BIRD RESPONSES TO HABITAT FRAGMENTATION AT DIFFERENT SPATIAL SCALES: ILLUSTRATIONS FROM MADAGASCAN AND AUSTRALIAN CASE STUDIES

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ABSTRACT

Despite increasing publicity, habitat loss and fragmentation remain a serious threat to biodiversity. The main objectives of this research were (i) to study the effects of forest fragmentation on the distribution and abundance of resident birds in the fragmented littoral forests of southeastern Madagascar and temperate woodlands of southeastern Australia at three spatial scales (patch, landscape and regional) and (ii) to place the results of these case studies within the realms of the equilibrium theory of island biogeography and its descendent theories, to ascertain whether it is appropriate to use these theories to derive conservation scenarios within these threatened regions.

Deforestation of Madagascar's remaining forests is considered a global concern due to both its current high intensity and the small amount of forest claimed to be remaining on the island. Surprisingly, very few studies have considered the impacts of forest fragmentation on bird diversity in Madagascar. A multi-scale study on the effects of littoral forest fragmentation and degradation on birds is therefore a major step forward for bird conservation on the island. Furthermore, prior to this study no known work has been conducted on the avifauna within the threatened littoral forests of eastern Madagascar. My results indicated that (i) the littoral forests contained bird species assemblages that were unique when compared to neighbouring forest habitats, (ii) many forest-dependent bird species were significantly affected by habitat structure and especially proximity to forest edge and (iii) many forest-dependent species were affected by landscape factors such as remnant shape and remnant size. No relationship was found between measures of landscape composition, remnant 'isolation' and bird distribution within littoral forest remnants.

The Australian analysis was conducted at a regional scale. Within the Australian temperate woodland belt, surprisingly little is known of how habitat fragmentation affects bird communities, even though deforestation due to agriculture and urbanisation has lead to destruction of much of its temperate vegetation, with as little as 7% intact woodland remaining. The Australian analysis was conducted in three similar fragmented woodland landscapes of southeastern Australia; these landscapes were located within 50 km of each other, contain fragments of similar age, size and spatial distribution, have similar proportions of woodland cover and experience similar climates. They differ principally in the properties of the landscape matrix surrounding the woodland remnants, with one being an urban environment (Canberra), another the surrounding peri-urban landscape and the third being a true agricultural environment. When woodland bird species incidence functions and area-isolation interactions were examined within the three landscapes, it became clear that bird species area-sensitivity and isolation-sensitivity were not consistent among the three fragmented landscapes. Although causation was impossible to determine, the differences in species distribution within the three landscapes appear most parsimoniously explained as a function of the differing properties of the matrix within which the three sets of woodland fragments are embedded.

The results of these two case studies have clear implications for bird conservation efforts in both southeastern Australia and southeastern Madagascar. Within Madagascar, greater efforts should be made to place littoral forests on the conservation agenda by conserving the largest remaining forest remnants and overcoming processes associated with habitat degradation and edge effects within them. In southeastern Australia, efforts should be placed not simply in making woodland remnants ‘bigger’ but by providing connectivity within the landscape matrix surrounding woodland remnants.

The results of these case studies have significant implications for theoreticians, researchers and modellers who continue to base their research on tenets of island theory and therefore view the effects of habitat fragmentation on biodiversity in a binary habitat-non habitat form. Using statistical inference I show that edge-effects, habitat structure, matrix composition and remnant shape all affected a number of habitat-dependent bird species in these fragmented systems. These processes must be given greater attention if any predictive general theory is to be produced on the effects of habitat fragmentation on biodiversity. I argue that a multi-scale approach to research that specifically looks at the processes and effects of fragmentation on the taxa of interest should be the first step in generating appropriate conservation guidelines for a particular fragmented system.

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PREFACE

This work brings together research conducted during three field expeditions in the littoral forests of southeastern Madagascar and a separate meta-analysis conducted on bird data collected from three fragmented woodland landscapes in southeastern Australia.

I did not originally envisage combining research from two completely different ecosystems within my doctoral thesis. When starting the thesis in 2001, I had intended to focus all my efforts in Madagascar. I believed that conducting research in the littoral forests of Madagascar would present a unique research opportunity to study an unknown, but seriously threatened ecosystem. As a large proportion (>80%) of the littoral forests in southeastern Madagascar lie in the middle of a proposed mining zone, I hoped that conducting research in these forests would also have important, practical conservation implications. Furthermore, it would provide an avenue to ask ecological and practically relevant questions about a system that has been little studied.

As my ideas on the effects of forest loss and fragmentation on birds evolved, I realised that I could not explore what 1 thought to be a very relevant (but little studied) research question-how did the landscape matrix composition (that is, the habitat surrounding the embedded fragmented habitat) affect birds within a fragmented landscape? The limitation with solely conducting research in the littoral forests in southeastern Madagascar was that the littoral forest landscape matrices were too similar for comparison for useful exploration of matrix effects.

Fortunately, I had an ongoing correspondence with ecologists from Australia's Commonwealth Scientific and Industrial Research Organisation (CSIRO), with whom I had conducted my honour's thesis. This led to a unique opportunity to utilise bird data sets that I had collected in 1999 and that CSIRO had collected in 2000. These data sets were from three, geographically close, fragmented woodland landscapes that had very different landscape matrix properties. The use of these Australian data allowed me to explore the ways in which different landscape matrix properties affect the distribution and abundance of resident woodland birds in fragmented landscapes.

As a consequence of studying in two different systems, this doctoral thesis can be divided into five main sections: the introduction, a literature review, a Madagascan littoral forest section, an Australian woodland section and the conclusion. The introduction situates the main topic of this work, describes the study sites and the goals of this thesis. It further gives an outline of the thesis. The literature review section places this research within the current literature concerning habitat fragmentation and develops the theoretical intentions of the thesis. The Madagascan littoral forest section comprises an introductory chapter that goes into further detail about the study site, and contains four empirical papers and a book chapter. The Australian woodland section comprises an introductory chapter that goes into further detail about the study site, and contains two empirical papers. Finally, the conclusion links all the chapters together, summarizing the most relevant findings of this study.

This thesis is submitted under departmental guidelines allowing that theses consist of at least four empirical chapters submitted for publication to refereed journals or books. The style and format required by the individual journals has been retained within the thesis. The following list outlines the status of the seven papers at the time of submission of this thesis.

Watson, J.E.M., Whittaker, R.J. & Dawson, T.P. (in press) The importance of littoral forest remnants for indigenous bird conservation in southeastern Madagascar. *Biodiversity and Conservation.*

Watson, J.E.M., Whittaker, R.J. & Dawson, T.P. (2004) Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. *Biological Conservation*, **120**, 315-331.

Watson, J.E.M., Whittaker, R.J. & Dawson, T.P. (2004) Avifaunal responses to habitat fragmentation in the threatened littoral forests of south-eastern Madagascar. *Journal of Biogeography*, **31**, 1791-1807.

Watson, J.E.M. (in press) Conservation of bird diversity in Madagascar's southeastern littoral forests. In: *Biodiversity conservation and mining in southeast Madagascar*, (editors: J.U. Ganzhorn, S.M. Goodman, J. Rabenantoandro, J.B. Ramanamanjato and M.Vincelette), Cambridge University Press.

O'Dea, N., Watson, J.E.M. & Whittaker, R.J. (2004) Rapid assessment in conservation research: a critique of avifaunal assessment techniques illustrated by Ecuadorian and Madagascan case study data, *Diversity and Distributions*, **10**, 55-63.

Watson, J.E.M., Whittaker, R.J., Dawson, T. P. & Freudenberger, D. (submitted) Variability of woodland bird incidence functions in different fragmented landscapes in southeastern Australia, *Ecography*. Submitted on 26th May 2004.

Watson, J.E.M., Whittaker, R.J., & Freudenberger, D. (in press) Bird community responses to fragmentation: how consistent are they across landscapes? *Journal of Biogeography*. Submitted on the 1st June 2004.

It must be noted that the O'Dea *et al.* (2004) manuscript presented in this thesis was not the majority of my work, and I do not include it as one of the four first-authored empirical papers necessary for a DPhil thesis. I have placed this manuscript within this thesis because it explains and justifies the bird methodology I employed in the littoral forests of southeastern Madagascar.

Journal authorship statements for all co-authored papers are attached at Appendix 1.

CHAPTER 1

INTRODUCTION

1.1 Conceptual framework

This thesis is concerned with the impact of anthropogenic habitat fragmentation at different spatial scales on bird communities in two distinct case study areas, the littoral forests of southeastern Madagascar and the woodlands of southeastern Australia. In the two regions of interest, little is known on how habitat fragmentation affects the bird communities, and yet threats of deforestation have exerted a strong influence on conservation and landuse planning in both systems. This thesis specifically examines the applicability of island theory as the basis for fragmentation research and as a tool to develop conservation strategies, within these two case study systems. I argue that since MacArthur and Wilson (1963, 1967) published their theory, there has been a strong and continued reliance on an island-habitat fragment analogy in research involving fragmented systems. Therefore, this thesis ultimately aims to contribute to an improved understanding of the effects of forest fragmentation on birds at different scales and to assess whether island theory is an appropriate research paradigm to use in these fragmented landscapes. It also aims to contribute to the application of appropriate conservation strategies in each region.

1.2 Context and rationale

Numerous factors, such as increasing human population, climate change, increasing use of pesticides, hunting and over-fishing, the introduction of pests and weeds and changing fire regimes, threaten the earth's biodiversity in complex ways (Lawton and May, 1995; Norris and Payne, 2002). Arguably, the greatest threat globally to biodiversity is anthropogenic modification, fragmentation and degradation of landscapes, primarily due to agricultural development, urbanisation and forestry practices such as clear-felling (Ehrlich and Wilson, 1991; Noss, 1991; Wilson, 1992; Pimm, 1998). It is now believed that there is little hope for the conservation of many indigenous species and the maintenance of biological diversity in modified ecosystems unless a detailed knowledge of the influence of habitat change on the persistence of species is obtained (Hobbs, 1994; Bierregaard *et al.*, 2001).

An increasing awareness of the ecological problems associated with habitat fragmentation and loss has led to a concomitant increased scientific focus on them. Historically, MacArthur and Wilson's (1967) equilibrium theory of island biogeography provided a theoretical framework for ecological research examining how habitat fragmentation impacts on the fauna and flora of terrestrial habitat 'islands'. Recent reviews (e.g Andrén, 1994; McGarigal and Cushman, 2002; Schmiegelow and Monkkonen, 2002) highlight the enormous amount of work conducted in the past two decades on assessing the effects of habitat loss and fragmentation on biodiversity and the numerous different ways researchers have tackled the research problem. Notwithstanding this tremendous research effort, there seems to be little consensus about the impacts fragmentation actually has on biodiversity (Mac Nally *et al.*, 2000; Bierregaard *et al.*, 2001; Watson, 2002) and understanding the effects of these processes on biodiversity is still considered a significant problem in ecology.

As will be discussed in more detail in Chapter 2, there are many reasons why there has been no unifying solution to the problem of ascertaining and predicting the effects of habitat fragmentation on biodiversity. The processes that drive habitat fragmentation are not simple, consistent and linear, but multi-scalar and multi-faceted. They therefore affect biodiversity in complex, often contradictory, ways (Lord and Norton, 1990; Wiens, 2002). For example, anthropogenic fragmentation of a habitat may affect biodiversity at a 'patch[1]' scale as it may lead to a loss of a specific resource (e.g. a type of plant species) within a habitat patch. At the 'landscape' scale, fragmentation of habitat will lead to the sub-division of habitat, patch

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[1] To avoid confusion over the definitions of terms in this thesis I have included a Glossary.

isolation, and edge effects, which, in turn, may affect plants and animals living within habitat patches. At the 'regional' scale, differences in the properties that make up the landscape matrix within which habitat fragments are embedded may affect species inhabiting the fragmented landscape. As biota inhabiting a fragmented system almost invariably 'experience' the process of habitat fragmentation in varying ways at each of these scales, and their responses to this affect the existence of other biota in the system, the process of describing and predicting the effects of habitat fragmentation on biodiversity is complicated.

These complications do not mean that ecologists should give up on trying to understand how biodiversity is affected by habitat fragmentation. Conservation issues are currently high on political agendas, as is reflected in the establishment of international conventions on biological diversity and recent changes in many national governments' environmental policies (Lindenmayer and Franklin, 2002; Randrianandianina *et al.* 2003). This increase in political awareness has meant that questions on how habitat loss, fragmentation and degradation are affecting biodiversity, ecosystem functioning, and ecosystem sustainability, are becoming increasingly important. Whilst many conservation-oriented questions remain value-based, and therefore beyond the realms of science, it is clear that public discourse on the subject is best informed by accurate scientific knowledge. In this context, this thesis aims to inform conservation policy, by investigating relevant issues involving the effects of habitat fragmentation and degradation on biodiversity.

The research presented in this thesis was conducted in two case study systems: the littoral forests of southeastern Madagascar and the woodland forests of southeastern Australia. As discussed below, both these systems are believed to be seriously threatened by habitat loss, fragmentation and degradation. This research addresses a number of questions on the impacts of forest fragmentation and degradation on bird species, including: how are bird communities affected by local, landscape and regional changes to their environment due to forest fragmentation? What species are threatened by habitat fragmentation and at what scale? What is the likely future impact of habitat fragmentation on bird species? What management strategies are likely to be most effective in limiting species' extinctions? Such questions are relevant to the conservation policy of the countries that the case studies have been conducted in. In addressing them I also hope to contribute to the development of theory and pragmatic approaches that focus on the fragmentation 'problem' in other threatened places on earth.

Birds were chosen as the focal taxa because they are (usually) conspicuous, easily identifiable and have a range of stereotypic and quantifiable behaviour - all of which simplifies experimental procedure. Even though birds are volant, they are threatened by habitat fragmentation at local, landscape and regional scales because they are territorial, have large home ranges and are area-demanding. Therefore, the reaction of birds to habitat fragmentation will often mirror the reaction of a wide range of other biota (Furness and Greenwood, 1993).

1.3 Habitat loss, fragmentation and degradation of Madagascar's forests

Madagascar is the world's fourth largest island, with an area of approximately 590 000 km^2. The island has been separated from Africa for approximately 165 million years. Madagascar's extant flora and fauna are well known for high levels of endemism, as well as for impressive radiations of plant and animal groups that arrived on the island during its long Mesozoic and Cenozoic isolation. Much of what has been written concerning the biota has, appropriately, emphasised the island's uniqueness. Madagascar has over 12000 plant species of which nearly 80% are endemic, 33 lemur species of which all are endemic and 90% endemism in its herpetofauna (Wilson, 1992; Wright, 1997; Hannah *et al.*, 1998; Garbutt, 1999). The Malagasy indigenous bird community, even with a relatively low number of species, also has a very high level of endemism. Including those species that occur on the Comoros Islands, 110 species are endemic and there are 37 endemic genera and five endemic families (Langrand, 1990; Langrand and Sinclair, 1994; Hawkins, 1999). This is exceptionally high considering only 209 species breed in the Madagascar and Comoros bioregion and, as a consequence, Madagascar has the highest proportion of endemic bird species of any relatively large country in the world (Hawkins and Goodman, 2003).

Madagascar is one of the poorest countries in the world, with most of the country's population living below the poverty line (UN, 2003). Nearly one in five children die before the age of five due to malnutrition or malnutrition related diseases (USAID, 1999). The traditional practice of slash and burn agriculture (tavy) and charcoal production is widespread and since the island's colonisation by humans approximately 1500 years ago, it has been argued that between 90 to 95% of Madagascar's forests have been lost (Nelson and Horning, 1990; Sussman *et al.* 1994; Conservation International, 1999). Different rates of recent forest loss have been estimated by several authors. For example, Green and Sussman (1990) argued that forest clearing rates averaged 110 000 ha per annum in eastern Madagascar between 1950 and 1985 and Smith (1997) argued that 61 000 ha per annum were being cleared in western Madagascar between 1950 and 1990. It must be noted that recent research (reviewed in Ingram, 2004) has shown that these statistics should be interpreted with caution due to the fact that the island was probably never fully covered in forest (Burney 1997). It is simply not known how much forest was on the island before human arrival and, hence, how much has been lost. Ingram (2004) shows that forest loss on the island is highly variable throughout space and time at regional and national scales.

What is indisputable is that there are now many fragmented landscapes in Madagascar. Pressure on fragmented forests is being maintained by a higher than average population growth rate that is doubling every 22 years (Daume, 1990), a low annual per capita income (US $260; World Bank, 2001), and high levels of subsistence agriculture (80% of the population; Gade, 1985; Kistler and Spack, 2003). Weed invasion, loss of soil fertility, and erosion of previously cleared land is becoming common in fragmented landscapes (Binggeli, 2003; Nicoll, 2003). Moreover, charcoal is the principal domestic energy source for

Madagascar and the equivalent of one to three percent of remaining forest cover is harvested annually, mostly from plantations in the north and east but also from other forests on the island (Pollock, 1986; Sussman *et al.*, 1994). Grazing is widespread in forest and savannas, and regular uncontrolled fires, started to promote fresh livestock fodder, destroy forest margins as well preventing forest regeneration and promoting erosion (Smith, 1997; Kull, 2002). All these factors put great pressure on Madagascar's remaining forests and there is a large international concern for Madagascar's unique biodiversity and the impacts of habitat and land degradation on it.

Although much is still not known about the biodiversity of Madagascar, there are examples of species extinction since human colonisation. Some well-known losses include seven genera of Lemurs (including twenty individual species) as well as all known Elephant bird species (an endemic group of large non-volant birds) (Simons, 1997). Due to the fact that most of these extinctions have closely coincided with human colonisation, many consider that rapid loss of habitat and hunting are the main reasons for the high extinction rate on the island (e.g. Goodman and Rakotozafy, 1997; Wells and Andriamihaja, 1997).

The high unique biodiversity value combined with the extent and pace of forest loss and accompanying extinctions have made Madagascar a biodiversity 'hotspot'. Both USAID and Conservation International have identified Madagascar as 'the single highest biodiversity conservation priority in the world' (Myers *et al.* 2000: 853). Yet, even with Madagascar being the focus of such attention from environmentalists and non-government organisations, it has been argued that the number of extinctions is set to increase because of habitat destruction and fragmentation (Durbin *et al.*, 2003). Twelve species or subspecies of lemur, including all four discovered in the past decade, are considered threatened by loss of habitat (Simons, 1997). Of the 31 threatened bird species endemic to Madagascar, only eight are not found in the eastern humid and coastal forests. It is believed that the other 23 species occur in forests where slash and burn itinerant cultivation and exploitation of firewood are common (Collar *et al.*, 1994; Wilme, 1996; Hawkins, 1999).

Efforts to conserve biodiversity in Madagascar have been focussed on the management of a network of 46 legally designated Protected Areas, which cover approximately 1.69 million ha or 2% of the land surface (Randrianandianina *et al.* 2003). However, inclusion of remnants in Protected Areas is no guarantee of biodiversity protection in Madagascar. The Malagasy government lacks the resources for effective staffing and management of Protected Areas (Smith, 1997; Erdmann, 2003; Nicoll, 2003; Randrianandianina *et al.*, 2003). Most reserves are under-staffed and threatened by ongoing agricultural encroachment, poaching, burning, and progressive degradation. Intensive, protected area management is largely confined to a limited number of Integrated Conservation and Development Projects (ICDPs), which seek to halt forest clearing by promoting sustainable agriculture in buffer zones surrounding reserves through financial compensation for loss of land through employment of locals as guides and guardians (Nicoll, 2003). While there is still considerable debate on the extent to which humans have cleared Madagascar's forests, it is clear that many habitats are fragmented, and there is little knowledge of how habitat fragmentation is affecting Madagascar's biodiversity outside and within these protected areas (Richard and O'Conner, 1997; Bollen, 2003; Ingram, 2004).

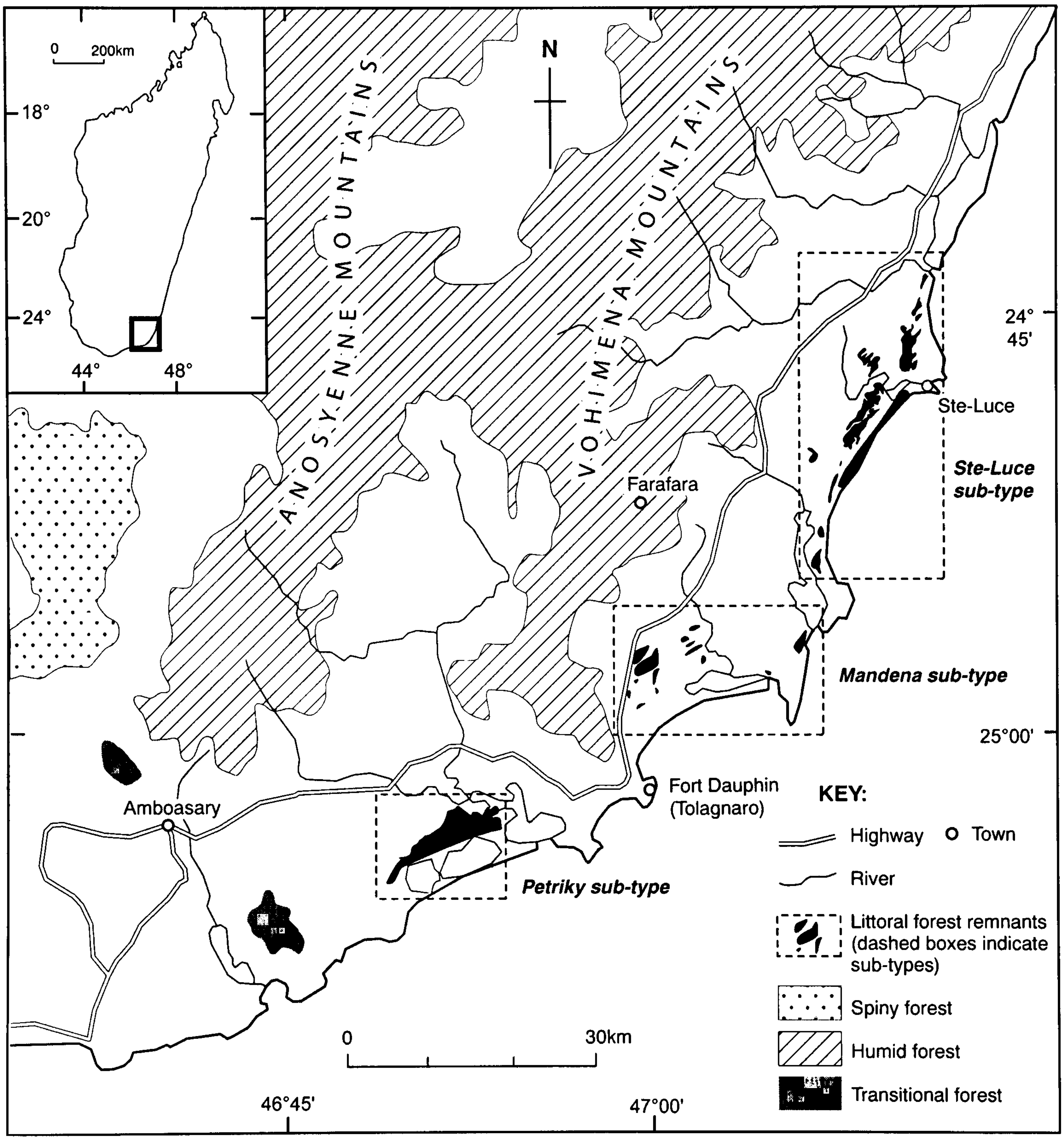
1.3.1 The littoral forests of southeastern Madagascar

The littoral forests of southeastern Madagascar (Figure 1.1) represent a particularly important study system in which to carry out fragmentation research. At present, the forests are considered degraded, highly fragmented and in urgent need of conservation management (Vincelette *et al.*, 2003). Like many other ecosystems in Madagascar, the period over which fragmentation of littoral forests occurred is unknown, but what is clear is that the forests now occur as a series of fragments. The high degree of endemism and biodiversity, the rarity of the forest type, and the urgent need for data on how habitat fragmentation affect birds in Malagasy ecosystems (Hawkins and Goodman, 2003), have all contributed to the choice of the littoral forests of the Fort Dauphin region for this research. Furthermore, the presence of QMM (QIT Madagascar Minerals), a company of QIT-Fer et Titane (a subsidiary of Rio Tinto plc, UK), means that the conservation status of these forests must be reviewed. The company is planning to mine heavy mineral sands on the coastal plain of the Fort Dauphin region. These sands are a source of titanium dioxide, principally in the form of ilmenite minerals. The core of the proposed mining area include 70% of the remaining littoral forest fragments. It is in landscapes such as these that management to attain conservation goals can still be proactive rather than reactive. Here efforts can be focussed on managing landscapes to reduce the effects of loss of biodiversity, rather than the much more difficult task of attempting to restore a severely altered ecosystem.

1.4 Habitat loss, fragmentation and degradation of Australia's temperate woodlands

Australia is the only nation to occupy an entire continent. In land area (7 682 300 km^2) it is the world's sixth largest nation. Australia has a tropical monsoon climate in the north, a temperate to Mediterranean climate in the south and a vast, arid interior. Important features of its climate are the highly irregular rainfall, the extreme rate of evaporation of available water, and the large temperature ranges. The continent has a generally flat land surface, with relatively low precipitation and run-off rates. Mountain ranges in the southeast are often snow-covered in winter, but Australia generally experiences mild winters and hot summers. Australia is the second driest continent in the world, with its freshwater and ground water resources having a limited capacity. Even though drought is a recurring climatic feature over most of the continent, Australia is home to a unique biodiversity. Approximately 85% of flowering plants, 84% of mammals, 45% of birds, and 89% of inshore, temperate-zone fish are endemic (IUCN, 2003).

Figure 1.1 The location of littoral forest remnants sub-types and the extent of humid forest and spiny forest in southeastern Madagascar. The matrix surrounding littoral forest remnants includes *marécage* swamp forest, *Melaleuca* forest, plantations of *Eucalyptus citriodora* and *E. robusta,* and heath-type vegetation consisting predominately of *Erica* spp. Forest extent was based on the figure presented in Ramanamanjato et al. (2002).



Evidence of human settlement in Australia has been dated at more than 60 000 years, although this is still being debated. The ancestors of Australia's indigenous peoples are believed to have entered the continent from the north as hunter-gatherers skilled in the use of wooden and stone tools and fire. There is still contention over how much influence Aboriginal people had on shaping the current vegetation of Australia, especially in the north and east of the country (Flannery, 1995; Bowman, 2000). It is now clear that savannah woodlands and rainforest discontinuity in the north vastly precede the arrival of humans in Australia even though it was formerly attributed to Aboriginal presence (Bowman, 1998; Bowman, 2000). Sharpe (2004) argues that the plethura of contrary assumptions about Australia's past vegetation, despite the current evidence, may have more to do with politics than with science. Aboriginal land claims are an ongoing issue in Australia, and assertions about the impact of Aboriginal stewardship on the Australian landscape may serve or become conflated with political ends.

European settlement dates from 1788, 18 years after the continent was claimed for Britain. It is well established that European colonisation led to vast vegetation clearance for agriculture, forestry and urbanisation within the past two centuries (Bennett, 1990; Saunders *et al.*, 1991), resulting in the fragmentation of many habitats (Hobbs, 1993; Watson *et al.*, 2001; 2003). These disturbances have placed stress on species and ecosystems that were poorly adapted to rapid change (Flannery, 1995; Ford *et al.*, 2001). Since 1788, at least 97 vascular plant species, 20 mammal species and 10 bird species have become extinct (IUCN, 2003). A further 1100 plant species, 118 mammal species and 36 bird species are considered endangered or threatened (Robinson and Traill, 1996; Lunney *et al.*, 1997; IUCN, 2003).

The report, *Australia: State of the Environment* (SOE, 1996: 13), presented to the Australian Government in 1996 suggested that:

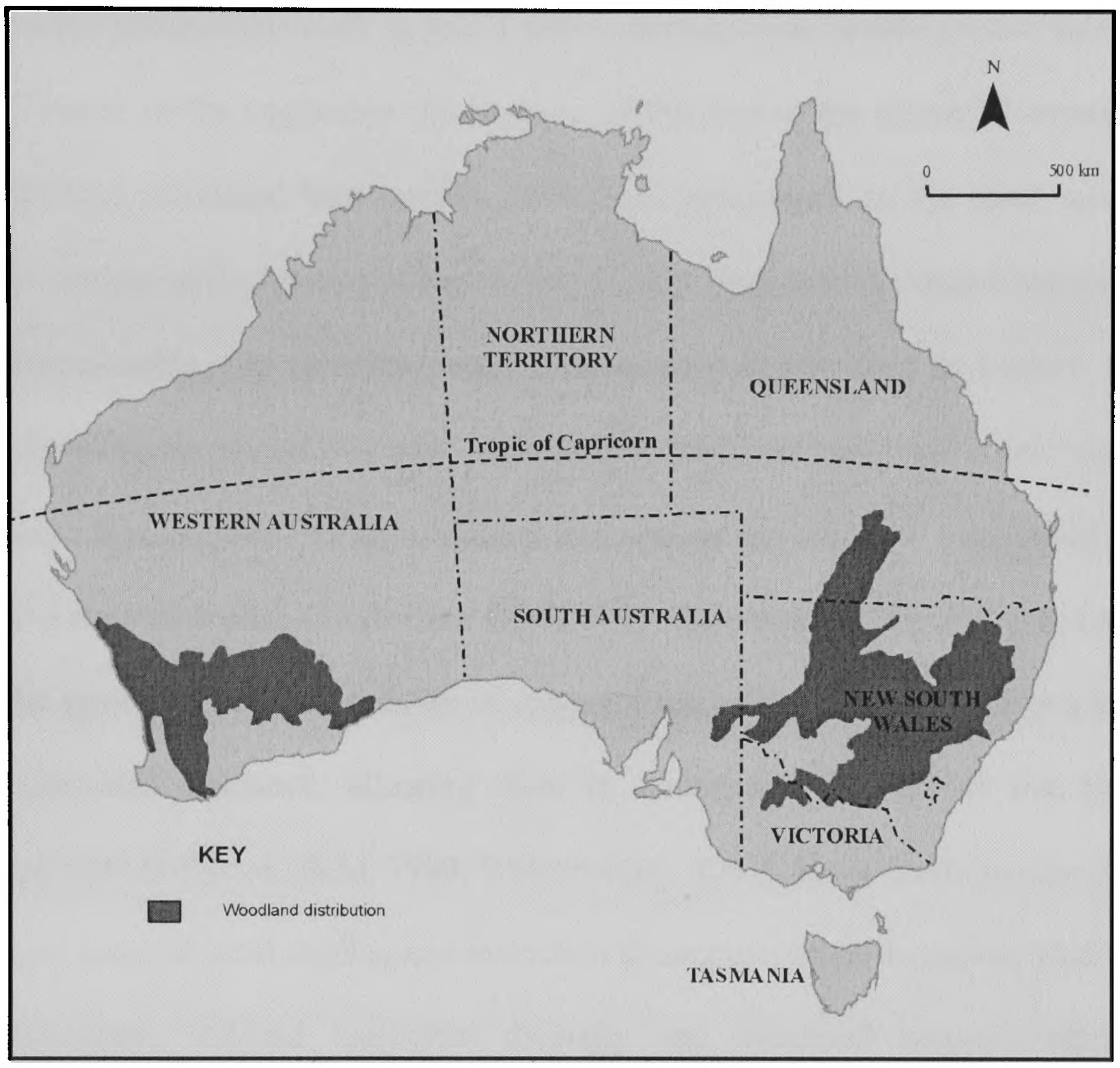
> *"The loss of biological diversity is perhaps our most serious environmental problem. Whether we look at wetlands or saltmarshes, mangroves or bushland, inland creeks or estuaries, the same story emerges. In many cases, the destruction of habitat, the major cause of biodiversity loss, is continuing at an alarming rate".*

1.4.1 The woodlands of southeastern Australia

Prior to European settlement, temperate woodlands dominated the inland plains of southeastern and southwestern Australia (Figure 1.2), where the mean annual rainfall is between 300 and 700 mm. These woodlands formed a transitional zone between the higher rainfall, forested margins of the continent and the shrublands and grasslands of the arid interior (Robinson and Traill, 1996). In the southeast of Australia, temperate woodlands occurred along the slopes and plains inland from the Great Dividing Range, from southern Queensland to the southern Flinders Ranges of South Australia (Moore, 1970). In the southwest of Western Australia, woodlands occurred on the inland plains, eastwards to the Nullabor Plain and northwards to the Nicholson Ranges (Saunders and Ingram, 1995).

Throughout both regions, woodlands occurred as part of a heterogeneous mosaic. At the time of European colonisation of Australia, woodlands formed the dominant landcover within this mosaic, with smaller areas of treeless grasslands on valley bottoms, and dry scherlophyll forests on stony oligotrophic hills (Beard, 1990; Hobbs *et al.*, 1993). The location of this mosaic of grassland and woodland west of the Great Dividing Range in eastern Australia is believed to be climate driven and not due to pre-European Aboriginal impact (Beard, 1990; Hobbs *et al.*, 1993). In less than a century, these woodlands have been cleared to the extent that it is now rare to find a landscape mosaic of woodland, grassland and forest anywhere in Australia (Hobbs and Yates, 1998). Since European settlement more than 85% of Australia's temperate woodlands have been cleared, making woodland communities the most endangered

Figure 1.2 The location of temperate woodlands at the time of European settlement. *Source*: adapted from Moore, 1970: 17.



and poorly conserved vegetation types within Australia (Benson, 1991; Hobbs and Yates, 1998). The intensity of vegetation clearance was linked to perceived economic potential (Woodgate and Black, 1988). The temperate regions suffered the brunt of vegetation clearance as they were the regions most suited to cropping and grazing regimes (Catteral *et al.*, 1997). Once described by Major Thomas Mitchell (1839: 3) as "... country ready for the immediate reception of civilized man... encumbered by too much wood", the temperate woodlands are now less encumbered. Due to widespread clearing for agriculture, they are amongst the most threatened ecosystems within Australia (Ford *et al.*, 2001).

Temperate woodlands provide core habitats for a distinctive group of woodland-dependent birds. Each species comprising this group has evolved in response to the long growing season and year round availability of food, the preponderance of *Eucalyptus* species and associated habitat components such as tree hollows, peeling bark, grassy ground layer and open canopy structure of the vegetation (Ford *et al.*, 1996). Due to the extent of woodland fragmentation, resident woodland bird species have been recognised as the most adversely affected of Australian birds in terms of the severity of their response to extreme habitat loss (Reid, 1999). For example, the paradise parrot (*Psephotus pulcherrimus*) is extinct, regent honeyeaters (*Xanthomyza phrygia*) - once recorded in 'immense numbers' - are now endangered, and more than a quarter of all woodland bird species are currently considered to be threatened or in a state of decline (Taylor and COG, 1992; Robinson and Traill, 1996; Ford *et al.*, 2001). At the same time, a small number of opportunistic native and exotic species have benefited from vegetation clearance, allowing them to spread and increase so that they now dominate regional avifaunas (Reid, 1999; Watson *et al.*, 2003). More insidious than these changes is the new wave of local decline and extinction among certain bird species. This trend towards local extinction, reduced biological diversity and increased homogenisation appears to be accelerating despite the fact that, in most regions, temperate woodland clearance has effectively halted (Smith *et al.*, 1996; Saunders *et al.*, 1999).

The Australian case study system is focussed in three different landscapes within the Australian Capital Territory and surrounding areas of New South Wales. These landscapes are located within 50 km of each other, contain fragments of similar age, size and spatial pattern distribution, have similar proportions of woodland cover and experience similar climates. As is shown in the empirical chapters (Chapters 10 and 11), these landscapes had vastly different matrix compositions and, as such, presented a special opportunity to examine the effects of fragmentation on birds at a regional scale.

Within the Canberra region, there is a growing concern that woodland biodiversity will not withstand the pressures of human-induced habitat fragmentation and that the reserve system is inadequate (Barrett *et al.*, 1994). Woodland management strategies now look to the development of a viable network of residual habitats extending beyond the formal reserve system and incorporate revegetation programs such as *Greening Australia* and *The million trees project* (Brooker and Margules, 1996; Binning, 1998). To implement and sustain successful interactive conservation networks, it is necessary to define the area, composition and spatial configuration of woodland remnants that must be present to meet the immediate needs of woodland biota (Ford and Barrett, 1995; Lindenmayer and Franklin, 2002). By conducting research in this region, this thesis builds on previous knowledge on the effects of fragmentation on biota and has important implications for the region's revegetation plans.

1.5 Thesis aims and objectives

One way of overcoming the general lack of knowledge on the effects of fragmentation on animals and plants is to rely on ecological theory to determine what the current and future effects of habitat fragmentation will be on biodiversity. A number of related theories – largely traceable as descendants of MacArthur and Wilson's (1967) equilibrium theory of island biogeography (ETIB) - have been used as bases for fragmentation-related research in the past three decades. A prominent example of the use of island theory today is Brooks *et al.*'s (2002) prioritisation of the 'hottest hotspots' within the 25 Conservation International global plant diversity hotspots (Myers *et al.* 2000). Brooks *et al.* (2002) apply a species-area approach, invoking one of the fundamental tenets of MacArthur and Wilson's (1967) ETIB, that of species *relaxation* in terrestrial habitat islands. Even though widely used, it is not known how appropriate these theories are for creating and implementing conservation policy in modified, threatened and under-studied fragmented systems.

This thesis has two over-arching aims. The first aim is to assess the effects of habitat fragmentation on bird species diversity in the littoral forests of south-eastern Madagascar and woodlands of southeastern Australia in order to help guide conservation policy in these regions. The second aim is to place the results of these case studies within the realms of island biogeography theory and its descendent theories, to ascertain whether it is appropriate to use these theories to derive conservation scenarios within the areas. In order to achieve both aims, it is necessary to understand: (i) what bird species occur in these ecosystems, (ii) how these bird species are affected by habitat fragmentation and degradation, and (iii) whether the relevant theory is applicable in these fragmented systems.

In order to achieve these aims, this research had seven objectives:

a) Review the effects of habitat fragmentation on birds and examine theory that has been used in habitat fragmentation studies.
b) Develop an appropriate way to conduct a rapid bird census in the littoral forests of southeastern Madagascar- a system that has never been thoroughly surveyed for birds before.
c) Determine which bird species inhabit the littoral forests of southeastern Madagascar, and how these species compositions compare to other forested habitats in the region.
d) Examine how fragmentation of littoral forests affect bird diversity at the patch and landscape scales, in order to identify appropriate conservation solutions for the region.
e) Examine how fragmentation of Australian woodland influences bird distributions at a regional scale, in particular focussing on how differences in the landscapes (i.e. matrix effects) are reflected in the distribution of birds in woodland fragments.
f) Determine the conservation implications of this research in both regions.
g) Consider the theoretical implications of this research.

These objectives are addressed through the thesis as described below.

1.6 Thesis structure

There are twelve chapters to this thesis. Figure 1.3 shows diagrammatically the broad outline of the thesis. As permitted under university regulations, the thesis comprises six scientific papers that are either published or submitted for publication in international peer-reviewed journals and one book chapter.

The present chapter has introduced the aims and objectives of the thesis, described problems associated with habitat loss, fragmentation and degradation in Madagascar and Australia, and provided a general outline of the thesis. The second chapter reviews how habitat fragmentation has affected bird communities in other regions of the world. It also comprises a literature review that critically assesses the theory that has been developed in fragmentation research. As such, Chapter 2 provides the theoretical framework within which the empirical case studies are evaluated.

Chapters 3 to 8 comprise the littoral forest case study. The third chapter describes the littoral forests of southeastern Madagascar in more detail than in this Introduction, and sets out and justifies the field methods employed. Chapter 4 describes and justifies the use of the rapid assessment bird census methodology employed in the littoral forest fragments. It does this by specifically showing that both bird species-accumulation and species-estimation curves plateau in the littoral forest patches. Moreover, this chapter contributes to the debate on the application of certain rapid assessment methodologies in species-rich and species-poor systems. Chapter 5 describes the bird communities that inhabit the littoral forests of southeastern Madagascar. As this was the first time a thorough bird survey had been conducted in this forest type, the analyses conducted in this chapter also examines whether these communities differed from the bird communities of other forested habitats in the region

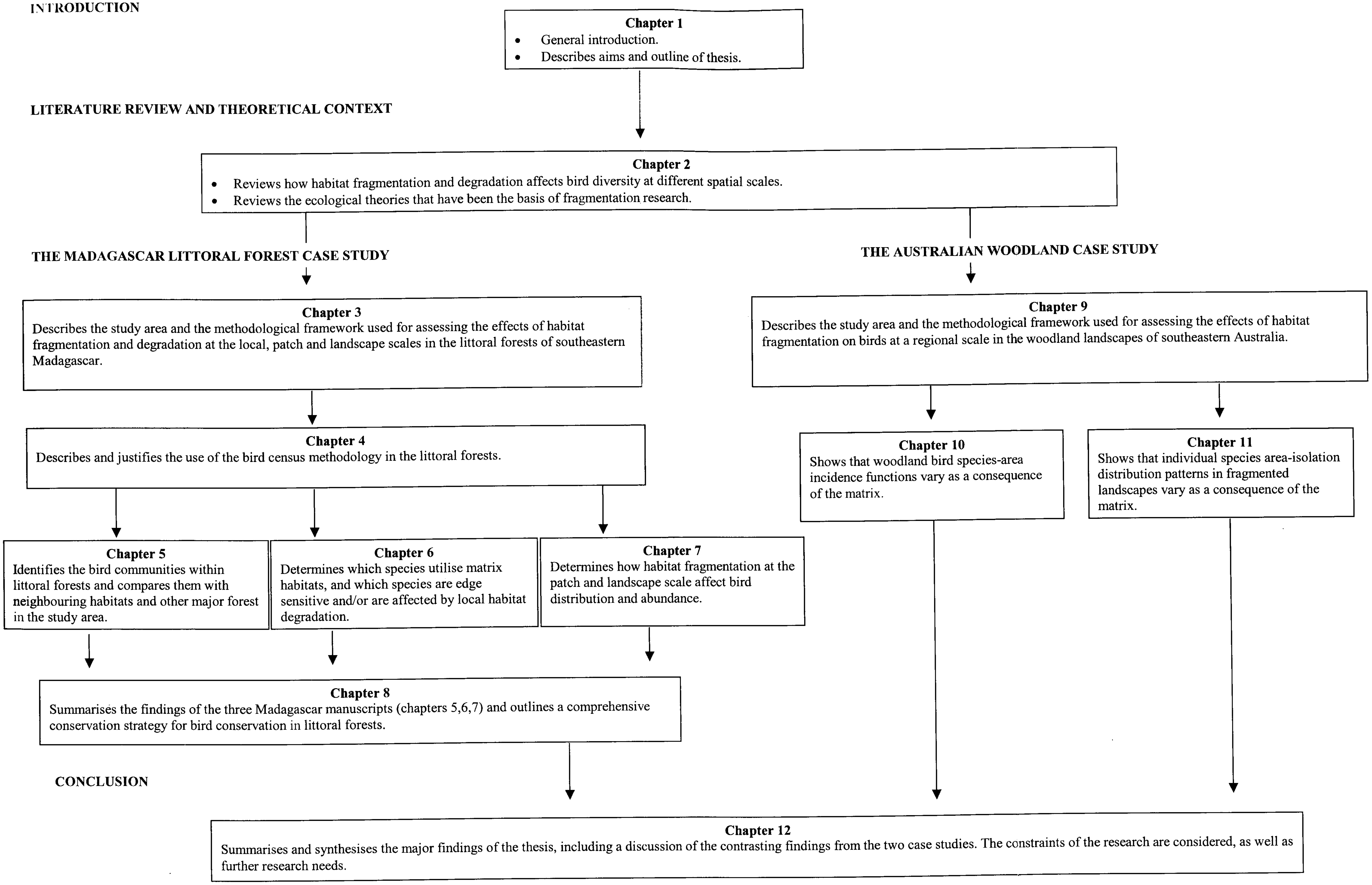


Figure 1.3 Outline of thesis

so as to assess the regional importance of the littoral forests for bird conservation. The last aim of this chapter was to determine if different sub-types of littoral forest within southeastern Madagascar possess different bird communities so as to identify the most important sub-types of littoral forest for bird conservation in the region. As very little research has been conducted in the littoral forests of southeastern Madagascar, it was an important component of this thesis to describe the bird communities and ascertain their distinctiveness before ascertaining the effects of habitat fragmentation and degradation.

Chapter 6 had a number of aims but focussed on the patch-scale effects of habitat fragmentation in the littoral forest system. The first aim was to determine which species were forest-dependent and which were habitat generalists. The second aim was to determine if there was a relationship between patch characteristics (in particular, vegetation structure) within littoral forest fragments and bird abundance across the landscape. The third aim was to determine if forest-dependent bird species inhabiting the littoral forests were utilising the dominant matrix. The fourth aim was to determine if the abundance of forest-dependent bird species were affected by proximity to remnant edge (i.e. edge effects). Chapter 7 primarily focused on the landscape-scale effects of habitat fragmentation in littoral forests. It did this by assessing the effects of landscape metric variables on the distribution of birds in the Ste-Luce and Mandena littoral forests, to determine if landscape-scale habitat fragmentation was affecting littoral bird composition. Chapter 8 places the results of the empirical papers of Chapters 4-7 in context with each other, and considers the conservation strategies needed to be implemented for bird conservation in Madagascar's southeastern littoral forests.

Chapters 9 to 11 comprise the Australian woodland case study. Chapter 9 describes the Australian woodland case study area in more detail and sets out and justifies the field methods employed. Chapter 10 examines the effects of woodland fragmentation at a regional scale by focusing on the area-incidence functions and minimum area requirements of six area-sensitive bird species to determine if they varied within three woodland landscapes that had different matrix composition. Chapter 11 examines the woodland bird community of the same three woodland landscapes and determines how species richness-area and species-isolation richness relationships varied between them. In addition to this, this paper looks at how area-isolation relationships at a species level vary across the three landscapes, showing a degree of variation that does not appear to have been documented in the literature hitherto.

The final chapter (Chapter 12) is the conclusion of the thesis. It summarises and synthesises the major findings of the thesis, including a discussion of the contrasting findings from the case study systems. The constraints of the research are considered, as well as further research needs.

CHAPTER 2

A REVIEW OF THE THEORETICAL AND OBSERVED EFFECTS OF HABITAT FRAGMENTATION ON BIRD DIVERSITY

2.1 Introduction

A full consideration of all theory that has been utilised in the conservation of fragmented landscapes globally is beyond the scope of this thesis. The aim here is a simple one: to describe the application of island theory, beginning with MacArthur and Wilson's (1967) equilibrium theory of island biogeography (ETIB), to the problem of fragmented ecosystems. I do this by first describing the tenets of ETIB and its descendent theories, and show how these theories have provided the basis for fragmentation related research. I then review the 'fragmentation literature' (in particular, the fragmentation research based on bird studies) of the past thirty years to describe how habitat fragmentation has affected bird diversity in different regions of the world.

In this chapter, I show that the development of MacArthur and Wilson's (1967) ETIB was, in essence, the start of fragmentation research. This theory led to the development of numerous other ideas and techniques – all based on the habitat fragment-island analogy - that have been used to assess the impacts of fragmentation on biota. These include Patterson and Atmar's (1986) ideas about nestedness and Diamond's (1975a) assembly rules. Even with the growth of landscape ecology in the past decade, island theory is still the dominant research paradigm in fragmentation research. This is because landscape ecology still lacks a strong theoretical framework that can be modified, developed and tested in fragmented landscapes. Therefore, even though it has been over forty years since the first publication of MacArthur and Wilson's (1967) theory, island theory is still playing a central role in both the development of conservation guidelines and the determination of future predictions of species loss, in fragmented landscapes. Moreover, new theories (e.g. Lomolino 2000a; Watson, 2002) based on the *habitat patch – hostile matrix* paradigm of ETIB, are still being developed and applied in fragmentation research. As a consequence, I use this review of the island theory literature as the theoretical basis for the empirical studies conducted in Madagascar and Australia, and discuss the implications of this research on these theories in the Conclusion Chapter.

By reviewing the empirical literature that has focussed on the effects of fragmentation on bird diversity, I show that it is essential to consider both spatial scale and landscape context in fragmentation research. This review shows that the process of fragmentation, from the creation of a habitat edge to the gradual isolation of small remnant habitats, has vastly different impacts on different species, guilds and entire communities. There are few general trends and little consistency among fragmented landscape systems. Moreover, as many studies are often focussed on either one scale, or on one of the many processes associated with fragmentation, it is often impossible to compare the effects of fragmentation between systems. Therefore, I use this literature review as the basis, and justification, for assessing the effects of habitat fragmentation at different spatial scales in the Madagascan and Australian case studies and for conducting this research in a site-specific manner.

2.2 The foundation of theories that formed the spearhead of habitat fragmentation research

Traditionally ecologists assumed that the most important ecological processes affecting populations and communities operated at fine spatial scales (Carothers *et al.*, 1974; Urban and Smith, 1989). For example, many ecologists at the start of the twentieth century believed that animal species richness and individual species abundance were solely functions of variation in local resource availability (reviewed in Cody, 1985). A growing awareness of the relationship between species richness and area (SPAR) accompanied a shift towards an appreciation that local scale processes alone may not adequately explain community and population dynamics within a habitat patch, or for that matter, within a landscape (Arrhenius, 1921). An appreciation of the general nature and form of SPARs was furthered by other researchers in the middle of the twentieth century (e.g. Darlington, 1957; Preston, 1960). However, it was only when MacArthur and Wilson (1963, 1967) developed the ETIB that the importance of the SPAR (as well as other landscape factors such as patch isolation) became fully recognised in respect of species persistence on islands and in habitat fragments (Whittaker, 1998). The development of the ETIB in the 1960s was the start of a new beginning on how ecological research was conducted in island and terrestrial systems. This is because it provided a new form of general model that could be modified, developed and tested by ecologists and because it opened up a research programme focussed on the idea of 'habitat fragmentation' (Whittaker, 1998; Lomolino, 2000a, b; Haila, 2002).

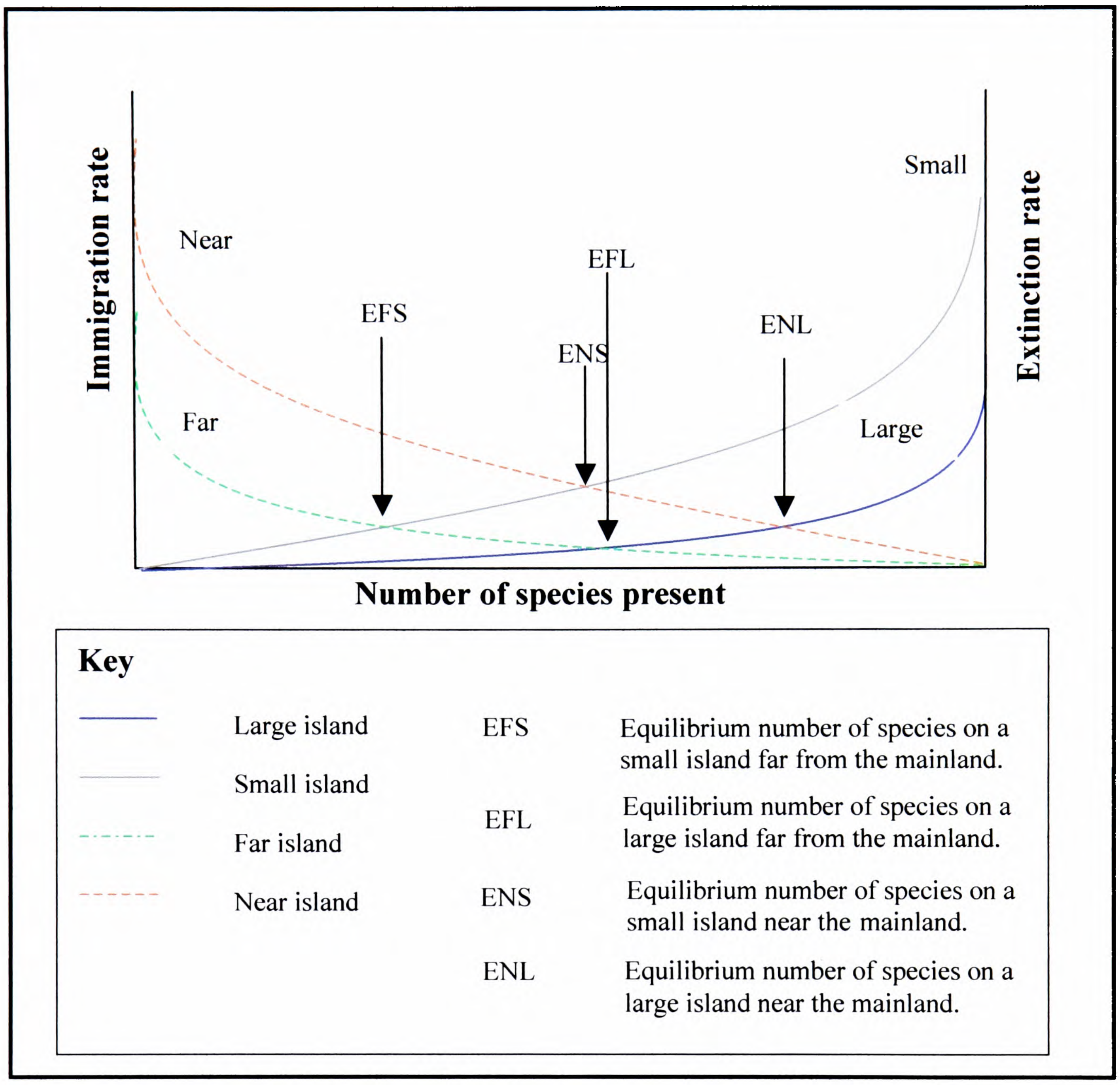
Before detailing the ETIB model, MacArthur and Wilson (1967) first discussed the existence of archipelagic SPARs: larger islands should tend to contain larger populations of species. They argued, using the findings of Darlington (1957) and Preston (1962) as a basis, that the number of species on a given island is usually approximately related to the area of the island, i.e. $S=cA^z$, where S is the number of species, A is the area, C is a constant that varies widely among taxa and according to the unit of area measurement, and z is a constant which falls in most cases between 0.20 and 0.35 for oceanic islands. They argued that when species counts are made from sample plots of increasing area on the same island or continent, z values are smaller, usually falling between the range of 0.12 and 0.17.

MacArthur and Wilson (1963, 1967) went beyond a demonstration of self-regulating diversity on oceanic islands. The main tenets of their ETIB was that there are two ways in which islands gain species, by immigration or by evolution of new forms, and that these means of increasing species richness will be balanced in the equilibrium condition by processes leading to a loss of species (MacArthur and Wilson, 1967). One major force for increase in species number (immigration) is likely to diminish as a fairly simple function with increasing distance from source pools while the other (speciation) will initially increase with distance from source pools but will sharply drop-off when individuals can no longer disperse the distance from the source pool to the island. Additionally, the greater resource base of larger islands should mean that extinction rates are lower for larger islands than for smaller. Thus, species richness (i.e. the number of species) is a consequence of an equilibrium between immigration and local extinction, and a reduction in island area and an increase in island isolation (i.e. the distance from a large source patch of immigrants) will result in predictable changes in rates of immigration and extinction and therefore lower species richness (Figure 2.1). By developing ETIB, MacArthur and Wilson (1967) defined the two derivatives that should be critical in determining species richness on an island: the rate at which species not on an island arrive on it, and the rate at which species on an island become extinct there (Rosenzweig, 1995; Whittaker, 1998). The MacArthur-Wilson theory, in its simplest form, argued that an island with no species can suffer no extinctions. An island with all the species of its mainland source pool can experience no further immigrations. In contrast, immigrants must be arriving at some positive rate on the island with no species and this rate should decline as the proportion of the mainland pool already on the island increase, and an island with as many species as possible must suffer extinctions at some positive rate with the rate increasing as the island accumulates more species. Thus, there has to be an intermediate diversity at which the two rates (immigration and extinction) neutralize each other, i.e. there has to be a point of dynamic equilibrium, predictable as a function of island area and isolation. So two islands at different distances, but of the same area, should have different steady states and the farther island will have a lower species richness.

2.2.1 The beginning of fragmentation research

MacArthur and Wilson (1967: 3-4) clearly foresaw the important role ETIB could play in research investigating the impacts of human-induced change on natural habitats. In their introduction, they argued:

Figure 2.1 A version of MacArthur and Wilson's (1963, 1967) equilibrium model, showing how immigration rates are postulated to vary as a function of distance, and extinction rates as a function of area. This is, in essence, the core of the equilibrium theory of island biogeography. *Source*: adapted from Whittaker, 1998: 119.



——	Large island
——	Small island
-·-·-	Far island
-----	Near island

EFS	Equilibrium number of species on a small island far from the mainland.
EFL	Equilibrium number of species on a large island far from the mainland.
ENS	Equilibrium number of species on a small island near the mainland.
ENL	Equilibrium number of species on a large island near the mainland.

'Insularity is moreover a universal feature of biogeography. Many of the principles graphically displayed in the Galápagos Islands and other remote archipelagos apply in lesser or greater degree to all natural habitats. Consider, for example, the insular nature of streams, caves, gallery forest, tide pools, taiga as it breaks up in tundra, and tundra as it breaks up in taiga. The same principles apply, and will apply to an accelerating extent in the future, to formerly continuous natural habitats now broken up by the encroachment of

civilisation, a process graphically illustrated by Curtis's maps of the changing woodland of Wisconsin…'

The implications of this statement were not lost and many researchers (e.g. Brown, 1971; Diamond, 1972; Terbough, 1974) were quick to test the tenets of ETIB on fauna in fragmented landscapes, on different island groups not considered in MacArthur and Wilson (1963, 1967), or in mountain tops isolated from North American desert basins. Arguably one of the most important papers of this period was Diamond's (1975a) *The island dilemma: lessons of modern biogeographic studies for the design of nature reserves* (Whittaker, 2004). Diamond (1975a), using MacArthur and Wilson's (1967) arguments that a distinction should be made between ancient oceanic islands that support an equilibrium number of species and recently isolated landbridge islands on which species number is above the extinction-colonisation equilibrium, developed and coined the hypothesis that species number *relaxes* to a lower number in habitats that have been fragmented in a predictable fashion. The 'proof' for this, Diamond (1975a) argued, could be derived from his studies of resident, non-marine bird communities inhabiting land-bridge islands off the coast of New Guinea. Diamond (1975a) used the assumption that before sea-level rose at the end of the Pleistocene and turned these land areas into islands, they would have shared close to a full quota of species now present on the mainland. Relaxation was defined as the process where if the island were reduced in area (i.e. in this case by sea-level rising), supersaturation of species would occur as immigration rate declines and extinction rate rises. This would eventually cause species loss towards a lower equilibrium. Diamond (1975a) empirically showed that New Guinea's land-bridge islands smaller than about 250 km^2 had very high extinction rates (as they lost their entire excess of bird species in 10, 000 years) while islands greater than this size had lost many but not all of their excess species in this time-frame, if these islands upon separation, held a full quota of species.

By using the results of this research, Diamond (1975a) argued that habitat fragmentation would produce similar, predictable patterns of species loss due to species relaxation over time. Relaxation, therefore, became an abstract theory founded on assumptions that a fragmented system passes from equilibrium (pre-isolation), to non-equilibrium (at isolation), to a new equilibrium condition. In this seminal paper, Diamond (1975a: 135) made some bold statements about our ability to predict total numbers of losses:

> *'a rough rule of thumb, corresponding to a z value of 0.30, is that a tenfold increase in island area means a twofold increase in the number of species...if 90% of the area occupied by a habitat is converted by man into another habitat and the remaining 10% is saved as an undivided reserve, one might expect to save roughly about half of the species restricted to that preserved habitat type.'*

Diamond (1975a: 139) also developed predictions on the rates of species loss in habitat fragments:

> *'Thus, the gradual decline of species number from a high initial value to a lower equilibrium value on land-bridge islands may furnish a model for what could happen when a fraction of an expanse of habitat is set aside as a reserve and the remaining habitat destroyed. ...for reserves of a few km^2, extinction rates of sedentary birds and mammal species unable to colonise from one reserve to another are so high to be easily measurable in a few decades.'*

Using these predictions as guidelines, Diamond (1975a), along with Wilson and Willis (1975), developed a set of general principles (Table 2.1) to guide the design of nature reserves. These ideas were supported by a number of authors (e.g. Diamond and May, 1976; Shafer, 1990; Noss and Cooperrider, 1994) but were heavily criticised by others (e.g. Simberloff, 1976; Simberloff and Abele, 1976; 1982), and formed the basis of the SLOSS

Table 2.1 Diamond's (1975a) reserve principles, which were supposedly derived from island biogeography studies.

Principle 1.	Large reserves are better than small reserves.
Principle 2.	A single large reserve is better than a group of small ones of equivalent total area [the basis of the SLOSS debate].
Principle 3.	Reserves close together are better than those far apart.
Principle 4.	A compact cluster of reserves is better than a line of reserves.
Principle 5.	Circular reserves are better than long, thin ones.
Principle 6.	Reserves connected by a corridor are better than reserves not connected by a corridor.

debate. By the late 1970s, results from research conducted using the tenets of ETIB and on Diamond's (1975a) subsequent ideas about species relaxation, were being widely applied in conservation decision-making processes in fragmented landscapes (Simberloff 1976; reviews in Zimmerman and Bierregaard, 1986, Doak and Mills, 1994; Boecklan 1997). For example, the IUCN's 1980 World Conservation Strategy (IUCN 1980) adopted these principles, and in Australia they were recommended for wildlife management in *Eucalyptus* forests (Davey, 1989).

A leading proponent of the ETIB and relaxation case is Professor Mike Rosenzweig, who provided an important review and meta-analysis of the SPAR in his 1995 book. Using the ETIB as a basis, Rosenzweig (1995) recognised three different SPARs (sample-area, archipelagic and inter-provincial) for different spatial scales, all with differing z-value ranges. He argued that sample-area SPARs occur from different-size samples within the same biological region and tend to have z-values that range from 0.1-0.3. Archipelagic SPARs are those SPARs for island systems within an archipelago and have z-values that range from 0.25-0.55. Inter-provincial SPARs are those SPARs that compare different biogeographical provinces and have z-values that range from 0.6 to 1. Using this framework, Rosenzweig

(1995) argued that to predict extinctions following habitat loss, researchers should apply a z-value within the sample-area SPARs, and that a value of z=0.25 was appropriate. Others have since used this z-value for predicting species loss in fragmented landscapes. Brooks *et al.* (1997) and (2002) used this z-value to predict the effects of deforestation on threatened birds in insular south-east Asia, and for identifying the most threatened of Myers *et al.*'s (2000) hotspots. Thomas *et al.* (2004) used this z-value to compare the estimated eventual extinction based on habitat loss and compared this with total extinction risk from climate change.

Interestingly, few questioned the validity of Diamond's relaxation predictions, even though such predictions appear to be derived largely from inferences based on studies of actual islands, rather than on studies of recorded losses from fragmented habitats within large land masses (but see Simberloff, 1992). But there were some who indirectly questioned it. Williamson (1988) showed by re-analysing three published data sets (Dony, 1970; Flessa and Sepkoski, 1978; Connor and McCoy, 1979; in Williamson, 1988), that oceanic islands have z-values that range from 0.05 and 1.132, habitat islands range from 0.09 to 0.957 and mainland samples range from –0.276 to 0.925. These z-values are clearly different from the ranges identified by MacArthur and Wilson (1967) and the subsequent analyses conducted by Rosenweig (1995). The results of other empirical studies bring into question the validity of species relaxation in fragmented landscapes. Gonzalez (2000), by manipulating a moss microcosm, showed that species loss was due more to community isolation rather than area, and that over the period of the experiment z values declined in the control communities and yet remained stable in the fragmented communities. He argued that predictions of species loss due to habitat fragmentation that do not take into account that z-values may not be constant, may lead to error-prone predictions of future losses. Honnay *et al.* (1999) surveyed the presence and absence of 75 forest-core plant species in 156 forest fragments in Western Belgium and concluded that forest plant extinctions in western Belgium were not caused by patch-area-dependent stochastic extinction processes resulting from shrinking forest size (i.e. species relaxation), but were due to deterministic processes caused by overall habitat deterioration. Unfortunately, there are only a few other studies that have explored the process of species relaxation in this detail.

Although little has been done on the applicability of a constant *z*-value, the form of the species-area curve has been recently reviewed (e.g. Ovaskainen and Hasnki, 2003; Scheiner, 2003; Storch *et al.*, 2003; Tjørve, 2003) and there have been many suggestions on improving the understanding of the relationship. For example, Triantis *et al.* (2003) introduce the term choros (*K*) to develop a species-area-habitat model and tested this against the traditional species-area relationship. To develop this new parameter they simply multiplied the number of habitats (*H*) within an area by the area (i.e. $K= H*A$). Triantis *et al.* (2003) showed that when replacing A with K in the species-area relationship that their new species-area-habitat relationship had a better fit in 20 of the 22 case studies examined. In another example Lomolino and Weiser (2001), by using break-point regressions, developed a methodology to examine the small-island effect in species-area relationships. By doing this, they were able to demonstrate a new, more general model of the species-area relationship, which help explains the richness of small islands in non log-log space. Although these developments are important, many ecologically important factors (e.g. the impact of spatial scale and landscape context) have been rarely considered in how they affect the species-area relationship (Whittaker, 1998).

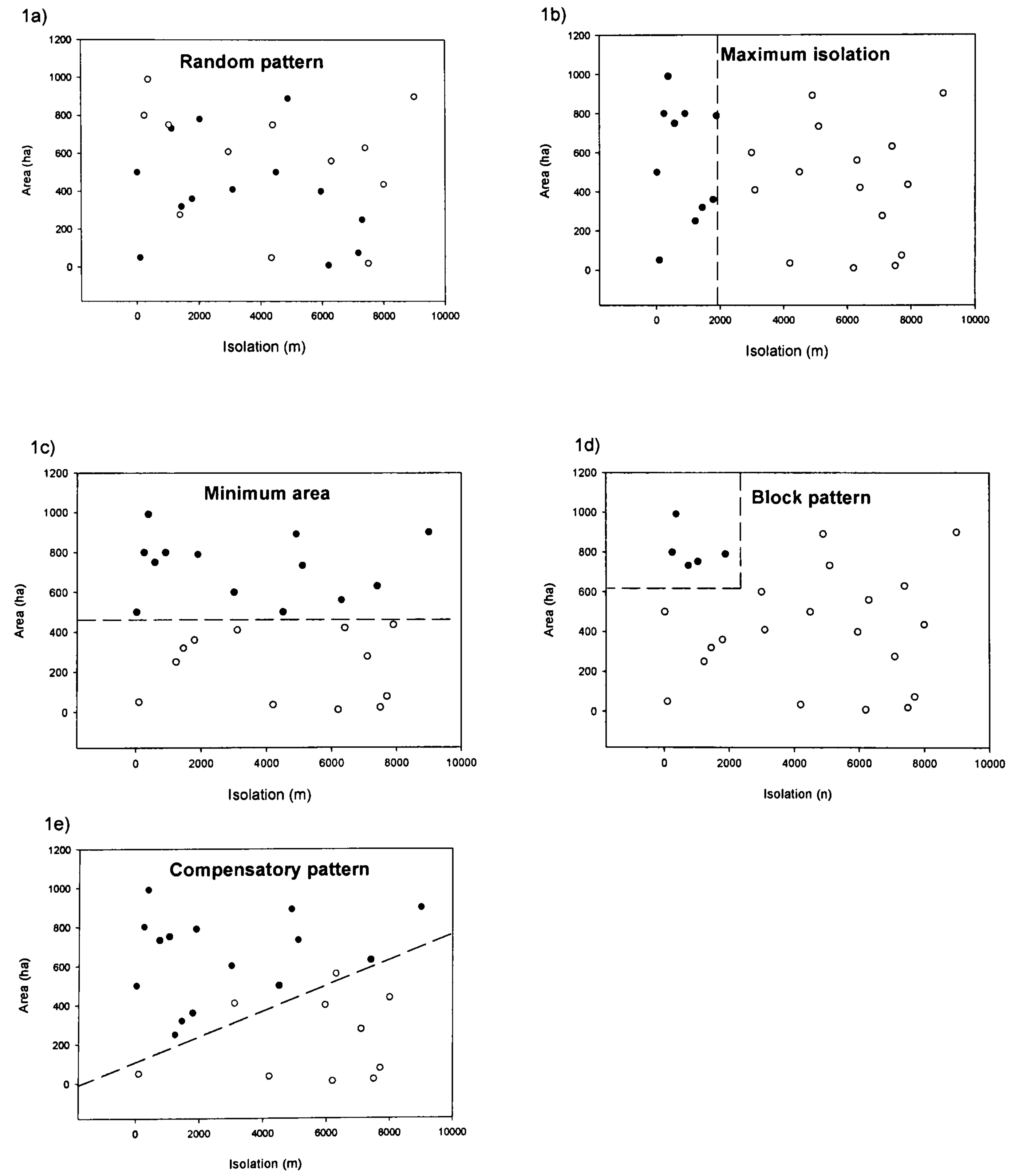
The idea of habitat fragmentation was a conceptual innovation adopted in ecology in the 1970s and the ETIB became the basis of fragmentation related research (Whittaker, 1998; Haila, 2002). As a consequence, island theory has become the driving theory behind many community-level studies of species assemblages occupying habitat remnants in fragmented terrestrial systems. It also led to the development of other associated theories on how species are distributed in fragmented landscapes.

2.2.2 Assembly rules

Following MacArthur and Wilson's (1967) attempt to explain species richness on islands, Diamond (1975a,b) assessed how similar species were distributed among islands. He was the first to describe the so-called assembly rules of birds, using examples of bird communities on the islands off New Guinea (Whittaker, 1998). Among other achievements, he coined the term 'super-tramps' in describing the patterns of species distribution among islands of different species richness and was also the first to recognize the importance of biogeographic checkerboard distributions of species on islands. His guild analyses revealed that exclusive distributions are often achieved by species segregating their realized distributions over different ranges of isolation and area, i.e. their distributions were dependent of both island area and isolation. Diamond's island assembly rules were criticized extensively (e.g. Simberloff, 1978; Connor and Simberloff, 1979; Lomolino, 2000a; see Whittaker, 1998 for a review), but his observations that species distributions were related to island area and isolation were significant. Lomolino (1986), for example, furthered Diamond's (1975a,b) research by developing five hypothetical insular patterns for the distribution of a particular species on an archipelago, which included species that were randomly distributed, had minimum area requirements, had maximum isolation requirements and two patterns (block and compensatory) that were combinations of minimum area and maximum isolation (Figure 2.2).

Another form of structure (assembly rules) is the degree of *nestedness* of biota inhabiting different islands (Patterson and Atmar, 1986; Whittaker, 1998). A nested distribution describes the situation where smaller insular species assemblages constitute subsets of the species found at all other sites possessing a larger number of species (Patterson and Atmar, 1986). Lindenmayer *et al.* (2002) argued that nested subset theory attempts to extend the species-area relationship that underpins island biogeography theory by tracking both the

Figure 2.2 Hypothetical distributions of species, arranged relative to fragment area isolation (after Lomolino 1986, Lawlor, 1998). Open circles are unoccupied fragments, while closed circles represent fragments in which the species occurs. (a) Random pattern, in which the distribution of species is not affected by area or isolation. (b) Maximum isolation pattern, in which species are dispersal limited, and recorded only in those fragments below a threshold-level of isolation. (c) Minimum area pattern, in which species are area-sensitive and inhabit only those fragments larger than a particular threshold. Two patterns may be exhibited by those species whose insular distributions depend on both area and isolation. (d) A 'block' pattern occurs when a species depends on both the resources of the largest remnants and has limited ability to immigrate. (e) A 'compensation' pattern, in which isolated fragments are occupied when of sufficient size, and small fragments are occupied when close to larger patches.



numbers of species and their identities on 'islands', although it is clear that the original theory was not based on area-ordered nestedness but rather richness-ordered nestedness (Whittaker, 1998). In the context of habitat fragmentation, nested subset theory states that species-poor small fragments should support assemblages that are subsets of larger, species-rich fragments (Patterson and Atmar, 1986). There is now considerable evidence of nestedness of biota in the fragmentation literature (e.g. Hansson, 1998; Butaye *et al.* 2001; Fernandez-Juricic, 2002a, b; Flieshman, 2002), although debate still occurs as to whether differential immigration or differential extinction is the chief reason why the pattern occurs, and, as such, whether nested assemblages are deterministic or stochastically based (Whittaker, 1998).

2.2.3 Metapopulation theory

Metapopulation theory arose out of the recognition that populations may be spatially subdivided rather than uniformly distributed across a landscape (Levins, 1969; Hanski and Gilpin, 1991). A metapopulation is a spatially structured assemblage of local populations with a level of interaction (e.g. dispersal) between them that has some effect on local population dynamics (Hanski and Simberloff, 1997). The theory is therefore similar to island biogeography in that habitat isolation is thought to play an important role in the extinction-colonisation dynamics of local populations. However, in the ETIB, the dynamic variable is the number of species on a particular island (or habitat fragment) while in metapopulation theory as formulated by Levins (1969), the dynamic variable is P, the number of habitat fragments occupied by a species, and the model is:

$$\frac{dP}{dt} = cP(T - P) - eP \qquad (1)$$

where T is the total number of fragments (assumed to very large) and *e* and *c* are the extinction and colonization parameters (Hanski and Thomas, 1994). The metapopulation model stresses the importance of within- and between- local population dynamics on the persistence of a species over time. Its concepts are intuitively appealing to researchers studying the dynamics of organisms living in anthropogenically fragmented landscapes because the distribution of many species is spatially subdivided. The concept of metapopulation dynamics has been used widely to describe the spatial arrangement of subpopulations of species in fragmented environments (e.g. Arnold *et al.* 1993; Hanski and Thomas, 1994), particularly those taxa susceptible to localized extinction and recolonisation (Hanski, 1998).

2.2.3 Other recent developments in island theory

Lomolino (2000a) presented an alternative to the ETIB based on the premise that many of the more general patterns in insular community structure result from non-random variation among species. The model presented was species-based. The fundamental component of the hierarchal model is the species insular distribution function (Figure 2.3), which describes how populations of a particular focal species should be distributed across the two geographical dimensions of island area and isolation. Although the majority of Lomolino's examples are from island archipelago systems, his research has implications for species diversity within habitat fragments. For example, Lomolino (2000a) showed the effects of 'immigration filters' of Hazel Grouse (*Bonasa Bonasa*) in fragmented forests in Sweden, using the results of Aberg *et al.*'s (1995) research, by arguing that the slope of the insular distribution function for this species increased where forests were surrounded by less hospitable habitats versus second growth, managed forests. In addition to this, Lomolino (2000a) argued that his species-based models were scale-dependent, which has important ramifications for interpreting minimum requirements of species with limited data (Figure 2.4).

In another attempt to build upon the ETIB, D.M. Watson (2002) developed a conceptual framework for studying species composition in fragments, islands and other 'patchy'

Figure 2.3. The general form of the insular distribution function for Lomolino's (2000a) focal species (dark symbols indicate presence, open circles indicate absence of a focal species). Adapted from Lomolino (2000a).

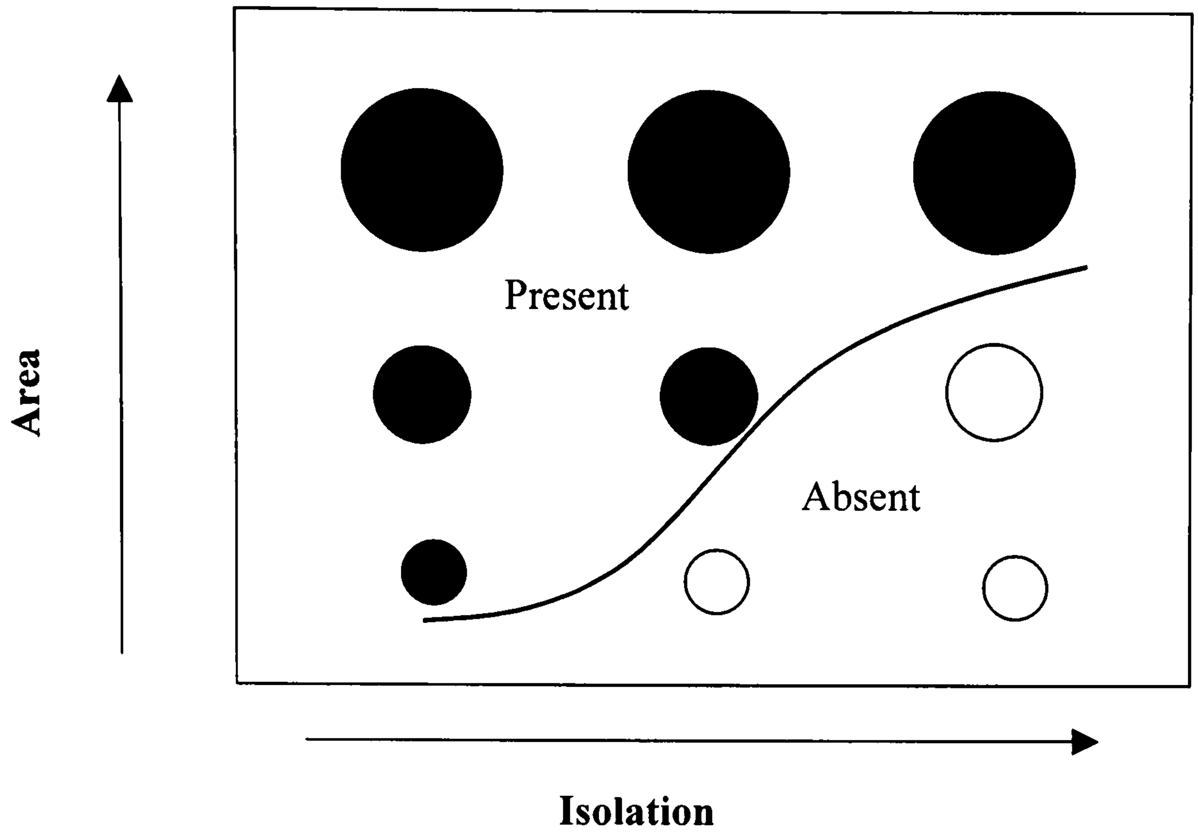
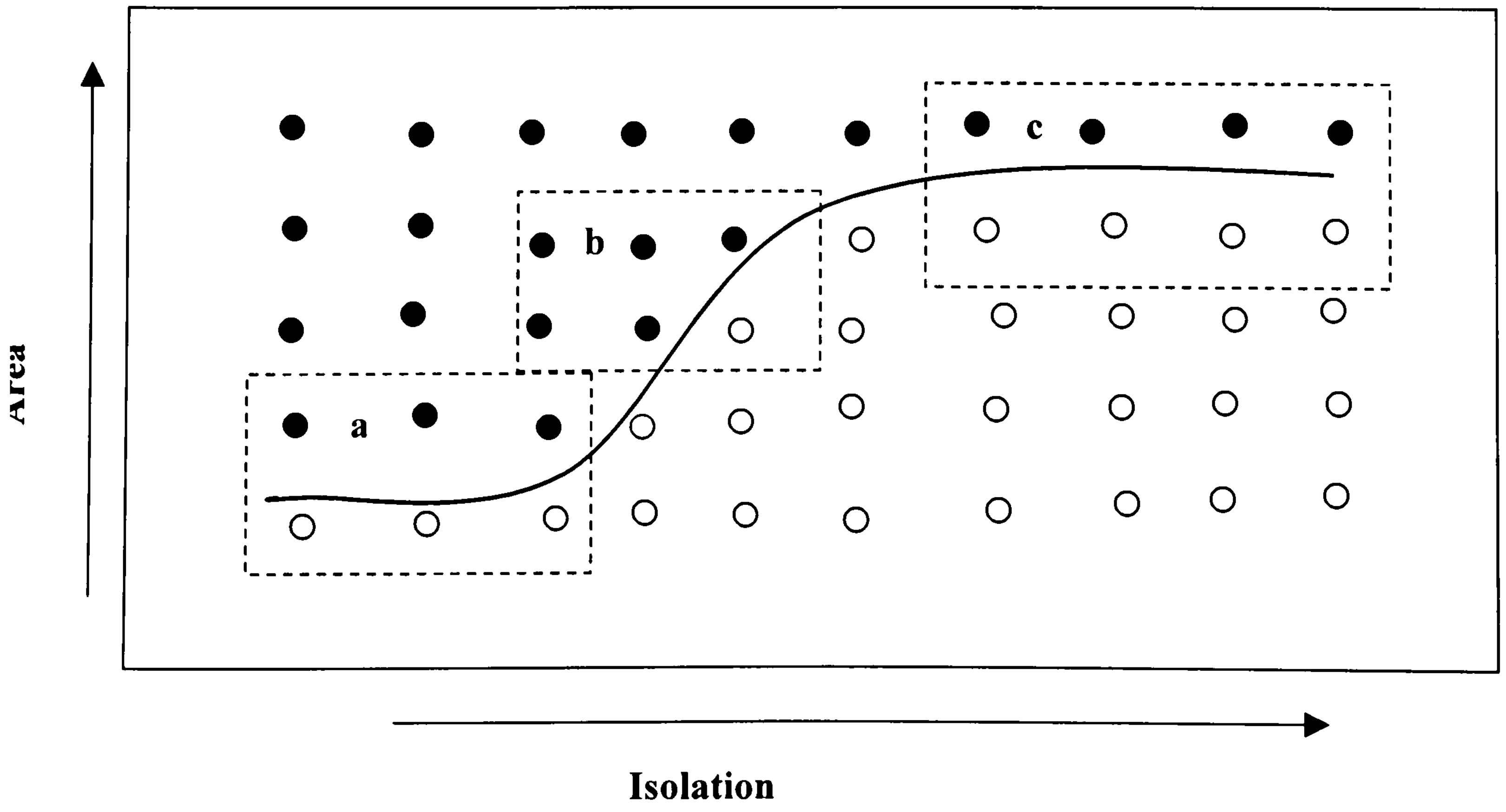


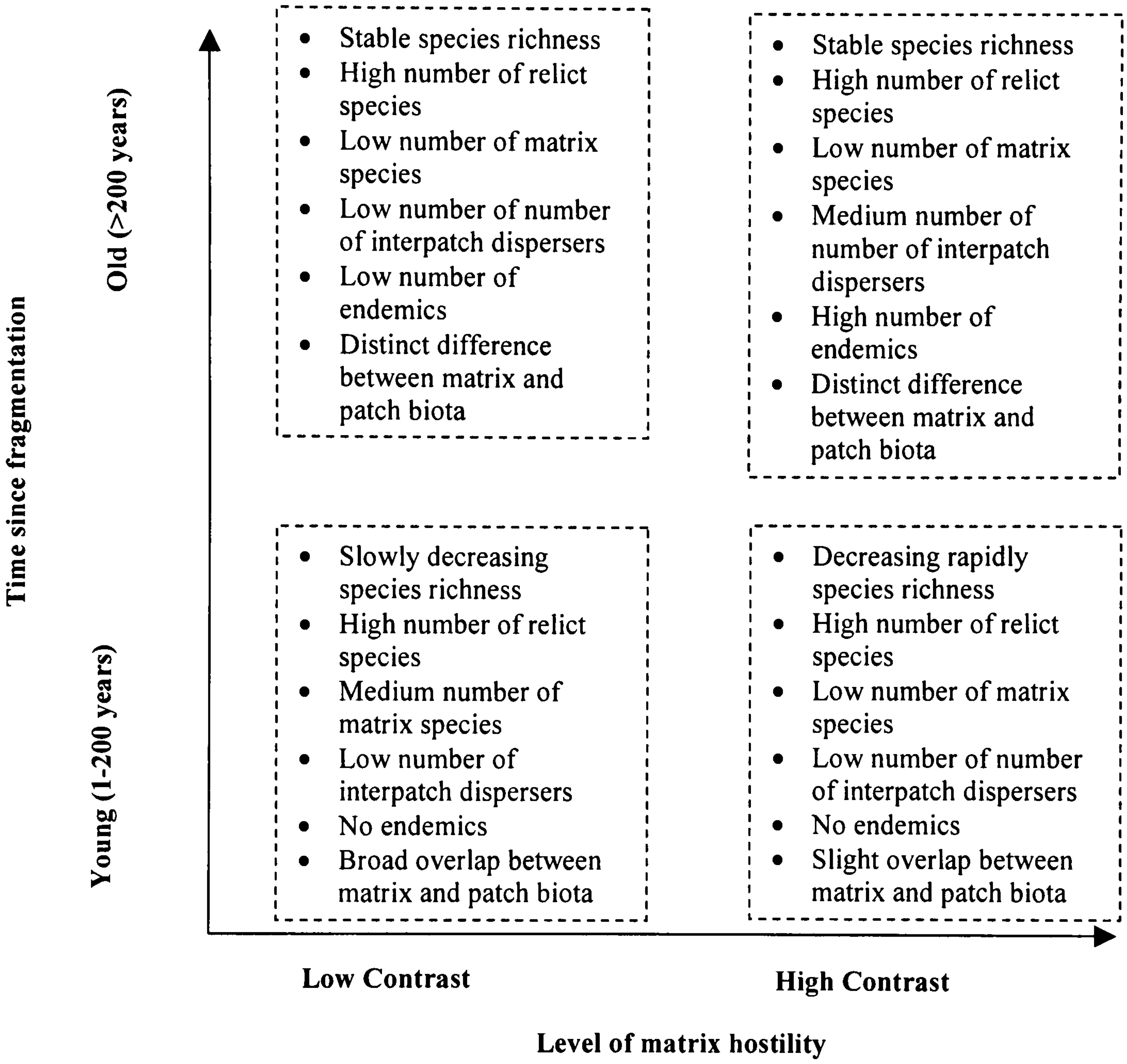
Figure 2.4. Effects of different sampling regimes on apparent patterns of distribution on a hypothetical species (darkened symbols depict presence, open symbols depict absence). Depending on the region sampled, the same species may appear to exhibit a variety of distribution patterns with respect to island area and isolation. If researchers were surveying habitats in regions **a** or **c**, they would conclude that the insular distribution is primarily limited by habitat or island area but would estimate different critical areas. Adapted from Lomolino (2000a).



ecosystems. Watson (2002) defined different matrix states to determine if a habitat island was low contrast (e.g. a forest fragment surrounded by grassland) or high contrast (e.g. an island surrounded by water) and also considered the history of isolation (i.e how long the habitat island had been 'isolated' for). In addition to this, Watson (2002) classified organisms as colonising, either from another patch (inter-patch dispersers) or from the matrix surrounding the patch (matrix-derived species). For the biota of fragments, those organisms that inhabited the patch prior to fragmentation were considered 'relict' species. Watson (2002) argued that for low contrast fragments soon after fragmentation, the biota of a patch is similar to pre-fragmentation conditions, composed primarily of relict species with some local extinctions because of the net loss of habitat caused by fragmentation. Within these patches there are few matrix-derived species (primarily habitat generalists) and a variable component of inter-patch dispersers. Subsequently, more matrix species enter and additional relict species become locally extinct through demographic (e.g. genetic extinction) and stochastic processes. Watson (2002) showed that these generalized patterns are exemplified by results of the Biological Dynamics of Forest Fragments Project (Lovejoy *et al.*, 1986). After fragmentation of the forest, butterfly, small mammal, understorey hummingbird and terrestrial frog diversity increased, as losses of forest-dependent relict species were more than compensated by an influx of matrix-derived specialists (see Watson, 2002 for further details).

By defining islands and species in this way, Watson (2002) was able to develop a framework for identifying four classes of habitat patch (after first separating true islands from habitat patches), and define a set of predictions for the biota that inhabit these patches (Figure 2.5). Even though only recently published, Watson's incorporation of matrix properties is potentially an important step-forward in fragmentation and ETIB related research. The development of this framework highlights the emergence of matrix-related ecological studies as a theme, as in previous comparative reviews, the confounding effects of patch: matrix contrast and age were not explicitly accounted for (Patterson and Atmar, 2000; Crooks *et al.*, 2001).

Figure 2.5 Schematic diagram of D.M. Watson's (2002) ideas of the characteristics of biota inhabiting four forms of habitat patch. These patches have been separated on a temporal (i.e. time since isolation) and matrix (i.e. hostility) basis.



2.2.5 Landscape ecology and fragmentation research

Landscape ecology deals with the causes and consequences of the spatial composition and configuration of landscape mosaics. Because changes in land use (e.g. deforestataion and habitat fragmentation) alter landscape composition and configuration, it has been argued that landscape ecology and biological conservation are closely linked (Gutzwiller, 2002). However, landscape ecology is still seen as a new academic discipline (Forman, 1995; Lindenmayer and Franklin, 2002) and there is still much uncertainty about what exactly constitutes landscape ecology (Wiens, 2002). As such, there are a number of broad definitions of what 'landscape ecology' is. Some authors consider landscape ecology to be a holistic, problem-solving approach to resource management (Barret and Bohlen, 1991). The emphasis on this approach is integrating many aspects of human activities with their environmental consequences - i.e. a geographically based resource-management approach. A second approach emphasises landscape as a level or scale; in essence, it is ecology writ large (Gutzwiller, 2002). Many of the questions asked using this approach are those that ecologists have traditionally addressed, but they are cast in a broader hierachical or spatial context. A third approach deals more explicitly with the effects of spatial pattern on ecological processes (Turner, 1989; Wiens, 1995). In this case, the level and scale are determined by characteristics of the organism or ecologically system of interest and the questions asked. The focus of this approach is on the mechanisms by which the spatial structure of the environment influences phenomena of conservation value such as populations or biodiversity. The scales on which these mechanisms are expressed (and thus the 'landscape') therefore will differ for different kinds of organisms.

Despite the debate over what the definition of landscape ecology should be, a number of researchers have attempted to produce landscape ecological models that were not solely based on the island-habitat patch analogy (Lindenmayer and Franklin, 2002). McIntyre and Barret (1992) proposed the concept of a 'variegated' landscape to account for cases where there could be gradients of habitat condition or quality within a landscape. Forman (1995) refined this idea, and produced the *corridor-patch-matrix* model, which differentiated between different types of patches, including the matrix. It was argued by some (e.g. McIntrye and Hobbs, 1999; Lindenmayer *et al.*, 2003) that this classification did not fundamentally address the tendency for investigators to use research models that assumed a binary habitat versus non-habitat classification. In order to present a more unified model of landscape alteration, McIntyre and Hobbs (1999) developed a *landscape continuum* model. In the landscape continuum model, landscapes are characterized by having different levels of vegetation cover within a continuum or gradient of possible conditions that range from an intact cover of native vegetation through to relictual levels of cover. Manning *et al.* (2004) developed a *Continua* (the concept of continua in nature) and *Umwelt* (individual species perception and response to changes in nature) model, as a further development on McIntyre and Hobbs (1999) landscape continuum model. In this model, the level and scale are determined by characteristics of the organism or ecological system of interest and the questions asked (cf. Whittaker, 1998; 2000). The focus of this approach is on the mechanisms by which the spatial structure of the environment influences phenomena of conservation value such as populations or biodiversity. The problem with these models (which the authors recognise themselves) is that it does not give a practical way forward in actually testing and developing them. These models are at best arbitrary in the real world of fragmentation.

Landscape ecology has been seen as a key advance by many ecologists who study habitat fragmentation (e.g. Gutzwiller, 2002; Lindenmayer and Franklin, 2002; Wiens, 2002) because it recognises the simple fact that ecological processes are not confined by anthropogenically created boundaries and the persistence of species may rely on the management of the entire landscape. However, landscape ecology (unlike the theories associated with island theory) still lacks a strong theoretical framework that can be tested and developed. Until landscape ecological models can be developed so that they can be tested easily in different fragmented systems, researchers will still have to rely on island theory as the basis of fragmentation research and the development of conservation strategies (Lindenmayer and Franklin, 2002). This is highlighted by a review of the most recent fragmentation studies published (e.g. Mac Nally and Horrocks 2002; Watson *et al.*, 2003; Deng and Zheng 2004, Maldonado-Coelho and Marini 2004; many others), as they all use the tenets of island theory and not landscape ecology as their basis.

2.3 What are the effects of habitat fragmentation on birds?

Since 1967 there has been, as some authors describe, an 'explosion' in the fragmentation literature. In this section, I aim to review the literature of the past three decades to describe the effects of habitat fragmentation on birds. For the sake of clarity, I use a spatial hierarchical structure based on Forman's (1995) landscape scale definitions (see the Glossary). This hierarchal structure was used to overcome a general weakness in ecological literature- the failure to distinguish factors relevant to particular scales of analysis (Whittaker *et al.*, 2001; Willis and Whittaker, 2002; Pearson and Dawson, 2003). The effects of landscape fragmentation are summarised at three spatial scales, 'patch', 'landscape' and 'regional', because habitat fragmentation affect ecosystem pattern and process at these scales (Lord and Norton, 1990; Wiens, 2002).

2.3.1 Patch scale effects of habitat fragmentation and degradation on birds

Increased human use of forest fragments often leads to the degradation of habitat. Processes associated with clear-felling, charcoaling, wood collecting and other related activities all inevitably lead to a change in vegetation complexity and composition within a habitat remnant. At the patch scale, degradation of habitat may also lead to major abiotic alterations in the local ecosystem, including changes to hydrologic regimes, mineral nutrient cycles, radiation balance, wind patterns and soil movement (Saunders *et al.*, 1991; Hobbs, 1993). These altered processes may affect vegetation structure and composition within the remnant; such changes can have a profound effect on the dynamics of bird communities (e.g. Mac Nally, 1990; Watson *et al.*, 2001). This is because different plant species are sources of food for particular bird species, while other plant species provide shelter and nesting materials for species (Carothers *et al.*, 1974; Urban and Smith, 1989). Two recent studies exemplify this: Major *et al.* (2001) found that the dominant tree type within woodland remnants had a significant ($p<0.05$) relationship with both the overall bird community composition and individual species distributions in eastern Australia and Herrando and Brotons (2002) found local habitat structure and floristics to be significant predictors of bird species in fragmented Mediterranean landscapes. Ultimately, loss or degradation of habitat may cause local extinction, especially for species restricted to the lost habitat (Connor and McCoy, 1979).

Degradation and habitat fragmentation also influence individual and bird community behaviour at the patch scale. It has been shown that as species compete for less resources (i.e. food, space) within a patch that is either smaller in size or has a changed vegetation composition, increased inter-specific and intra-specific competition may occur (Newton, 1998). Reductions in population sizes can adversely affect inter-specific interactions if lost individuals belong to species playing mutualistic roles in the patch habitat (Desouza *et al.*, 2001; Dick, 2001). This may cause a decrease in the reproductive success of individuals in the patch, reducing even further their population sizes. However, a decrease in population densities may lead to the reduction of competitive interactions, if resources have been unaffected by fragmentation (Newton, 1998). Indirect biological changes may also occur as predator-prey relationships are altered within a patch habitat. In some cases, predation pressures may be diminished or disappear entirely (Marcström *et al.*, 1988; Newton, 1998).

These reduction or increases in inter-specific and intra-specific interactions may either ease the increment of population size on resident species through density compensation (Case 1975) or increase the 'invasibility' of the remnants by immigrants (Tilman, 1997). Density compensation occurs when extant populations grow in such a way that the community in the fragment will present the same total numbers of individuals as before fragmentation, but these individuals will be distributed over fewer species. Density compensation may lead to a secondary increase in either intra or inter-specific competition, which in turn, may lead to the elimination of individuals from a remnant.

2.3.2 Landscape and regional scale effects of habitat fragmentation and degradation on birds

At the landscape and regional scales, it is now believed that dynamics of bird populations are influenced by five interrelated processes associated with habitat loss and subsequent fragmentation: habitat loss, subdivision of habitat, patch isolation, edge effects and compositional changes in the landscape matrix (Forman, 1995; Lindenmayer and Franklin, 2002). The last four factors are defined as habitat fragmentation – the subdivision of habitat patches – and need to be distinguished from habitat loss, which is the overall depletion of habitat (Andrén, 1994). Theoretically, habitat loss can occur without habitat fragmentation, as shown by Forman's (1995) landscape modification models (i.e. perforation, dissection and shrinkage). In the majority of cases it is extremely difficult to separate the effects of habitat fragmentation from the effects of habitat loss (Andrén 1997; Harrison and Bruna, 1999; McGarigal and Cushman, 2002). The two processes are nearly always confounded. However, it is now generally agreed among ecologists that below certain thresholds of habitat cover (normally cited to be around 30% of cover in a given landscape), the loss of species and populations declines of individual taxa are more substantial than predicted from habitat reduction alone (e.g. Rolstad and Wegge, 1987; Andrén, 1994; Enoksson *et al.*, 1995; Newton, 1998; McCarthy and Lindenmayer, 1999; With and King, 1999).

2.3.3 The effect of sub-division of habitat

Habitat fragmentation leads to the sub-division of habitat, with different sized parcels of habitat occurring throughout the landscape. The effect of remnant patch size on biodiversity is arguably the most well studied aspect of fragmentation and numerous studies have found that species are sensitive to a loss of habitat area (Turner, 1996; Debinski and Holt, 2000). The most obvious reason for this (and one that was described in MacArthur and Wilson's ETIB) is that a species requires enough habitat to support an adequate number of individuals for the maintenance of a long-term viable population, and, therefore, a reduction in patch area will lead to a smaller population of a given species (Diamond, 1975b; Wilson and Willis 1975). Small populations are more prone to extinction for a variety of reasons including: (i) they are more prone to extinction by chance events than are large populations (stochastic events) (Soulé, 1986), (ii) there is a higher chance that individuals will mate with closer relatives, which may produce few offspring or offspring that are weak or sterile (inbreeding depression) (Templeton *et al.*, 1990), (iii) there is likely to be a paucity of mates which may lead to out-breeding depression (McCarthy *et al.*, 1994); and (iv) they have their fitness affected by genetic drift (the chance increase or decrease of alleles) (Nei *et al.*, 1975).

Studies have shown that it is not a non-random selection of bird species that are area-sensitive, with the majority being 'patch-interior' (sensu Villard, 1998) or 'relictual' (sensu Watson, 2002) species. These specialist bird species are often affected by the sub-division of habitat because they experience high rates of nest predation (Robinson *et al.*, 1995), high rates of nest parasitism (Robinson, 1992), increased interspecific competition (Ambuel and Temple, 1983; Grey *et al.*, 1998), fewer adequate breeding microhabitats (Wilcove *et al.*, 1986), reduced pairing success (Van Horn *et al.*, 1995; Hagan *et al.*, 1996; Hinsley *et al.*, 1999), altered intra-specific dynamics leading to Allee effects (Allee *et al.*, 1949; Ims *et al.*, 1993) and are affected by mesopredator release (Soulé *et al.*, 1988; Crooks and Soulé, 1999) in smaller patches. This may reduce populations of some species to nonviable levels.

The result of having area-sensitive species in a fragmented landscape is that bird communities will change with patch size. The majority of bird community studies show a strong relationship between patch habitat area and bird species richness (e.g. Cornelius *et al.*, 2000; Watson *et al.*, 2001; Beier *et al.*, 2002). Furthermore, a number of studies (e.g. Watson *et al.*, 2000; Martin and Catterall, 2001; Park and Lee, 2002; Mac Nally and Horrocks, 2002) have found that remnants of different sizes have significant differences in their community composition. However, two recent studies show that smaller patches may contain more or similar number of patch-interior species than large remnants (Estades and Temple, 1999;

Fischer and Lindenmayer, 2002a) and a number of other studies (e.g. Schieck *et al.*, 1995; Pattanvobool and Dierdren, 2002) have found little to no effect of area on species richness or composition. There have been a number of reasons given for why small patches experience an increase in species richness after fragmentation: (i) they have an increase in matrix-tolerant species post fragmentation leading to a greater species richness in the remnant (Yahner, 1988), (ii) a 'spillover' of species from nearby large remnants into small remnants may occur (Debinski *et al.*, 2001) and, (iii) in landscapes comprised mostly of small patches, species may sample several patch types (i.e. habitat sampling, Debinski *et al.*, 2001). The lack of area-effects in some studies (e.g. Fischer and Lindenmayer, 2002a) may be simply due to a limited range in area of patches sampled (cf. Whittaker, 1998, 2000).

2.3.4 Remnant shape changes

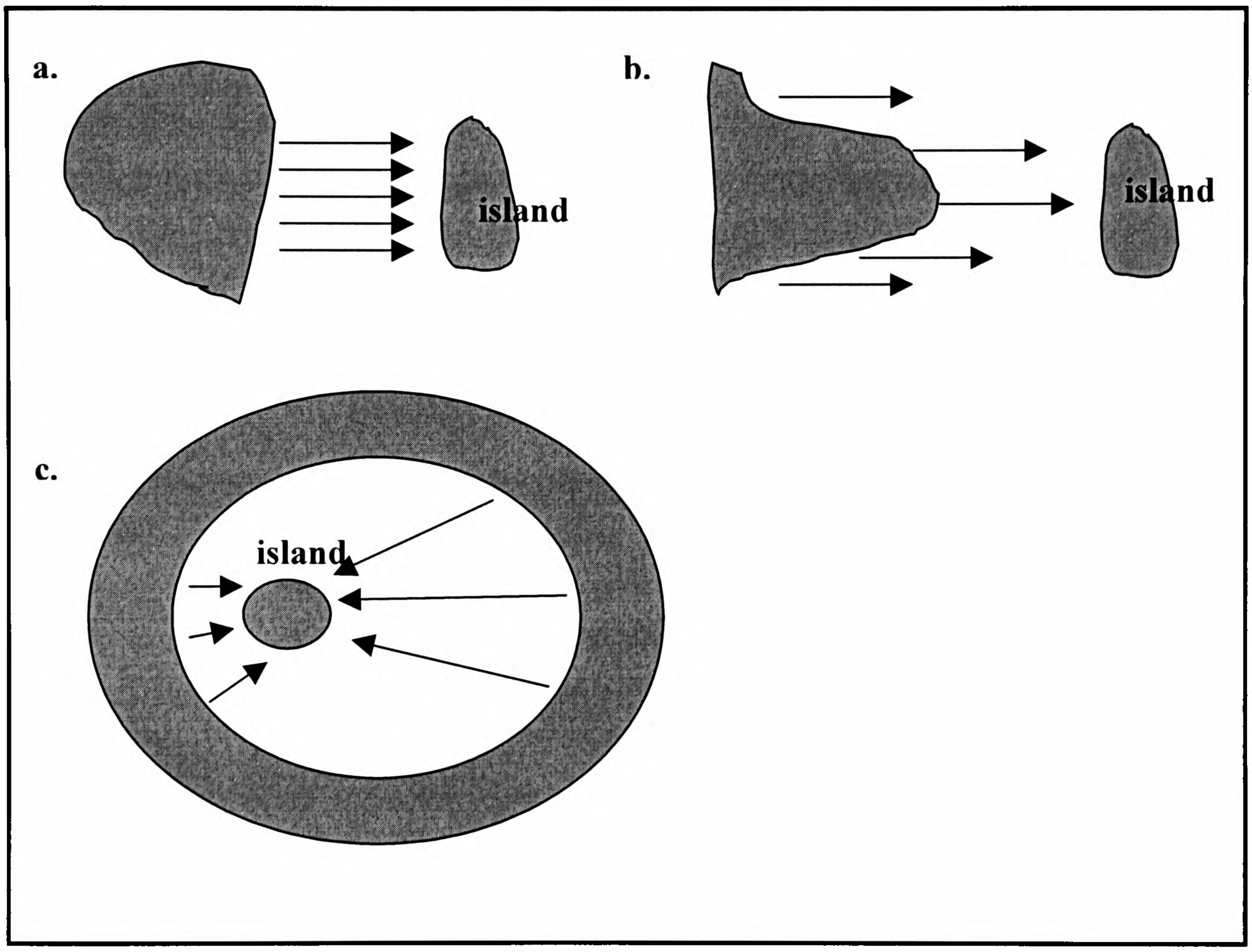
Habitat fragmentation not only reduces the amount of habitat available for organisms to live in but also affects the spatial arrangement of habitat, i.e. it will inevitably lead to a change of shape (i.e. perimeter to area ratio or amount of core habitat available) of habitats (Sisk and Margules, 1993). A change in shape may alter the proportion of edge habitat for that habitat. For example, a small irregular shaped remnant will contain proportionally more edge habitat than a small round habitat and therefore be exposed to greater amounts of edge effects. A number of studies have shown that the shape of a patch may affect reproductive success, bird behaviour and the composition of communities in different ways (Sisk *et al.*, 1997; Restrepo and Gomez, 1998). Temple and Cary (1988) found that the abundance of forest-interior species in temperate forests declined in patches with increasing edge-to-area ratios. Perhaps a more interesting discovery was Helzer and Jelinski's (1999) finding that that the perimeter-area ratio, which reflects both the area and the shape of a patch, is a stronger predictor of both individual species presence and overall species richness of birds inhabiting fragmented grasslands in Nebraska, than area alone.

In addition to the potential deleterious effects of an increased edge, immigration rates can also be affected by the shape of both the fragment and the potential source habitat (Taylor, 1987; Figure 2.6). According to this model, straight-line shores should 'release' more colonisers than do pointed peninsulas, at least for passive dispersers. Similarly, an island in the centre of a circular lake should receive more immigrants than if it were located eccentrically, close to the shore. An island in the centre of a lake can receive colonisers from the entire lake perimeter, whereas an island near one shore might not receive colonisers from the more distinct margin (Figure 2.6). The same can be true for the shape of the fragment: the number of propagules 'hitting' the fragment should increase when the side of the site facing the source population expands and its position approaches a perpendicular to the main direction of colonists' travel. Therefore, shape effects may promote both lower and higher accessibility of the site by immigrants, as compared to its original status within the forest. Higher accessibility implies the arrival of more immigrants, with consequences discussed above. Lower accessibility implies that fewer immigrants reach the site, which may lead to local extinction through inbreeding depression and demographic stochasticity (Harrison, 1991; Desouza *et al.*, 2001). To my knowledge, this has never been empirically tested for birds.

2.3.5 Remnant isolation

At the landscape scale, habitat fragmentation results in habitat remnants being isolated to varying degrees (Wilcove *et al.*, 1986). The configuration of habitat within a landscape impacts on a species persistence in a fragmented landscape, as a population must rely on its dispersal capabilities between remnant habitats (MacArthur and Wilson, 1967). Therefore, isolation of remnant habitats may make sub-populations more vulnerable to extinction through stochastic demographic fluctuations, loss of genetic diversity, and decreased immigration (Lord and Norton, 1990; Stacey and Taper, 1992). As such, patch isolation has

Figure 2.6 Shape effects in colonisation rates for passive dispersers (adapted from Desouza *et al.*, 2001). According to this model, straight-line shores (ie. a) should 'release' more colonisers than do pointed peninsulas (i.e. b), at least for passive dispersers. Similarly, an island in the centre of a circular lake (i.e. c) should receive more immigrants than if it were located eccentrically, close to the shore. An island in the centre of a lake can receive colonisers from the entire lake perimeter, whereas an island near one shore might not receive colonisers from the more distinct margin.



been a key consideration in numerous empirical studies that have examined the influence of habitat fragmentation on wildlife populations (Saunders *et al.* 1991; Newton, 1998).

Patch isolation as a spatial phenomenon is a difficult attribute to quantify and many metrics have been used in the literature to describe it (see Bender *et al.*, 2003). Remnant isolation is most often characterized by simple isolation measures that reflect the structure of a landscape (e.g. distance to nearest remnant, distance to source remnant) or the configuration of the landscape (e.g. the density of remnants surrounding a remnant habitat, the density of edge habitat that surrounds a remnant habitat). A number of studies have found strong relationships between landscape structure and/or configuration with bird species richness, diversity or individual abundance. For example, Saab (1999) found that the measures 'distance to source', 'distance to nearest neighbour' and 'landscape edge contrast' was related to species richness and the presence of certain species in cottonwood patches in North America. McCoy and Mushinsky (1999) showed that there was a negative relationship between shrub remnant isolation and the abundance of five bird species in the fragmented Florida shrublands. Calme and Desrochers (2000) found that the abundance of two bird species inhabiting Quebec's peatlands was significantly negatively related to patch isolation. Schmeigelow *et al.* (1997) were able to show that forest bird species turnover occurred at a significantly ($p<0.05$) higher rate in isolated boreal forest fragments than in fragments that were not isolated.

A number of studies do not find strong interactions between species richness or individual species abundance and measures of remnant isolation (e.g. Estades and Temple, 1999; Miller and Cale, 2000; Watson *et al.*, 2001). There are a number of possible reasons for this. Firstly, in some study areas many bird species may be so mobile that they are not affected by isolation to the extent that other taxa are, and as such, immigration may not be an issue (Margules *et al.*, 1982; Ambuel & Temple, 1983; Renjifo, 1999). Secondly, the lack of an isolation effect in this system might be simply due to scale effects, as many studies' isolation data range might not have a broad enough range to capture an isolation effect (Whittaker, 2000). Finally, the measures of isolation may not actually capture the effect of remnant isolation on birds. This is because linear measures of distance between remnants or measures that examine configuration may be poor measures of 'connectivity' within the landscape (Haila, 1999; Manning *et al.*, 2004).

The time since deforestation and habitat isolation can be an important determinant of the biotic response to fragmentation (Saunders *et al.*, 1991; Stratford and Stouffer, 1999). It has been found that when habitat fragmentation occurs (i.e. when a habitat fragment becomes isolated) there may be an initial, dramatic increase in the densities of forest birds within the remaining habitat patches (Bieeregaard and Lovejoy, 1989). Hagan *et al.* (1996) argued that when habitat loss is not an ongoing process and the onset of fragmentation is not a recent event, the dynamics of populations are governed by other effects rather than displacement phenomena. That is, put simply, remnant isolation becomes more important as time goes by. Crooks *et al.* (2001) supported this when they found that fragment age was one of the most important variables in influencing extinction and colonization rates in remnants in scrub birds in fragmented southern Californian chaparral and coastal sage shrub. However, a number of studies either do not support these findings or find inconsistencies among bird guild types. For example, Mac Nally and Horrocks (2002) found that historical influences such as remnant age and isolation had little effect on woodland bird diversity in eastern Australia. In this study, the remnant age (1963-1996) may have been too short a period for a biological response. Stouffer and Bierregaard (1995a, b) showed that responses to time since isolation (nine years) were guild specific at the Biological Dynamics of Forest Fragments Study Site in the Amazon Basin, with the abundance and species richness of understorey insectivores declining dramatically after the isolation of tropical forest remnants but the abundance of some understorey hummingbirds species becoming more common.

2.3.6 The creation of a habitat edge

Habitat loss and subsequent habitat fragmentation creates habitat edges, which are the junctions or ecotones between plant community types, successional stages or landuses (Yahner, 1988; Murcia, 1995). The creation of a habitat edge has been shown to affect bird diversity because it may create a change in micro-climate gradient within the particular habitat and a biological change of the community along the new edge. Micro-climatic changes may include factors such as an increased amount of sunlight, wind and temperature variation (Chen, 1993; Matlack, 1993; Murcia, 1995). This, in turn, may result in increased mortality of trees, ground herbs and epiphytic lichens at edges, which in turn may affect food availability for birds (Kapos *et al.*, 1997; Villard, 1998; Laurance, 2001). Some studies (e.g. Beier *et al.*, 2002) argue that different habitat structure and composition along the edge of forest remnants leads to a different bird community, while other studies (e.g. Laurance *et al.*, 1997; Burke and Nol, 1998) argue that micro-climatic changes near the patch edge can make the patch unsuitable for some bird species. To make matters more complicated, there are often biological side-effects to the creation of an edge, including increased predation and nest predation because of increased presence of predators at forest edges (Robinson *et al.*, 1995; Hartley and Hunter, 1998), increase in brood parasitism (Robinson *et al.*, 1995) and a displacement effect where species displaced by habitat loss encroach on communities that exist on the edges of habitat (Dunning *et al.*, 1992).

When an edge habitat is created, it has been found that some species are sensitive to the habitat edge (i.e. 'edge-avoiders'), some are tolerant ('edge-tolerant') and some are encountered more commonly near the edge (an 'edge species') (Wilcove *et al.*, 1986; Reese and Ratti, 1988; Sisk *et al.*, 1997). These definitions are supported by studies that show certain species reach their highest or lowest abundances at particular habitat edges (Kroodsma, 1984; Lynch and Whigham, 1984; Dale *et al.*, 2000). However, what is clear when reviewing the 'edge' literature is that there is no clear general pattern whereby particular species or guilds can confidently be forecast to be more affected by the creation of edge habitat - proximal explanations for edge-avoidance vary across systems and species. For example, of the many studies that assess the impacts of predators on edges versus in the core of a habitat (e.g. Bayne and Hobson, 1997, 1999; Heske *et al.*, 1999; Flaspohler *et al.*, 2001; Keyser, 2002; Morrison and Bolger, 2002), only a few have found that the edge affected the amount of nest predation (King *et al.*, 1998; Estrada *et al.*, 2002). Furthermore, when investigators looked at specific species and how distance to habitat edge affected their breeding success (Friesen *et al.*, 1999; Morse and Robinson, 1999; Flaspohler *et al.*, 2001; Huhta and Jokimaki, 2001; Morrison and Bolger, 2002), most studies found no edge-effect on the breeding success of these species (e.g. Friesen *et al.*, 1999; Flaspohler *et al.*, 2001; Huhta and Jokimaki 2001).

Where investigators have examined how bird composition changed between edge and the interior of habitats, most identified a change in either community structure or individual species abundance (Sisk *et al.*, 1997; Restrepo and Gomez, 1998; Dale *et al.*, 2000; Mancke and Gavin, 2000; Graham and Blake, 2001). For example, in a study on the effects of forest fragmentation in semi-deciduous forest fragments in Ghana, Beier *et al.* (2002) found approximately 20% of species to be edge-sensitive while Dale *et al.* (2000) found that 54% of species increased in numbers with increasing distance from the edge in logged tropical forests in Uganda.

Hagan *et al.* (1996) argue that sensitivity to edges depends on a number of factors including the species' sensitivity to area effects, the duration and rate of habitat loss and fragmentation, and the proximity of a forest stand to disturbance. Further, they argue that incipient forest fragmentation may affect populations differently from later stages of fragmentation, when the geometry of the landscape has reached a more stable configuration. Studies in South America complement this argument, showing that penetration of edge effects on bird abundance declines over a time-scale of decades (Restrepo and Gomez, 1998). However, it is clear that the hostility of the matrix compared to the core habitat (i.e. the nature of the edge) is also a very important determinant. Saurez *et al.* (1997) were able to define different edge types (abrupt to gradual) and found that nest predation rate of indigo buntings (*Passerina cyanea*) was nearly twice as high in harsh edges than in gradual edges. This was supported by Morse and Robinson's (1999) study on the effects of edge on Kentucky warblers (*Oporornis formosus*) in Shawnee National Forest in southern Illinois, as they found edge effects occurred along an agricultural boundary but not along other edges. This variation in harshness likely accounts for the differences in the reports of how far edge effects are felt within fragments. Dale *et al.* (2000) found that bird species edge effects were operating up to 400 m from the edge in logged rain forests of Uganda, while Canaday (1997) reported that edge effects in Amazonia could reach up to 2 km into primary forest if clearings were large and disturbed enough; these differences may be best explained by the different composition of the matrix surrounding the remnants in the two studies.

2.3.7 The effect of landscape composition

Deforestation and habitat fragmentation not only reduce the size of habitat remnants but also involve the creation of a landscape matrix that is often extremely different to that of the original habitat. Although the impacts of the landscape matrix on bird communities that inhabit the embedded habitat fragments has been less well studied than other processes associated with habitat fragmentation (Lindenmayer and Franklin 2002), a number of studies provide evidence of landscape matrix effects on bird communities.

The greater probability of occurrence of some taxa in smaller remnant habitats has been attributed a species' ability to utilize resources within the surrounding matrix habitats (Diamond *et al.,* 1987; Dunning *et al.*, 1992; Estrades and Temple, 1999). A number of studies have shown that different matrices have different resources within them, and therefore have differential carrying capacity for different bird species. These studies were able to identify species that were matrix-tolerant species. For example, Cornelius *et al.* (2000) found 17 species that utilised both matrix habitats and remnant habitats and nine species that used matrix habitats only in a relict, fragmented temperate forest landscape in semi-arid Chile. This meant they could ascertain which species would be threatened by further loss of habitat and which species would be threatened if matrix habitats changed. Lindenmayer *et al.* (2002) found that many 'area-sensitive' species lived in very small *Eucalyptus* forest remnants that were next to highly heterogeneous matrix habitats in southeastern Australia. They argued that the matrix habitat supported many of these species in the small remnants and hence was an important aspect of Eucalyptus forest bird conservation in the region (Lindenmayer *et al.*, 2002). Saab (1999) argued that surrounding matrix should be a primary consideration for selecting riparian reserve areas, as matrix composition was a significant predictor of bird species occurrence in cottonwood riparian forests in the USA. Estades and Temple (1999) found that bird community composition in forest fragments varied in relation to the features of the surrounding matrix in a fragmented forest landscape surrounded by pine plantations in Brazil. These studies have two implications. Firstly, if species can utilize the surrounding matrix they may be less prone to the effects of habitat fragmentation. Secondly, if a particular bird species cannot use the resources of a particular matrix, they may be more affected by habitat fragmentation as they will require larger areas of the remnant habitat to persist (Cook *et al.*, 2002, Lindenmayer *et al.*, 2003).

The suitability of the landscape matrix for bird movements (i.e. dispersal across) has been found to influence population persistence in patchy environments (Sisk *et al.,* 1997; Gascon *et al.*, 1999). A pioneer study in central Amazonia has demonstrated that the type of secondary vegetation surrounding forest fragments influences the use and recolonisation of fragments by understorey birds. Some understorey birds, such as hummingbirds, are less affected by fragmentation and surrounding matrices than others, such as understorey insectivores and species associated with mixed flocks (Stouffer and Bierregaard, 1995a,b; Bierregaard and Stouffer, 1997). Therefore, the contrast between fragments and matrix may determine the degree of isolation a local population experiences, because the suitability of the landscape matrix may affect the ability of individuals to move through it, which will influence population persistence in fragmented landscapes (Stouffer and Bierregaard 1995a,b; Sisk *et al.*, 1997; Gascon *et al.*, 1999; Renjifo 2001; Wethered and Lawes 2003).

As already mentioned in the edge effects section (section 2.3.6), the 'edge-contrast' between remnant and matrix has been shown to be an important predictor for bird diversity within fragmented landscapes. These effects range from the influx of species from the matrix into remnant habitat to a differential impact on the capacity of forest organisms to move among forest edges (Andrén, 1992, 1994; Stouffer and Bieergaard 1995a,b; Sisk *et al.*, 1997). All these factors affect the distribution of species in fragmented landscapes, and all would potentially change if matrix composition alters.

2.4 Conclusion

This chapter has described the dominant theories that have been incorporated in fragmentation research and highlights the important role island theory stills plays in modern fragmentation studies. This chapter has also described the myriad of effects that habitat fragmentation has on bird species at different scales, in different areas of the world. As a result, this chapter forms the theoretical basis of this thesis. The following empirical chapters utilise the theory described in this review as foundations for assessing the effects of habitat fragmentation on birds in the woodlands of southeastern Australia and the littoral forest birds in southeastern Madagascar. In these empirical chapters, I discuss whether the bird communities in these two case studies are reacting in ways observed in other fragmentation studies and whether they conform to the theory outlined herein.

CHAPTER 3

THE MADAGASCAN CASE STUDY

3.1 Introduction

One of the main objectives of this thesis is to assess the effects of habitat fragmentation and degradation on birds in the unknown, but seriously threatened, littoral forests of southeastern Madagascar. The first aim of this chapter is to describe these littoral forests and the ecological research that has been conducted within them in the past. The second aim is to describe the involvement of the international mining company, Rio Tinto, in the region. This mining company has made plans with the Malagasy government to clear a substantial amount (approximately 80%) of littoral forest in the next 50 years and in doing so, has placed the previously forgotten littoral forests on the world stage. Many conservation NGOs are now concerned about the proposed mining operation, especially its expected impact on local people and on the region's biodiversity. It is simply not possible to ignore this situation in the present thesis, as any practical conservation strategy determined from my work must be placed within this political dynamic.

3.2 The Fort Dauphin region

The Fort Dauphin region of southeastern Madagascar is arguably the most diverse on the island (Goodman *et al.*, 1997). The region's size (approximately 10000 km^2, or about 1.7% of the total land area of island) is small, but it contains a large variety of habitats, including different forest types, coastal zones, high mountains and areas of inland freshwater habitat. Three major forest types (humid forest, spiny forest and littoral forest) occur in the region (Figures 3.1 and 3.2). The humid forests occur almost exclusively on lateritic soils at the base of, and on, the Anosyenne and Vohimena Mountains, while the spiny forests occur on drier, sandy soils to the west of these mountain ranges (Goodman *et al.*, 1997; Ramanamanjato *et al.* 2002). The littoral forests, the most threatened habitat of the region, occur on the sandy soils next to the coast (Ganzhorn *et al.*, 1997; Ramanamanjato, 2000; Ramanamanjato and Ganzhorn, 2001). As a result of this forest variety, the southeast region of Madagascar has the highest recorded numbers of species – regardless of taxa – when compared to any other region on the island. For example, Goodman *et al.* (1997) found 189 bird species within the area, representing 68% of the birds known in Madagascar. This is impressive considering the region's small size.

Figure 3.1 Example of littoral forest. This photograph was taken in the remnant known to locals as S17 (Ste-Luce) in October 2002

Figure 3.2 Example of spiny forest. This photograph was taken in spiny forest north of Amboasary in October 2003.

In southeastern Madagascar, there is only one national reserve (Andohahela PN) which contains 76 020 ha of forest in three separate parcels. Two other private reserves (Berenty Reserve north of Amboasary-Atsimo and Nahampoana, approximately 15 km west of Fort Dauphin) are also found in the region. The main habitats of all these reserves are humid evergreen forest, xerophilous thickets, and spiny forests (Randrianandianina *et al.*, 2003). As such, no reserve in the region contains littoral forest.

The largest town in the region, Fort Dauphin (Tolagnaro), is home to 47 000 inhabitants. The geographic location of the town is particularly significant, as it is where two ethnic groups with very different cultural backgrounds cross; the Tandroy people live in the spiny forest region to the south of Fort Dauphin while the Tanosy live on the coastal lowlands to the north of the town. The growth of Fort Dauphin in recent years has lead to a large Tandroy migration to the region and a number of small villages have appeared close to the town, with Tandroy people now utilising the littoral forests (which were formerly only used by Tanosy people).

3.3 The littoral forests of southeastern Madagascar

For some time the littoral forests have been classified among the evergreen forests of the eastern domain of the island (Ingram, 2004). Yet they represent floristically distinct ecosystems with endemic invertebrates and special combinations of vertebrate fauna (Dumetz, 1999; Ganzhorn *et al.*, 2000). Littoral forests are classified as possessing a canopy layer ranging from 6 m to 12 m, with emergents to 20 m (canopy closure varies from 30-90%), a sub-canopy layer ranging from 5 m to 8 m, a shrub layer ranging from 1 m to 4 m in height and a herbaceous layer (Lowry and Faber-Langendoen, 1991). They now only occur along the coastal margins of southeastern Madagascar, at less than 40 m above sea level, on sandy soils.

At least 278 species of terrestrial vertebrates occur within these forests, of which three reptiles are locally endemic (Lewis Environmental Consultants, 1990). In addition to this, the littoral forests contain 29 plant species that are either restricted to littoral forests, are small relict populations of species endemic to Madagascar or are IUCN-listed threatened species (Henderson, 1999). The littoral forests contain no bird species unique to that habitat. The near exception is the giant coua (*Coua gigas*), a species inhabiting the southwestern portion of the island and whose range extends into the littoral forests of southeastern Madagascar (Goodman *et al.*, 1997; Langrand, 1990).

The littoral forests near Fort Dauphin occur in three separate areas: Petriky, Mandena and Ste-Luce (Figure 3.3). The littoral forests in these sub-regions are considered Madagascar's most intact littoral forests (Dumetz 1999). These forests occur in fragments that vary in size, shape

Figure 3.3 The view of the Mandena region from Pic St. Louis (near Fort Dauphin). Arrows point to examples of littoral forest remnants. Photograph taken by Jennifer Quilter, October 2003.

and degree of anthropogenic impact. Petriky occurs as one large remnant while a mixture of small and large remnants make up the littoral forest communities in Ste-Luce and Petriky. Approximately 20 000 people inhabit and utilise resources from these forests. The majority of these people live within the Mandena region and the least populated sub-region is Petriky. Henderson (1999) and Vincelette *et al.* (2003) argue that the littoral forests that surrounded Fort Dauphin were originally a contiguously forested area, and that they have become fragmented within the past century.

Recent research based on aerial photography and remotely sensed image shows that deforestation is occurring within the littoral forests (Vincelette *et al.*, 2003; Ingram, 2004), but there is evidence to suggest that the remnants that occur now have been isolated for at least five decades and that the spatial arrangement of remnants has been quite stable during this period (J. Carter Ingram, pers. comm). The matrix surrounding these remnants includes *Melaleuca* swamp forest, plantations of *Eucalyptus citriodora* and *E. robusta,* and heath-type vegetation dominated by *Phillippia* sp. grassland (Figure 3.4; Ramanamanjato and Ganzhorn, 2001).

3.4 Plans for mining in the littoral forests zone

QMM (QIT Madagascar Minerals), a company of QIT-Fer et Titane (subsidiary of Rio Tinto plc, UK) conducted an extensive exploration program along the east coast of Madagascar for heavy mineral sands in 1986. These investigations led to the discovery of a potentially economically viable ore body near Fort Dauphin, with the major deposits located underneath the littoral forest remnants. QMM argue that these forests are under severe pressure from the local human population, which depends on them for wood, medicine and charcoal for cooking and construction. The company conducted a deforestation assessment of the area in 2000 and argued that 60% of the littoral forest had been lost over the past 50 years (Vincelette *et al.*, 2003).

After review of the Social and Environmental Impact Assessment (SEIA) documents, issuance of the environmental permit from the Office National pour l'Environnement (ONE) and an investment decision from QMM, the proposed mining is likely to start in the Mandena region in 2008, followed several decades later by mining in Ste-Luce and Petriky. QMM has identified four conservation zones within the 4000 ha of littoral forest, with Mandena having 390 ha of littoral forest, Sainte Luce having two blocks making 430 ha and Petriky having 60 ha. These conservation zones were selected in consultation with people living in the surrounding communities, Eaux et Forêts authorities, and experts collaborating with the project. 'Their preservation, in concert with well designed restoration activities, should permit

Figure 3.4 Example of a small littoral forest surrounded by *Erica*. This photograph was taken in the spiny forest remnant north of Amboasary in October 2003.

the maintenance of a significant portion of biodiversity in the mining zone beyond the end of the proposed mining activities' (Vincelette *et al.*, 2003: 1536). To support the conservation initiatives, 500 ha of exotic and native tree plantations will be established over the next five years prior to the mining. QMM argues that the plantations should provide wood and fuel products needed to 'offset current exploitation of native forests and thereby assure the preservation of conservation and restoration zones' (Vincelette *et al.*, 2003; 1537). However, there is no knowledge of (i) what impacts this forest loss will have on indigenous biodiversity of littoral forests in southeastern Madagascar and (ii) what the impact of encouraging exotic plant species will have on the biodiversity of the region.

3.5 Ecological research in the littoral forests

A review of the published and unpublished literature in Madagascar and internationally, shows that there has been increasing interest in the littoral forests. This is primarily due to the development of a QMM scientific team located within Fort Dauphin since the early 1990s. Part of QMM's first environment program was conducting preliminary assessments on the project's feasibility and the potential effects of proposed activities on both the human and natural environment. Biodiversity studies were conducted on fauna and flora between 1989-1991. These studies are available in the SEIA submitted to the Office National pour l'Environnement (ONE) in May, 2001 (QMM 2001).

Work to data has predominately focussed on lemurs (e.g. Ganzhorn 1998; Ramanamanjato and Ganzhorn, 2001; Ramanamanjato *et al.*, 2002) rodents (e.g. Ramanamanjato and Ganzhorn, 2001) amphibians and reptiles (Ramanamanjato *et al.*, 2002) and plants (e.g. Dumetz, 1999; Henderson, 1999; Cadotte *et al.*, 2002; Bollen, 2003; Ingram, 2004), with most studies documenting species lists in the different forest fragments. Apart from the initial bird surveys conducted in 1989 in all three sub-types, no work has been conducted on birds within the forests.

There has been limited attention given to the effects of fragmentation within the forests, and this has focussed on lemur and rodent populations in the Mandena region (Ramanamanjato and Ganzhorn, 2001). However, in her PhD thesis, Bollen (2003) examined the role of fruit-frugivore interactions in the littoral forests and highlighted the importance of lemurs, and possibility the vasa parrots, in dispersing some species of trees and that connectivity within the landscape is important. Moreover, Ingram (2004) recently showed that the plant communities of different littoral forest remnants were distinct from each other; indicating that simply conserving a small number of remnants in each sub-type may not adequately conserve all species within the littoral forest region.

3.5 Conclusion

This chapter has described the littoral forests of southeastern Madagascar and explored the ecological research that has been conducted within them in the past. It has also described the involvement of the international mining company, Rio Tinto, in the region, highlighting their conservation aims pre- and post- the proposed mining operation. This chapter therefore sets up the stage for the following five chapters. These chapters are the empirical research papers conducted on the bird communities of these littoral forests. As mentioned in the introduction, Chapter 4 describes and justifies the use of the rapid assessment bird census methodology employed in the littoral forest fragments. Chapter 5 describes the bird communities that inhabit the littoral forests of southeastern Madagascar. As this was the first time a thorough bird survey had been conducted in this forest type, the analyses conducted in this chapter also determined whether these communities differed from the bird communities of other forested habitats in the region so as to assess the regional importance of the littoral forests for bird conservation. Chapter 6 explores the relationships between patch characteristics (in particular, vegetation structure) within littoral forest fragments and bird abundance across the landscape. Chapter 7 primarily focuses on the landscape-scale effects of habitat fragmentation in littoral forests. It did this by assessing the relationships between landscape metric variables and the distribution of birds in the Ste-Luce and Mandena littoral forests, to determine if landscape-scale habitat fragmentation was affecting littoral bird composition. Chapter 8 places the results of the empirical papers of Chapters 4 - 7 in context with each other, and considers the conservation strategies needed to be implemented for bird conservation in Madagascar's southeastern littoral forests.

CHAPTER 4

RAPID ASSESSMENT IN CONSERVATION RESEARCH: A CRITIQUE OF AVIFAUNAL ASSESSMENT TECHNIQUES ILLUSTRATED BY ECUADORIAN AND MADAGASCAN CASE STUDY DATA

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4.1 Abstract

The urgency of conservation concerns in the tropics, linked with the limitations imposed on research efforts by the tropical environment has resulted in the development of methods for rapid assessment of biological communities. One such method, the MacKinnon list technique, has been increasingly applied in avifaunal surveys worldwide. Using paired tropical bird data sets from Ecuadorian cloud forest and Madagascan littoral forest, we compare the performance of the MacKinnon list with that of the more standard method of point counts in indicating when a site has been adequately surveyed, estimating the magnitude of species richness, quantifying relative species abundance, and providing an α-index of diversity. In species-rich Ecuadorian cloud forest, neither method produced data indicating adequate survey effort, despite extensive sampling, whereas in the relatively species-poor Madagascan littoral forests, data collected by both methods indicated that the area had been sufficiently surveyed with comparable sampling effort. Species richness estimates generated from MacKinnon list data provided a more accurate estimate of the magnitude of the species richness for the Ecuadorian avifauna, whereas estimates for the Madagascan avifauna stabilised with relatively few samples using either method. Data collected by each method reflected different patterns of relative abundance among the five most abundant species, with MacKinnon list data showing a bias towards solitary and territorial species and against monospecific flocking species relative to the point count data. As a consequence of this bias, MacKinnon list data also fail to reflect accurately the structure of communities as quantified by an index of community evenness. Point counts, on the other hand, failed to capture the full species complement of the species-rich Ecuadorian study area. As techniques for the rapid assessment of unsurveyed areas, both methods are subject to biases that limit their value if used alone, in collecting data of scientific and management value. We propose a hybrid rapid assessment methodology that capitalises on the strengths of both techniques while compensating for their weaknesses.

Key words: birds, community structure, conservation, Ecuador, rapid assessment, point counts, Mackinnon lists, Madagascar, species richness, tropical forest

4.2 Introduction

The challenge of obtaining scientific information on previously unknown ecosystems and ensuring the comparability of such information across study areas has led to the development of several techniques for rapid assessment. These have found particular application in the tropics, where researchers often have to contend with heavily vegetated, steep, and otherwise inaccessible terrain, high species diversity and clustered species distributions, which make the application of systematic field methodologies developed in temperate areas difficult, if not impossible. Rapid assessment techniques acknowledge these constraints and provide means of accelerating the collection of scientific data in understudied areas.

One recently developed approach to rapid assessment, the 'MacKinnon list' method of avifaunal assessment (MacKinnon & Phillips, 1993), has been increasingly adopted for tropical bird studies worldwide, from Indonesia (MacKinnon & Phillips, 1993; Trainor, 2002b, a), to mainland Africa (Fjeldsa, 1999), Madagascar (James Watson, unpublished data) and South America (Poulsen *et al.*, 1997a, b). It has also been promoted as a potentially useful technique in a recent manual on bird census methods (Bibby *et al.*, 2000). Poulsen *et al.* (1997b: 65) claim that the method is "suitable for judging (a) when a site is adequately surveyed, (b) the magnitude of the species richness, (c) the relative abundance of each species and (d) an index of α-diversity." Researchers employing MacKinnon lists argue that the method is subject to no more bias than other survey methods (Poulsen *et al.*, 1997b; Fjeldsa, 1999), and that it is less biased than mist-netting (Fjeldsa, 1999). The advantages claimed for the technique relative to more widely used point counts or transects include time efficiency and relatively greater observer independence; the entire available time period is used to collect data and, hence, there is far less 'data loss' than in other survey methods. While a basic familiarity with the resident avifauna is necessary to ensure that reliable results are obtained, the method allows for a certain degree of difference in observer ability, since the data collection is not timed and, therefore, more time can be spent searching out and identifying unknown birds. Authors have recommended the adoption of this straightforward technique for examining the impacts of habitat modification in the tropics (Fjeldsa, 1999; Trainor, 2002b).

Another technique frequently employed in studies of tropical ecosystems that have not previously been formally surveyed is the point count methodology (Poulsen & Krabbe, 1998; Marsden *et al.*, 2000). Point counts are a powerful method of measuring relative abundances efficiently (Whitman *et al.*, 1997). They are also the traditionally preferred avian survey method where inferences are to be drawn about habitat associations because bird data collected can be directly related to the habitat measured (Bibby *et al.*, 2000).

In this paper we make use of paired tropical bird data sets from two localities, Ecuadorian cloud forest and Madagascan littoral forest, to assess the effectiveness of the MacKinnon list and point count methods. Specifically, we assess their relative performance in: (i) providing a reliable measure of effort, indicating when a site has been adequately surveyed; (ii) providing a robust estimation of the magnitude of species richness; (iii) accurately reflecting species abundance distributions; and (iv) providing an α-index of diversity. Overall, our purpose is to address this question: if practicality dictates the need for rapid assessment, which of these methods will provide more informative and ultimately useful data?

4.3 Materials and Methods

4.3.1 Study Areas

The Madagascar study site is located near the township of Fort Dauphin in the southeast of the island (24° 47' S, 47° 12' E). This region has a semi-tropical climate with mean annual precipitation ranging from 1000-1600 mm and daily minimum and maximum air temperature averaging 15-28 °C (Goodman *et al.*, 1997). The study covered an area of approximately 5000 ha with an altitudinal range between 0 and 50 m asl. Due to its location, the region possesses a distinct precipitation gradient, with the eastern coast having a tropical damp climate and the west having a semi-arid climate (Lewis Environmental Consultants, 1990; Goodman *et al.*, 1997). The littoral forests grow as a series of remnants along a narrow band of sand and alluvium along the coast of the region, and are considered Madagascar's most intact littoral forests (Dumetz, 1999).

The matrix surrounding these forests includes *Melaleuca* swamp forest, plantations of *Eucalyptus citriodora* Hook and *E. robusta* Blakely, and heath-type vegetation consisting predominately of *Erica* spp. (formerly *Phillippia* spp.) (Ramanamanjato & Ganzhorn, 2001). These forests have never been extensively surveyed (Goodman *et al.*, 1997), so the purpose of these surveys was to determine their avian species composition.

The Ecuadorian study site was located in the Maquipucuna and Santa Lucia Reserves and adjacent lands (0° 7' S N, 78° 36' W) on the western slope of the Andes in the Pichincha province of northern Ecuador. The study covered an area of approximately 3000 ha with an altitudinal range between 1100 and 1850 m asl. Mean annual precipitation is 3200 mm and daily minimum and maximum air temperature average 17-26 °C at 1200 m asl, with little seasonal change (Rhoades & Coleman, 1999). Following Holridge *et al.* (1971), the natural vegetation can be classified as lower montane wet forest. The forest vegetation of the area is a mixture of mature and 20-year-old regrowth forest embedded within a matrix of agricultural land, including pastures, sugar cane fields and fruit tree plantations. Compiling records from various sources as well as data from a year of weekly survey work, Parsons (1996) listed 326 bird species for the area.

4.3.2 Field Methods

In the Madagascar case study area, fourteen littoral forest remnants, as well as sites in the surrounding matrix, were surveyed for birds using both point counts and the MacKinnon list methodology in November and December 2001. In Ecuador, forest and sites in agricultural land were surveyed using both point counts and MacKinnon lists in June and July 2002.

Proposed by MacKinnon and Phillips (1993), the MacKinnon list methodology is a standardised rapid assessment technique for tropical bird communities, providing an index of effort for bird encounters recorded opportunistically. Using this methodology, all species seen or heard are grouped into consecutive lists of equal length and a species accumulation curve is generated from adding those species not recorded on any previous list to the total species number. This number is then plotted as a function of list number. In the present study, we used 10-species lists, recommended by Herzog *et al.* (2002) as representing the best compromise between stable richness estimation curves and robust sample size. Thus, in each habitat sampled, we consecutively recorded each new species encountered, starting a new list once 10 different species had been recorded. All species seen or heard were recorded on the lists. We compiled MacKinnon lists while slowly walking trails through forested and open land, stopping periodically to search out and record individual species or flocks.

Point counts are a more widely used method of avifaunal assessment in which birds are recorded at fixed stations separated by fixed distances (Bibby *et al.*, 2000). The point count stations in both of our study areas had a radius of 25 m and were located at least 100 m apart to minimize the risk of counting the same individual twice. Ten minutes were spent at each station, allowing for the identification of all birds present while minimising the likelihood of double-counting individuals arriving or moving during the count period. Bird species recorded in the point counts were also recorded in MacKinnon lists to ensure maximum sampling using the MacKinnon list methodology. In Madagascar, surveys were confined to the periods 0600 – 1000 hr and 1500 – 1900 hr. In Ecuador, the point counts were confined to 0600 – 1000 hr, while MacKinnon lists were compiled from 1400 – 1600 hr as well as in the morning period. All surveys were conducted on days without rain or strong wind.

All point count and MacKinnon List surveys in Ecuador and Madagascar were conducted by N. O'Dea and J. Watson, respectively. Thus, problems associated with biases attributed to differences among observers were avoided. Compact disks of all bird species that could occur in each study area were produced before the study commenced, and both observers trained to recognise the recorded songs of all species that could be encountered in each study area. In addition to this training, local ornithologists accompanied each observer for a period of a week to ensure that the observer was familiar with all bird species (and their calls) within the study area, before surveying began. In the Ecuadorian case study area, a local ornithologist accompanied the observer throughout the survey period.

4.3.3 Analysis

Simple species accumulation curves are generated and compared for data collected using the two methods for forest habitat in each study area. A plateau in the species accumulation is defined here as the point where the rate of species accumulation over a ten-sample interval falls below 0.10. The Chao 2 (Chao, 1987) species richness estimator was also calculated for these data:

$$S_{Chao} = S_{obs} + F_1^2/2F_2 \qquad \text{eqn 1}$$

where S_{obs} is the number of species observed, F_1 is the number of species with exactly one individual and F_2 is the number of species with exactly two individuals. Several authors recommend Chao 2 as the most robust estimator of species richness where most species are infrequent (Colwell & Coddington, 1994; Chazdon *et al.*, 1998). Curves generated indicate whether sufficient sampling effort has been undertaken to capture the total species richness of the habitat in question. They also indicate whether differences exist in the expected total species richness of these habitats. Both species accumulation and species richness estimator curves represent the average values from 50 randomisations of sample order. We analyse the recorded distributions of species abundances by comparing the rank abundances of the five most abundant species recorded in forest habitats using each method. Indices of α-diversity are only comparable where the method of data collection is held constant. In order to compare the performance of the two methods in providing an index of α-diversity, we compare the rank diversity of communities in forest and non-forest habitat within each study area as recorded by each method. For this purpose we apply the log-series α index, weighted towards species-richness and the Brillouin E index, weighted towards community evenness, to examine how data from each method reflects these aspects of diversity (Melo *et al.*, 2003). Equations used to calculate these indices are available in Krebs (1989). The significance of differences in diversity between habitats was determined by Bootstrap analysis with 10 000 random permutations. All analyses were performed using Species Diversity and Richness, version 3.02 (Pisces Conservation, 2002).

4.4 Results

4.4.1 Sampling effort

In both the Ecuador and Madagascar study areas, considerably more hours were spent in the collection and subsequent entry of data for Mackinnon lists (Table 4.1). In Ecuador, 132 additional hours, including time spent on 14 additional survey days, were spent compiling MacKinnon lists than was spent conducting point counts, while in Madagascar, an additional 60 hours were spent on MacKinnon list compilation.

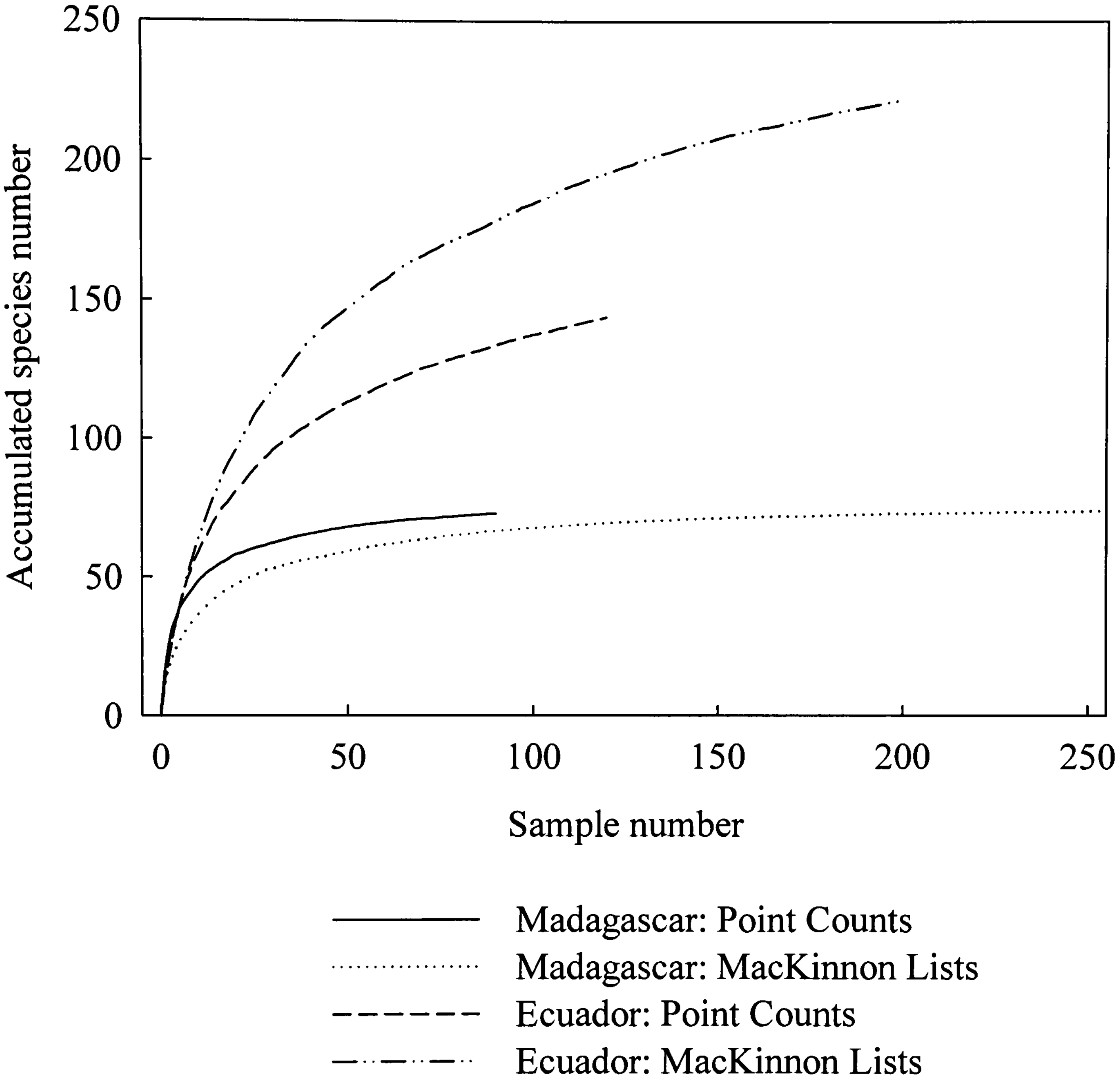
In Ecuador, 78 species in addition to those recorded during the point count survey were recorded using the MacKinnon list method (Table 4.1), while in Madagascar only one additional species was recorded using the MacKinnon list method. In the Ecuadorian data there is no plateau in the species accumulation curves despite recording 120 individual point counts and 200 10-species lists (Fig. 4.1).

Table 4.1. Summary of the sampling effort using MacKinnon list and point count methodologies in the littoral forests of Madagascar and the Cloud forests of Ecuador. MacKinnon lists were compiled continuously, including during point counts.

	Ecuador		**Madagascar**	
	MacKinnon Lists	Point Counts	MacKinnon Lists	Point Counts
Number of counts/lists	200	120	255	90
Time spent in data collection	180h in 24 days	48h in 12 days	90h in 15 days	30h in 12 days
Time spent in data entry[1]	16h40min	10h	21h15min	7h30min
Species Count Total	222	144	74	73

[1] The time spent in data entry was calculated at the rate of 5 minutes per list.

Figure 4.1. Species accumulation curves for bird communities in the Ecuadorian cloud forests and Madagascan littoral forests using MacKinnon list (1 sample = 1 10-species list) and point count (1 sample = 1 point count) methodologies. Each curve represents the average values of 50 randomisations of sampling order.



In the Madagascan data, the rate of species accumulation drops below 0.10 (plateaus) with relatively few samples: 69 point counts and 91 MacKinnon lists. In contrast to the Ecuadorian data, the Madagascan point count survey accumulates more species per sample than the MacKinnon list survey and reaches a plateau at a smaller sample size.

4.4.2 Total species richness estimation

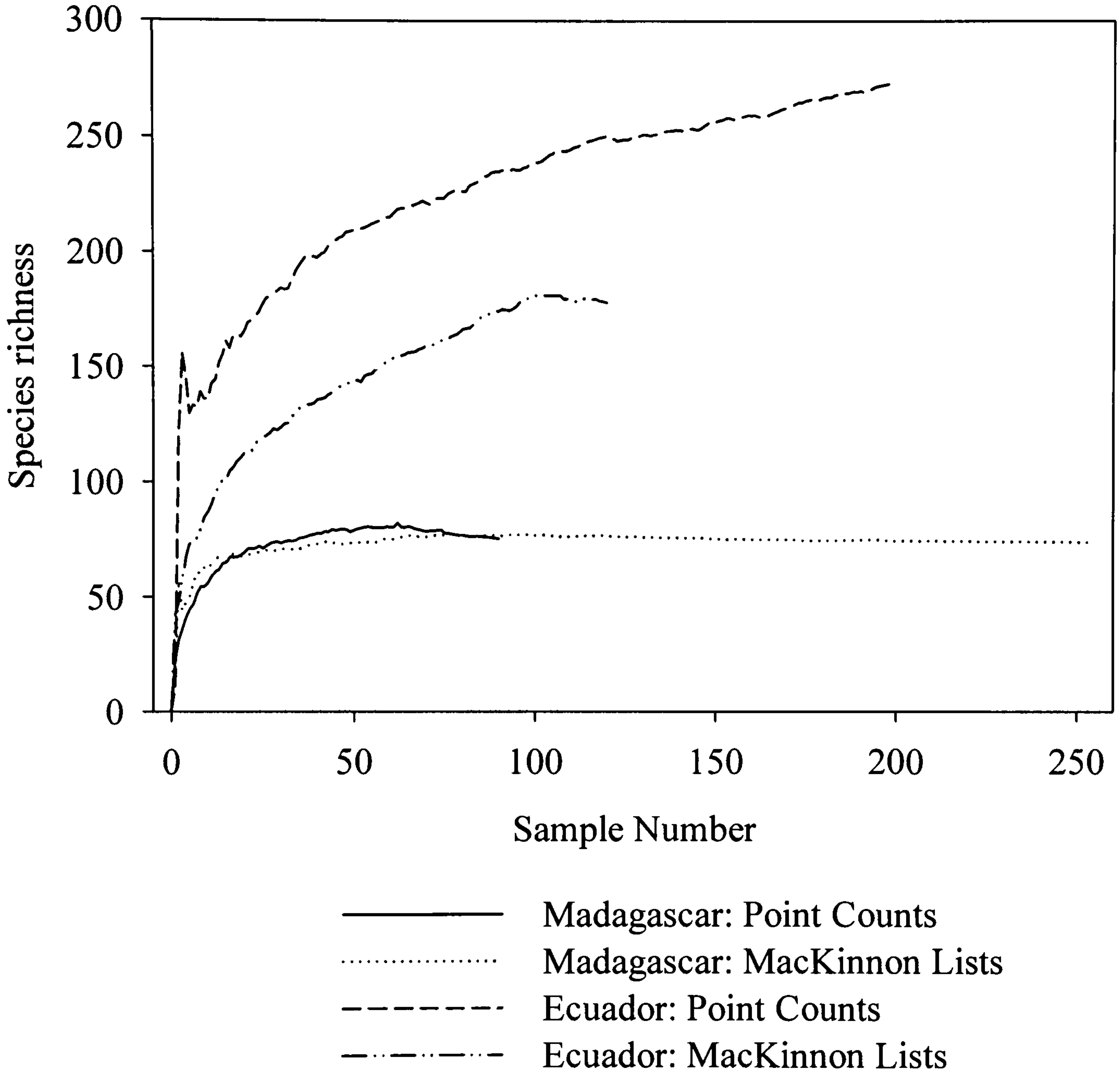
Figure 4.2 shows the change in the estimation of total species richness calculated by the Chao 2 estimator as sample size increases in both study areas. In the Madagascar case study, species richness is estimated at 75 after 90 point counts and 74 after 255 MacKinnon lists. These numbers are close, and for MacKinnon list data identical, to the actual number of species encountered (Table 4.1, Fig. 4.2). The curves for both point count and MacKinnon list data plateau after approximately 50 samples. Standard deviations in the Chao 2 estimate fall to below 5% of the estimated species richness within 83 point counts and 107 MacKinnon lists.

For the Ecuadorian data, total species richness is estimated at 274 species after 200 MacKinnon lists and 180 species after 120 point counts (Fig. 4.2). The richness estimate appears to stabilise between 100 and 120 samples for the point count survey, However, as for the simple species accumulation curve, no plateau in the estimate of total richness was achieved for the MacKinnon list data. Standard deviations remain above 5% of the estimated species richness for both data sets.

4.4.3 Relative abundance

Comparing the rank abundance of the five most abundant species for each study area as recorded using the MacKinnon list and point count methodologies, differences were apparent (Table 4.2). For Madagascan littoral forests, the two top-five lists shared four species, although with differing relative abundances. The Madagascar Bulbul *Hypsipetes madagariensis* Müller and Souimanga Sunbird *Nectarinia souimanga* Gmelin were similarly abundant, each holding either the first or second position in the abundance ranking in data for each method. The Common Jery, *Neomixis tenella* Hartlaub is a gregarious, flocking species; it was the third most abundant bird in littoral forests as recorded using the point count methodology but only sixth as recorded in the MacKinnon lists. The Madagascar Bee-eater

Figure 4.2. Species estimation curves using Chao 2 estimator (Chao, 1987) for bird communities in the Ecuadorian cloud forests and Madagascan littoral forests using MacKinnon list (1 sample = 1 10-species list) and point count (1 sample = 1 point count) methodologies. Each curve represents the average values of 50 randomisations of sampling order.



Merops superciliosus L., a nomadic insectivore, was among the five most abundant species in MacKinnon list data but was not among the five most abundant species in the point count data. In the Ecuadorian data, while the overall ordering of abundances is similar, one species appears among the top five most abundant species in data for each methodology that does not appear in that of the other. For point count data this species was the monospecific flocking Plumbeous Pigeon *Columba plumbea* Vieillot, recorded as the fourth most abundant species,

Table 4.2. Comparison of the five most abundant species recorded in point counts and MacKinnon lists in the Ecuador and Madagascan study areas. The numerical abundances as recorded by each method, followed in brackets by the rank abundances, are reported for each species. * indicates equal rank abundance.

Ecuador			**Madagascar**		
Species Name	Point Counts	MacKinnon Lists	Species Name	Point Counts	MacKinnon Lists
Henicorhina leucophrys Tschudi	119 (1)	79 (1)	*Hypsipetes madagariensis* Müller	271 (1)	187 (2)
Euphonia xanthogaster Tschudi	106 (2)	58 (3*)	*Nectarinia souimanga* Gmelin	264 (2)	198 (1)
Basileutris tristriatus Tschudi	92 (3)	58 (3*)	*Neomixis tenella* Hartlaub	240 (3)	131 (6)
Columba plumbea Vieillot	75 (4)	47 (7)	*Streptopelia picturata* Temminck	203 (4)	156 (4)
Parula pitiayumi Vieillot	70 (5)	49 (4)	*Centropus toulou* Müller	196 (5)	177 (3)
Lophotriccus pileatus Tschudi	68 (8)	64 (2)	*Merops superciliosus* L.	146 (8)	143 (5)

whereas for MacKinnon lists, it was the territorial and largely solitary Scale-crested Pygmy-Tyrant *Lophotriccus pileatus* Tschudi, recorded as second most abundant.

4.4.4 Diversity indices

Using the log-series α index of diversity, we found that both data collection methods provide the same ranking of diversity between forest and non-forest habitats (Table 4.3). Despite differences in the actual values calculated, data obtained by both methods rank the forest bird communities as significantly more diverse than the non-forest communities at $p<0.05$. However, results were inconsistent for the Brillouin E index, which reflects evenness in the distribution of species abundances in the community. In the Ecuadorian study area, the forest community was ranked as significantly more even than the non-forest community for point counts, but was less even according to the MacKinnon list data at $p<0.05$. In the Madagascan case study area the results were consistent in ranking evenness at $p<0.05$, but the Brillouin E index values derived from MacKinnon list data were more similar between forest and non-forest habitats than those for the point count data (Table 4.3).

4.5 Discussion

In the cloud forests of northwest Ecuador, a species-rich environment, a total of 222 species were recorded during the course of MacKinnon list surveys, while 144 species were recorded during point counts. Differences were also apparent in the indices of total species richness and relative abundance. In the littoral forests of southeastern Madagascar, a relatively species-poor environment, we recorded approximately the same number of species, but found differences in the relative abundances of species, using the two methods. Inconsistencies also emerged in ranking the evenness of communities in forest and non-forest habitats within each study area. Such differences are indicative of biases implicit in data collected using both the MacKinnon list and point count methodologies. Below, we discuss the nature of these biases and their influence on the relative usefulness of each approach in the context of rapid assessment in previously unsurveyed areas.

4.5.1 Sampling effort

Because the entire period of the point count survey as well as time outside this period could be used for compiling MacKinnon lists, the MacKinnon list method allowed a greater proportion of the available field time to be spent collecting bird data than did point counts. Consistent with other authors (Poulsen *et al.*, 1997b; Herzog *et al.*, 2002), we found the MacKinnon list method suitable for determining when a site has been adequately sampled. In the relatively species-poor Madagascan study area, species accumulation curves for littoral

Table 4.3. A summary of the different diversity indices that were found using species list and point count methodologies in the cloud forests of Ecuador and the littoral forests of Madagascar. Significance tested by Bootstrap analysis with 10 000 random permutations. * higher diversity (at p<0.05).

Diversity Index	Method	**Ecuador**		**Madagascar**	
		forest	non-forest	forest	non-forest
Log-series α	Point Counts	36.78*	25.65	16.43*	7.99
	MacKinnon Lists	63.84*	50.59	14.28*	4.55
Brillouin E	Point Counts	0.8510*	0.8214	3.65*	2.57
	MacKinnon Lists	0.8843	0.9186*	3.51*	2.84

forest remnants plateau at the same species number for both MacKinnon list and point count data. By contrast, in Ecuador no plateau was reached within the confines of available sampling for either method. Therefore, even with 200 lists or 120 point counts, sampling effort was still insufficient to capture the heterogeneity and diversity of this particular bird community. The 200 MacKinnon lists compiled in the Ecuadorian survey was a far greater number than that needed to achieve asymptotic species accumulation curves in other MacKinnon list studies (Poulsen *et al.*, 1997b; Fjeldsa, 1999). This attests to the difficulty of applying any rapid assessment technique in such a species-rich environment. It should be noted, however, that the MacKinnon list species accumulation curve approached the recorded species richness of the area far more closely.

4.5.2 Species richness estimation

In the littoral forests of Madagascar, the Chao 2 estimator applied to the Mackinnon List data set estimated the exact number of species actually recorded in the remnants surveyed and estimated one additional species using the point count data set. This is because the Chao 2 estimate of total species richness will equal the recorded richness once all species have been recorded more than once. Thus, in a relatively species-poor environment, both techniques were effective and time efficient for estimating total species richness.

In the Ecuadorian cloud forest, the estimate of total species richness did not stabilise within the available sampling effort for either data set because we continued to encounter new species throughout the sampling period. As such, it is not possible to state with confidence the magnitude of species richness for the area based on the data, even after extensive sampling. However, if we take the Parsons (1996) inventory of 326 species as representative of the area's total species richness, the Chao 2 estimate for the MacKinnon list data approached this number more rapidly than that for the point count data. In fact, the point count data appeared to plateau at approximately 180 species between 100 and 120 samples, indicating a systematic under-sampling of the avian community relative to MacKinnon lists. This is a known property of the point count technique (Bibby & Buckland, 1987; Whitman *et al.*, 1997; Pagen *et al.*, 2002), since certain species, particularly those which are nocturnal or crepuscular, will often not be represented. As well, the MacKinnon list method may better record rare and vagrant species because it allows continuous recording and active searching. Notably, of species only recorded in MacKinnon lists, 77% were encountered only once or twice, including six additional restricted-range species and seven additional at-risk species. At its simplest, and recognizing that the actual richness of birds present in the Ecuadorian study area at the time of the 2001 sampling is unknowable (as is the number of breeding species); all we can state with confidence is that the number of species that were present must have fallen somewhere between the 222 species observed in the study and the figure of 326 species comprising all records (including vagrants) for the reserve. On this basis, where the purpose of a survey is simply to assess the overall species richness of an area, MacKinnon lists appear to be the more effective tool.

4.5.3 Relative abundance

Differences in the rank abundance of species as determined by MacKinnon list and point count methods illustrate a tendency of the MacKinnon list method to weight regularly-spaced territorial species as more abundant than flocking species. For example, in Ecuador, when abundance at each encounter was recorded in the point count survey, the Scale-crested Pygmy-Tyrant *L. pileatus* had only 57% of the abundance of the most abundant species, *H. leucophrys* and was the eighth most abundance species (Table 4.2). However, when recorded on MacKinnon lists, the abundance of this solitary and highly territorial *L. pileatus*, jumped to 82% of that of *H. leucophrys*, becoming the second most abundant species (Table 4.2). Thus, even if, as suggested by other authors (Poulsen *et al.*, 1997b; Herzog *et al.*, 2002), obviously territorial species are not double-counted, the method still overestimates their relative abundance. In Madagascar, even though abundant species were being encountered at much greater rates than in the Ecuador, similar weighting occurred. Species that readily form flocks, like *H. madagariensis* and *N. tenella* (Langrand, 1990; Eguchi *et al.*, 1993a; Eguchi *et al.*, 1993b), ranked lower in abundance for MacKinnon list data.

While MacKinnon list data are weighted towards territorial species, it could be argued that point count data are similarly weighted towards monospecific flocking species, which might be present at fewer sites, but in greater abundance. However, unlike MacKinnon list data, point count data record both abundance at sites and ubiquity (presence/absence) across sites, representing two facets of relative abundance. There is the further possibility that the same widely and rapidly ranging flocks could be recorded in different point counts (Raman, 2003), again weighting them as more abundant. The systematic separation in space and short duration of consecutive point counts are means of reducing this bias, but this provides no guarantee against double counting on different days. Nevertheless, the MacKinnon list method is subject to the same bias and provides no systematic way of controlling for it.

Poulsen *et al.* (1997a; 1997b) acknowledged that relative abundances recorded by MacKinnon lists may be biased and call for further investigation. In a recently published study, Herzog *et al.* (2002) modelled the behaviour of data collected using the MacKinnon list methodology. They support Poulsen *et al.*'s (1997b) contention that MacKinnon lists are appropriate for judging sampling effort and magnitude of species richness, but argue that differences in detectability of species mean that relative abundances can only be compared within species across habitats or sites. We concur, but argue further, that the incomparability of relative abundances is due not only to differences in detectability, but also to biases in the technique of recording abundance. Point counts do not provide a perfect measure of abundance either. They are biased relative to the very time-consuming spot-mapping method (Raman, 2003), considered the only reliable means of determining absolute abundance (Terborgh *et al.*, 1990; Stratford & Stouffer, 1999). However, the advantage of point counts relative to MacKinnon lists is that their spatial and temporal standardisation means that their biases are more readily quantifiable and controllable.

4.5.4 Diversity indices

Due to the bias in measuring relative abundance, Herzog *et al.* (2002) argue that MacKinnon list data are also unsuitable for the calculation of diversity indices. The distribution of abundances within the community will appear more even for MacKinnon list data than for point count data because the abundance of a species at a given encounter is not quantified. Thus, in both our case study areas, while the log-series α index, weighted towards species-richness, consistently identified the forest bird community as more diverse than non-forest bird communities for both point count and MacKinnon list data, the Brillouin E, reflecting community evenness, provided inconsistent results; MacKinnon list data failed to capture the greater unevenness in the non-forest bird community resulting from the presence of a few hyper-abundant flocking species. In order to provide more information than the simple species richness, all α-diversity indices incorporate this relative abundance into their formulae. As such, we consider MacKinnon list data sub-optimal for the calculation of diversity indices and recommend the use of point count data for this purpose.

4.5.5 General discussion

Table 4.4 summarises our findings relating to the use of the MacKinnon list and point count survey techniques in species-rich cloud forests of northwest Ecuador and species-poor littoral forests of southeast Madagascar. Without the constraints imposed by timed counts, the MacKinnon list technique allowed a greater proportion of the available field time to be spent in the field collecting bird survey data. More species were recorded using the MacKinnon list technique in the Ecuadorian case study. This is due to the flexibility of the technique in continuously recording data and actively searching out new species. However, we caution that this searching may introduce an additional bias into the data: the act of searching out a potentially new species, which is evading detection, may distract the data recorder from registering more commonly encountered species in his or her surroundings. Trainor (2002b) expressed similar concerns. Such bias towards novel species could account for the steeper species accumulation curve observed and for the greater number of restricted-range and at-risk species recorded. This bias is controlled in the point count technique because the observer's objective is to record accurately everything seen and heard from a standing position within a fixed time period.

Herzog *et al.* (2002) suggest that the abundance of species be recorded for the MacKinnon list technique in order to ensure maximum flexibility in the choice of list length. While this may be practicable for certain species, recording a monospecific flock of 20 individuals would be excessively time consuming if each one had to be noted in its order of appearance relative to other species present. Moreover, another bias is introduced in that the sequence of recording can have a potentially large influence on the relative abundance calculated for a given species. For instance, if two individuals of a species occur at the end and beginning of consecutive

Table 4.4. Summary of study findings comparing MacKinnon list and point count survey techniques in Madagascar and Ecuador.

	MacKinnon lists	**Point Counts**
Percentage of field time spent in data collection	more	less
Time spent in data collection	more	less
Continuous recording?	yes	no
Total species count	more	less
Individual birds recorded at every sighting?	no	yes
Bias in relative abundance estimate	more	less
Bias in α-diversity estimate	more	less
Observation weighted to rare/novel species?	yes	no
Minimum unit of standardization	habitat/fragment	point
Minimum unit of comparison with environmental landscape variables	habitat/fragment	point

lists, their relative abundance will double relative to that if they fell in the middle of a list sequence.

Fjeldsa (1999) and (Trainor, 2002b) advocated the application of MacKinnon lists as a standardised design for examining the impacts of habitat disturbance on bird communities. We feel that for this purpose, among the most important in conservation research, conducting MacKinnon list surveys may not be enough. Authors applying the MacKinnon list method acknowledge that comparison across sites can only be made if habitat diversity, altitude and size of surveyed areas are held constant (Poulsen *et al.*, 1997b; Fjeldsa, 1999; Trainor, 2002b). This is difficult to achieve in the field and directly undermines surveys aimed at examining the effect of these variables. The lack of sampling standardisation in a MacKinnon list survey makes it difficult to relate observed patterns within avian communities to patterns in the environment. Whereas in a point count survey, the sampling protocol can be standardised to correct for environmental heterogeneity, in a MacKinnon list survey the lack of standardisation in the sampling protocol necessitates standardising the environmental heterogeneity. Further, point counts allow for the direct comparison of bird and environmental data at each point, because bird and environmental data can be collected for each point (Bibby *et al.*, 2000). On the other hand, a point count survey alone may fail to provide an accurate indication of an area's species richness, particularly in extremely species-rich areas.

Given the advantages and limitations of each method for the rapid assessment of previously unsurveyed areas, we propose a synthetic method combining the best qualities of both. We argue that research efforts should focus on conducting systematic point count surveys to examine aspects of bird community structure and species composition, and their relation to environmental factors (Thiollay, 1997; Galetti & Aleixo, 1998; Estades & Temple, 1999; Saab, 1999; Reynaud & Thioulouse, 2000). However, if, as suggested by Herzog *et al.* (2002), birds encountered during, between, and after point counts are recorded in MacKinnon lists, these additional data can be use to generate a comparative index of sampling effort and to ensure a more accurate assessment of the magnitude of species richness in an area.

The concerns raised here, while focused on birds, may not be restricted to the rapid assessment of birds. Rapid assessment techniques are used in the study of many tropical taxa, from butterflies to reptiles (Lande *et al.*, 2000; Thompson & Withers, 2003). We propose that rapid assessments should wherever possible set out to generate data suitable for estimating both richness and other aspects of community structure, such as equitability, as well as data concerning the habitat relationships of species. Thereby, rapid assessments can generate high quality data sets to inform conservation policy for understudied and relatively unknown tropical areas.

4.6 Conclusions

Authors who have assessed the efficacy and biases of the MacKinnon list approach argue it to be a 'best compromise' approach, given limitations of time, funding and personnel, and the urgency of conservation needs (Poulsen *et al.*, 1997b; Fjeldsa, 1999; Herzog *et al.*, 2002). While evaluations of species richness have value in guiding conservation efforts, we would caution that the type of information these surveys provide on their own contributes relatively little to our understanding of how or what to conserve. As acknowledged by Poulsen *et al.* (1997b), MacKinnon list surveys, when standardised, are neither easier nor superior to point counts; what they provide is an efficient means of determining species richness in a species-rich environment, as well as cataloguing the species systematically missed by point count.

Research efforts must concentrate on understanding the causes of species loss rather than merely cataloguing the species that are about to disappear. MacKinnon lists provide a first step in conservation research, offering an inventory of species present, a robust measure of the adequacy of sampling effort, and a means of estimating the magnitude of species richness. However, the need for rapid assessment is driven by constraints of time and funding. As such, initial rapid assessment surveys should not only document the bird species (or indeed other taxa) of new areas, but should also improve our scientific understanding of mechanisms driving their distribution and abundance. We argue that for birds, using the Mackinnon list method in conjunction with point counts will provide robust rapid-survey data, including both an accurate assessment of species richness as well as compositional and relative abundance data that can be directly related to environmental variables.

4.7 Acknowledgments

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CHAPTER 5

THE IMPORTANCE OF LITTORAL FOREST REMNANTS FOR INDIGENOUS BIRD CONSERVATION IN SOUTHEASTERN MADAGASCAR

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5.1 Abstract

The littoral forests of Madagascar are relatively unexplored ecosystems that are considered seriously threatened by deforestation and habitat fragmentation. We set out to describe the bird communities inhabiting the littoral forest remnants in three different sub-regions of southeastern Madagascar to determine the national importance of these forests for bird conservation. In total, 77 bird species were found inhabiting 14 littoral forest remnants. Of these species, 40 are endemic to Madagascar and a further 21 are endemic to the Indian Ocean sub-region, consisting of Madagascar, the Comoros and the Mascarenes. The matrix habitats (*Melaleuca* forests, *marécage* swamp forest, *Eucalyptus* plantations and *Erica* grassland) that immediately surround the littoral forests were depauperate of bird species and contained few species that were found within the littoral forests. The geographic location of littoral forest remnants had an important role in determining what bird species occurred within them, with the northern remnants having similar bird communities to nearby humid forest whilst the most southern remnant had a bird community that resembled those of nearby spiny forest habitats.

Eleven bird species that have been previously described as being habitat-restricted endemics to either spiny forests or humid forests, were found in littoral forest remnants. These results suggest that these littoral forests may play an important transitional role between the two other major natural habitats (spiny forest and humid forest) of southeastern Madagascar. On this basis we advocate that the littoral forest remnants of southeastern Madagascar should be afforded continuing conservation priority.

Key words: Madagascar, Fragmentation, Deforestation, Littoral Forests, Spiny Forests, Humid Forests, Birds, Conservation

5.2 Introduction

Madagascar's indigenous bird community, even with a relatively low number of species, has a very high level of endemism (Goodman and Patterson 1997). Of the 204 breeding birds that occur in Madagascar and surrounding islands, 120 are endemic, of which 80 are dependent on forest habitats (Langrand 1990; Morris and Hawkins 1998). Considering the high rate of endemism in the Malagasy bird community and the threat of continued deforestation and habitat degradation on the island, it is critical to identify the bird communities in all of Madagascar's different ecosystems to define baselines for the development of conservation strategies (Jolly et al. 1984; Stephenson et al. 1994; Hannah et al. 1998; Dumetz 1999). Within the past decade, research in Madagascar has increasingly focussed on describing the communities of previously unsurveyed habitats (Safford and Duckworth 1988; Goodman 1993; Goodman et al. 1996a; Goodman and Putnam 1996; Thornstrom and Watson 1997; Dumetz 1999) and on the ecology of endangered bird species (Wilme and Langrand, 1990; Goodman et al. 1996b; Thorstrom and Lind 1999). Yet, there are still numerous ecosystems that have not been surveyed thoroughly, and therefore large gaps still exist in our knowledge of the distribution of bird species on the island.

The littoral forests of Madagascar are one example of a relatively unexplored ecosystem (Lewis Environmental Consultants 1990; Ganzhorn et al. 2000; Ganzhorn et al. 2003). These floristically distinct forests grow along a narrow band of sand and alluvium along the east coast of the island (Lowry and Faber-Langendoen 1991; Schatz 2000). Human activities (e.g. selective logging and 'tavy' farming) and natural catastrophes (e.g. cyclones and fire) have reduced this forest type to the extent that in 1979 no more than 450 km^2 remained (Du Puy and Moat 1996; Ganzhorn et al. 2001). Due to their high floristic endemism, the littoral forests of southeastern Madagascar are ranked among the habitat types of highest conservation priority on the island, but even with this distinction there has been only one avifaunal study conducted within them (Goodman et al. 1997). This study, conducted in 1989, was part of a larger survey of birds within southeastern Madagascar - a region of some 10 000 km^2 - and as a result did not include many littoral forest remnants (Goodman et al. 1997). Moreover, since 1989 the littoral forests have been subject to loss and degradation due to fire, deforestation and other anthropogenic impacts (Henderson, 1999; Ramanamanjato and Ganzhorn, 2001).

The primary aim of this paper is to describe the bird communities that inhabit the littoral forests of southeastern Madagascar and to determine if these communities differ from the bird communities of other forested habitats in the region so as to assess the regional importance of the littoral forests for birds. The secondary aim of this paper is to determine if different bird communities occur in the different sub-types of littoral forest within southeastern Madagascar so as to identify the most important sub-types of littoral forest for bird conservation in the region.

5.3 Study area

The southeast of Madagascar has a subtropical climate with a regional mean annual minimum temperature of 15 °C, mean maximum temperature of 28 °C, and mean annual rainfall ranging from 500 - 3000 mm (Goodman et al. 1997). Due to its location, the region possesses a distinct precipitation gradient, with the eastern coast having a tropical damp climate and the west having a semi-arid climate (Lewis Environmental Consultants 1990; Goodman et al. 1997). As a result, the littoral forests located in the west of the study area are noticeably drier with distinctly less rainfall than the littoral forests on the eastern coast (Dumetz 1999).

The study area is located near Fort Dauphin and includes the littoral forests of three different sub-regions: Mandena, Petriky and Ste.-Luce (Figure 1.1). The littoral forests in these sub-regions are considered Madagascar's most intact littoral forests (Dumetz 1999). These forests occur in fragments that vary in size, shape and degree of anthropogenic impact. Dumetz (1999) found that the littoral forests of Petriky, St-Luce and Mandena each have different plant compositions, different stand densities and differences in vegetation structure and are therefore distinct 'sub-types'. The matrix surrounding these forests includes *marécage* swamp forest, *Melaleuca* forest, plantations of *Eucalyptus citriodora* and *E. robusta,* and heath-type vegetation consisting predominately of *Erica* spp. (formerly *Phillippia* spp.) (Ramanamanjato and Ganzhorn 2001). Two other major forest types (humid forest and spiny forest) also occur in the study area. The humid forests occur almost exclusively on lateritic soils at the base of, and on, the Anosyenne and Vohimena Mountains, while the spiny forests occur on drier, sandy soils to the west of these mountain ranges (Goodman et al. 1997; Ramanamanjato et al. 2002).

5.4 Materials and Methods

Fourteen littoral forest remnants were surveyed, ranging in size from 17 ha to 855 ha, with a median size of 42 ha (Table 5.1). The areas of these remnant patches were determined from a Landsat TM satellite image acquired on 11 November 1999 and from rectified aerial photographs taken in December 2000. Selection of remnants for sampling was constrained by the difficulty of obtaining permission to survey birds on privately held land. Of the 14 remnants surveyed, 7 remnants were located in the sub-region of Ste.-Luce, 6 remnants were

Table 5.1 Geographic data and species richness estimates for the littoral forest remnants.

Remnant name	Sub-type	Lat/Long	Area (ha)	Species number	Chao estimate
M2	Mandena	24° 58′ 01″ S 47° 00′ 33″ E	116	45	46.1
M3	Mandena	24° 59′ 21″ S 46° 59′ 51″ E	73	33	33.7
M4	Mandena	24° 57′ 37″ S 47° 01′ 01″ E	47	30	30.2
M5	Mandena	24° 56′ 49″ S 47° 06′ 17″ E	25	25	26
M6	Mandena	24° 56′ 57″ S 47° 01′ 33″ E	17	21	21.2
M9	Mandena	24° 57′ 14″ S 47° 04′ 23″ E	23	19	19.4
P1	Petriky	25° 04′ 31″ S 46° 53′ 10″ E	855	53	55.1
S6	Ste.-Luce	24° 48′ 43″ S 47° 08′ 31″ E	297	46	47.7
S7	Ste.-Luce	24° 47′ 17″ S 47° 09′ 12″ E	254	42	44.1
S8	Ste.-Luce	24° 46′ 12″ S 47° 09′ 09″ E	172	44	45.3
S9	Ste.-Luce	24° 45′ 39″ S 47° 10′ 19″ E	464	58	60.3
S10	Ste.-Luce	24° 44′ 22″ S 47° 11′ 51″ E	17	28	29.4
S15	Ste.-Luce	24° 45′ 01″ S 47° 10′ 55″ E	126	42	43.4
S16	Ste.-Luce	24° 43′ 07″ S 47° 11′ 08″ E	31	28	29.2

Note: Species richness was determined using 20 Mackinnon Lists of 10 species per list. The Chao estimate was determined using the Chao 2 species richness estimator (Chao 1987).

located in the sub-region of Mandena and one in the sub-region of Petriky (Table 5.1). Only one remnant was surveyed in Petriky because it was the sole remnant left that was accessible.

Bird species presence/absence data were obtained for all 14 littoral forest remnants using a MacKinnon list census technique (MacKinnon and Phillips 1993). This method has been promoted as a suitable, rapid assessment technique for determining bird species communities in habitats that are relatively unknown and when a rapid assessment is necessary (Poulsen et al. 1997). The method should minimise observer bias, whilst enabling the calculation of species richness per remnant. The observer is able to produce bird lists for a particular site and amalgamate them to generate a 'species-discovery' curve, where the cumulative total of species recorded is plotted against survey effort (Bibby et al. 1998; O'Dea et al. 2004). The unit of effort in the MacKinnon list technique is the time taken for an observer to record a pre-determined number of species. This method is less susceptible to differences in ability between observers and loss of concentration by an observer and therefore significantly reduces observer bias (Bibby et al. 1998). Another benefit of this method is that it identifies the minimum amount of effort needed to survey an area, as a plateau is achieved when fewer new species are discovered with continuing effort (MacKinnon and Phillips 1993; Herzog et al. 2002). This approach enabled the observer (JW) to visit a large number of remnants within a short period of time.

We decided to use 10-species species lists for the surveying and subsequent analysis because Trainor (2002a) determined that this species list number generated the most accurate species richness estimations in a species poor environment and Herzog et al. (2002) recommended it as the best compromise between stable richness estimation curves and robust sample size. All 14 littoral forest remnants were surveyed by the first author using this technique between November and December 2001 and again in October and November 2002. Only species sighted within littoral forest fragments were recorded as present, although calls were used to locate birds and to aid identification. Surveys were confined to the periods 0600 – 1000 hr and 1500 – 1900 hr on days without rain or strong wind.

Birds were also surveyed in the other major habitats of the region but the emphasis was placed on determining the species composition within littoral forest remnants. Three *Eucalyptus* plantations and five *Melaleuca* forest patches that immediately surrounded littoral forest remnants within Mandena were surveyed using MacKinnon lists. Due to the difficulty of finding discrete patches of *Erica* vegetation (as it dominated the study area), an area limit of approximately 1 km^2 was used when surveying birds within the *Erica* vegetation with each surveyed area separated by a distance of at least 1 km. Five surveys were conducted in this way. Bird species presence/absence data were also obtained for two areas of lowland humid forest that surround the village of Farafara and three areas of spiny forests north of Amboasary using MacKinnon lists (Figure 1.1). Bird surveys were also conducted within the coastal habitats and rice-paddies of the region to construct a total species list for the study area.

5.5 Analysis

Similarity measures using presence/absence (binary) data was used to assess the extent to which habitats in the study area had species in common. There are many simple measures of the extent to which two habitats have species in common (se Legrendre and Legrendre (1983) for a review). Following previous approaches in Madagascar (e.g. Wilme 1996; Ganzhorn 1998), bird species similarities between littoral forest remnants of different sub-types and spiny and humid forest habitats of the study area were calculated using Jaccards' Index. The Sorensen's Index was also calculated to compare with the Jaccards' Index results. These similarity indices were calculated using the following formulas.

$$\text{Jaccards' Index} = \frac{a}{a+b+c} \qquad (1)$$

$$\text{Sorensen's Index} = \frac{2a}{2a+b+c} \qquad (2)$$

where a = the species present in both samples, b = the species present at one locality and not the other and c = the species found at the second locality and not the first (Legendre and Legendre 1983). In both these indices, the higher the similarity score the more similar the bird communities are to each other.

Non-metric multidimensional scaling (NMDS), using Sorensen's similarities, was used to provide a visual interpretation of the similiarity in species composition of different forested habitats in the study area (Kruskal and Wish 1977). NMDS was conducted in Community

Analysis Package (CAP) software (Pisces Conservation 2002). We chose NMDS because it overcomes two major weaknesses in other ordination techniques: it has greater flexibility both in definition and conversion of dissimilarity to distance and its rationale is the preservation of these relationships in low dimensional ordination space (Carr 1994). We used one-way analyses of similarities (ANOSIMs) to compare habitats for compositional differences/similarities (Clarke 1993). There are N(N-1)/2 combinations for N groups in pair-wise comparisons, so we employed a sequential Bonferroni procedure (Holme 1979) to test for statistical significance. All compositional analyses were based on presence/absence data and Bray-Curtis indices.

An estimation of total species richness in the littoral forest remnants utilising the species lists was calculated using the Chao 2 species richness estimator. Developed by Chao (1984; 1987) this estimator is:

$$\text{Species number} = S(obs) + \frac{G^2}{2M} \qquad (3)$$

where G is the square of the number of species that only occur in one sample, M is the number of species that occur in only two samples and *S(obs)* is the observed species number. By looking at the progressive change in the estimates it was possible to assess if sufficient samples had been taken to stabilize the estimate (Colwell and Coddington 1994; Chazdon et al. 1998).

5.6 Results

Species accumulation curves plateau after approximately 10 lists had been completed and in all cases 15 MacKinnon lists of 10 species accurately determined the species number in each littoral forest remnant and in other forested habitats of the study area (Figure 5.1). Therefore, our basic sampling effort for each forest habitat remnant within the study area became 15 MacKinnon Lists.

5.6.1 What species are found within the littoral forests?

A total of 109 bird species were identified within the study area, with 77 species identified within 14 littoral forest remnants (Appendix 2). Table 5.1 shows the estimate of species richness in the littoral forest remnants utilising the MacKinnon Lists and the Chao 2 species richness estimator. The species richness estimates using the Chao 2 algorithm were within three species of observed richness for all 14 remnants and therefore we believe our survey efforts identified the majority (>95%) of species occurring within these remnants.

The scientific and English names (Langrand 1990) of all species identified are included in Appendix 2, as well as their breeding status: (1) resident, (2) local migrant, including species breeding in or near the study area but not present all year and (3) local migrant, present over winter but not breeding in the area. Information regarding breeding status for many Malagasy birds is scarce. The field guides for the birds of Madagascar (Langrand 1990; Morris and Hawkins 1998), for example, gives a breeding status and notes on how species nest, but this information is limited. Therefore, Appendix 2 is supplemented by Goodman et al.'s (1997) and our observations of birds actively nesting within the study area or from observations of recently fledged birds.

The littoral forests contained no bird species unique to that habitat. Of the species identified within the littoral forests, 40 were island endemic species (species that are endemic to Madagascar) and a further 21 were endemics to the biogeographic sub-region of Madagascar, Comoros and Mascarenes (Appendix 2). Three species (Madagascar Cuckoo Falcon, Eleonora's Falcon, Madagascar Long-eared Owl) were found only in littoral forest remnants and not in other forested habitats of the study area. Two species (Madagascar Crested Ibis and

Figure 5.1 Species accumulation curves using MacKinnon list (1 sample = 1 10 species-list) methodologies for bird communities in all habitat sites surveyed in the study area: 2a) Mandena and Petriky sub-regions; 2b) Ste.-Luce sub-region; 2c) *Eucalyptus* plantations; 2d) *Erica* heathland.

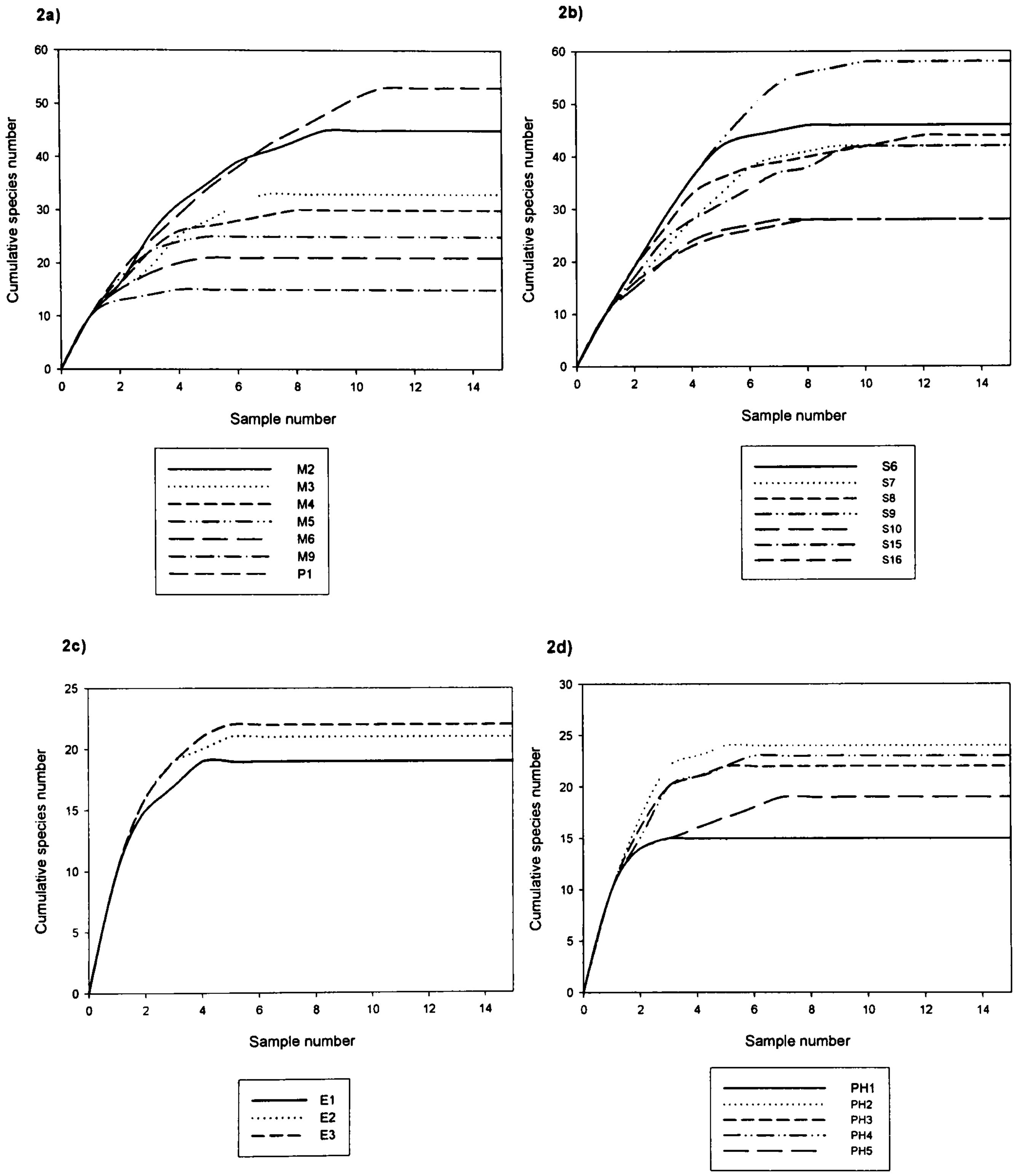
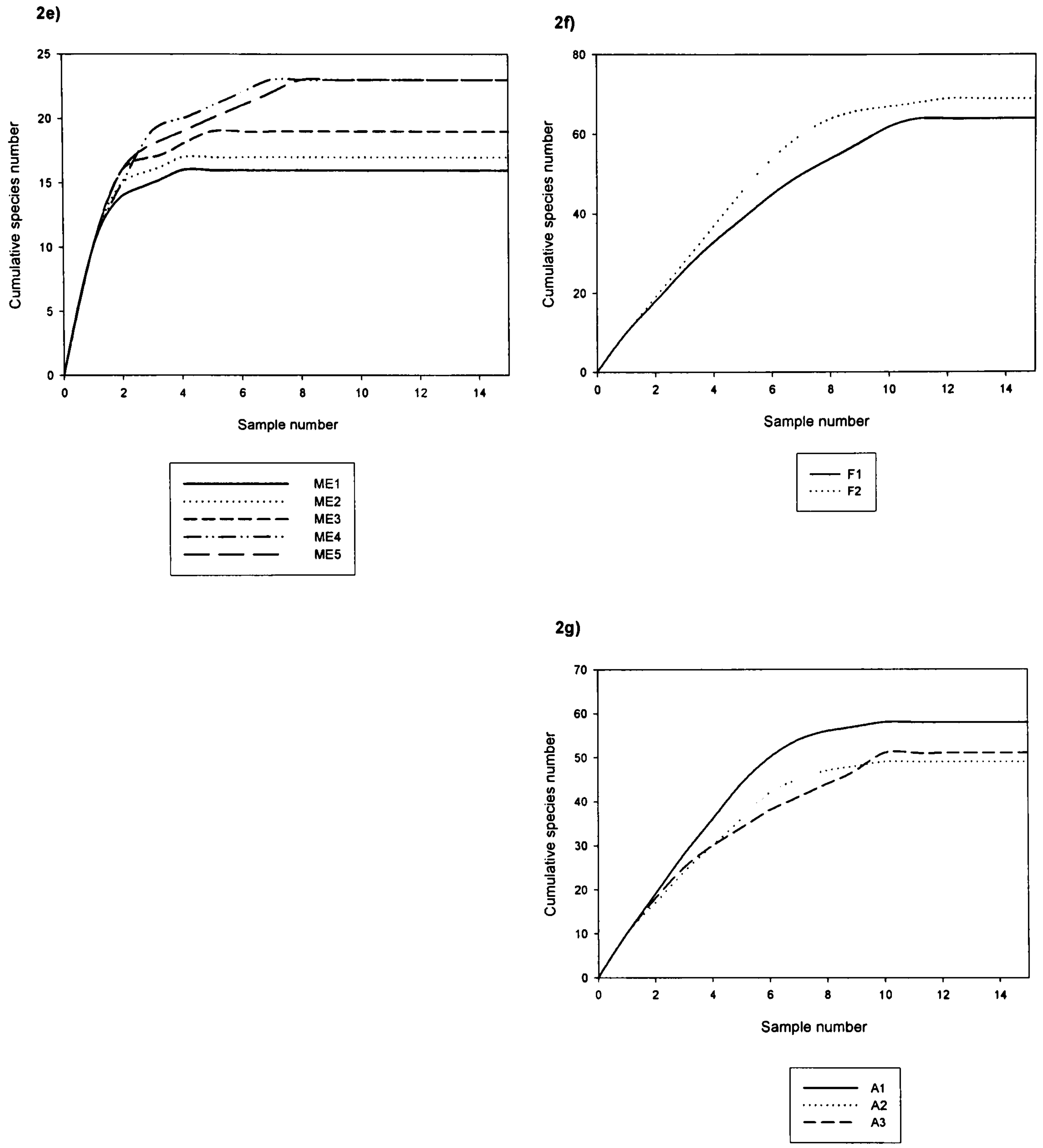


Figure 5.1 cont. Species accumulation curves using MacKinnon list (1 sample = 1 10 species-list) methodologies for bird communities in all habitat sites surveyed in the study area: 2e) *Melaleuca* forest; 2f) Fara Fara humid forest; 2g) Amboasary spiny forest.



Henst's Goshawk) encountered within the littoral forests are considered 'near-threatened' and declining (Thorstom and Watson 1997; Morris and Hawkins 1998) and seven species (Eleonora's Falcon, Madagascar Cuckoo-Falcon, Greater Vasa Parrot, Madagascar Long-eared Owl, Brown-throated Sand Martin, Green Jery and Forest Fody) are considered uncommon in a regional setting (Goodman et al. 1997).

5.6.2 Is bird species composition affected by littoral forest location?

The geographic location of littoral forest remnants appears to play an important role in bird distribution within the study area. A total of 72 species were found within the seven Ste.-Luce remnants, compared to 51 species in the six Mandena remnants and 52 in the single Petriky remnant (Appendix 2). Fourteen species were found solely within the Ste.-Luce littoral forests remnants, four species were found solely found in the Petriky Forest (Crested Coua, White-browed Owl, Lantz's Brush-Warbler, White-headed Vanga) whilst one species (Eleanora's Falcon) was found only in Mandena littoral forest remnants. When the species composition of littoral forest fragments in each sub-type was lumped, we found that Mandena and Ste.-Luce had the most similar bird communities, next in similarity was Mandena and Petriky, and the least similar pair is Ste.-Luce and Petriky (Table 5.2).

NMDS ordination of the sites indicated that two dimensions were sufficient to provide a good overall 'fit' for the bird composition data (stress <0.1; Kruscal and Wish 1977). This ordination shows that geographic location played a role in determining bird composition within the littoral forest remnants, as the Petriky littoral forest remnant was more similar to the spiny forests than the other littoral forest remnants (Figure 5.2). The ordination also showed that the Mandena and Ste.-Luce littoral forest remnants were very similar in bird composition.

Table 5.2 Similarity indices for lumped data between littoral forest sub-regions (Ste.-Luce, Mandena and Petriky) and for spiny forest and humid forest habitats within the study area. Above the diagonal is Jaccard's Index and below the diagonal is Sorensen's Index.

	Ste.-Luce	**Mandena**	**Petriky**	**Humid forest**	**Spiny forest**
Ste.-Luce		0.69	0.37	0.65	0.34
Mandena	0.81		0.52	0.55	0.37
Petriky	0.53	0.68		0.53	0.72
Humid forest	0.77	0.71	0.65		0.42
Spiny Forest	0.52	0.55	0.85	0.66	

When the remnants of different sub-regions were treated independently, the highest similarity was between small sites (<50 ha) irrespective of region. Comparisons involving larger (>50 ha) sites show a tendency for within region pairings to be more similar than between region pairings. The lowest similarity was for pairs of large versus small sites drawn from separate regions (Table 5.3).

These analyses show two things. Firstly, the bird communities that inhabit different littoral forest sub-regions are different, especially the Petriky littoral forest bird community compared to the Ste.-Luce littoral bird community. This is because each sub-region had bird species that were only found within their sub-region (Appendix 2). Secondly, this geographic effect appears to disappear when remnants are below approximately 50 ha in area, as all the small remnants from the Mandena and Ste.-Luce regions had very high Jaccard's and Sorensen's similarity values with each other and low values with the larger remnants of their same sub-type.

5.6.3 Is the bird species composition of littoral forests similar to those of surrounding habitats?

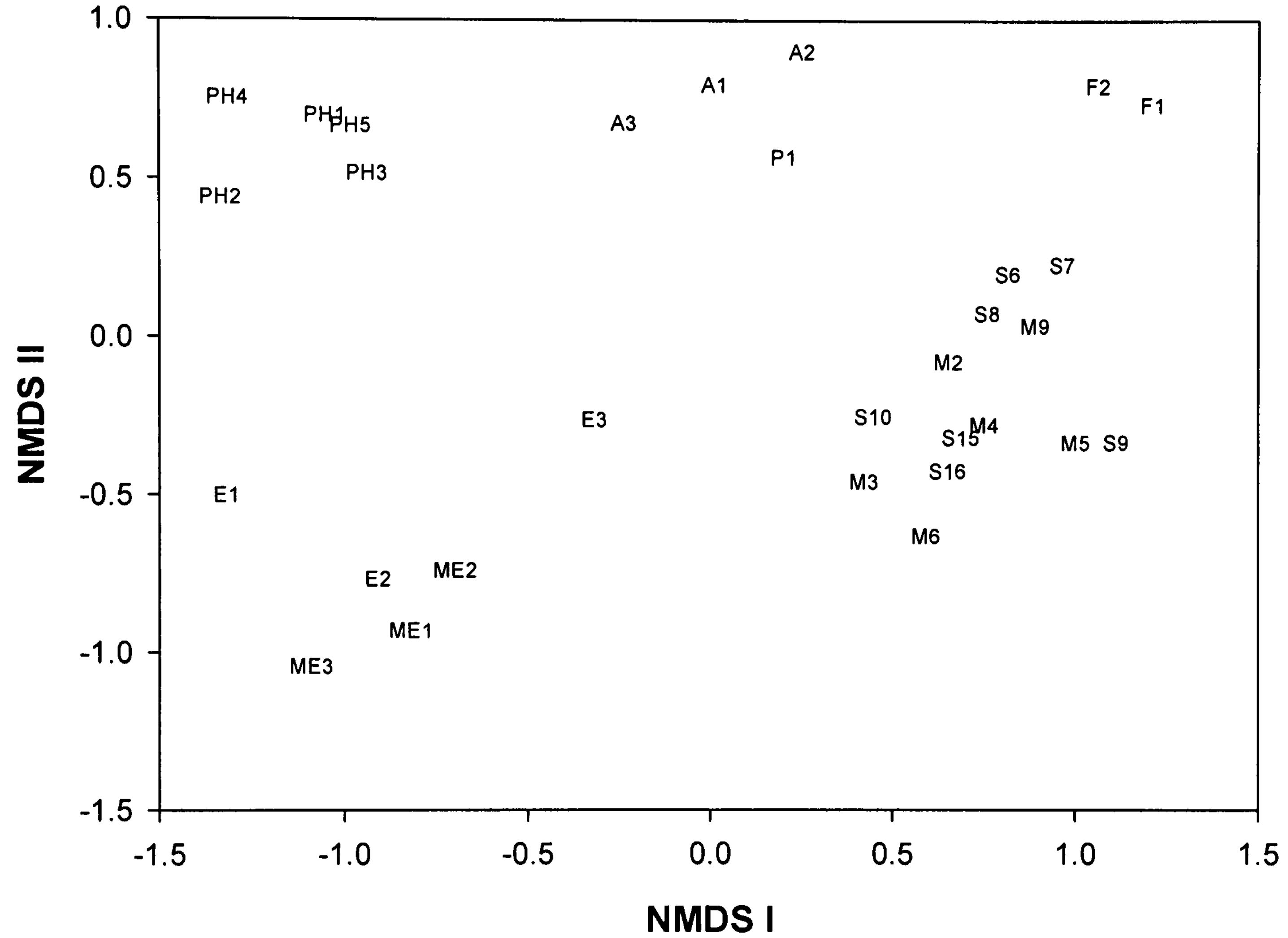
Of the 53 bird species found within the other habitats that immediately surround the littoral forests within the study area, 16 were endemic to Madagascar and 12 others were endemic to the region of Madagascar, Comoros and Mascarenes (Appendix 2). Fourteen of these 53 species were not encountered within the littoral forest remnants; and, 10 of the 14 species were found solely in the aquatic habitats of the *marécage* swamp forests of the study area. The other four species (Kittlitz's Plover, Madagascar Snipe, Peregrine Falcon and Stonechat) all prefer non-forested, open habitats. The other forested habitats that surrounded the littoral forest had very few species compared to the littoral forests. The five *Erica* vegetation patches had bird species richness ranging from 15 to 24 species, with a total of 24 species found within the habitat type (Figure 5.2). The three *Eucalyptus* plantations contained 19, 21 and 22 species with a total of 22 species within the habitat type and the five *Melaleuca* forest patches had species richness ranging from 16 to 23 species, with a total of 23 species recorded from the habitat type (Figure 5.2).

As demonstrated in the NMDS ordination, there was a significant effect of habitat type on the bird community composition (ANOSIM: Global $R = 0.351$; $P < 0.001$). The bird communities of the largest remnant in each sub-type, when compared to the bird communities of the matrix habitats surrounding littoral forest remnants (*Erica* heath, *Eucalyptus* plantations, *Melaleuca* forest), were statistically distinct ($p < 0.05$; Table 5.4). Ordination of the sites showed a high degree of separation of all habitats within the study area and highlighted the distinction between the littoral forests and their surrounding habitats (Figure 5.2).

5.6.4 Are the bird communities that inhabit littoral forests the same as other forested habitats of southeastern Madagascar?

In total, 69 species were found in the two sites in lowland humid forest that surrounds the township of Farafara and 56 species were found within the three sites of spiny forests north of

Figure 5.2 Non-metric multidimensional scaling plot of sites showing degree of separation of forest types based on bird communities. The analaysis included bird communities of seven Ste.-Luce littoral forest remnants (S); six Mandena littoral forest remnants (M); one Petriky littoral forest remnant (P); five *Erica* (PH) quadrats; three *Melaleuca* stands (ME); three Amboasary spiny forest remnants (A); three *Eucalyptus* plantations (E); two Fara Fara humid forest remnants (F)



Amboasary. Of the 77 bird species found within littoral forests, 59 were found also in the Farafara lowland humid forest samples and 48 bird species that were found in the spiny forests north of Amboasary. Twenty-one species found in littoral forests were found in the humid forests but not found in the spiny forests and a further 10 littoral forest species were found in the spiny forests but not in the humid forests (Appendix 2). When bird species communities were lumped per littoral forest sub-region and per habitat type, the Ste.-Luce and Mandena littoral forest bird communities had high similarity values with the humid forest bird communities of Farafara but low similarity values with the spiny forest bird communities

Table 5.3 Comparison of bird communities using the Jaccard's Index within large (>50 ha) and small (<50 ha) littoral forest remnants of different sub-regions. Remnant area is given in Table 5.1.

	<50 ha and < 50 ha	**<50 ha and > 50 ha**	**> 50 ha and > 50 ha**
Mandena *v* Mandena	0.72, 0.73, 0.74, 0.76, 0.75, 0.74	0.54, 0.52, 0.51, 0.54, 0.53, 0.55, 0.53, 0.55	0.67
Mandena *v* Ste.-Luce	0.72, 0.74, 0.71, 0.72, 0.73, 0.75, 0.74, 0.75	0.39, 0.41, 0.42, 0.44, 0.45, 0.44, 0.46, 0.46, 0.46, 0.47, 0.47. 0.49, 0.48, 0.47, 0.41, 0.42, 0.43, 0.42, 0.41, 0.45 0.44, 0.43, 0.48, 0.45	0.56, 0.55, 0.54, 0.52, 0.48, 0.49, 0.51, 0.53, 0.54, 0.56
Ste.-Luce *v* Ste.-Luce	0.72	0.67, 0,64, 0,68, 0.69, 0.64, 0.64, 0.65, 0.67, 0.68, 0.69	0.69, 0.71, 0.68, 0.67, 0.68, 0.70, 0.68, 0.69, 0.66, 0.65, 0.72, 0.73, 0.69, 0.68, 0.70, 0.73, 0.74, 0.69, 0.68, 0.67

north of Amboasary (Table 5.2). The Petriky littoral forest remnant had high similarity values with the spiny forest bird communities north of Amboasary but low similarity values with the humid forest bird communities of Farafara (Table 5.2). Note, however, that the sampling effort varies in these comparisons. To check if this had influenced the results we compared only one (the largest) site from each littoral forest sub-region alongside one site from the humid and spiny forests (Table 5.4). The largest remnants of Mandena and Ste.-Luce had significantly ($p<0.05$) distinct bird communities from the spiny forests north of Amboasary, whilst the Petriky remnant had significantly distinct communities from the humid forests of Fara Fara (Table 5.4). The NMDS analysis shows that all three forest types (littoral forest, spiny forest and humid forest) contain distinct avifaunal communities but also supports the contention that the bird communities in the larger Ste.-Luce and Mandena remnants are closer in affinity to the humid forest communities while the Petriky littoral forests are more similar to the spiny forest communities (Figure 5.2).

Table 5.4 Analysis of similarities (ANOSIMs) between bird communities of littoral forest remnant sub-types and other forest habitats of the study area. The largest remnant of each forest type was chosen to represent the bird communities of that type.

Each ANOSIM produces a global test of the null hypothesis (Global R), that there are no differences between groups. The Global R is approximately zero if the null hypothesis is true. The significance statistic is interpreted as the probability that the observed group means could have occurred if the null hypothesis were actually true.

Comparison group	**Global R**	**Significance Statistic (%)**
Ste.-Luce sub-type		
S9 *v* Fara Fara humid forest (F1)	0.315	7.2
S9 *v* Amboasary spiny forest (A1)	0.385	2.4*
S9 *v Phillipea* (PH1)	0.910	0.1**
S9 *v Eucalyptus* stand (E1)	0.656	0.2**
S9 v *Melaleuca* stand (ME1)	0.391	0.9 *
Mandena sub-type		
M2 *v* Fara Fara humid forest (F1)	0.334	6.4
M2 *v* Amboasary spiny forest (A1)	0.354	3.9*
M2 *v Phillipea* (PH1)	0.905	0.1**
M2 *v Eucalyptus* stand (E1)	0.643	0.2**
M2 v *Melaleuca* stand (ME1)	0.372	1.1*
Petriky sub-type		
P1 *v* Fara Fara humid forest (F1)	0.364	1.7*
P1 *v* Amboasary spiny forest (A1)	0.286	10.2
P1 *v Phillipea* (PH1)	0.922	0.1**
P1 *v Eucalyptus* stand (E1)	0.674	0.2 **
P1 v *Melaleuca* stand (ME1)	0.410	0.8*

* $p<0.05$ ** $p<0.01$

5.7 Discussion

In surveys conducted in 1989, Goodman et al. (1997) found 96 species within the same study area. Our study found 22 species within the study area that Goodman et al. (1997) did not find, of which 17 species were found within littoral forest remnants (Appendix 2). This increase is likely a reflection both of the methodology (MacKinnon list census technique) used herein and of the larger number of remnants visited in this study.

It could be argued that littoral forests are not an important habitat for birds when considered in a national context. The littoral forests have no nationally or globally threatened species (Collar et al. 1994). They contain only two near-threatened species (Madagascar Crested Ibis and Henst's Goshawk) and the 77 species found within them in the present study only equates to 28% of all bird species found within Madagascar (Hawkins 1999; Lagrand 1990). In comparison, the evergreen Malagasy humid forests contain 87 bird species and of these, 39 are endemic species that are confined to that habitat (Hawkins 1999). However, our data support the importance of littoral forest of southeastern Madagascar as a refuge for forest bird diversity at the regional scale. When bird endemism is considered, these forests contain 57% of all the island- and regional- endemic species found within Madagascar (Appendix 2). The littoral forests also contains 42% of all the species found in southeastern Madagascar, and 64% of all bird species that have been identified to live in or utilise forest habitats within this region (Goodman et al. 1997). They also contain two endemic species (Madagascar Cuckoo Falcon, Madagascar Long-eared Owl) that were not found within other forested habitats in the present study.

The importance of littoral forests as a reservoir for regional bird diversity is highlighted when the matrix habitats surrounding these forests are considered. All habitats surrounding the littoral forests were depauperate in bird species diversity. The dominant matrix habitat (*Erica* heath) contained 24 species, with all species considered widespread in the region and on the island (Langrand 1990; Goodman et al. 1997; Morris and Hawkins 1998). The *Eucalyptus* plantations surrounding the littoral forest remnants in Mandena also contained a disproportionately small number of species compared to the littoral forests. They had no species occurring within them that were not found within the littoral forests, and many littoral forest bird species that seem to be able to adapt to secondary forest environs (e.g. Long-billed Sunbird, Common Newtonia) did not utilise *Eucalyptus* forests. Interestingly, Ramanamanjato and Ganzhorn (2001) reported that the endemic mammals that occurred in littoral forest were likewise not found in the *Eucalyptus* plantations that bordered them. In other fragmented tropical areas, the matrix has been found to have a varying influence on the bird composition within fragmented forests. Renjifo (2001), for example, found that the matrix played an important role in determining bird species composition and abundance in sub-Andean tropical forests while Cornelius et al. (2000) found that the nature of the matrix had little effect on bird composition in fragmented temperate forest in Chile. The results of the present study indicate that differences between the particular matrix habitat surrounding these littoral forest areas do not have a strong influence in determining what bird species occur within littoral forest remnants, as very few forest species were found within matrix habitats.

Goodman et al. (1997: 90) argued that there was little difference between the bird communities of Ste.-Luce and Mandena and Petriky, and that the species richness in littoral forests 'did not differ markedly from that of adjacent humid forest'. Our results demand a reassessment. We found that the littoral forests had distinct bird species composition compared to the humid forests of the study area. Geographic location of littoral forests (even at a regional scale) played an important role in determining their bird species composition. For example, the Petriky littoral forest contained a number of species (e.g. Crested Coua, Lantz's Brush-Warbler) that are normally found in the spiny forests of the southern domain (Lagrande 1990) and were found to be significantly ($P<0.05$) dissimilar to the humid forests in nearby Fara Fara (Table 5.4).

The Ste.-Luce remnants had bird species communities resembling those of the lowland evergreen humid forests of the Anosyenne Mountains and Parcel 1 of the Reserve Naturelle Integrale d' Andohahela (Goodman et al. 1997; Hawkins and Goodman 1999). Six species (Madagascar Wood Rail, Red-fronted Coua, Blue Coua, Green Jery, Rufous Vanga, Forest Fody) hitherto described as only inhabiting humid forests (Lagrand 1990; Morris and Hawkins 1998) were found within the Ste.-Luce littoral forest remnants. This humid forest influence could be a result of the northerly location of these remnants or the close proximity to the humid forests of the Vohimena Ranges. However, the Ste.-Luce remnants also contained a number of spiny forest species (e.g. Giant Coua, Archbold's Newtonia). Interestingly, Archbold's Newtonia was found within the Ste.-Luce littoral forests but not in the Petriky forest. This species has been described as being found only in the dry *Didierea* forests of Madagascar's southern domain (Morris and Hawkins, 1998). Ganzhorn et al. (2000) also found two dry forest lemurs (*Cheirogaleus medius, Microcebus murinus*) in the littoral forests of Mandena and Ste.-Luce but not in Petriky.

The sub-regional effect was lost when remnants occurred below a certain size. Smaller littoral forest remnants had fewer bird species and were more similar to each other (regardless of sub-type) than to larger remnants within their sub-type (Table 5.3). This is an important outcome, as fragmentation of littoral forest may lead to the homogenisation of bird communities between the different sub-types, which in turn could have serious effects on bird diversity at the regional scale.

We suggest that the littoral forests are playing an important regional role in determining the overall range distributions of many bird species within the region. One example of this is the occurrence of Lantz's Brush Warbler (considered confined to spiny forest) (Schulenberg et al. 1993). A second example is the presence of the Madagascar Brush Warbler (considered confined to humid and secondary forest) in Ste.-Luce and Mandena. In addition to these species, we found that a number of species considered habitat-restricted by Langrand (1990), either to spiny forest species (e.g. Giant Coua, Crested Coua, Lantz's Brush-Warbler, Archbold's Newtonia) or humid forest (e.g., Red-fronted Coua, Blue Coua, Green Jery, Madagascar White-eye, Rufous Vanga, Tylas Vanga, Forest Fody) occurred in littoral forests remnants. These habitat-restricted endemics, by definition, should occur within a certain habitat type yet they were found together within the same littoral forest remnants. There were also numerous other species that are not considered habitat-restricted endemics, which only occurred in humid and littoral forest or spiny and littoral forest within the study (see Appendix 2). This could mean that the littoral forests are acting as a transitional zone for forest bird species, with some species occurring in all three major habitats, while others occur in only two. In a survey of avian diversity within different habitat types in the Masoala Peninsula, northeastern Madagascar, Thorstom and Watson (1997) report a similar result, as the littoral forests had the lowest species richness compared to all other habitats surveyed. They also found, like the littoral forests in southeastern Madagascar, a number of supposed habitat-restricted endemics (Red-breasted Coua, Red-fronted Coua, Blue Coua, Scaly Ground-Roller, Long-billed Greenbull, Scaly Ground-Roller and Nelicourvi Weaver) inhabiting them. These species were all found to be common in neighbouring lowland humid forest (Thorstom and Watson 1997).

The littoral forests are missing many species that are commonly found in lowland humid forests (e.g. Common Sunbird-Asity, Long-billed Greenbul, Spectacled Greenbul, White-throated Oxylabes, Crossley's Babbler, Dark Newtonia, Pollen's Vanga, Nuthatch Vanga, Nelicourvi Weaver) and spiny forests (e.g. Running Coua, Sickle-billed Vanga, Sakalava Weaver) of southeastern Madagascar (Goodman et al, 1997). The littoral forest's low altitude could be one reason for this, as elevation has been shown to affect bird composition in many areas of the tropics (Terborgh 1971; 1977; Beehler 1982), including Madagascar (Goodman et al. 1997; Hawkins 1999). Other ecological reasons may also be important, such as the availability of suitable resources for particular bird species. However, these reasons may not be valid because many of these bird species were found in littoral forests in the north of the island (Thorstom and Watson 1997). The absence of these species may be a reflection of the amount of human pressure these forests are presently enduring or a reflection of long-term isolation from nearby lowland humid forest and spiny forest.

The complete lack of habitat-restricted endemic bird species within the littoral forests could be a reflection of the comparatively small amount of habitat for species radiation to have taken place or lack of sufficient habitat and food resource differentiation between the littoral habitats and adjacent ecosystems. There is no firm information available on how large the littoral forests were before human settlement but it has been estimated to be around 4500 km^2 (Ganzhorn et al. 2001). Therefore, it is unlikely that the Madagascar littoral forests have ever been large enough to allow for the radiation of highly localised vertebrate taxa at any time in their evolutionary history (Ganzhorn et al. 2000). As demonstrated by the high similarity of species found between littoral forests and spiny forests and between littoral forests and humid forests, the geographic proximity of these three forest types may have also inhibited the differentiation of locally endemic bird species in the littoral forests.

5.8 Conclusion

The littoral forests contain no bird species that are unique to them, and their bird communities resemble a mixed assembly of species that occur in nearby humid forests and spiny forests. However, their comparatively low number of bird species does not mean that they are of minor importance from a conservation perspective and at least two factors emphasise the importance of the littoral forest ecosystem. Firstly, the geographic location of these forest remnants raises the possibility that these remnants may enhance connectivity for birds through the landscape by functioning as ‘stepping stones’ for birds reticent to cross large expanses of hostile matrix. This could include dispersal of humid forest species in the Vohimena Ranges between the littoral forest remnants of Mandena and Ste.-Luce. Secondly, these forests had three species (including two endemic species) not found anywhere else in the study area in our surveys, and also a number of species that are considered ‘restricted’ to humid-forest and spiny-forest ecosystems. In some instances, these habitat-restricted species were found only in one littoral forest sub-types, while others (regardless of which habitat they were supposed to be restricted to) were found in all three sub-types. Therefore, the littoral forests contain a bird community that is unique in the sense that no other habitat on the island contains a mixture of both spiny-forest and humid forest bird communities. As such, the littoral forests have a conservation value in their own right.

Only three remnants of littoral forest are situated within protected areas of which none are located in southeastern Madagascar (Ganzhorn *et al.*, 2001). We believe that the littoral forests are an important regional habitat for indigenous bird communities in the region and recommend that this be kept in consideration if more nature reserves are to be developed. Since the forests are highly fragmented and only small parcels are left, the question arises whether the low species diversity is a true reflection of what the littoral forest hitherto comprised or is a reflection of recent species loss. Future research should focus on the direct effects of fragmentation in these forests, as this would greatly aid the establishment of effective conservation strategies.

5.9 Acknowledgements

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CHAPTER 6

HABITAT STRUCTURE AND PROXIMITY TO FOREST EDGE AFFECT THE ABUNDANCE AND DISTRIBUTION OF FOREST-DEPENDENT BIRDS IN TROPICAL COASTAL FORESTS OF SOUTHEASTERN MADAGASCAR

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6.1 Abstract

Despite the fact that Madagascar is classified a biological 'hotspot' due to having both high levels of species endemism and high forest loss, there has been no published research on how Madagascan bird species respond to the creation of a forest edge or to degradation of their habitat. In this study, we examined how forest bird communities and different foraging guilds were affected by patch habitat quality and landscape context (forest core, forest edge and matrix habitat) in the threatened littoral forests of coastal southeastern Madagascar. We quantified habitat use and community composition of birds by conducting 20 point counts in each landscape contextual element in October and November 2002. We found that littoral forest core habitats had significantly ($p<0.01$) more bird species than forest edge and matrix habitats. Thirty-one (68%) forest dependent species were found to be edge-sensitive. Forest edge sites had fewer species, and a higher representation of common species than forest interior sites. Twenty-nine species were found in the matrix habitat, and the majority of matrix-tolerant forest species had their greatest abundance within littoral forest edge habitats. Guild composition also changed with landscape context. Unlike other tropical studies with which we are familiar, we found that frugivorous species were edge-sensitive while sallying insectivores were edge-preferring. The majority of canopy insectivores (n=15, 88%), including all six endemic vanga species, were edge-sensitive. When habitat quality was assessed, the distributions of nine edge-sensitive species were significantly ($p<0.01$) affected by changes in habitat complexity and vegetation vertical structure in core or edge point counts. Therefore, we believe that changes in vegetation structure at the edge of littoral forest remnants may be a key indicator of mechanisms involved in edge sensitivity of forest dependent species in these forests. Our findings indicate that habitat fragmentation and degradation affect Madagascan bird communities and that these processes threaten many species. With continued deforestation and habitat degradation in Madagascar, we predict the futher decline of many bird species.

Keywords: Habitat fragmentation; Madagascar; Edge-effects; Birds; Habitat degradation; Matrix-effects; Tropical forest

6.2 Introduction

Deforestation and habitat degradation in tropical countries represent major threats to global biodiversity (Myers 1984, 1988; Laurance and Bierregaard, 1997). When deforestation occurs, the amount of habitat available to indigenous forest species is reduced, and the original forest matrix is replaced by habitats created and maintained by human activities (Forman, 1995). Forest fragmentation often occurs alongside deforestation, and if habitat fragments become too small, they will be subjected to both a large array of edge effects and an increase in human pressure, resulting in habitat degradation (Watson et al., 2001; Beier et al., 2002). Many forest-dependent species have been shown to be detrimentally affected by habitat loss and degradation and there are cases of species going locally extinct when forest fragments are either too small or too degraded to support viable populations (e.g. Kattan et al., 1994; Turner, 1996; Renjifo, 1999). It is essential to ascertain how communities and individual species are affected by deforestation, habitat fragmentation and degradation to derive appropriate ecosystem management options.

Due to its size, climate and long history of separation, Madagascar has exceptional concentrations of endemic species (Smith, 1997). Over the past two millennia, Madagascar's forests have been reduced so substantially that it is estimated that only between 10% (Myers et al. 2000) and 20% (Du Puy and Moat, 1998) of 'primary' forest cover is left on the island, although there is still debate over the extent and rate of forest loss (Smith, 1997; Ingram et al., submitted, 2003a, b). On the basis of the number of endemic plant species and the extent of habitat loss and degradation on the island, Madagascar has been identified by Myers et al. (2000: 853) as 'the single highest biodiversity conservation priority in the world'. Degradation of the remaining forests is occurring as a consequence of many factors, most notably logging, slash and burn agriculture (tavy), charcoal production and fuelwood collection (Jolly and Jolly, 1984; Lowry et al., 1997; Kull, 2002). Surprisingly, there are very few published studies on how deforestation and habitat degradation is affecting Madagascar's biodiversity (Langrand and Wilme, 1997; Ramanamanjato and Ganzhorn, 2001; Vallan, 2002).

In this paper, we aimed to assess how processes associated with deforestation and habitat degradation affected a Madagascan forest bird community. Birds have often been used as 'bio-indicators' as they are easy to quantify (Furness and Greenwood, 1993; Turner 1996) and a number of other studies have shown that deforestation and habitat degradation affect bird communities in tropical forests (Bierregaard and Lovejoy, 1989; Newmark, 1991; Kattan et al, 1994; Stouffer and Bierregaard, 1995a; Dale et al., 1999). Our study system comprised areas of threatened littoral forests of southeastern Madagascar (Ganzhorn et al., 2001). The bird communities that exist in these forests are of special interest, as they contain a number of 'near-threatened' species and species hitherto thought to be restricted to either rain forest or spiny forest habitat (Watson et al., in press a; Chapter 5).

Our first aim was to determine if bird species differed in their use of three distinct landscape elements within the littoral forest landscape. These landscape elements were the cores of littoral forest patches, the edges of littoral forest patches and the surrounding matrix habitat. We chose to measure bird species distribution and abundance in the matrix because we wanted to identify which species moved through or utilized the matrix resources. This is because the suitability of the landscape matrix and the ability of animals to move through it may influence population persistence in fragmented landscapes (Stouffer and Bierregaard, 1995b; Sisk et al., 1997; Gascon et al., 1999; Renjifo, 2001; Wethered and Lawes, 2003). The capacity for movement among forest patches (i.e. connectivity) is an important factor in the maintenance of organisms in fragmented habitats (Beier and Noss, 1998), enabling persistence of populations and metapopulations (Whittaker, 1998). It has been found that high connectivity can favour higher abundances of local populations in fragments through immigration (Haas, 1995; Brooker et al., 1999). If the matrix limits recolonisation, however, deterministic or stochastic processes can lead to the decline of local populations and even to local extinction (Opdam, 1990; Whittaker, 1998; Wethered and Lawes, 2003). The contrast between fragments and matrices may determine the degree of isolation of the local population of a given species and, thus, its abundance in fragmented forests.

Our second aim was to determine which species were forest specialists, and of these species, which were sensitive to the forest edge (‘edge-avoiders’) and which were tolerant (‘edge-tolerant’) (Sisk et al., 1997; Lopez de Casenave et al., 1998). A forest edge may have different abiotic conditions to the core of the forest, including increased amounts of sunlight, higher wind speeds, and larger fluctuations in temperature and humidity (Saunders et al., 1991; Murcia, 1995). This, in turn, could potentially affect plant community composition and structure (Malcolm, 1994; Kapos et al., 1997) and hence bird communities. Many studies have shown that certain species reach their highest or lowest abundances at particular habitat edges (e.g. Kroodsma, 1984; Lynch and Whigham, 1984; Dale et al., 2000), but there has been no published study on how forest birds in Madagascar respond to edge effects.

Our third aim was to assess how habitat degradation affected bird communities in littoral forests. Local people use littoral forests to obtain wood for fire, to build houses and pirouges (canoes), and collect plants for medicinal and food purposes, and it appears that this use of the forest may be more common at the edge of littoral forest remnants (Ingram, et al., submitted a, b; JW and TD pers. obs.). In addition to this, the process of deforestation and subsequent habitat fragmentation may mean that a remnant's vegetation structure and floristic diversity is altered because decreasing the size of a remnant can often remove a number of species from a remnant (Cadotte et al., 2002). As a remnant decreases in size it may be more subject to other disturbances, such as fire, disease or wind, and an increase in overall human pressure, which also may affect the vegetation structure and floristic composition of the remnant. We define this change to vegetation complexity and structure as 'habitat degradation'. The degradation of a remnant has often been found to have a profound effect on the community and dynamics of bird communities (Mac Nally, 1990). This is because different plant species are sources of food for particular bird species, while others provide shelter and nesting materials (Carothers et al., 1974; Urban and Smith, 1989). In addition, a change in vegetation structure (e.g. number of vegetation layers) has been shown elsewhere to affect individual bird communities and specific feeding guilds (Santos et al., 2002; Watson et al., 2003).

Our fourth aim was to determine if different functional groups used landscape elements differently. It has been shown in other parts of the world that species of different foraging guilds, with different habitat associations or with different relative abundances, respond unevenly to forest fragmentation (Seiving and Karr, 1997; Lopez de Casenave et al., 1998; Renjifo, 1999; Beier et al., 2002). Therefore, we were interested in identifying if a response to each landscape element and habitat structure were species specific or if certain functional groups were more threatened by the creation of forest edges and/or degradation of their habitat.

Few studies have examined how forest loss and fragmentation have affected birds in Africa or its surrounding islands (but see Newmark, 1991; Brooks et al., 1999; Dale et al., 2000; Beier et al., 2002; Wethered and Lawes, 2003). Given the high human disturbance and extent of fragmentation in Madagascar's forests, our over-riding goal was to determine which bird species were affected by the creation of forest edges and degradation of habitat and hence determine the conservation potential of remnants of different habitat structure and with different amount of edge habitats for bird conservation. Work elsewhere in the tropics suggests the following hypotheses:

1. Forest-dependent bird species that are matrix-tolerant are better adapted to forest edges and the degradation of forest habitat;
2. Some bird species occur restrictively in the core habitat of forests and are adversely affected by habitat degradation; and
3. Specific feeding guilds benefit from the creation of a forest edge (e.g. frugivores and nectivores) while others (e.g. terrestrial insectivores) do not.

In this study, we based our investigation on these hypotheses.

6.3 Materials and Methods

6.3.1 Study area

The Fort Dauphin region of southeastern Madagascar has three major forest types: littoral forest, humid forest and spiny forest (Goodman et al., 1997; Watson et al., in press a). The littoral forests grow along a narrow coastal band of sand and alluvium (Lowry and Faber-Langendoen 1991; Schatz 2000) while the humid forests occur almost exclusively on lateritic soils at the base and on the Anosyenne Mountains and the spiny forests occur on drier sandy soils to the west of these mountain ranges (Goodman et al. 1997). The littoral forests are arguably the most threatened forest-type in the region and are ranked among the habitat types of highest conservation priority on the island (Ganzhorn et al. 2001). These forests now exist as a series of fragments along the eastern coast of Madagascar, and are surrounded by a vastly different matrix habitat mostly comprised (>95%) of *Erica*-dominated heathland (Ramanamanjato and Ganzhorn, 2001). These forests are under varying degrees of human pressure and some remnants are heavily degraded due to slash and burn agriculture, charcoal making and firewood harvesting (Cadotte et al. 2002; JW & TD, personal observations).

We conducted the study in the littoral forest remnants that surround the small township of Ste-Luce (24° 47' S, 47° 12' E; Fig. 6.1). The 18 littoral forest remnants that occur near Ste-Luce cover approximately 1260 ha and the elevation ranges from 0 to 50 m (J. Carter Ingram, unpublished data). Total annual rainfall in southeastern Madagascar ranges from 500 - 3000 mm, with a regional mean annual minimum and maximum temperature of 15°C and 28°C respectively (Goodman et al., 1997).

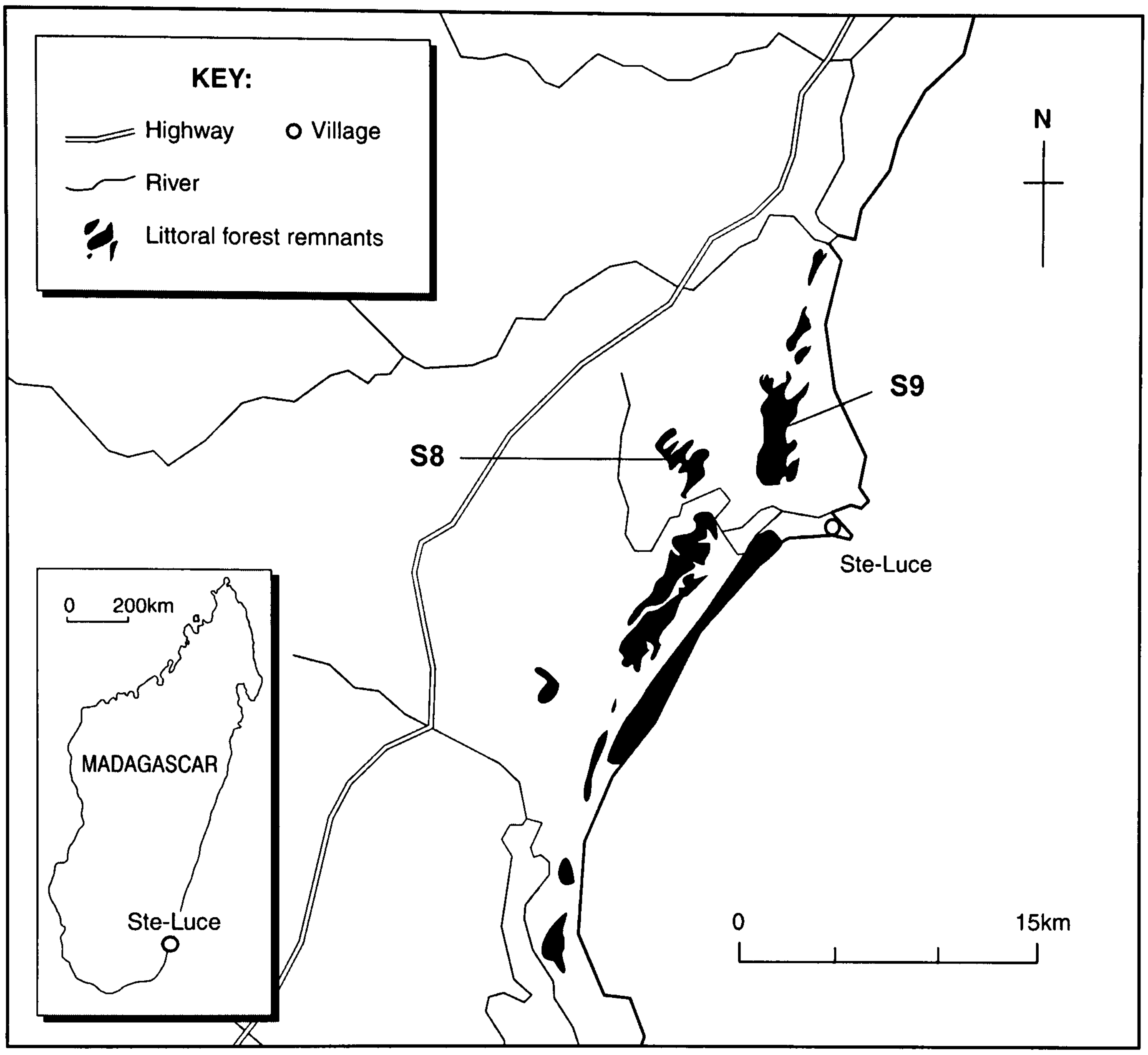
6.3.2 Site selection

We selected three site types: littoral forest edge sites (n=20), littoral forest core habitats (n=20) and the dominant matrix habitats (n=20), hereafter edge, core and matrix respectively. All core sites were located in two large forest blocks, known as S8 and S9, and all edge sites were located on their edges (10 on each). S8 is a 172 ha block and S9 is a 254 ha block, occurring within 1000 m of each other and possessing a relatively uniform vegetation and mostly flat topography (Cadotte et al., 1999; Fig. 6.1). Core habitats were defined as forest areas 300 m from the edge of the forest remnant. Matrix sites were defined as non-forest areas 300 m from the edge of the forest remnant. We determined ten areas of core forest in both S8 and S9 and each core and edge point count were paired.

6.3.3 Bird and habitat measurements

Bird abundance in each of the three landscape elements was quantified using point-count surveys (Bibby et al., 2000) in October and November 2002. Birds occurring within 25-m fixed-

Fig. 6.1 Location of study area showing the distribution of littoral forest remnants near the township of Ste-Luce and the location of our study sites (S8 and S9). The matrix adjacent to these remnants is predominately composed of *Erica* spp. heathland.



radius of each station were recorded because it was often not possible to identify species past this distance. Each station was located at least 100 m apart to minimize the risk of counting the same individual twice. Each station was visited twice. The twenty edge sites were placed so that that the edge of each point count was touching the edge of the remnant (i.e. the centre of the point count was 25 m from the edge of the remnant). To reduce time-of-day effects, the order in which sites were sampled was reversed each week. For two weeks prior to data collection, JW undertook training to estimate distances to the site and sound of the bird and to become familiar with the bird species of the study area. Ten minutes were spent at each station. Surveys were confined to the periods 0600 – 1000 hr and 1500 – 1900 hr on days without rain or strong wind. All point counts were conducted by one observer (JW) to minimise observer effects (Ralph et al., 1993). In addition to conducting point counts, JW conducted an area-search survey using the species-list technique of Mackinnon and Phillips in both remnants (1993). These data show that species richness captured in point count stations in edge and core stations provides a good representation of the species richness in each remnant (O'Dea et al. 2004).

We visually estimated vegetation structure and habitat complexity within each point count. We used eight habitat variables to define vegetation structure and habitat complexity (Table 6.1). Four represented vegetation vertical structure (low shrub cover, medium shrub cover, tall shrub cover and canopy cover) and two represented vegetation density (number of small trees and number of large trees). Two other measures (percentage litter cover and the maximum height of vegetation) were chosen to afforce the other measures in giving an overall measure of how complex the forest habitat was in each point count site (Table 6.1). All habitat variables were recorded as continuous (not categorical) data and were collected at every edge and core point count station, using the same perimeter (i.e. 25 m radius) used for the bird sampling. For example, for the habitat variable 'number of large trees', JW counted the number of large trees (i.e. those trees > 10 m; see Table 6.1) within the 25 m point count radius while for the variable 'litter cover', JW estimated the percentage of leaf litter and fallen dead vegetation within the 25 m point count radius. The eight categories defined in Table 6.1 were chosen to represent a wide range of vertical structure, tree density and habitat complexity measurements, all of which are affected when a habitat is degraded by human activity, such as fire wood collection (Bentley et al., 1997; Cadotte et al., 2002; Vallan, 2002).

Bird species in the littoral forests were classified into predominant foraging substrate and predominant foraging guilds using the species accounts in Langrand (1990), Morris and Hawkins (1998) and Goodman et al. (1997) and other literature surveys (Eguchi et al., 1993a, b;

Table 6.1 Description and mean values (1 SD in parentheses) for vegetation structural measures for forest edge (n=20) and forest core stations (n=20) in two littoral forest fragments in southeastern Madagascar. The results of paired *t*-tests that assessed the difference between the means of each habitat variable are also reported. Note that the variables measured as a percentages were arc-sine square rooted prior to the analysis (Dytham, 1999).

Variable	**Description**	**Forest edge (n=20)**	**Forest core (n=20)**	***t*-value**
Number of large trees	Number of trees > 10 m in height	13.4 (2.5)	18.9 (3.1)	6.1**
Number of small trees	Number of trees between 6 and 10 m in height	21.8 (4.7)	23.4 (5.5)	0.9
Maximum vegetation height	The maximum height of vegetation (m)	12.7 (0.9)	14.5 (1.2)	5.1**
Canopy cover	Percentage of crown cover of trees > 10 m high	72.7 (7.5)	81.9 (6.1)	4.4**
Litter cover	Percentage of leaf litter and fallen dead vegetation	78.7 (8.1)	85.7 (6.4)	3.1**
Low shrub cover	Percentage of shrub cover between 0 and 0.5 m high	49.5 (14.1)	36.7 (22.8)	-1.5
Medium shrub cover	Percentage of shrub cover between 0.5 and 2m high	48.5 (10.1)	36.6 (9.9)	-2.1*
Tall shrub cover	Percentage of shrub cover between 2 and 6 m high	54.5 (17.4)	38.7 (9.98)	-3.4**

* $p<0.05$, **$p<0.01$

Bohning-Gaese et al., 1995; Wilme, 1996; Bleher and Bohning-Gaese, 2000) and field observations. The 11 guilds identified were terrestrial granivores, canopy granivores, terrestrial insectivores, shrub insectivores, canopy insectivores, sallying insectivores, aerial insectivores, canopy frugivores, canopy nectivores, canopy carnivores and aerial carnivores.

6.3.4 Statistical methodology and analysis

All habitat and bird abundance variables were tested for normality using the Kolmogorov-Smirnov test in SPSS software version 11.5 (Dytham, 1999; Kinnear and Gray, 2000). We used several procedures to compare bird species abundance and species richness among the three landscape elements. We conducted two analyses of variance (ANOVA) to compare the total number of individuals and species richness by landscape element. These analyses allowed us to detect differences among the three landscape elements and to determine whether the differences were consistent across time. Species accumulation curves were also generated for each element, in the order in which the censuses were conducted.

Non-metric multidimensional scaling (NMDS), using Sorenson's similarities, was used to provide a two dimensional summary of the similarity in bird species composition of the three habitat types in the study area (Kruscal and Wish 1977). NMDS was conducted using the Community Analysis Package (CAP) software (Pisces Conservation, 2002). We chose NMDS because it overcomes three major weaknesses in other ordination techniques: it has greater flexibility both in definition and conversion of dissimilarity to distance, its rationale is the preservation of these relationships in low dimensional ordination space and it does not need to meet parametric assumptions of other ordination techniques (Carr 1994).

Following Beier et al. (2002), we evaluated the difference in bird species abundance between edge and core point counts using paired *t*-tests using SPSS software (Kinnear and Gray, 2000). Bird abundance data per point count were logarithmically transformed prior to the analysis to improve the normality of the data (Kent and Coker, 1992; Dytham, 1999). We analysed only those species that were found in both landscape elements (i.e. core habitat and edge habitat). This allowed us to determine which species were edge-tolerant, edge-preferring and edge-sensitive.

We used paired *t*-tests to assess the difference between the means of each habitat variable between core and edge sites. The habitat variables that were measured using percentage values (i.e. maximum vegetation height, canopy cover, litter cover, low shrub cover, medium shrub cover, tall shrub cover) were transformed using the arcsine root formula prior to the analysis, to improve the normality of the data.

In order to understand how habitat degradation affected bird species distribution between landscape elements, we used a logistic step-wise regression procedure to examine how individual species distribution (i.e. presence/absence) corresponded with habitat variables at core and edge point counts. Colinearity was found to exist between the habitat variables 'canopy cover' and 'height of vegetation', when an r-value = 80 was used as the cut-off (Soulé *et al.*, 1988; Kent and Coker, 1992; Pisces Conservation, 2002). We therefore removed 'height of vegetation' from the step-wise regression analysis as it explained less of the variance when considered independently. These statistics were calculated using SPSS software (Kinnear and Gray, 2000).

6.4 Results

6.4.1 General patterns of birds in the three landscapes

We identified 74 species of birds during the counting period. Sixty-two species were found within core littoral forest habitat, 44 species were found within edge habitats and 29 species were found within the matrix (Table 6.2). Twenty-nine species (40% of all species recorded) were found in only one landscape type: 24 were only found in core habitat and five species were only found in the matrix habitat (Appendix 3). A further six species were found only in the matrix and edge habitat and one species was found in core and matrix habitats but not in edge habitat (Appendix 3). Only 18 (24%) species were found in all three landscape habitats.

Numbers of species and individuals per point count differed between habitat types (Table 6.2, repeated measures ANOVA: richness, $F_{2,57}$= 41.5, $p<0.01$; abundance, $F_{2,57}$=38.6, $p<0.01$). Species accumulation curves plateau for each habitat type, i.e. by the end of each census no new species were being found (Fig. 6.2). The NMDS ordination produced an adequate fit in two dimensions (stress= 0.14; Fig. 6.3; Kruscal and Wish, 1997). This ordination clearly showed that there were differences in the bird composition among the different landscape elements. Predictably, there was greater overlap between the core forest and forest edge than between forest and matrix habitats.

6.4.2 Individual species and guild response to landscape composition

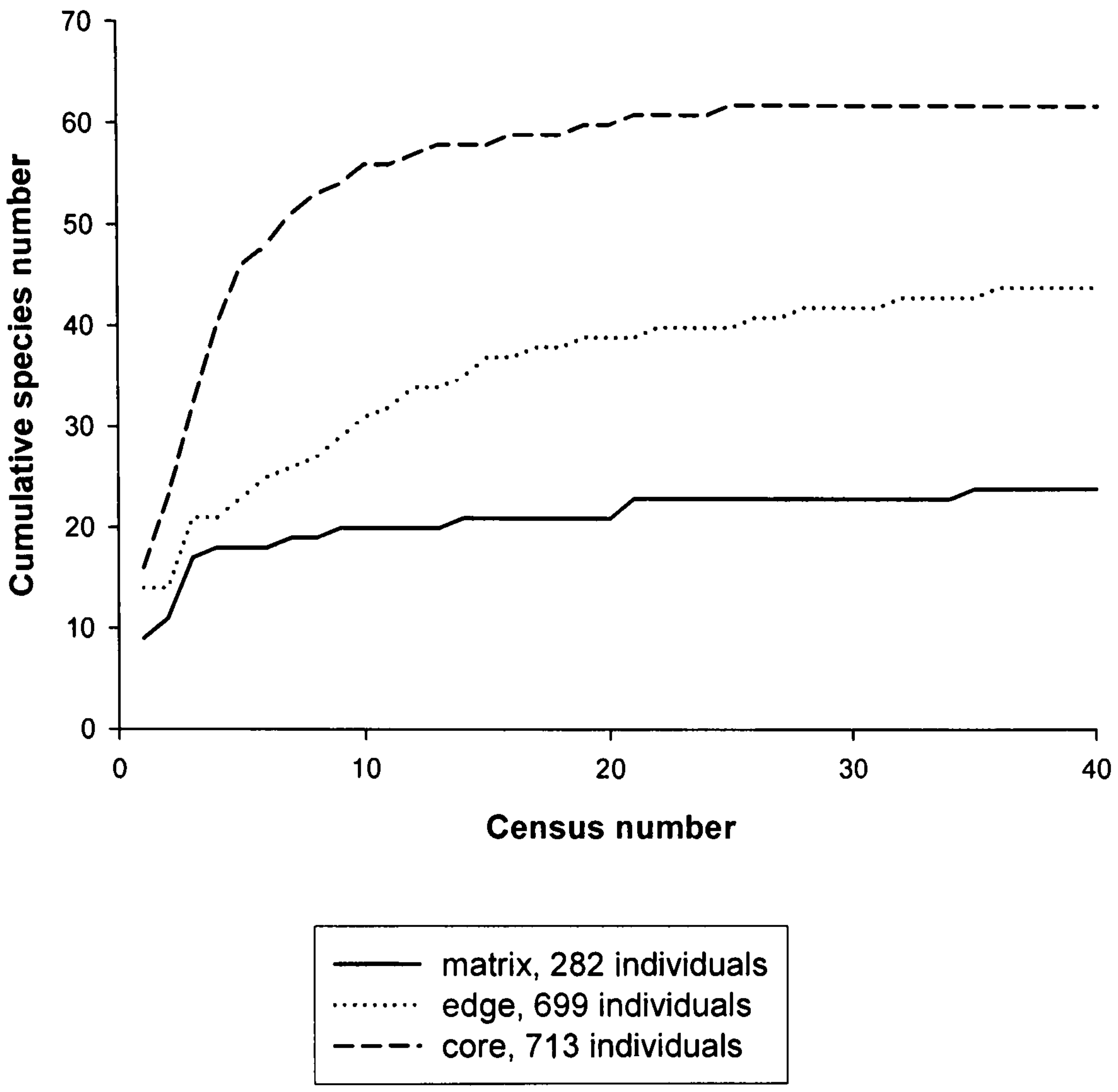
Apart from the 24 species found only in core habitats, a further six species, Madagascar green pigeon (*Treron australis*), lesser vasa parrot (*Coracopsis nigra*), blue coua (*Coua caerulea*), ashy cuckoo-shrike (*Coracina cinerea*), Madagascar white-eye (*Zosterops maderaspatana*) and hook-billed vanga (*Vanga curvirostris*) were found to be significantly ($p<0.05$) edge sensitive, based on their mean abundance in edge and core point stations, using paired *t*-tests (Appendix 3). These species (hereafter 'edge-avoiders') had much higher relative abundances at core point stations than edge stations and none were found in the matrix habitats (Appendix 3).

Ten species were found to be uniformly distributed across core and edge forest sites but were not found in matrix habitat (hereafter 'edge-tolerant') (Appendix 3). A further four species were found in littoral forest only, but showed a significant ($p<0.05$) preference for the forest edge (hereafter 'edge-preferers'). These species were Frances's sparrowhawk (*Accipter francesii*) (core n=1, edge n=5), malagasy kingfisher (*Alcedo vintsioides*) (core n=1, edge n=7),

Table 6.2 Mean numbers of species and individuals recorded during bird counts for all sites combined and by landscape element (i.e. core, edge, matrix); standard deviations are in parentheses. The sample size is the number of point counts within each landscape element class.

Variable	**Forest core (n=20)**	**Forest edge (n=20)**	**Matrix habitat (n=20)**	**Total (n=60)**
Species accumulated over all point counts	63	44	29	74
Species per point count	12 (4.2)	10.7 (2.5)	5 (2.5)	9.3 (4.4)
Species per count after samples were added together	18.2 (5.7)	13.6 (2.2)	7 (2.6)	12.9 (5.9)
Individuals accumulated over all counts	713	699	282	1694
Individuals per count	17.8 (6.8)	17.4 (4.8)	7.1 (3.6)	14.2 (7.2)

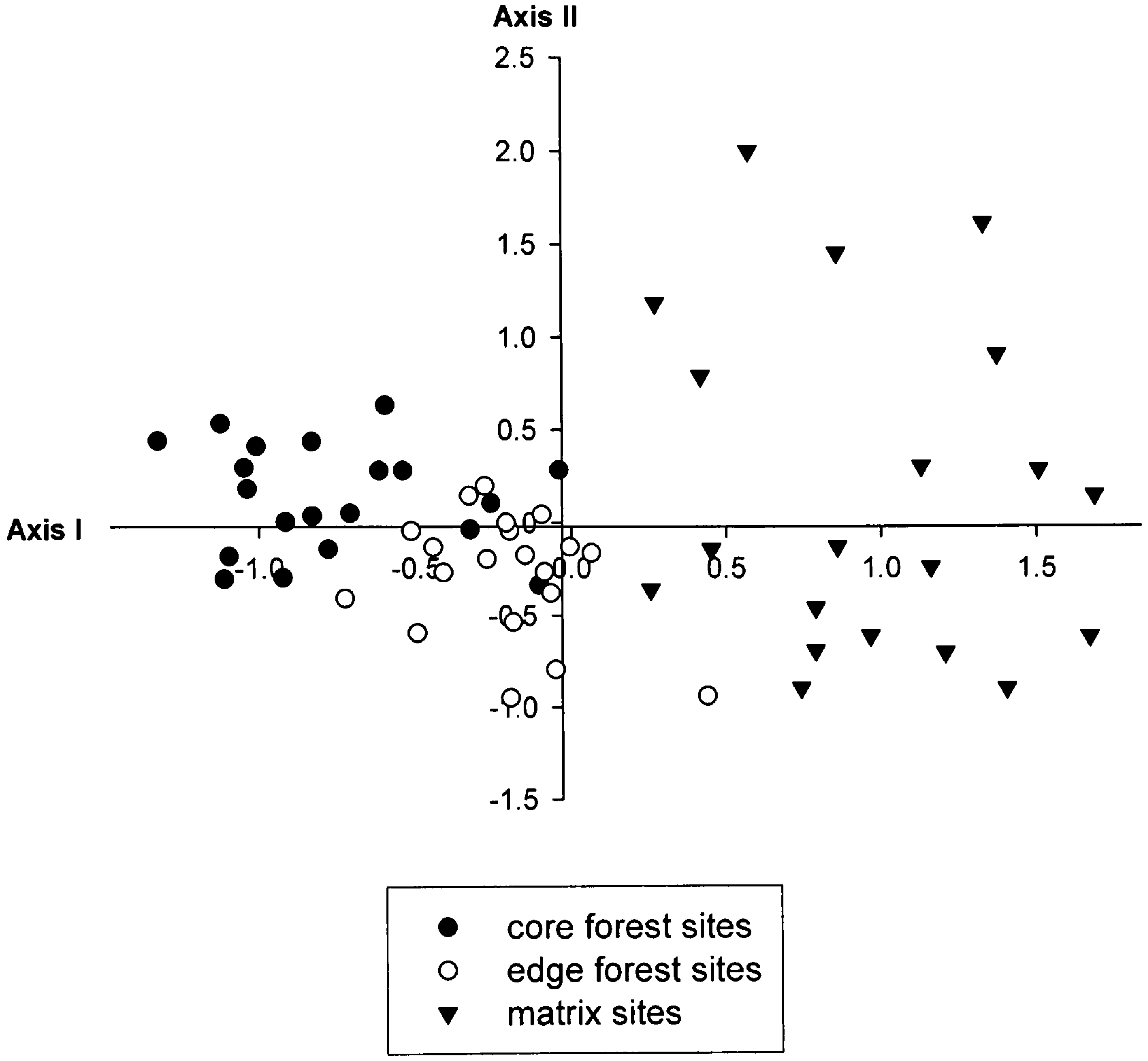
Fig. 6.2 Species accumulation curves based on the sequence in which the bird censuses were conducted for each of three landscape elements.



Madagascar wagtail (*Motacilla flaviventris*) (core n=2, edge n=8) and broad-billed roller (*Eurystomus glaucurus*) (core n=2, edge n=8).

Eighteen species showed no significant bias towards or against any landscape element (hereafter 'ubiquitous'). Of these, ten species were commonly encountered in all three landscape elements, while the others species were rarely recorded (Appendix 3). Five of the ubiquitous species identified were swifts or swallows, which hunt in the air well above the vegetation and are therefore unlikely to be associated with the landscape elements measured in this study.

Fig. 6.3 Two-dimensional non-metric multidimensional-scaling ordination, using Sorenson's similarities, of bird species composition in 60 point count stations located in three different landscape elements (n=20 for matrix, edge and core habitats).



A number of guilds were found to be strongly associated with one landscape element. Of six frugivorous species, only Madagascar green pigeon (*T. australis*) and lesser vasa parrot (*C. nigra*) was found in the edge sampling stations, and these species were found at significantly (P<0.05) lower abundances than in the core sampling stations (Table 6.3; Appendix 3). The rest of this guild was found only in littoral forest core habitats. The abundance of sallying insectivores was higher in edge and matrix habitats than in core sampling stations. The majority

(88%) of canopy insectivores, including all six endemic vanga species identified in this study, were dependent on littoral forest core habitats, as they were either not found in littoral forest edge habitats, or were found at significantly ($p<0.05$) lower abundances and frequencies at edge sampling stations (Appendix 3). Six (46%) of the terrestrial insectivores were found to be edge-avoiders while only two (25%) of shrub favouring insectivores were edge sensitive. The majority (83%) of terrestrial granivorous species were found to be associated with the matrix habitats. The majority (80%) of carnivores were found to be associated with the matrix or forest edge habitats, and only Madagascar harrier-hawk (*Polyboroides radiatus*) and Madagascar long-eared owl (*Asio madagascariensis*) were considered edge-sensitive.

6.4.3 The relationship between remnant habitat variables and bird species distribution

General patterns of birds

Vegetation density, habitat vertical structure and habitat complexity varied between core and edge sampling stations. On average, core habitats had significantly ($p<0.01$) higher density of large trees, a higher maximum height of vegetation, more canopy cover and a higher percentage of litter cover. The edge habitats had significantly ($p<0.05$) higher amounts of low and medium shrub cover (Table 6.1).

Individual bird and guild response to habitat variables

The relationships between individual bird species presence and habitat structure were analysed separately for core point counts (Table 6.4) and edge point counts (Table 6.5). All species found in either landscape element were analysed independently to determine if their presence or absence within point counts could be explained, at least partially, by habitat variables. Therefore, 63 species were analysed in core sites (Table 6.4) and 44 species were analysed in edge sites (Table 6.5).

Table 6.3 The relationship between bird foraging guild and site type in the littoral forests of southeastern Madagascar. The values represent the number of species within each guild classified to be part of the following landscape association: forest species, edge-avoiding forest species, edge-preferring forest species, matrix species, or ubiquitous species. See Appendix 3 for definitions for each species' predominate foraging substrate, predominate foraging guild and landscape association.

Guild	**Littoral forest species**			**Matrix**	**Ubiquitous**
	Edge-avoider	Edge-tolerant	Edge-preferrer		
Insectivore					
Terrestrial	6	1	1	5	
Shrub	2	2		1	3
Canopy	15	2			
Sallying			1		1
Aerial		1			7
Granivore					
Terrestrial		1		3	2
Canopy		1			1
Frugivore					
Canopy	6				
Nectivore					
Canopy		1			1
Carnivore					
Canopy	1		1		
Aerial	1	1	1	2	3

Habitat variables significantly ($p<0.05$) explained the distribution of seven species in core forest sampling stations (Table 6.4). Of these species, five were 'edge-avoiders', one was 'edge-tolerant', and one was 'ubiquitous' (section 3.2; Appendix 3). The edge-avoiding species had significant ($p<0.01$) relationships with the amount of canopy cover ($n=2$) and the percentage of litter cover ($n=2$), with one species (Archbold's newtonia *Newtonia archboldi*) having a significant relationship with both low shrub cover and litter cover. The amount of low shrub cover ($n=2$) and the number of small trees ($n=1$) were the habitat variables that significantly ($p<0.01$) explained the variance of edge preferring and ubiquitous species, at the core stations, with one species being significantly ($p<0.01$) affected by both (Table 6.4).

Variance in presence/absence data of seven species within edge sampling sites were explained ($p<0.05$) by one or more habitat variables (Table 6.5). Four of these species were 'edge-sensitive', two were 'edge-tolerant' and one was considered 'ubiquitous' (section 3.2; Appendix 3). All four edge-sensitive species that were found to have a relationship with a habitat variable, were affected by canopy cover. One edge-tolerant species (Madagascar brush warbler *Nesillas typica*) was affected by both the amount of low shrub cover and number of small trees, as it was in core forest sites (Table 6.4), while the other (long-billed green sunbird *Nectarinia notata*) was affected by the amount of tall shrub cover. The single significant model for a ubiquitous species (Madagascar cisticola *Cisticola cherina*) was based on the amount of low shrub cover.

When foraging guild was considered, both of the terrestrial insectivores (Madagascar crested ibis *Lophotibis cristata* and Madagascar flufftail *Sarothrura insularis*) found to have habitat variables significantly ($p<0.05$) explain their variance in abundance, were more common in areas with high amounts of litter cover. All the canopy frugivores and insectivores featured in Tables 6.4 and 6.5 were found to be at higher abundances in areas of thick canopy cover, except for Archbold's newtonia (*N. archboldi*), which preferred areas that had a higher percentage of low shrub cover and high litter cover. Unsurprisingly, the shrub insectivores featured in Tables 6.4 and 6.5 were most abundant in areas of high shrub cover and/or high density of small trees.

6.5 Discussion

Our first aim was to determine how bird communities differed between three landscape elements: littoral forest core habitat, littoral forest edge habitat and matrix habitat. We found that core sites contained significantly more species than edge and matrix habitats. The forest edges contained very similar numbers of birds to the core but at a much lower diversity. The

Table 6.4 Results of individual logistic regression models for 63 species when related to local vegetation variables for 20 core littoral forest point counts. Bird species are classified as: edge-sensitive, edge-preferring, edge-tolerant and ubiquitous (see Appendix 3).

Only bird species that had a significant relationship with habitat variables are shown. Habitat variables are defined in Table 6.1. Latin names for species identified in this table and the names of species that did not have a significant relationship are found in the Appendix 3.

Species, by group	**Model**	χ^2	**d.f.**
Edge sensitive forest species			
Madagascar flufftail	4.6-5.7(litter cover)	10.3**	1
Madagascar crested ibis	3.6-4.2(litter cover)	10.5**	1
Madagascar blue pigeon	-2.28+ 2.5(canopy cover)	9.8**	1
Madagascar pygmy kingfisher	-3.5+2.7(canopy cover)	8.2**	1
Archbold's newtonia	-9.6+7.27 (low shrub cover)-2.8(litter cover)	14.3**	2
Edge-tolerant forest species			
Madagascar brush warbler	-58.8+40.3(low shrub cover)+ 9.8(number of small trees)	16.9**	2
Ubiquitous species			
Madagascar cisticola	-1.2+ 2.9(low shrub cover)	13.7**	1

** $p<0.01$

matrix habitat was very depauperate in both species richness and numbers of individuals. Only a small proportion of species were habitat generalists, i.e. utilised the forest and non-forest environs. Our results contrast with several similar studies which have shown that many bird species inhabiting forest remnants also use matrix habitats for food and other resources, such as nesting material (e.g. Bayne and Hobson, 1997; Saab, 1999; Renjifo, 2001). Where birds do use the matrix, survival in the remnants is likely to be enhanced. For example, a study in central Amazonia demonstrated that the type of secondary vegetation surrounding forest fragments influenced what species were found within forest fragments (Laurance and Bierregaard, 1997).

Table 6.5 Results of individual logistic regression models for 44 species when related to local vegetation variables for 20 edge littoral forest point counts. Bird species are classified as: edge-sensitive, edge-preferring, edge-tolerant and ubiquitous (see Appendix 3).

Only bird species that had a significant relationship with habitat variables are shown. Habitat variables are defined in Table 6.1. Latin names for species identified in this table and the names of species that did not have a significant relationship are found in the Appendix 3.

Species, by group	**Model**	χ^2	**d.f.**
Edge sensitive forest species			
Madagascar green Pigeon	-1.4+2.7(canopy cover)	10.1**	1
Lesser vasa parrot	29.7 -25.4(canopy cover)	12.4**	1
Common newtonia	-114.7 + 104.1(canopy cover)	20.1**	1
Hook-billed vanga	0.8+2.49(canopy cover)	5.9*	1
Edge-tolerant forest species			
Madagascar brush warbler	-45.6+51.6(low shrub cover)+ 14.7(number of small trees)	20.1**	2
Long-billed green sunbird	-2.9 -5.8(tall shrub cover)	7.1*	1
Ubiquitous species			
Madagascar cisticola	-1.59+ 3.1(low shrub cover)	10.3**	1

** $p<0.01$, * $p<0.05$

Some guilds (e.g. hummingbird species) were unaffected or less affected by forest loss and fragmentation because of their ability to use the surrounding matrix (Stouffer and Bierregaard, 1995a,b; Bierregaard and Stouffer, 1997). Saab (1999), Renjifo (2001) and Wethered and Lawes (2003) also found that the nature of the matrix was very important in determining bird communities in forest fragments of north and central America, and in South Africa. In our study system it appears that the matrix was simply too hostile for many forest bird species, as it was dominated by small *Erica* shrubs with no trees. As it lacked shelter or food resources for many species, the only bird species found were shrub and terrestrial foraging insectivores, granivores, and aerial insectivores.

In addition to determining which species utilised the matrix habitats and which did not, we aimed to determine which species were 'forest specialist', and of these species, which were sensitive to the forest edge. We found 45 species in littoral forest habitats (core or edge) that were not found within the matrix habitats. Of these 'forest-dependent' species, 31 were sensitive (i.e. had significantly lower abundances) or did not occur at the edge of the littoral forest remnants. This is a very high proportion (68%) of the forest-dependent species found within this study. Other studies in tropical Africa have shown marked edge effects within forest bird communities but (to our knowledge) not to this degree. For example, in a study on the effects of forest fragmentation in semi-deciduous forest fragments in Ghana, Beier et al. (2002) found approximately 20% of species to be edge sensitive while Dale et al. (2000) found no understorey species showed significant edge avoidance in a logged Ugandan forest, although 54% of species increased in numbers with increasing distance from the edge.

It is unclear why the littoral forests have so many edge sensitive species. Hagan et al. (1996) argue that sensitivity to edges depends on a number of factors including the species' sensitivity to area effects, the duration and rate of habitat loss and fragmentation, and the proximity of a forest stand to disturbance. Further, they argue that incipient forest fragmentation may affect populations differently from later stages of fragmentation, when the geometry of the landscape has reached a more stable configuration. Studies in South America complement this argument, showing that penetration of edge effects on bird abundance declines over a time-scale of decades (Restrepo and Gomez, 1998). However in our study area, the geometry of the landscape has probably remained stable for at least 30 years (J. Carter Ingram, unpublished data). Using Hagan et al.'s (1996) argument, one would expect to find that far fewer species would be affected by forest edge effects than we have encountered. What is clear from the data herein is that species richness is reduced close to edges, as reported by several other tropical studies

(Lovejoy et al., 1986; Restrepo and Gomez, 1998; Dale et al., 1999; Beier et al., 2002 but see Lopez de Casenave et al., 1998), which seems to be opposite to the effect seen in temperate regions, where edges often correspond with higher bird diversity (Hansson, 1983).

Proximal explanations for edge-avoidance vary across systems and species. For instance, habitat structure and composition may be different on the edge (Lopez de Casenave et al., 1998; Beier et al., 2002), and micro-climatic changes near the patch edge can make the patch unsuitable for some bird species (Laurance at al., 1997; Burke and Nol, 1998; Beier et al., 2002). In the present study, we found that the edge habitats had significantly ($p<0.05$) more shrub cover and a less complete canopy and less litter cover than the core habitats (Table 6.1). This change in vegetation structure and complexity is likely the result of human-induced change as local activities such as the chopping down of trees were often seen at the edge of forests (JW and TD pers. obs.). However, it has been shown in other tropical forests that changes to forest structure at remnant edges can also be exacerbated by changes to micro-climate, such as increased amounts of sunlight, higher wind speeds, and larger fluctuations in temperature and humidity at remnant edges (Laurance, 2001). We found that four edge-avoiding species had a significant ($p<0.01$) portion of the variance in their distribution among edge sites explained by canopy cover (Table 6.5). Moreover, a further five species had a significant ($p<0.01$) portion of their variance explained by canopy cover or litter cover in core sampling stations. All five species were not encountered at any of the littoral forest edge sampling stations. Therefore, for these nine species it is possible that the cause of their edge-sensitivity, at least in part, is due to a lack of a canopy cover and litter cover on the edge of littoral forest remnants.

It should be noted, however, that there is no evidence for an edge effect due to changed forest structure for 21 edge-avoiding birds, as these species did not have their variance explained by habitat variables at either core and edge sites. One possible explanation for this is that bird species are edge sensitive because they are mapping onto some unmeasured resource such as food. Food supply for insectivores, for example, has been shown to vary with fragment size as a result of edge effects, because invertebrates, especially surface dwellers, are prone to desiccation and may not survive well in edge habitat, which is often warmer and drier than the forest interior (Matlock, 1993; Didham et al., 1996; Zanette et al. 2000). Moreover, there may be fewer fruiting and flowering trees near littoral forest remnant edges, resulting in an edge-effect for nectivorous and frugivorous species (Githiru et al., 2002; but see Lopez de Casenave et al., 1998; Restrepo et al., 1999). Another possible explanation is that predation, or avoidance of predation, near the edges may make a number of species 'edge-sensitive' (Robinson et al., 1995), but as far as we are aware there is no direct evidence of this from tropical studies. Whilst we have no data on predation, we did observe a significantly greater number of raptors on the edge of the littoral forest than in the core, including one specialist bird hunter (*A. francesii*), giving circumstantial evidence that this may be a reason why potential prey species are 'edge-avoiders'. Another possibility is that there is increased competition on the edge of littoral forest remnants from matrix-tolerant species (Andrén, 1994; Marzluff and Ewing, 2001). This is supported by the fact that the majority of species found in littoral forest remnants and in the matrix (labelled 'ubiquitous' species; Appendix 3) occurred at their higher abundances at the edge of remnants. Therefore a displacement effect may be occurring at the edges of littoral forest remnants, where species tolerant to matrix habitats encroach on communities that exist on the edges of the forest habitat forcing them to become 'edge-sensitive' (Dunning et al., 1992). Much of this is speculation but we hope will provide some initial hypotheses for future tests that examine the mechanisms that contribute to such a high number of species within littoral forest remnants in Madagascar being edge-sensitive.

Our third aim was to assess how habitat degradation affected bird communities in littoral forests. We defined habitat degradation as a change to vegetation complexity, density or structure. We found that there was variability in the amount of vertical structure within the core habitats (Table 6.1). We also found that the forest edge had significantly ($p<0.01$) fewer trees, less canopy cover and less litter cover and greater shrub cover than the core habitat (Table 6.1). This variability between sampling stations is undoubtedly related to human use of the forest, as some sampling sites were more exploited and, as such, more degraded than others. We found relationships between canopy cover and six edge-sensitive species and litter cover and three edge-sensitive species (Tables 6.4 and 5). We argue that these species are affected by internal degradation of forest habitat, in particular a loss of the larger trees. These types of changes have been found to influence species richness and individual species abundance in other tropical studies (Beier et al., 2002).

Our fourth aim was to determine if different functional groups used landscape elements differently. The effect of landscape composition was observed in foraging guild composition. Whereas sallying insectivores, carnivores and nectivores were in general, more common close to the edge, frugivores were more common away from the edge. Other studies elsewhere in the world have typically found frugivores to be edge-tolerant species and sallying insectivores to be biased to the forest-interior (Johns, 1991; Lambert, 1992, Kattan et al., 1994; Plumptre, 1997; Restrepo and Gomez, 1998; Dale et al., 2000; Beier et al., 2002). Differences in the relative abundance of frugivores from forest edge to forest core might be partially explained by changes in the distribution of the resource base as fruit abundance may decline dramatically from the edge of the forest to the interior (Restrepo et al., 1997; Githiru et al., 2002 but see Restrepo et al., 1999). The decline in the abundance of nectivores from edge to interior may also be resource based, as similar studies have shown in Colombia (Restrepo et al., 1999) and central Brazil (Bierregaard and Stouffer, 1997).

The results concerning guild relationships to edge are interesting. It appears that certain foraging guilds (e.g. canopy frugivores) may be suffering from habitat loss and the creation of a habitat edge in a very different manner to those same guilds in South America, mainland Africa or Asia. This may ultimately lead to a change of vegetation structure and type on the edge of forests, as frugivorous seed dispersers may not disperse certain tree species' seeds on the edge of forests (Hubbell, 1979; Bleher and Bohning-Gaese, 2000). Our results do ultimately question the generality of foraging guild responses to fragmentation but it must be noted that the distribution of guilds in relation to landscape composition may vary throughout the year depending on breeding requirements and foraging habits outside of the breeding season (Restrepo and Gomez, 1998). Further research is needed to determine if our findings hold over time and in Madagascar generally or just for littoral forests surrounded by *Erica* dominated heathlands.

6.5.1 The conservation of birds in littoral forests

We hypothesized that the littoral forest remnants would: (i) contain forest-dependent bird species that are matrix-tolerant and thus better adapted to forest edges and the degradation of forest habitat, (ii) contain bird species that occur restrictively in the core habitat of forests and which are thus adversely affected by habitat degradation, and (iii) have specific feeding guilds that benefited from the creation of a forest edge. We found that the littoral forests had many species that were at lower abundances or did not occur at the forest edge. None of the 'edge-sensitive' community, which included one near-threatened species (*L. cristata*), occurred in the dominant landscape matrix (Langrand, 1990). We also found that certain functional groups were more edge-sensitive, specifically, the majority of frugivorous species and canopy insectivores were found to be 'edge-sensitive'. These findings have clear implications for conservation of forest-dependent birds in littoral forests (and other fragmented habitats) in Madagascar. We suggest that forests blocks be maintained so they have the largest area of core forest habitat possible. In addition to this, we argue that the degradation of littoral forest remnants via the extraction of large logs or tavy farming may conflict with the conservation of some forest birds, as nine species were affected by reductions in canopy cover or loss of litter cover. It is also clear from our analyses that a change from littoral forest to an *Erica* spp. matrix would be disastrous for the forest bird communities (especially the edge-sensitive species) within the region, and would result in a severely reduced bird community.

Our findings show that for many forest bird species *it is* appropriate to view the forests as isolated 'island' habitats surrounded by an inhospitable 'sea' of matrix (cf. Whittaker, 1998). Following MacArthur and Wilson (1967), bird populations within these islands should be governed by factors such as time since remnant isolation and island size and not just how much edge a remnant has. Therefore, future studies within these forests should assess if remnant area plays a role in species distribution and if species are affected by littoral forest remnant isolation (Diamond, 1975; Wilson and Willis 1975; many others). We hypothesize that many edge-sensitive species will also be found to be area-sensitive, and that the species that were using the matrix habitats are more likely to be found within smaller forest fragments at abundances comparable to or greater than those in continuous littoral forest (Renjifo, 2001).

There were some limitations to this study. We were unable to determine how far edge effects extend into the littoral forests. Dale et al. (2000) found that bird species edge effects were operating up to 400 m from the edge and Canaday (1997) reported that edge effects in Amazonia could reach up to 2 km into primary forest if clearings were large enough. However, we found that a distance of 300 m was significant in finding a core-edge relationship in the littoral forest bird community, and so regardless of the exact range of edge effects we suggest that littoral forest set aside for conservation of birds and other organisms may benefit from large size and a low proportion of edges.

Our results were based on a 2-month study in two relatively large forest remnants, and the matrix that surrounds them. Conclusions based only on two large forest patches may suffer from a limited generality. It is also possible that edge effects have a seasonal pattern (Restrepo and Gomez, 1998), so it would be useful to do similar studies at other times of the year or even in different years. Because there have been no similar studies conducted in Madagascar, we can have no idea how representative our results may be.

6.5.2 Conclusion

The littoral forests contain a distinctive forest bird assemblage but are threatened by deforestation and degradation. The main findings of this study were that there was a significant difference between the bird species richness found in matrix, edge and core habitats, and that many forest-dependent species avoided both the edge of the littoral forest and the surrounding *Erica* spp.-dominated matrix. Moreover, our findings indicate that a fair proportion of edge-sensitive forest species are affected by changes to vegetation structure (in particular canopy cover) and the amount of litter cover. From a conservation perspective, we would argue that the species we have identified as edge-avoiders and the species that are affected by habitat degradation should receive the most attention. Many of these species are considered common and widespread in Madagascar but we predict that these species may be the next suite of 'decliner species' on the island, as they seem adversely affected by deforestation, habitat fragmentation and habitat degradation. We recommend that our study be replicated elsewhere in Madagascar to establish the generality of our findings. But, based on the findings reported herein, we would recommend that large littoral forest remnants, with a low proportion of edge, be conserved in southeastern Madagascar, so that these species (and other biodiversity) can persist. We also recommend that conservation strategies be applied to ensure that littoral forest remnants have a high area/perimeter ratio (to reduce edge effects) and to limit the destruction and degradation of habitats within the core of these larger remnants.

6.6 Acknowledgements

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CHAPTER 7

AVIFAUNAL RESPONSES TO HABITAT FRAGMENTATION IN THE THREATENED LITTORAL FORESTS OF SOUTH-EASTERN MADAGASCAR

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7.1 ABSTRACT

Aim Madagascar's lowland forests are both rich in endemic taxa and considered to be seriously threatened by deforestation and habitat fragmentation. However, very little is known about how these processes affect biodiversity on the island. Herein, we examine how forest bird communities and functional groups have been affected by fragmentation at both patch and landscape scales, by determining relationships between species richness and individual species abundance and patch and landscape mosaic metrics.

Location Littoral forest remnants within south-eastern Madagascar.

Methods We sampled 30 littoral forest remnants in southeastern Madagascar, within a landscape mosaic dominated by *Erica* spp. heathland. We quantified bird community composition within remnants of differing size, shape and isolation, by conducting point counts in November - December in 2001 and October - November 2002. Each remnant was characterised by measures of remnant area, remnant shape, isolation, and surrounding landscape complexity. We used step-wise regression to test the relationship between bird species richness and landscape structural elements, after correcting for sampling effort. Relationships between bird species abundances and the landscape variables were investigated with Canonical Correspondence Analysis and binomial logistic regression modelling.

Results Bird species richness and forest-dependent bird species richness were significantly ($p<0.01$) explained by remnant area but not by any measure of isolation or landscape complexity. The majority of forest-dependent species had significant relationships with remnant area. Minimum area requirements for area-sensitive species ranged from 15-150 ha, with the majority of species having area requirements > 30 ha. Surprisingly, there was no relationship between bird body size and minimum area requirement. Forest-dependent canopy insectivorous species and large canopy frugivorous species were the most sensitive functional groups, with >90 % species sensitivity within each group. The distribution of four forest-dependent species also appeared to be related to remnant shape where remnant area was less than <100 ha.

Main conclusions The majority of forest-dependent species, including many that are considered widespread and common, were found to have significant relationships with fragment size, indicating that they are sensitive to processes associated with habitat loss and fragmentation. As deforestation and habitat fragmentation remains a serious problem on the island, it follows that many forest-dependent bird species will decline in abundance and become locally extinct. At the regional scale, we urge that large (>200 ha) blocks of littoral forest are awarded protected status to preserve their unique bird community.

Keywords Littoral forest, fragmentation, isolation, species-area relationship, shape index, birds, island biogeography, Madagascar, incidence function, passive sampling

7.2 INTRODUCTION

Deforestation and habitat fragmentation are having a profound effect on species distributions and abundance in many parts of the world (reviews in Turner, 1996; Debinski & Holt, 2000). In the past two decades there has been an increasing response to these ongoing threats, with research being conducted in many different ecosystems using many methodologies (McGarigal & Cushman, 2002). The vast majority of these studies have been conducted in temperate ecosystems of the 'developed' world, and there is compelling evidence that changes to landscape composition and structure that accompany fragmentation are affecting species in Europe, North America and Australia (Robinson *et al.*, 1995; Hinsley *et al.*, 1996b; Watson *et al.*, 2003). However, there have been relatively few studies on the impact of habitat fragmentation and deforestation in tropical developing countries (especially Africa and its surrounding islands), where the impacts of deforestation seem to be most serious (Whitmore, 1997; Laurance, 1999). The studies that have been conducted have shown that there is a strong, but variable, response to habitat fragmentation and all emphasise the need for more research to be conducted (Dale *et al.*, 2000; Beier *et al.*, 2002). The present paper is the first analysis of the effects of forest fragmentation on birds in Madagascar that considers both patch and landscape mosaic measures.

The island of Madagascar - one of the poorest countries in the world - is no exception to the phenomena of deforestation and habitat fragmentation (Smith, 1997; Mittermeier *et al.*, 1998; Dufils, 2003). Madagascar has been identified as a biodiversity 'hotspot' as it is an island with an exceptional concentration of endemic species that is experiencing rapid loss of habitat (Myers *et al.*, 2000). Deforestation and human-induced habitat fragmentation are occurring primarily because of extractive logging, burning for pasture, and slash-and-burn agricultural practices (Jolly & Jolly, 1984; Kull, 2002; Kistler & Spack, 2003). Forest loss is non-uniform and dynamic on the island and, as such, some ecosystems are considered more threatened than others (Du Puy & Moat, 1998; Ingram, 2004). The littoral forests that are distributed within a narrow band of sand and alluvium along the east coast of the islands are considered one of

Madagascar's most threatened ecosystems (Ganzhorn *et al.*, 2001). They now occur as a series of forest fragments along the length of the island, with the largest intact blocks occurring in southeastern Madagascar (Schatz, 2000).

In this study we assess the effects of deforestation and fragmentation on littoral forest bird communities and different functional groups, by identifying the patch and landscape characteristics that best explain the distribution of bird species richness and individual bird species occupation in littoral forest fragments. From over 60 metrics that have been developed to characterize landscape configuration (McGarigal & Marks, 1994), we identified eight that are associated with deforestation and habitat fragmentation (Trzcinski *et al.*, 1999; Boulinier *et al.*, 2001; Wiens, 2002). These metrics included patch-based measures (remnant area, degree of isolation, reserve shape) and landscape structural measures (density of edges and patches and the area of remnants within a perimeter of the patch in question). As destruction of habitat involves habitat loss, reduction in habitat size and habitat isolation, often acting in concert, these eight metrics were deemed most promising for this study (Haila, 2002; McGarigal & Cushman, 2002). Specifically, we assess how individual bird species distribution and bird assemblages were related to patch and landscape mosaic characteristics by asking the following questions:

(i) what are the relationships between patch and landscape mosaic characteristics and bird species richness?

(ii) are littoral forest-dependent species more affected by patch and landscape mosaic characteristics than habitat generalist species?

(iii) is there a relationship between functional group distribution and patch and landscape mosaic characteristics?

By assessing how patch and landscape mosaic characteristics correlate with bird species distribution and richness within this system, we hoped to achieve three broad aims. Firstly, we aimed to identify associations between bird communities and mappable landscape elements so that we could provide recommendations on key attributes that should be addressed in efforts to conserve bird species within the region (following Major *et al.*, 2001). Secondly, we sought to identify which species or functional groups were affected by fragmentation to aid in forecasting future declining species, as it has been shown elsewhere that bird responses to landscape context can, in part, be explained by bird life history attributes (Stratford & Stouffer, 1999; Lindenmayer *et al.*, 2002). Thirdly, we aim to determine if bird species distribution in fragmented littoral forests conforms to expectations drawn from the dynamic, equilibrium theory of island biogeography and other related theory (e.g. passive sample hypothesis) (MacArthur & Wilson, 1967; Connor & McCoy, 1979; Whittaker, 1998). Information generated by this research may be applied directly into management strategies as the research identifies the species that are likely to be affected by future conservation programs involving regeneration and restoration of littoral forest remnants.

7.3 STUDY AREA

The study was conducted in littoral forest remnants located to the west and north of the township of Fort Dauphin, southeastern Madagascar (Fig. 1.1). This region is considered to have some of Madagascar's most intact littoral forests (Dumetz, 1999). The mosaic surrounding these forests includes small patches of *Melaleuca* swamp forest and plantations of *Eucalyptus citriodora* Hook and *E. robusta* Blakely, and a dominant heath-type matrix consisting of *Erica* spp. (formerly *Phillippia* spp.) (Ramanamanjato & Ganzhorn, 2001). The southeast of Madagascar has a subtropical climate with a regional mean annual minimum temperature of 15 °C, mean maximum temperature of 28 °C, and mean annual rainfall ranging from 500 - 3000 mm (Goodman *et al.* 1997). Three different sub-types of littoral forests have been identified in this region: in the Mandena, Petriky and Ste-Luce areas, respectively (Dumetz, 1999; Fig. 1.1). Watson *et al.* (in press a) showed that the Mandena and Ste-Luce littoral forests contained similar bird communities while the Petriky remnant was quite distinct. As a result, we limited this study to the bird communities of Mandena and Ste-

Luce to minimise the effect of forest sub-type on bird species distribution within littoral forest remnants.

7.4 FIELD METHODS

Species richness and abundance of birds were determined using the point-count method (Bibby *et al.*, 1992). A total of 90 point count stations were placed in 30 littoral forest remnants. Selection of remnants for sampling was constrained by the difficulty of obtaining permission to survey birds on privately held land and by the number of remnants available within each sub-type (Fig. 1.1). Of the 30 remnants surveyed, 16 remnants were located in the sub-region of Ste-Luce and 14 were located in the sub-region of Mandena. Following other similar studies (e.g. Helzer & Jelinski, 1999; Saab, 1999), the number of point count stations varied depending on the area of the remnant: one station in remnants < 1 ha; two stations in remnants of 1-10 ha; three for 10-20 ha remnants; four for 20-40 ha remnants; and five for remnants > 40 ha. Each station had a fixed radius of 25 m and stations were located at least 100 m apart to minimize the risk of counting the same individual bird twice. Circles of 25 m radius were selected because this was as far as an observer could reasonably see in littoral forest, and the smallest littoral forest patches in our survey approximated this width. Ten minutes were spent at each station. For each encounter, an estimated distance from the observer to the bird when first detected was recorded. Distances to birds that were poorly seen were estimated by measuring the distance to vegetation immediately in front of or behind the bird (Shaw & Shewry, 2001).

Bird surveys were carried out by JW during November and December 2001 and in October and November 2002. Each station was visited twice. JW wore drab clothing to avoid detection biases induced by bright colours (Gutzwiller & Marcum, 1993). To reduce time-of-day effects, the order in which sites within a local area were sampled was reversed each week. For two weeks prior to data collection, JW trained to estimate distances to the site and sound of the bird and to become familiar with the bird species of the study area. Surveys were confined to the periods 0600 – 1000 hr and 1500 – 1900 hr on days without rain or strong wind. In addition to conducting point counts, JW conducted an area-search survey using the species-list census technique of MacKinnon & Phillips (1993). These data show that species richness captured in point count stations provides a good representation of the species richness in each remnant (O'Dea *et al.*, 2004).

One of the strongest criticisms of research examining species-area relationships is that organisms are often considered independently of their association with the habitat under consideration (Marini, 2001). To overcome this, we categorised species by their forest-dependence based on Watson *et al.* (in press b). We classified species *a priori* as forest-restricted if they were (1) two or more times more abundant in littoral forest patches than in other habitats; or (2) at low abundance in, or absent from, other habitats. We confirmed our classifications using the species accounts in Wilmé and Goodman (2003) and found a close match between our definitions of forest dependence and theirs. In order to examine the effects of fragmentation on functional groups of avifauna, resident littoral forest bird species were categorised into guilds based on their body weight (<20 g, 20-100 g, >100 g), foraging niche (insectivore, nectivore, frugivore, granivore) and the foraging substrates they exploit (ground, foliage, canopy, air), using the species accounts in Langrand (1990), Eguchi *et al.* (1993a,b), Wilmé (1996), Goodman *et al.* (1997), Morris & Hawkins (1998), Ravokatra *et al.* (2003) and Wilmé and Goodman (2003).

7.5 LANDSACPE STRUCTURE DATA

We selected eight parameters that assessed the patch-based measures and landscape mosaic measures mentioned in the Introduction. These were the area of each remnant (AR), distance to nearest large (>1000 ha) block of forest (DS), distance to the nearest remnant > 100 ha (DR), distance to nearest remnant (DRN), area of nearest remnant (ANR), a littoral forest remnant shape index (SI), patch density (PD) and edge density (ED) (Table 7.1). Measurements from the edge, rather than the centre of the patch, were used in calculating edge and patch density to exclude the area of the patch of interest, because that measurement (remnant area) was included as a landscape metric. We analysed numerous shape indexes obtained from a number of sources (see Helzer & Jelinski, 1999; Liu & Chen, 2000) but discovered all were auto-correlated with the variable remnant area in our system. We decided to use the formula in Table 7.1 because it most reduced the autocorrelation between these two parameters and has been used in other similar studies (e.g. Hinsley *et al.*, 1995; Watson *et al.* 2000; Santos *et al.*, 2002). According to this formula, a circle has a shape index of one; a perfect square has a shape index of 0.88, with a lower number indicating a higher edge to area ratio. All eight patch and landscape mosaic variables were determined from a supervised classified Landsat TM satellite image acquired on 11 November 1999 using ArcView GIS software.

Table 7.1 Definition and summary statistics, with adopted transformations, for landscape structural metrics of 30 littoral forest remnants in southeastern Madagascar. Landscape environmental attributes were determined from a Landsat TM satellite image acquired on 11 November 1999.

Code	Description	Units	Minimum	Maximum	Mean
Shape Index (SI)	SI= $\frac{A/P}{R/2} x100$ where R is the radius of a circle with area A and perimeter P	0-1	0.27	0.94	0.707
Edge Density (ED)	Density of littoral forest edge within 500 m of each remnant's edge multiplied by 100	0-1	0.07	0.51	0.28
Patch Density (PD)	Density of littoral forest remnant area within 500 m of each remnant's edge	0-1	0.02	0.38	0.18
Distance to source (DS)	Distance to the nearest block of forest > 1000 ha	m	4813	17502	9965
Distance to large remnant (DR) [1]	Distance to the nearest remnant with an area > 100 ha	m	45	3968	903
Distance to nearest remnant (DNR) [2]	Distance to the nearest remnant	m	55	1600	132
Area of nearest remnant (ANR) [1]	Area of nearest littoral forest remnant	ha	0.40	464	96
Remnant Area (AR) [1]	Total area of the remnant	ha	0.30	464	58

[1] ln transformed; [2] square-root transformed for analyses

7.6 ANALYSIS

A step-wise regression analysis (holding P to enter =0.05 and P to remove =0.1) was used to explore the relationships of species richness and forest dependent specific richness (dependent variable) with the patch and landscape mosaic variables recorded for each fragment in order to build the best predictive model for each richness value. The problem of analysing patterns of species richness in fragments of differing size is that it is difficult to eliminate the effects of decreasing sampling area; both fragmentation and decreasing sampling area should result in decreasing species richness (Stratford & Stouffer, 1999). To overcome this problem, we average species richness per point count per remnant. The variables 'area', 'area of the nearest remnant' and 'distance to the nearest remnant > 100 ha' were logarithmically transformed while the parameter 'distance to nearest remnant' was square-root transformed prior to analyses (Sokal & Rohlf, 1981; Table 7.1). As multicolinearity was found between the two independent variables 'shape' and 'area', we removed the variable 'shape' from the step-wise, as it explained less of the variance in both analyses (Soulé *et al.*, 1988; Table 7.2).

We attempted to estimate the density of bird species encountered within littoral forest remnants using the distance sampling technique (Buckland *et al.*, 1993). Due to a low encounter rate of most (>90%) species within the littoral forests, we could only accurately estimate individual species densities for the most abundant species within the littoral forest system. Therefore, we used a measure of 'relative abundance', which we defined as individual species abundance per point count station in each remnant. To account for potential biases created by having different numbers of stations per patch, the mean number of occurrences observed among all stations surveyed within each patch was used to calculate a species' frequency of occurrence in a single patch (Saab, 1999). For example, if a species was recorded as one individual on one occasion at each of five sampling stations surveyed four times within a large littoral forest patch, the index of occurrence would be five observations divided by 20 visits, for a mean of 0.25. This frequency of occurrence would be equal to that

Table 7.2 Pearson correlations between landscape variables. See Table 7.1 for how landscape variables were calculated.

	Remnant Area	Shape Index	Distance to large remnant	Distance to source	Patch Density	Edge Density	Distance to nearest remnant	Area of nearest remnant
Remnant Area	1	-0.81*	-0.02	0.46	-0.26	-0.51	-0.08	-0.24
Shape Index		1	-0.08	-0.22	0.25	0.51	0.02	0.27
Distance to large remnant			1	-0.26	-0.14	-0.28	0.50	-0.41
Distance to source				1	-0.13	-0.09	-0.01	0.35
Patch Density					1	0.59	-0.60	0.27
Edge Density						1	-0.56	0.46
Distance to nearest remnant							1	-0.20
Area of nearest remnant								1

* $p<0.05$

of a small patch with one sampling station where only one individual is recorded once across all 4 visits, for a mean of 0.25. The bird density data from the point stations were combined because the co-efficient of variation for individual species' abundances and species turnover rates did not differ significantly among years (Saab, 1999).

Relationships between relative bird species abundances and the landscape structural variables were investigated using Canonical Correspondence Analysis (CCA) using CANOCO 4.5 (ter Braak, 1986; ter Braak & Smilauer, 2002). We used CCA as it has been proven to be useful in determining relationships between environmental variables and bird species abundance in other studies (e.g. Calme & Desrochers, 2000; Shochat *et al.*, 2001). This is because CCA is a direct gradient analysis in which the ordination axes extracted are selected by multiple regression using linear combinations of the environmental variables (ter Braak, 1986).

Relative abundance per point count at each remnant was used as the biological data and seven landscape metrics were used as the environmental data. The significance of the first three canonical axes were tested by way of a Monte Carlo test with 10000 permutations.

Binomial logistic regression was used to identify landscape variables associated with the probability of occurrence of individual species (Watson *et al.*, 2001). Logistic regression was used instead of linear regression because of the low number of species found in many patches. Logistic regressions were modelled using a likelihood ratio test based on the presence/absence data for littoral forest bird species in all 30 littoral forest remnants. These regressions were then used to examine the relationships between the presence or absence of a species and individual landscape variables. Minimum requirements for all sensitive species identified in the binomial logistic regression were estimated for each significant landscape metric with incidence functions calculated using logistic regression. An incidence of 50% in the logistic models (the point at which the model predicts a 50% probability of the species occurring in a given patch) was used to define the minimum requirement of the landscape parameter for a sensitive species (after Robbins *et al.*, 1989; Helzer & Jelinksi, 1999). All regression analyses were calculated using the statistical package SPSS (Kinnear & Gray, 2000).

7.7 RESULTS

7.7.1 Avifauna of the region

In total, 70 bird species were found in the 30 littoral forest remnants, of which 39 species were identified as 'forest-dependent'. The mean number of bird species detected in each point count was 15.4 (± 6.1 S.D.), of which 5.14 (± 5.08 S.D) were considered forest-dependent. The seven most commonly encountered species were Madagascar bulbul *Hypsipetes madagascariensis* Müller, souimanga sunbird *Nectarinia souimanga* Gmelin, Madagascar coucal *Centropus toulou* Müller, Madagascar turtle-dove *Streptopelia picturata* Temminck, crested drongo *Dicrurus forficatus* L., Madagascar bee-eater *Merops superciliosus* L. and common jery *Neomixis tenella* Hartlaub. Each of these species had > 50 % probability of detection in any point count and all were considered habitat generalists, as defined by Watson *et al.* (in press b). The three most commonly encountered forest-dependent species were hook-billed vanga *Vanga curvirostris* L., lesser vasa parrot *Coracopsis nigra* L. and Madagascar green pigeon *Treron australis* L.; each of which occurred in > 25% of point counts. Eleven forest-dependent species (Madagascar cuckoo falcon *Aviceda madagascariensis* Smith, Madagascar sparrowhawk *Accipiter madagascariensis* Smith, Henst's goshawk *Accipiter henstii* Schlegel, greater vasa parrot *Coracopsis vasa* Shaw, Madagascar lesser cuckoo *Cuculus rochii* Hartlaub, red-fronted coua *Coua reynaudii* Pucheran, Madagascar scops owl *Otus rutilus* Pucheran, Madagascar long-eared owl *Asio madagascariensis* Smith, green jery *Neomixis viridis* Salomonsen, rufous vanga *Schetba rufa* L., forest fody *Foudia omissa* Rothschild) and five habitat generalist species (Eleonora's falcon *Falco eleonorae* Gené, sooty falcon *Falco concolor* Temminck, Malagasy spine-tailed swift *Zoonavena grandidieri* Verreaux, alpine swift *Apus melba* L., brown-throated sand martin *Riparia paludicola* Vieillot) were found in fewer than three point count stations and as a result, were treated as 'rare' species and were excluded from the likelihood ratio, CCA and incidence function analyses.

7.7.2 The relationship between landscape metrics and bird species richness

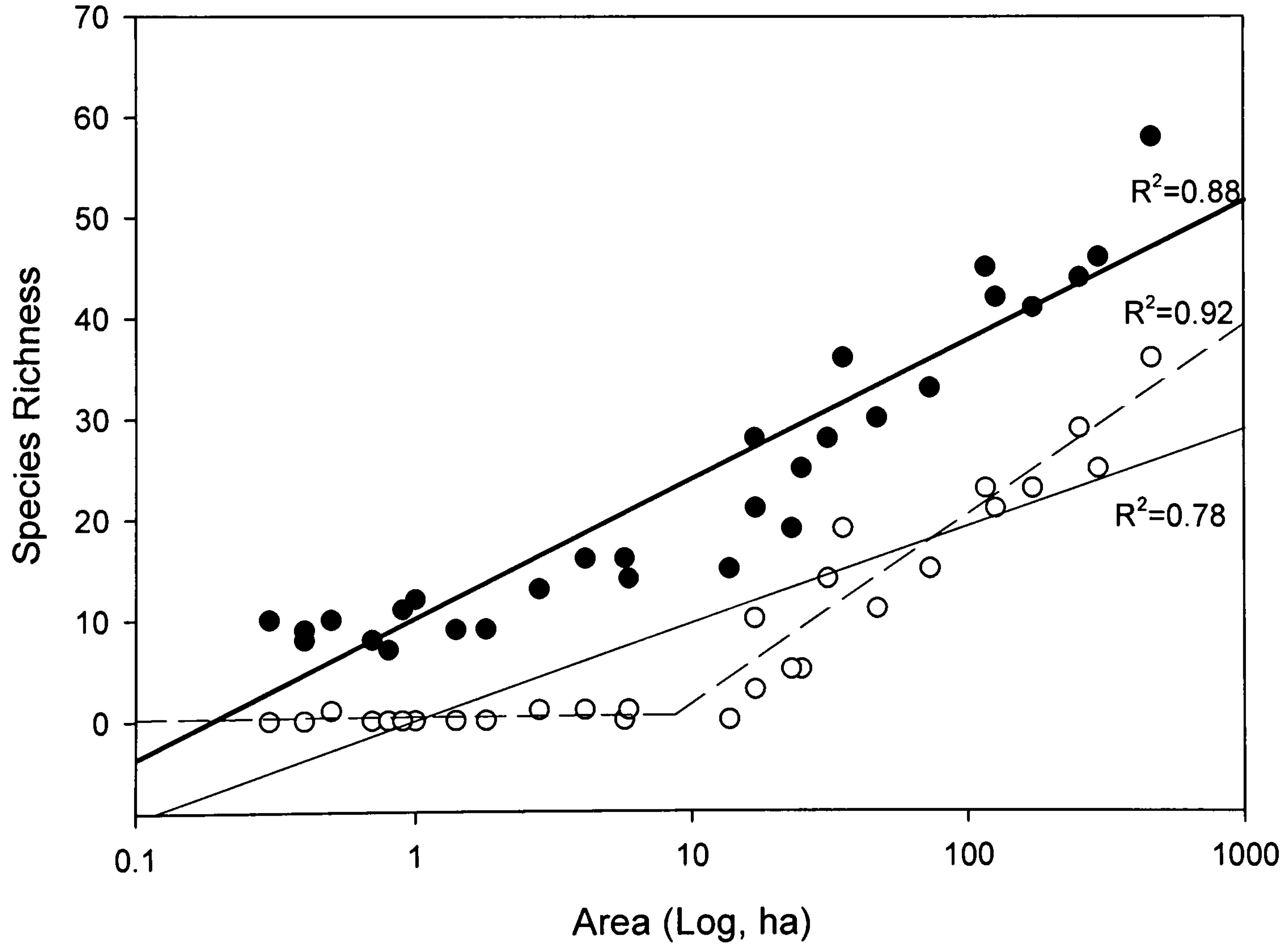
The step-wise regression model selected remnant area as a significant ($p<0.01$) factor that explained variation in total species and forest bird species richness. Variance in total and forest-dependent species richness accounted for by the other variables in the step-wise regression was negligible in each case and they were not selected in either model.

When considered independently, total species richness and forest-dependent species richness were significantly correlated with fragment size (total species richness $F_{1,28} = 15.3$, $P<0.001$; forest-dependent species richness $F_{1,28} = 18.1$, $P<0.001$). As it is important to see what function fits the species-area relationship best, we conducted linear regressions of log-species on log-area for all species and for forest-dependent species, and compared the output for accuracy of fit to untransformed or semi-log plots (Scheiner, 2003; Tjørve, 2003). We found that the species-log area regression provided the best fit in both cases (Fig. 7.1). However, as only one forest-dependent species (Madagascar green pigeon) was found in remnants of <10 ha, we conducted an additional break-point regression analysis for the forest-dependent species: area relationship (Lomolino & Wieser, 2001). This improved the r^2 value by 14% and highlighted the small-area effect for forest-dependent species in littoral forest remnants.

Figure 7.1 Bird species richness-area in the littoral forests of southeastern Madagascar, including regressions.

Two classifications of species richness were considered: total species richness (closed circles) and forest-dependent species richness (open circles). Classification of forest dependency followed Watson *et al.* (in press b).

Linear regressions: unbroken lines; break-point regression: dashed line. The break-point regression procedure followed Lomolino and Wieser (2001). All regressions are significant (p<0.01).



To assess how the 'island effect' in our study system compared to other systems, we calculated z using the log species (S) - log area (A) formula following MacArthur and Wilson (1967). In the littoral forest system, S = 2.1 + 0.34A (i.e $z = 0.34$).

7.7.3 The relationship between landscape metrics and individual bird species and guild structure

Individual species distribution

The variable 'area' was strongly correlated with the first axis of the CCA while 'distance to source' and 'patch density' were correlated with the second. Therefore, the first ordination axis separated species according to whether they were associated with patch remnant area while the second axis separated landscape structural components (Fig. 7.2a, b). The first two environmental axes explained, respectively, 43% and 15% of the variance of the species-environment relationship (Table 7.3). The first canonical axis was significant according to the Monte Carlo test (eigenvalue= 0.252; F-ratio= 3.798; P=0.006; Table 7.3).

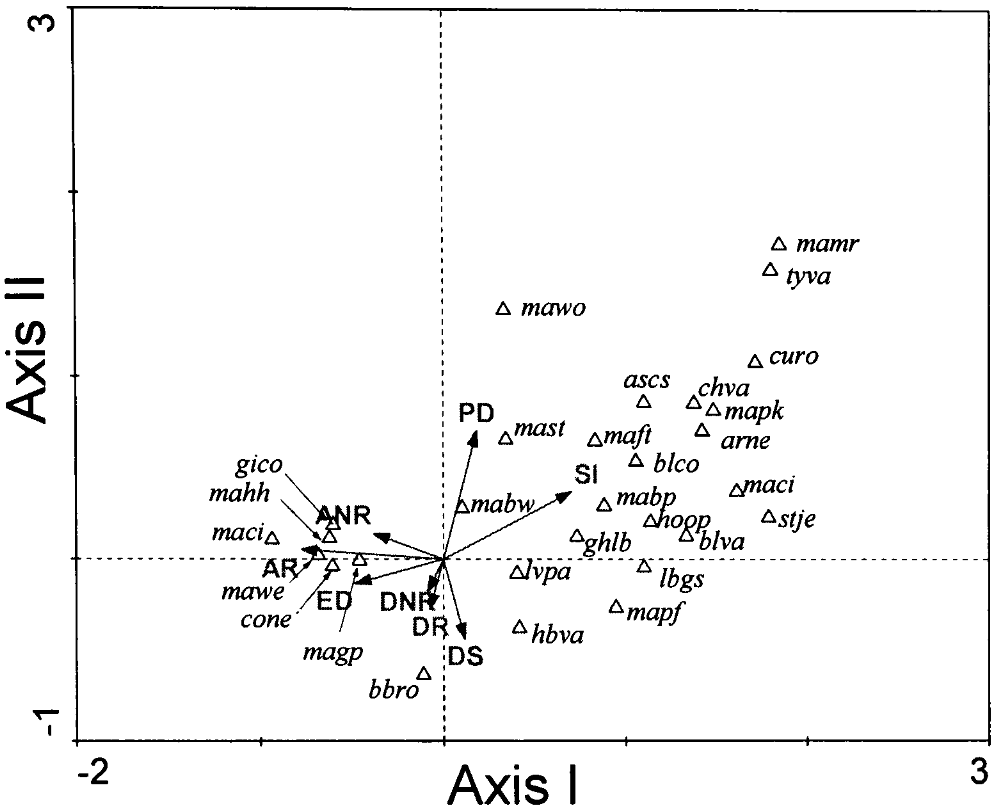
The CCA highlighted the general association between forest-dependent species and the landscape variables remnant area and remnant shape and to a lesser extent, distance to source (Fig. 7.2a). It also highlighted the relationship between some habitat generalist species with

Table 7.3 Results of CCA showing the distribution of birds species in 30 littoral forest remnants of southeastern Madagascar, in multivariate environmental spaces. Species CCA biplots are shown in Fig. 7.2.

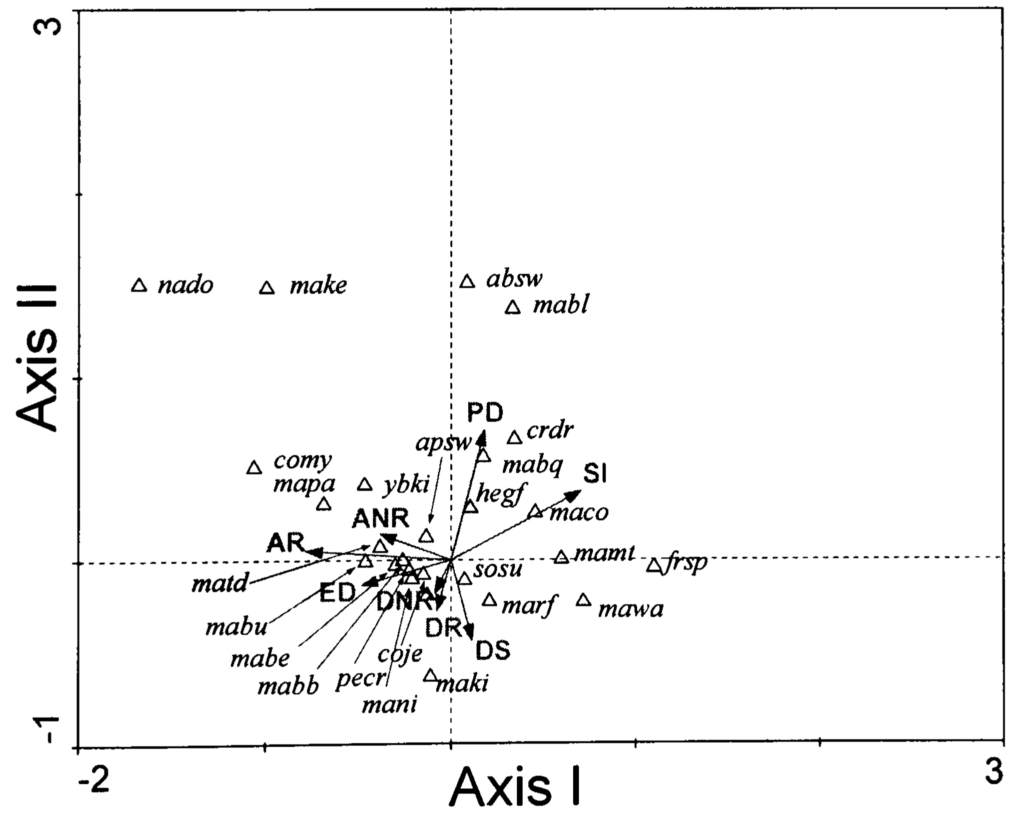
	Axis I	Axis II
Canonical eigenvalues	0.25	0.11
Species variance accounted by axes (%)	43	15
Species-environment correlations	0.94	0.84
Monte Carlo simulation, P-Values	<0.01	0.10

Figure 7.2 CCA biplots showing the distribution of bird species in multivariate environmental space. Figure 7.2a) consists of forest-dependent species and 7.2b) consists of habitat generalist species. Species were separated into their forest dependency following Watson *et al.* (in press b). Species codes are as in the Appendix 4, variable codes are as in Table 7.1.

7.2a)



7.2b)

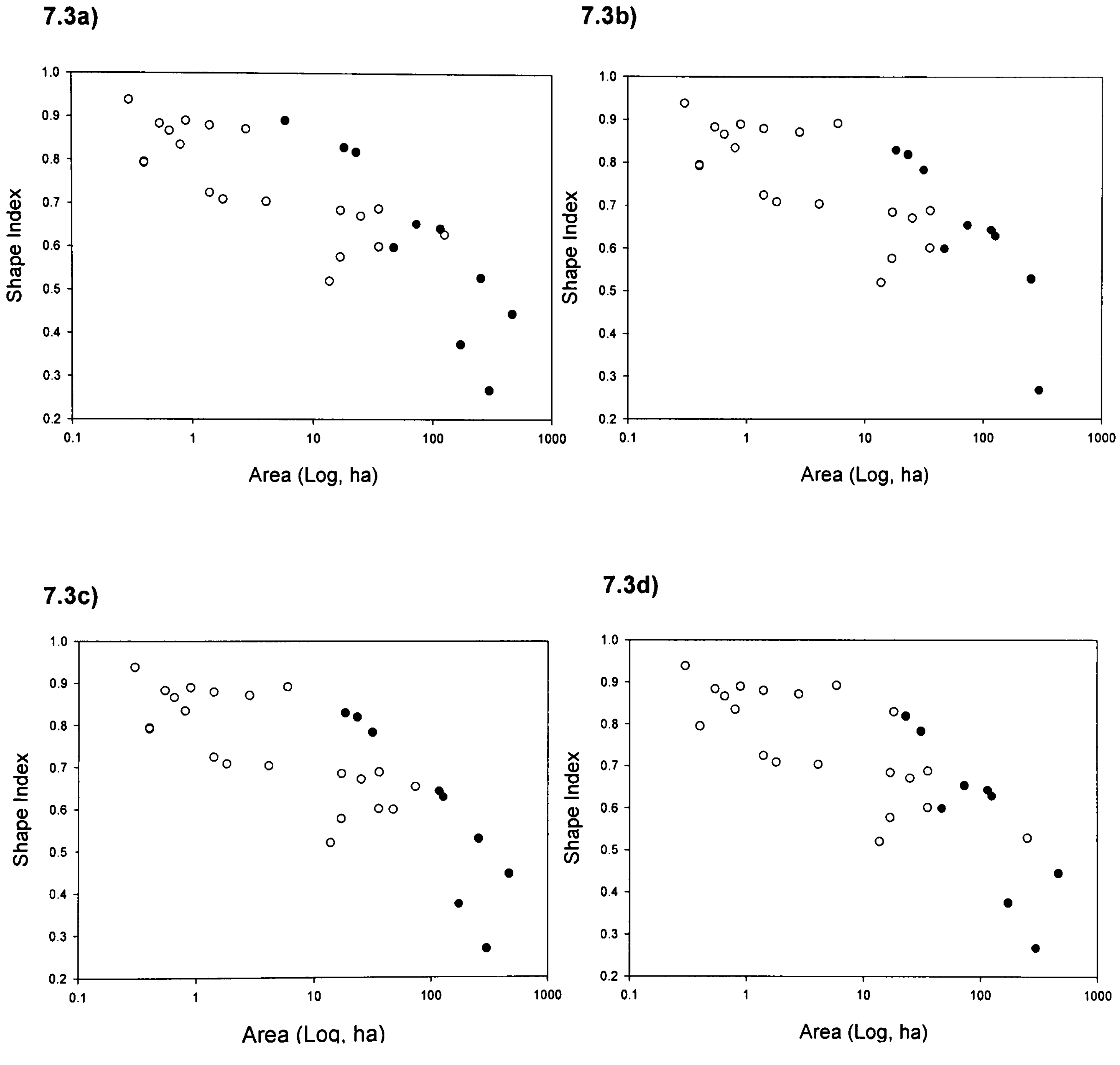


the landscape complexity metrics patch edge and patch density. However, the majority of the habitat generalist species displayed no general relationships with patch or landscape variables (Fig. 7.2b). Moreover, the CCA did not show any clear structure when life history traits were considered.

When individual landscape variables were considered in determining the probability of occurrence of individual species, remnant area explained a significant ($p<0.05$) portion of the deviance in the logistic models for 22 species (Appendix 4). All these species were classified as 'forest-dependent'. The minimum area requirements identified from each species' incidence function varied from 15 to 150 ha (Appendix 4). Remnant shape also explained a significant ($p<0.05$) portion of the deviance in the log/linear models for 12 species, all of which were classified as forest-dependent (Appendix 4). This was not surprising, considering that the variable 'remnant shape' was strongly correlated with the variable 'remnant area' (Table 7.2) and for most species this sensitivity was most likely an artifact of 'remnant area'. However, we discovered an interesting shape-area interaction for four forest-dependent species (ashy cuckoo-shrike *Coracina cineria* Müller, common newtonia *Newtonia brunneicauda* Newton, stripe-throated jery *Neomixis striatigula* Sharpe, Madagascar white-eye *Zosterops maderaspatana* L.) within littoral forests remnants, when the species presence/absence were considered graphically against both variables (Fig. 7.3). As opposed to the species that were solely area-sensitive, these species each occurred in remnants below 100 ha only when they were regular in shape; finally disappearing when remnants became too small for their existence (approximately 10 ha). This suggests that these four species are both area and shape sensitive. Finally, no isolation or landscape complexity measurement significantly ($p<0.05$) explained the deviance for any species (Appendix 4).

Figure 7.3 Presence or absence of a) ashy cuckoo-shrike *Coracina cinerea*, b) common newtonia *Netownia brunneicauda* c) stripe-throated jery *Neomixis striatigula* d) Madagascar white-eye *Zoesterops maderaspatana* in littoral forest remnants of different sizes and shape indices. See Table 7.1 for definitions of these measurements.

Closed circles indicate species presence and open circles indicate species absence within the littoral forest remnant.



Foraging guilds and body size distribution

In total, 38 species of insectivores were found in this study, including 21 forest-dependent species (Appendix 4). Seventeen forest-dependent insectivorous species had a significant ($p<0.05$) relationship with remnant size, including four (80%) terrestrial insectivores, three (75%) understorey insectivores and nine (90%) forest-dependent canopy insectivores (Table 7.4). Of the ten aerial insectivores, the Broad-billed Roller *Eurystomus glaucurus* Müller (the only forest dependent species within this functional group) was the only species that had a significant ($p<0.05$) relationship with remnant area. Remnant shape explained a significant ($p<0.05$) portion of the deviance in the logistic models for ten insectivorous species, all of which were forest dependent.

All five frugivores found within the study area were considered forest-dependent (Watson *et al.* in press b). Remnant area explained a significant ($p<0.05$) portion of the deviance in the logistic models for all large (Madagascar green pigeon, Madagascar blue pigeon *Alectronenas madagascariensis* L. and lesser vasa parrot) frugivores, and in two of these cases, remnant shape was also significant. Of the nine carnivorous species, only one species (Madagascar harrier hawk *Polyboroides radiatus* Scopoli) had a significant relationship with a patch or landscape metric, in this case, remnant area ($p<0.05$).

When body mass was considered in isolation, we found that approximately half the species in each weight category were forest-dependent; eight (53%) of the small species, nine (42%) of the medium-sized species and 11 (42%) of the large species (Table 7.4). We found that the small and large categories were more sensitive to remnant area and remnant shape. For example, eight (80%) of the large forest dependent species and seven (88%) of the small forest dependent species were affected by remnant area, while only four (44%) of the medium sized forest dependent species were affected.

Table 7.4 Summary of the number of area-sensitive species and shape-sensitive species in avifaunal functional groups and their minimum area ranges.

Guild association and size was determined using species accounts in Langrand (1990), Egushi *et al.* (1993), Wilmé (1996), Goodman *et al.* (1997), Morris & Hawkins (1998), Ravokatra *et al.* (2003) and Wilmé and Goodman (2003).

Species were determined area-sensitive if their probability of occurrence in littoral forest remnants was explained significantly ($p<0.05$) in a binomial logistic regression. As remnant shape was strongly correlated with remnant area, species were determined to be shape-sensitive by analysing their presence/absence distribution among littoral forest remnants graphically (Fig. 7.3).

Numbers in brackets are the total forest-dependent species in each foraging guild following Watson *et al.* (in press b).

Minimum area requirements for all area-sensitive species were determined using incidence functions calculated from logistic regressions models. An incidence of 50% in the logistic model was used to define the minimum area.

Foraging niche	Area	Shape	Minimum area range
Small (n=15)	**7 (7)**	**3 (3)**	
Terrestrial granivores (n=1 (0))	-	-	
Shrub insectivores (n=4 (3))	2(2)	1 (1)	25
Canopy insectivores (n=5 (4))	4(4)	2(2)	15-150
Canopy nectivores (n=2 (1))	1(1)	-	15
Canopy granivore (n=1 (0))	-	-	
Aerial insectivores (n=2 (0))	-	-	
Medium (n=19)	**5 (5)**	**1 (1)**	
Terrestrial insectivores (n=4 (1))	1(1)	-	
Terrestrial granivores (n=1 (0))	-	-	
Shrub insectivores (n=1 (1))	1(1)	-	110
Canopy insectivores (n=6 (5))	3(3)	1 (1)	15-150
Canopy frugivores (n=2 (2))	-	-	
Aerial insectivores (n=7 (0))	-	-	
Large (n= 24)	**10 (10)**	-	
Terrestrial insectivores (n=5 (4))	3(3)	-	150
Terrestrial granivores (n=4 (0))	-	-	
Shrub insectivores (n=1 (0))	-	-	
Canopy insectivores (n=2 (2))	2(2)	-	25-35
Canopy frugivores (n=3 (3))	3(3)	-	20-25
Canopy carnivores (n=1 (0))	-	-	
Aerial carnivores (n=7 (1))	1(1)	-	25
Sallying insectivores (n=1 (1))	1(1)	-	15

7.8 DISCUSSION

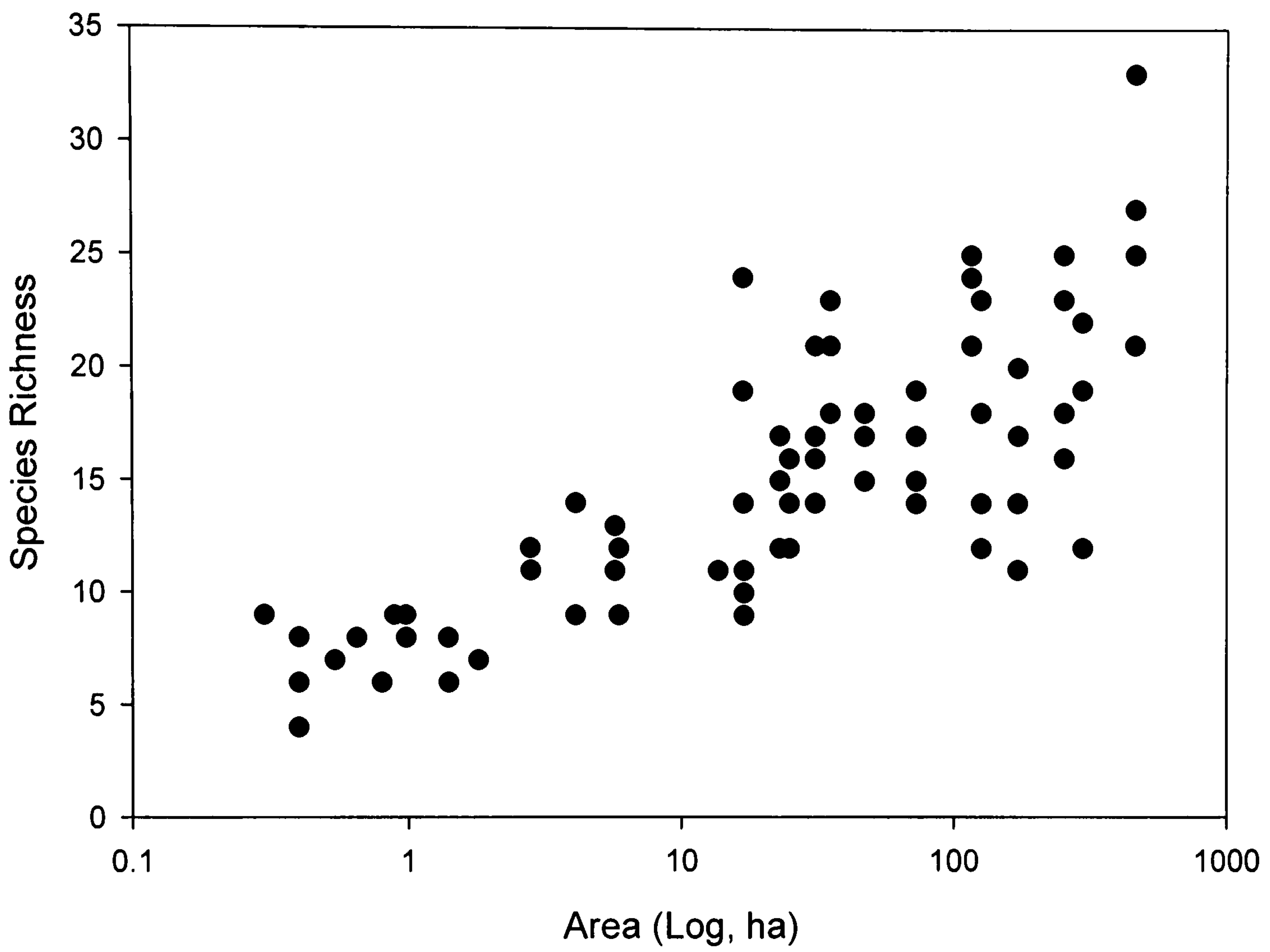
7.8.1 Avifauna of the littoral forests

Of 189 native land birds that occur in southeastern Madagascar (Goodman *et al.*, 1997), 70 were recorded within 30 littoral forests remnants in this study. This may seem a small proportion, but when forest-dependent species are considered, the littoral forests contained 55% of all forest-dependent species recorded within the region (Goodman *et al.* 1997; Watson *et al.*, in press a), a very high proportion considering that the littoral forests contain no species endemic to them and have a very limited altitudinal range. Both of these factors have been correlated with species richness elsewhere in Madagascar (Hawkins, 1999; Wilmé and Goodman, 2003). They also had three species (Madagascar sparrowhawk, Henst's goshawk and Madagascar crested ibis *Lophotibis cristata* Boddaert) that are considered 'near-threatened' (Birdlife International, 2000; Hawkins and Goodman, 2003). On this basis, the littoral forests are an important forest habitat for bird conservation in southeastern Madagascar.

7.8.2 The relationship between landscape metrics and bird species richness

We found that the size of littoral forest remnants played a very important role in determining species richness. This marked relationship between total species richness and forest-dependent species richness and remnant size was not unexpected (e.g. Opdam *et al.*, 1985; Hagan *et al.*, 1996; Watson *et al.*, 2001; Beier *et al.*, 2002; Santos *et al.*, 2002). There have been a number of explanations given why forest–dependent species numbers decrease with decreasing area. Connor & McCoy (1979) argue that the increase in species richness with increasing patch area may be due simply to the larger population of individuals found in large patches, i.e. the passive sampling hypothesis. Following Andrén (1994), we tested this hypothesis in our study area by using point counts of equal area from each remnant. As species richness per point count is highly correlated with remnant area, it is unlikely that birds are distributed through the littoral forest landscape according to the passive sampling hypothesis (Fig. 7.4).

Figure 7.4 Mean total bird species richness per point count per remnant versus area in the littoral forests of south-eastern Madagascar.



The more likely reason why the littoral forest system has a very strong species-area relationship is the lack of forest-dependent species found in small littoral forest remnants. We found that only one forest-dependent species occurred in remnants <10 ha in size, and many species needed remnant areas > 15 ha, (with some up to 150 ha) to have a probability of greater than 50% of occurrence within them (Appendix 4). The steepness of the slope in the species-area relationship (*z*=0.34) highlights the very low species richness in small remnants and suggests that species loss is occurring at a faster rate than in other fragmented tropical forests (e.g. *z*=0.15, Warburton 1997; *z*=0.15, Stratford & Stouffer, 1999; z=0.16, Langrand & Wilmé, 1997) and temperate forests (e.g. *z*=0.07, Wethered & Lawes, 2003). However, as there are no base-line data on the species richness of littoral forests before fragmentation, it is impossible to determine the extent of species loss in small littoral forest remnants. Other studies have shown that small remnants have insufficient resources to support a large number of species (Recher *et al.*, 1987), fewer adequate breeding microhabitats (Wilcove *et al.*, 1986), a higher degree of mesopredator release (Soulé *et al.*, 1988; Crooks & Soulé, 1999); and experience greater edge-effects, including increased predation and parasitism (Robinson *et al.*, 1995; Christiansen & Pitter, 1997; Villard, 1998). Bird populations in small littoral forest remnants could be suffering from any one of these processes and further study is needed to ascertain which processes are contributing to the small-island effect. However, the 'edge-effect' hypothesis appears to be supported for some species, evidenced by the apparent remnant shape-area interaction for four forest-dependent species (Fig. 7.3). These species only occurred in remnants that were more regular shaped, until the remnant was greater than approximately 100 ha in size.

We found that no measure of remnant isolation or landscape complexity was related to bird species richness in littoral forest remnants. The lack of an 'isolation' effect is contradictory to: (i) the equilibrium theory of island biogeography, which states that both remnant area and isolation are important in determining the number of species on a habitat island (MacArthur & Wilson, 1967); (ii) Andrén's (1994) assertion that remnant isolation assumes greater importance at higher levels of habitat loss and fragmentation; and (iii) the many studies which have shown that remnant isolation has an important influence on both numbers and occurrence of bird species in fragmented landscapes (e.g. Lynch & Whigham, 1984; McCollin, 1993; Hinsley *et al.*, 1995). There are several possible explanations for the relative lack of importance of isolation in our data. For instance, it may be that the bird species found in the study area are so mobile that they are not affected by isolation to the extent that other taxa are, and as such, immigration may not be an issue (Margules *et al.*, 1982; Ambuel & Temple, 1983). Those species that are not highly mobile may be able to disperse through the landscape matrix, again removing an isolation effect (Andrianarimisa *et al.*, 2000; Renjifo, 2001). As the dispersal capabilities of Madagascan birds are unknown, it is impossible to resolve this issue. The lack of an isolation effect in this study may not in fact be generalisable to Madagascan birds, as it may reflect the relatively limited range of isolation in the present study (cf. Whittaker, 2000).

The lack of a relationship between forest-dependent species richness and individual species distribution and landscape complexity is less surprising. The strong relationship between remnant area and individual forest-dependent species presence indicates that these species do not use a number of patches for their home-territory, i.e. their territorial range is solely within the forest remnant. Therefore the landscape composition surrounding a remnant will likely not affect the forest-dependent species living within them.

J.C. Ingram (unpublished data; and see Vincelette *et al.*, 2003) has undertaken an analysis of forest loss in the littoral forests of the Fort Dauphin region (Fig. 1.1) based on aerial photographic and satellite imagery. Her analyses show that these forests have undergone a gradual process of attrition but that the fragments involved in the present study have been relatively stable in form over the last 30 years. On this basis, we cannot assume that the bird communities have reached a dynamic equilibrium (MacArthur & Wilson, 1967; Diamond, 1975; Simberloff, 1992) across these landscapes, and even within the fragments themselves, thirty years is a comparatively short period in terms of forest dynamic processes that might in due course lead to further alterations in the carrying capacity for particular species (Bush & Whittaker, 1991; Whittaker, 1998). Therefore, if anything, our estimates of area effects may be conservative, as lagged species losses from smaller remnants can be expected to accrue over time (Brooks & Balmford, 1996; Robinson 1999).

7.8.3 The relationship between landscape metrics and functional group

Over 85% of forest-dependent insectivores had a significant relationship with the patch variable 'remnant area'. Other studies have also found that insectivores are particularly affected by habitat loss and fragmentation, with terrestrial and understorey insectivores being the most sensitive group (Karr, 1982; Kattan *et al.*, 1994; Canaday, 1996; Langrand and Wilmé, 1997; Stratford & Stouffer, 1999; Beier *et al.*, 2002). It has been postulated that this foraging guild is particularly sensitive to fragmentation events because the process changes micro-climate within forests, which in turn affects foraging substrates (Johns, 1997). We found that 75% of large terrestrial insectivores had a significant ($p<0.05$) relationship with remnant area, but we were unable to find any small terrestrial insectivores within the littoral forests (Table 7.4). This is surprising considering that two terrestrial insectivorous species (white-throated oxylabes *Oxylabes madagascariensis* Brisson, Crossley's babbler *Mystacornis crossleyi* Grandidier) are found commonly in the rain forests just to the east of the littoral forests and other species that inhabit these rain forests are found within littoral forests (Goodman *et al.*, 1997; Watson *et al.*, in press a, b). One possibility is that smaller terrestrial insectivores once did occur in littoral forest remnants and have become locally extinct. Interestingly, we found that canopy insectivores were the most area sensitive foraging guild, with nine (90%) forest-dependent species having minimum area requirements >20 ha.

The three large forest-dependent frugivore species were each found to be sensitive to remnant area. Frugivorous species have been found to be affected by forest loss in other tropical areas (Guindon, 1996; Price *et al.*, 1999; Pattanavibool & Dearden, 2002) and reasons for this include a loss of connectivity between foraging areas, which may severely restrict access to a year-round food supply for frugivorous species, and a loss of large trees, which affects reproductive success in species that use hollows. However, as no measure of remnant isolation or landscape complexity appeared to affect the distribution of these species, it is more likely that these species were area-sensitive due to a lack of fruiting trees in smaller littoral forest remnants.

We found that there was little relationship between minimum area requirements of littoral forest bird species and body mass (Appendix 4; Table 7.4). This is surprising considering the well-known correlation between body size and home range (e.g. Belovsky, 1987; Mysterud *et al.*, 2001) and that other studies have found body mass to be a very good indicator for species vulnerability to fragmentation, especially to remnant area reduction (e.g. Recher *et al.*, 1987; Beier *et al.*, 2002). Moreover, our study showed no general relationship between similar life-history traits of bird species and minimum area requirements (cf Davies *et al.*, 2000; Fagan *et al.*, 2001; Table 7.4). Our work suggests that body size or life-history traits alone will not be enough to predict area requirements precisely for littoral forest dependent bird species. The requirements of each bird species have to be considered independently to determine suitable conservation strategies.

7.8.4 Conservation implications

The most conspicuous outcome related to bird conservation is the poor capability of small littoral forest patches to maintain forest-dependent bird species. We found that 76% of the forest-dependent species assessed had a statistically significant relationship with remnant area. A further 12 forest-dependent species, removed from the individual and community analyses due to their rarity, were found solely in the very largest littoral forest remnants. If our results turn out to be indicative of how Madagascan bird species are coping with fragmentation in other forested habitats, then a whole suite of species that are considered either 'common' or 'widespread' may become threatened by ongoing processes of forest fragmentation and loss. These processes are occurring throughout the island at an alarming pace (Smith, 1997; Kull, 2002). When functional groups are considered, large frugivores and all insectivores were found to be prone to landscape fragmentation effects. A loss of certain functional groups, such as insectivores and frugivores, could have serious implications for a forest ecosystem, inhibiting important functions such as pollination or dispersal of seeds from occurring, and altering the structure and form of food chains (Terborgh, 1986; Bierregaard and Lovejoy, 1989; Bollen, *et al.* submitted). We urge that more research be conducted in Madagascar on processes associated with habitat fragmentation to test the generality of our results.

On a regional scale, our findings suggest that approximately 60% of forest dependent bird species will be absent from a reserve system composed solely of small patches of less than about 10-20 ha. To preserve the existing forest-dependent bird community, we recommend that as much continuous forest be conserved as soon as possible and, if this not possible, we recommend the protection of a number of large core littoral forest areas in Mandena, Ste-Luce and Petriky (>200ha). As remnant shape also played an important role in explaining the presence/absence of a number of forest-dependent species when remnants were <100 ha (Fig. 7.3), we suggest that where possible, reserves should minimize perimeter to area ratios. Even though our results indicate that remnant isolation and landscape complexity are having little effect on the distribution of forest-dependent birds within the littoral forest system, we strongly encourage matrix management as part of an overall conservation strategy. This includes both the maintenance of connectivity between littoral forest remnants and the maintenance of landscape heterogeneity within the fragmented littoral forest landscape. Connectivity within the landscape will influence processes such as population persistence and recovery, the exchange of individuals and genes between isolates, and the occupancy of habitat patches, and thereby reduce the impacts of habitat fragmentation on sensitive bird species (Lindenmayer & Franklin, 2002). The maintenance of landscape heterogeneity will lead to the conservation of greater species diversity, as it may provide the particular environments required by habitat-specialist species.

We must emphasize that we do not write off small littoral forest patches as having no value in this system. Although small littoral forest patches do not contain many forest dependent bird species, such patches may harbour many species of native plants, insects, birds and mammals that could provide important 'ecosystem services' in both the littoral forests and surrounding matrix. For example, they could harbour common species that are pollinators and seed dispersers for littoral forest trees (Beier *et al.*, 2002; Bollen *et al.* submitted). In addition to this, the absence of a bird species from a small remnant does not mean that that the remnant is not used by the species when moving through the landscape. Because only one movement per generation may be sufficient to prevent inbreeding (Mills & Allendorf, 1996), movement events that have a low probability of detection still have a great biological significance. Small remnants could be acting as stepping stones for species between larger littoral forest remnants or between nearby lowland humid forest and the littoral forest (Matlock *et al.*, 2002).

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CHAPTER 8

CONSERVATION OF BIRD DIVERSITY IN MADAGASCAR'S SOUTHEASTERN LITTORAL FORESTS

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8.1 ABSTRACT

The littoral forests of southeastern Madagascar are relatively unexplored ecosystems that are considered severely threatened by habitat fragmentation and degradation. In this chapter, the bird communities inhabiting the littoral forest remnants of three different sub-regions are described. Processes associated with habitat fragmentation and degradation were assessed to determine how they affected the bird communities inhabiting these forests. In total, using a standardized sampling system, I found 77 bird species in 31 littoral forest remnants. Of these 61 were endemic to the island or to the Indian Ocean sub-region consisting of Madagascar, the Comoros and the Mascarenes. In comparison, the matrix habitats surrounding the littoral forests were depauperate of species, with the *Erica* spp. heathland containing 29 species, and *Eucalyptus* and *Melaleuca* forest patches containing 22 and 23 species, respectively. At the patch-scale, 31 species were found to be edge-sensitive, and nine species were affected by changes in habitat complexity and

vegetation structure at core or edge point counts. At the landscape scale, 20 species were affected by remnant size, and four species were affected by remnant shape. No species appeared to be affected by any measure of isolation. I encourage a multi-faceted approach to conservation and management of these forests, and recommend that (1) as much littoral forest be formally protected as possible in each of three sub-types, (2) preserving the largest littoral forest remnants be a priority, (3) efforts should be made on planting and restoring the native vegetation in and around remnants, and (4) special efforts should be made to make the smaller remnants more compact. I do not encourage a fortress-style conservation scenario where local people are excluded from their forests. Although our results indicate that some species are threatened by habitat degradation and fragmentation, there is no evidence that the local people's activities are to blame.

8.2 INTRODUCTION

Because of its size, climate and long history of separation from a continental landmass, Madagascar has exceptional concentrations of endemic species. The flora of Madagascar is one of the richest in the world in proportion to its area (Dumetz 1999) while endemism exceeds 90% for mammals, reptiles and amphibians (Groombridge 1992; Garbutt 1999). Due to high estimates of deforestation (Green and Sussman 1990; Du Puy and Moat, 1996; Smith, 1997), Madagascar now receives considerable attention as a high priority for global biodiversity protection (Mittermeier *et al.* 1998; Myers *et al.* 2000). However, only 3 % of the island has protected status (Godfrey *et al.* 1997) and as Madagascar is one of the poorest countries in the world with high population growth, pressure on remaining forests is increasing (Smith *et al.* 1997). Activities such as slash and burn agriculture, wood harvesting and charcoal production are widespread on the island, meaning that the large proportion of the island's forests that are unprotected are threatened by habitat fragmentation and degradation (Goodman *et al.* 1997).

The enormity of deforestation and degradation forests in Madagascar is paralleled only by our ignorance about the way these processes affect Madagascar's biodiversity (Goodman and Benstead, 2003). Many recent studies have documented the distribution of species on the island (e.g. Goodman, 1993; Goodman and Putnam, 1996). To develop sound and practical strategies to restore and conserve biodiversity in Madagascar's degraded and fragmented landscapes, we need to know more than the number of species that occur within them (Pimm *et al.* 1995). Processes associated with habitat degradation and fragmentation are complex and many issues must be individually and collectively understood for effective conservation action to take place (Bierregaard *et al.* 2001). Therefore, when conducting conservation related studies, researchers need to ask a multiplicity of questions at different spatial scales, to adequately formulate appropriate conservation strategies (Lindenmayer and Franklin 2002).

In this study I use a multi-scale approach to examine the effects of habitat degradation and fragmentation on bird communities in the threatened littoral forests of southeastern Madagascar. I present the current understandings of what bird species occur in littoral forests of southeastern Madagascar, and reveal the way in which processes associated with habitat fragmentation (specifically the creation of habitat edges, the reduction and isolation of littoral forest remnants, the changing of remnant shape and the role of the surrounding matrix) and habitat degradation affect these bird communities. It must be noted that this paper is partly a summation of results that have been published (Watson *et al.* in press a, b, c) and partly additional analysis. In the conclusion, I use the results of this research to devise a comprehensive conservation strategy for bird conservation in littoral forests.

8.3 MATERIALS AND METHODS

8.3.1 Bird Surveys

The MacKinnon list census technique (MacKinnon and Phillips 1993), with 10-species species lists was used to determine the species composition of littoral forest remnants in each of the three sub-types. This method has been promoted as a suitable, rapid assessment technique for determining bird species communities in habitats that are relatively unknown and when rapid assessment is necessary (see O'Dea *et al.* 2004 for a critical review of this methodology). Fourteen littoral forest remnants > 17 ha in size between November and December 2001 and 31 remnants in October and November 2002 were surveyed using this technique (Table 8.1). In order to determine if littoral forest bird communities differed from other habitats in the study area, three *Eucalyptus* plantations and five *Melaleuca* forest patches that immediately surrounded littoral forest remnants within Mandena were also surveyed using MacKinnon lists. Due to the difficulty of finding discrete patches of *Erica* vegetation (as it dominated the study area), an area limit of approximately 1 km^2 was used when surveying birds within the *Erica* vegetation, with each surveyed area separated by a distance of at least 1 km. Five surveys were conducted in this way.

A point count sampling strategy was employed to determine how patch characteristics and landscape fragmentation affected bird composition (Table 8.1). A total of 90 point count stations were placed in 30 littoral forest remnants of varying sizes in the sub-types of Mandena and Ste-Luce. Point counts were carried out during November and December 2001 and in October and November 2002. Selection of remnants for sampling was constrained by the difficulty of obtaining permission to survey birds on privately held land and by the number of remnants available within each sub-type. Following other similar studies (e.g. Helzer and Jelinski 1999; Saab 1999), the number of point count stations varied depending on the area of the remnant: one station in remnants < 1 ha; two stations in remnants of 1-10 ha; three for 10-20 ha remnants; four for 20-40 ha remnants; and five for remnants > 40 ha.

In order to assess how birds respond to the forest edge 20 littoral forest edge sites and 20 littoral forest core habitats were surveyed using point counts in October and November 2002. All core sites were located in two large forest blocks, known as S8 and S9, and all edge sites were located on their edges (10 on each). Core habitats were defined as forest areas 300 m from the edge of the forest remnant.

For the point counts, birds occurring within 25-m fixed-radius of each station were recorded because it was often not possible to identify species past this distance. Each station was located at least 100 m apart to minimize the risk of counting the same individual twice. Each station was visited twice. To reduce time-of-day effects, the order in which sites were sampled was reversed each week. For each surveying period, the author undertook training to estimate distances to the site and sound of the bird and to become familiar with the bird species of the study area, before conducting point counts. Ten minutes were spent at each station. Surveys were confined to the periods 0600 – 1000 hr and 1500 – 1900 hr on days without rain or strong wind.

8.3.2 Habitat surveys

Vegetation structure and density was visually estimated using eight categories (variables) to define the structure and numbers of trees of differing size (Table 6.1). Four represented vegetation vertical structure (low shrub cover, medium shrub cover, tall shrub cover and canopy cover) and two represented vegetation density (number of small trees and number of large trees). Two other measures (percentage litter cover and the maximum height of vegetation) were chosen to give a measure of how complex the forest habitat was. These eight categories were chosen to represent a wide range of vertical structure, tree density and habitat complexity measurements, all of which are affected when a habitat is degraded by human activity, such as fire wood collection

Table 8.1 Geographic data, species richness and number of endemic species per littoral forest remnant. The number of species found in one-sub type was defined as the species restricted to found only in Mandena, Ste-Luce or Petriky.

Remnant name	Sub-type	Lat/Long	Area (ha)	Species number	Number of regional endemics	Number of island endemics	Number of species found in one sub-type
M1	Mandena	24° 45′ 01″ S 47° 10′ 55″ E	126	42	15	19	
M4	Mandena	24° 57′ 37″ S 47° 01′ 01″ E	47	30	10	12	
M5	Mandena	24° 56′ 49″ S 47° 06′ 17″ E	25	25	8	9	
M6	Mandena	24° 56′ 07″ S 47° 01′ 51″ E	17	21	9	5	
M7	Mandena	24° 56′ 57″ S 47° 01′ 33″ E	13.7	15	6	4	
M15	Mandena	24° 58′ 01″ S 47° 00′ 33″ E	116	45	17	19	1
M16	Mandena	24° 59′ 21″ S 46° 59′ 51″ E	73	33	14	12	
M20	Mandena	24° 57′ 14″ S 47° 04′ 23″ E	23	19	8	6	
MA	Mandena	24° 56′ 36″ S 47° 01′ 02″ E	0.8	7	2	2	
MB	Mandena	24° 56′ 52″ S 47° 00′ 21″ E	0.4	8	3	2	
MC	Mandena	24° 56′ 32″ S 47° 00′ 52″ E	0.9	11	4	3	
MD	Mandena	24° 56′ 20″ S 47° 02′ 16″ E	2.8	13	6	3	
ME	Mandena	24° 58′ 01″ S 46° 59′ 33″ E	5.9	14	6	4	
MF	Mandena	24° 56′ 17″ S 47° 00′ 48″ E	1.8	9	2	3	
MG	Mandena	24° 58′ 02″ S 46° 59′ 09″ E	4.1	16	7	3	
P1	Petriky	25° 04′ 31″ S 46° 53′ 10″ E	855	53	16	25	4
S1	Ste-Luce	24° 43′ 07″ S 47° 11′ 08″ E	31	28	12	9	1
S7	Ste-Luce	24° 47′ 17″ S 47° 09′ 12″ E	254	42	15	20	7
S8	Ste-Luce	24° 46′ 12″ S 47° 09′ 09″ E	172	44	15	17	8
S9	Ste-Luce	24° 45′ 39″ S 47° 10′ 19″ E	464	58	17	30	10
S10	Ste-Luce	24° 44′ 22″ S 47° 11′ 51″ E	17	28	11	12	
S11	Ste-Luce	24° 44′ 20″ S 47° 10′ 44″ E	35.3	36	11	18	4
SH	Ste-Luce	24° 46′ 41″ S 47° 09′ 47″ E	0.4	10	1	3	
S17 (S6)	Ste-Luce	24° 48′ 43″ S 47° 08′ 31″ E	297	46	17	21	6
SA (S13)	Ste-Luce	24° 46′ 01″ S 47° 09′ 49″ E	0.4	9	3	3	
SB (S14)	Ste-Luce	24° 46′ 41″ S 47° 09′ 55″ E	1.4	9	4	2	
SC (S1)	Ste-Luce	24° 48′ 55″ S 47° 08′ 46″ E	5.7	16	5	6	1
SD (S2)	Ste-Luce	24° 46′ 14″ S 47° 09′ 35″ E	1	12	4	3	1
SE (S3)	Ste-Luce	24° 46′ 57″ S 47° 08′ 46″ E	0.5	10	3	5	
SF (S4)	Ste-Luce	24° 46′ 51″ S 47° 08′ 52″ E	1.4	9	3	2	
SG (S5)	Ste-Luce	24° 47′ 01″ S 47° 08′ 51″ E	0.7	8	1	2	

(Cadotte *et al.* 2002; Vallan 2002; Ingram *et al.* submitted). These data were collected at every point count station, with the same perimeter (i.e. 25 m radius) used for the bird sampling.

8.3.3 Patch and landscape structure data

Eight parameters were selected to describe the landscape at the patch and landscape scale: area of each remnant (AR), distance to nearest large block of forest (DS), distance to the nearest remnant > 100 ha (DR), distance to nearest remnant (DRN), area of nearest remnant (ANR), a littoral forest remnant shape index (SI), patch density (PD) and edge density (ED) (Wiens, 2002; Table 7.1). Formulas for patch density and edge density were calculated are given in Table 7.1. All eight patch and landscape mosaic variables were determined from a supervised classified Landsat TM satellite image acquired on 11 November 1999 using ArcView GIS software.

8.3.4 Analysis

A step-wise regression analysis (holding P to enter =0.05 and P to remove =0.1) was used to explore the relationships of species richness (dependent variable) with the patch and landscape mosiac variables recorded for each fragment in order to build the best predictive model for each richness value. When analysing patterns of species richness in fragments of differing size it is difficult to eliminate the effects of decreasing sampling area; both fragmentation and decreasing sampling area should result in decreasing species richness (Stratford and Stouffer 1999). To overcome this problem, an average was taken for species richness per point count per remnant. The variables 'area', 'area of the nearest remnant' and 'distance to the nearest remnant > 100 ha' were logarithmically transformed while the parameter 'distance to nearest remnant' was square-root transformed prior to analyses (Sokal and Rohlf 1981; Table 7.1). As multicolinearity was found between the two independent variables 'shape' and 'area', the variable 'shape' was removed from the step-wise, as it explained less of the variance in both analyses (Soulé *et al.* 1988).

I used several procedures to compare bird species abundance and species richness among the three landscape elements. I conducted two analyses of variance (ANOVA) to compare the total number of individuals and species richness by landscape element. These analyses allowed me to detect differences among the three landscape elements and to determine whether the differences were consistent across time. Species accumulation curves were also generated for each element, in the order in which the censuses were conducted. Following Beier et al. (2002), I evaluated the difference in bird species abundance between edge and core point counts using paired *t*-tests using SPSS software (Kinnear and Gray, 2000). Bird abundance data per point count were logarithmically transformed prior to the analysis to improve the normality of the data (Kent and Coker, 1992; Dytham, 1999). I analysed only those species that were found in both landscape elements (i.e. core habitat and edge habitat). This allowed us to determine which species were edge-tolerant, edge-preferring and edge-sensitive.

I used paired *t*-tests to assess the difference between the means of each habitat variable between core and edge sites. The habitat variables that were measured using percentage values (i.e. maximum vegetation height, canopy cover, litter cover, low shrub cover, medium shrub cover, tall shrub cover) were transformed using the arcsine root formula prior to the analysis, to improve the normality of the data.

In order to understand how habitat degradation affected bird species distribution between landscape elements, I used a logistic step-wise regression procedure to examine how individual species distribution (i.e. presence/absence) corresponded with habitat variables at core and edge point counts. Colinearity was found to exist between the habitat variables 'canopy cover' and 'height of vegetation', when an r-value = 80 was used as the cut-off (Soulé *et al.*, 1988; Kent and Coker, 1992; Pisces Conservation, 2002). I therefore removed height of vegetation from the step-wise regression analysis as it explained less of the variance when considered independently. These statistics were calculated using SPSS software (Kinnear and Gray, 2000).

8.4 RESULTS

8.4.1 Bird diversity in the littoral forests

In total, these surveys found 77 species inhabiting 31 littoral forest remnants (Table 8.1). This included 17 species that were not found by Goodman *et al.*'s (1997) survey of the littoral forests in 1990 (Watson *et al.* in press a). The forests have no unique species[1] but contained 57% of all the island's and region's endemic species, including three threatened bird species (Birdlife International, 2000). Moreover, the littoral forests contained a unusual bird assemblage when compared to neighbouring humid and spiny forest sites. It appears that the littoral forests are playing an important regional role in determining the overall range distributions of many bird species within the region as a number of species considered habitat-restricted by Langrand (1990), either to spiny forest species (e.g. Giant Coua, Crested Coua, Lantz's Brush-Warbler, Archbold's Newtonia) or humid forest (e.g., Red-fronted Coua, Blue Coua, Green Jery, Madagascar White-eye, Rufous Vanga, Tylas Vanga, Forest Fody) occurred in littoral forests remnants. These habitat-restricted endemics, by definition, should occur within a certain habitat type yet they were found together within the same littoral forest remnants.

The location of littoral forest remnants was an important determinant in what species occurred within them. For example, 14 species were found solely within the Ste-Luce littoral forests

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[1] The taxonomic status of Archbold's Newtonia *Newtonia archboldi* inhabiting littoral forest fragments in Ste-Luce has yet to be verified (Watson and Ellis, in press). This species presence in the Ste-Luce littoral forests, and its slight differences in plumage compared to populations in the southern spiny forests, indicate that this population could be taxonomically distinct.

remnants and four species were found solely found in the Petriky Forest (Appendix). Of the 14 species solely found in Ste-Luce littoral forests, seven are considered humid forest dependent. This humid forest influence could be a result of the northerly location of these remnants or the close proximity to the humid forests of the Vohimena Ranges. However, the Ste-Luce remnants also contained a number of spiny forest species (e.g. Giant Coua, Archbold's Newtonia). Interestingly, Archbold's Newtonia was found within the Ste-Luce littoral forests but not in the Petriky forest. This species has been described as being found only in the dry *Didierea* forests of Madagascar's southern domain (Morris and Hawkins, 1998).

An important finding in our overall surveys, was the depauperate nature of the matrix habitats surrounding littoral forest remnants. The dominant matrix habitat (*Erica* heath) contained 29 species, with all species considered widespread in the region and on the island (Langrand 1990; Goodman *et al.* 1997; Morris and Hawkins 1998). This vegetation type did have four species (Kittlitz's Plover, Madagascar Snipe, Peregrine Falcon and Stonechat) that were not found in littoral forest remnants, but all prefer non-forested, open habitats. The three *Eucalyptus* plantations surveyed contained a total of 22 and the five *Melaleuca* forest patches had a total of 23 species, with all species found also in littoral forest remnants. The vast majority of species (n=48) in this study were found only in littoral forest habitat, and were classified as forest-dependent (see Watson *et al.* in press a) for further details).

8.4.2 The effect of habitat degradation

I found that there was variation in the vegetation density, habitat vertical structure and habitat complexity between core and edge sampling stations. On average, core habitats had significantly ($p<0.01$) higher density of large trees, a higher maximum height of vegetation, more canopy cover and a higher percentage of litter cover. The edge habitats had significantly ($p<0.05$) higher amounts of low and medium shrub cover. Interestingly, I found that there was as much variation between habitat variables in point counts in the same remnant as there was between point counts in different remnants. This finding supports Ingram's (2004) findings that littoral forest remnants have high internal heterogeneity and that it is not appropriate to classify a littoral forest patch as being in a certain state or 'condition'.

The relationships between individual bird species presence and habitat structure were analysed separately for core point counts (Table 6.4) and edge point counts (Table 6.5). All species found in either landscape element were analysed independently to determine if their presence or absence within point counts could be explained, at least partially, by habitat variables. Therefore, 63 species were analysed in core sites (Table 6.4) and 44 species were analysed in edge sites (Table 6.5).

Habitat variables significantly ($p<0.05$) explained the distribution of seven species in core forest sampling stations (Table 6.4). Of these species, five were 'edge-avoiders', one was 'edge-tolerant', and one was 'ubiquitous' (section 3.2; Appendix). The edge-avoiding species had significant ($p<0.01$) relationships with the amount of canopy cover ($n=2$) and the percentage of litter cover ($n=2$), with one species (Archbold's Newtonia *Newtonia archboldi*) having a significant relationship with both low shrub cover and litter cover. The amount of low shrub cover ($n=2$) and the number of small trees ($n=1$) were the habitat variables that significantly ($p<0.01$) explained the variance of edge preferring and ubiquitous species, at the core stations, with one species being significantly ($p<0.01$) affected by both (Table 6.4).

Variance in presence/absence data of seven species within edge sampling sites was explained ($p<0.05$) by one or more habitat variables (Table 6.5). Four of these species were 'edge-sensitive', two were 'edge-tolerant' and one was considered 'ubiquitous' (section 3.2; Appendix). All four edge-sensitive species that were found to have a relationship with a habitat variable, were affected by canopy cover. One edge-tolerant species (Madagascar Brush Warbler *Nesillas typica*) was affected by both the amount of low shrub cover and number of small trees (Table 6.4), while the other (Long-billed Green Sunbird *Nectarinia notata*) was affected by the amount of tall shrub cover. The single significant model for a ubiquitous species (Madagascar Cisticola *Cisticola cherina*) was based on the amount of low shrub cover.

8.4.3 Edge effects

I observed a considerable edge-effect in the littoral forests, in terms of both species-richness and the individual number of birds. Sixty-two species were found within core littoral forest habitat while only 44 species were found within edge habitats. Numbers of species and individuals per point count differed between the two habitat types (repeated measures ANOVA: richness, $F_{2,57}$= 41.5, $p<0.01$; abundance, $F_{2,57}$=38.6, $p<0.01$). Based on their probability of occurrence in edge and core stations in univariate tests, I identified 30 species that are edge sensitive (Table 6.4; see Watson *et al.* (in press c) for further details).

8.4.4 The effect of habitat fragmentation at patch and landscape scales

When all landscape variables measured were considered in a step-wise regression model, only remnant area was a significant ($p<0.01$) factor that explained variation in both the total species and forest bird species richness. Variance in total and forest-dependent species richness accounted for by the other variables in the step-wise regression was negligible in each case. They were therefore not selected in either model.

When individual landscape variables were considered in determining the probability of occurrence of individual species, I found that remnant area explained a significant ($p<0.05$) portion of the deviance in the logistic models for 20 species (Appendix 4). The minimum area requirements identified from each species' incidence function varied from 15 to 150 ha (Table

7.4). This is most probably an underestimation of the species affected by remnant area reduction, as a further 12 species were removed from both individual analysis due to their rarity, were solely found in the very largest littoral forest remnants.

No isolation or landscape complexity measurement significantly ($p<0.05$) explained the deviance for any species. Remnant shape explained a significant ($p<0.05$) portion of the deviance in the log/linear models for 12 species but this was not surprising, considering that the variable 'remnant shape' was strongly correlated with the variable 'remnant area' and for most species this sensitivity was most likely an artifact of 'remnant area'. However, an interesting shape-area interaction was discovered for four forest-dependent species (ashy cuckoo-shrike *Coracina cineria*, common newtonia *Newtonia brunneicauda*, stripe-throated jery *Neomixis striatigula*, Madagascar white-eye *Zosterops maderaspatana*) within littoral forests remnants, when the species' presence/absence were considered graphically against both variables (Table 7.4; see Watson *et al.* (in press b). As opposed to the species that were solely area-sensitive, these species all only occurred only in regular shaped remnants when the remnants were below approximately 100 ha until the remnants became too small for their existence (approximately 10 ha). This suggests that these four species are both area and shape sensitive, as they were found to occur in irregular shape remnants only when they are greater than approximately 100 ha.

8.5 DISCUSSION

8.5.1 General findings

An important finding in this study was the high number of bird species found inhabiting littoral forest fragments. These littoral forests were once considered depauperate because of their low species diversity and richness (Goodman *et al.* 1997). The results of this study indicate (i) that the littoral forests have a distinct bird species composition compared to other forested habitats and (ii) though the fragments are relatively small and degraded, they are of national importance for bird conservation because they contain a high proportion of the national endemic species. Littoral forest should no longer be considered the poor cousins when compared to the other forest habitats in the region.

Another important finding is the clear relationship between bird species richness and individual abundance of some bird species with patch-scale factors such as vegetation structure and remnant edge, and landscape-scale factors such as remnant area, remnant shape and the geographic position of remnants in the landscape. In this study I could not show any causal link between degradation and habitat fragmentation and bird diversity reduction, as the base-line data was not available (cf McGarigal and Cushman 2002). However, these strong relationships suggest that processes associated with habitat degradation and fragmentation are affecting the distribution of many bird species. This, in turn, is affecting the species richness in littoral forest fragments. I predict that if the littoral forests are degraded and/or cleared at an unsustainable rate, there will be a large loss of forest-dependent bird species, eventuating in the homogenization of the littoral forest landscape. Apart from the obvious moral concerns that are associated with human-induced localized extinction, a loss of forest-dependent bird species may result in a change in the functioning of the littoral forest ecosystem. For example, the species lost could be important pollinators or seed dispersers within the littoral forest landscape (Bollen *et al.* submitted), or could play important roles in predator-prey interactions (Newton, 1998).

8.5.2 Strategies for bird conservation in the littoral forests

The multi-scale nature of this research has meant that I can consider a number of conservation scenarios. In recent years, a ‘bigger is better’ attitude toward reserve acquisition has held sway in the conservation community (Miller and Cale, 2000). One reason for this attitude is that larger reserves are likely to support more species than smaller reserves. If the goal is to maximize the number of native bird species in the littoral forests, large habitat remnants are the logical starting point for avian conservation efforts. These results indicate that most forest-dependent bird species occurring in the littoral forest landscape will be present in such remnants without the need to consider detailed information about degradation within the individual patch.

If our conservation goals were to conserve the bird diversity of Madagascar while also conserving the uniqueness of the littoral forest remnants, I argue that the remnants S9, S8, S17, S11, P1 and M15 be given the highest priority. These remnants had the highest species richness, highest numbers of regional and island endemics, and also the highest number of species found in one sub-type (Table 8.1). These remnants are 'irreplaceable' (Margules and Pressey, 2000) as they each contain a unique bird community on the island. However, there are a number of problems associated with a conservation scenario focused on just conserving these six remnants. With limited options and resources for reservation, a successful reserve network needs complementarity (Pressey *et al.* 1993) as one disaster could lead to local extinction of a unique bird community. Therefore, I would argue that the other large remnants in be placed in a form of network reserve. A second concern is that in southeastern Madagascar, large remnants are few in number and measured in hundreds, not thousands, of hectares. Some species may need very large remnants to survive and they may even require groups of remnants to satisfy their habitat needs or to ensure population-level persistence. Therefore, a landscape perspective is especially important, and an emphasis should be placed on conservation reserve networks and careful consideration given to the spatial arrangement and complementary of habitat fragments (Pressey *et al.* 1993). Larger remnants might represent core areas, but smaller remnants also have a key role to play and may be especially important in this context (Fischer and Lindenmayer 2002a).

As littoral forest remnant size decreases, I argue that details assume more importance. I found that remnant shape, location of edge and amount of habitat degradation affected the abundance of a number of forest-dependent bird species (Table 6.4; Table 6.5). Many of these affected species were found in remnants as small as 20 ha. As a remnant gets smaller, edge-effects and degradation will invariably play more of a role in species distribution within the landscape. Therefore, efforts need to be made to overcome over-exploitation of smaller littoral forest remnants. As most of the very small patches (e.g. 10 ha) in our study appeared to have few species within them one could argue that they should not be involved in an overall conservation strategy as they appear to have little conservation value. However, I argue that small littoral forest remnants should not be ignored. Small remnants have been proven to be useful stepping stones in other areas for bird dispersal (e.g. Potter 1990; Date *et al.* 1996; Law *et al.* 1999), butterfly dispersal (e.g. Neve *et al.* 1996; Schultz, 1998) and plant dispersal (e.g. Collingham and Huntley 2000) because only one movement per generation may be sufficient to prevent inbreeding (Mills & Allendorf, 1996; Matlock *et al.*, 2002). The number of small remnants in the landscape may be one reason why remnant isolation is not appearing to have an impact of littoral forest bird communities.

One conservation strategy that has begun to be implemented in this landscape is the creation of habitat corridors between littoral forest remnants[2] (QIT Madagascar Minerals 2001; Bollen 2002). There is good scientific reason to use habitat corridors as a conservation tool: they connect isolated fragments (Beier and Noss 1998). A habitat corridor may enhance plant and animal movement among patches and hence improve population viability (e.g. Haas 1995; Downes *et al.* 1997), as well as facilitate the pollination and seed dispersal (Wunderle 1997). In the littoral forest system, Bollen (2003: 143) encourages the use of corridors in this system for seed dispersal as 'seed of forest plant species will be dispersed at greater distances from their source through continuous forest than through open field or pasture, so corridors should ideally be contiguous with the native seed source'.

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[2] A corridor was created between the remnants M4 and M5 with 20% endemic plant species and 80% exotic plant species (Bollen, 2002).

Though I do not disagree with this contention, and, in fact, encourage any form of active regeneration in the region, I do urge caution in any emphasis placed on habitat corridors as a sole conservation solution. This current study found that the exotic plantations of *Eucalyptus* contained very few bird species and although there is no data available on how littoral forest species move through these plantations, the costs of having such a conservation strategy for birds is not known. Moreover, it has been found in other studies that corridors can encourage edge-adapted species which, in turn, can start to dominate the species the patches that the corridors connect (Yahner, 1988). Experimental and observational studies have shown a significantly greater level of predation and parasitism among edge-adapted species (e.g. Small and Hunter 1988; Yahner and Scott 1988; Major *et al.* 1999) and that some corridors simply act as conduits for invasives, predators, pests and diseases that otherwise would not have been spread (Hobbs, 1992). If corridors encourage the invasion of edge specialists into a remnant, it may negate any conservation value the corridor may have and lead to a loss of certain core species. Given the fact that remnant area significantly ($p<0.05$) affected the distribution of some 20 species, and 31 species appeared to be intolerant of forest edges (Appendix 3, 4), I believe that the current enthusiasm for creation of habitat corridors should not be at the expense of restoration and sympathetic management of littoral forest remnants. I encourage the practice of making the smaller remnants larger and more compact, by planting native vegetation around them, over the use of habitat corridors.

8.5.3 Conservation recommendations

A multi-faceted approach to conservation and management of the littoral forests is strongly encouraged. The adoption of multiple approaches is more likely to provide conditions needed by different species different parts of the landscape. More-over, a multi-faceted approach means if any one strategy is found to be ineffective, others will be in place that might better protect sensitive elements of biodiversity. This form of *risk-spreading* (sensu Lindenmayer and Franklin, 1997) in littoral forest management can only lead to a greater chance of conservation success.

The conservation recommendations that emerge from this research are:

1) As much continuous littoral forest should be formally protected as soon as possible.

2) All three littoral forest sub-types are important for bird diversity in the region and all three have different bird assemblages. I urge that large blocks of littoral forest in all three sub-types be protected.

3) Since littoral forests > 200 ha retain percentages greater than 95% of the species pool of the forests, preserving large littoral forests should be a priority. These large littoral forest remnants are vital for conservation of littoral forest bird communities.

4) Edge effects and remnant shape affect the distribution of a number of forest-dependent bird species. Efforts should be made to make linear or irregular shape remnants more compact by planting indigenous trees on the edges of remnants and through forest restoration management. I would also argue, the larger, more circular remnants should be given priority when choosing which remnant to protect.

5) Even though very small remnants appear to not hold much significant conservation value, I encourage the restoration and conservation of these remnants. These remnants increase the connectivity within the landscape matrix and may provide homes for important keystone species for littoral forests.

6) Further to 4) and 5), efforts should be placed on planting and restoring the native vegetation in and around littoral forest remnants. I argue that these efforts should replace the current efforts of planting non-native plantations in the matrix surrounding the littoral forest remnants.

7) Since a number of habitat variables (litter cover, canopy cover) associated with forest complexity positively affect the presence in fragments of a number of forest-dependent species, management of degradation by preventing or reducing severe human impacts (tavy farming, firewood collection) should be regarded as a complementary measure. However, it must be noted that even though I found a number of species associated with canopy cover and litter cover, I also found species that had positive relationships with less canopy cover, and more shrub cover. As such, I believe that natural disturbance and non over-exploitive human use of the forest may also have a positive effect on bird biodiversity within littoral forest remnants.

8) Maintenance of landscape heterogeneity is important. The natural littoral forest landscape is not homogenous (Ingram 2004), as it comprises a mosaic of patches representing different forest composition and age classes where different structural conditions occur, as well as patches of *marécage* swamp vegetation and abutting aquatic wetlands within them. Maintaining the landscape heterogeneity will also aid in preserving the integrity of the aquatic ecosystem. Given the fundamental importance of the aquatic ecosystem to the human societies surrounding the littoral forests, this should be one of the chief objectives in the management of littoral forest communities.

8.6 CONCLUSION

The littoral forest vegetation in southeastern Madagascar does not have any formal protection. They contain no bird species unique to them, and bird species richness is low compared to other habitats on the island (e.g. high montane humid forests, Hawkins, 1999). Although recognized by

Dumetz (1999) and Ganzhorn *et al.* (2001) as one of the most threatened ecosystems in Madagascar, they are often ignored by the wider scientific and NGO communities. This research has shown that the littoral forests contain bird communities found nowhere else in Madagascar and have threatened bird species inhabiting them, and as such, have a conservation value in their own right.

The future of avian diversity in the littoral forests depends not only our ability to establish and manage a network of remnants, but also on the cooperation of local people who utilize the forests for their day to day needs (Ingram *et al.* submitted a). Ultimately, for conservation to succeed, there must be incentives for rural villages to maintain or increase the habitat value of remnant vegetation. I agree with Bollen's (2002) assertion that the greatest chance of conservation success in the region is to develop an integrated approach combining research, conservation and development aid in the region. Eco-tourism could be one approach. The region, especially the northern region, has beautiful beaches, fishing, swimming, diving, a wide range of charismatic mammals, and of course, some beautiful birds. Sharing revenues from forest entrance fees may be one way to fully distribute benefits from tourism to local villages. This could also facilitate the training of locals in guiding and running small tourist ventures. Other economic opportunities should be offered to locals if management plans are to be taken seriously in these forests. QMM have proposed butterfly farming, and implemented small scale fish farming and bee keeping as other economic opportunities (Bollen, 2002). Another possibility of diminishing degradation and local impact on the forest is to offer alternative materials for fishing equipment (e.g. synthetics).

As the majority of Madagascar's human population lives below the poverty line, conservation of the forest's unique biodiversity may be considered to be a luxury. If we ignore possible future mining actions, the greatest threat to the littoral forests is an increase in degradation and fragmentation of littoral forest remnants, due to increased human pressure (Cincotta, *et al.*, 2000).

Our research does not show that current human activity in the forests is detrimental to bird conservation at the moment and I do not encourage fortress style conservation management of the forests. Humans are just another taxa that use and inhabit these forests (Ingram *et al.*, submitted), and they have successfully managed and lived among the littoral forests for a very long time. There is no evidence that the forests have become fragmented or have been over-exploited by local people in the region.[3] It is clear that with an increasing population, there is more chance of people using the forest, especially in terms of collecting wood. Therefore, there is an urgent need for alternative resources necessary to provide the people with fuel, construction and tool wood. A possible solution is the establishment of plantations of fast-growing non-invasive species (Bollen, 2002).

Although this study was able to demonstrate that a large number of species' distributions had significant relationships with landscape components such as remnant area and habitat complexity, our research had some limitations. This research addressed only the pattern of bird distribution across the landscape and has not provided any new data on process. For example, I was unable to assess for what purpose habitat patches (in particular small patches) were used by various bird species, and if their usage changed through space and time. The presence of birds in a particular remnant does not mean that the sub-population is viable, nor does it mean that the particular remnant is making a positive contribution to the metapopulation (Donovan *et al.* 1995; Lens *et al.* 2002). More auto-ecological studies should be conducted to understand minimum viable populations within this landscape. Such data will be necessary considering the current mining plans in the region. In addition to this, it is important to determine how different bird species use the matrix habitats, as well as small littoral forest remnants in the matrix, and which habitats are the most suitable for species dispersing through them (following Ramanamanjato and Ganzhorn's

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[3] The only evidence of littoral forest fragmentation in the past 50 years is from the remnant known locally as M3. Charcoalers have devastated this remnant in the past five years. It is now established that these charcoalers are not local people but Antandroy migrants from the southern Androy region.

(2001) research). This type of research would be directly applicable to the reforestation guidelines suggested in this research, as it would assess both the possible effects of creating natural buffer zones around littoral forest remnants and the benefits of having corridors linking remaining forest fragments.

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CHAPTER 9

THE AUSTRALIAN CASE STUDY

9.1 Introduction

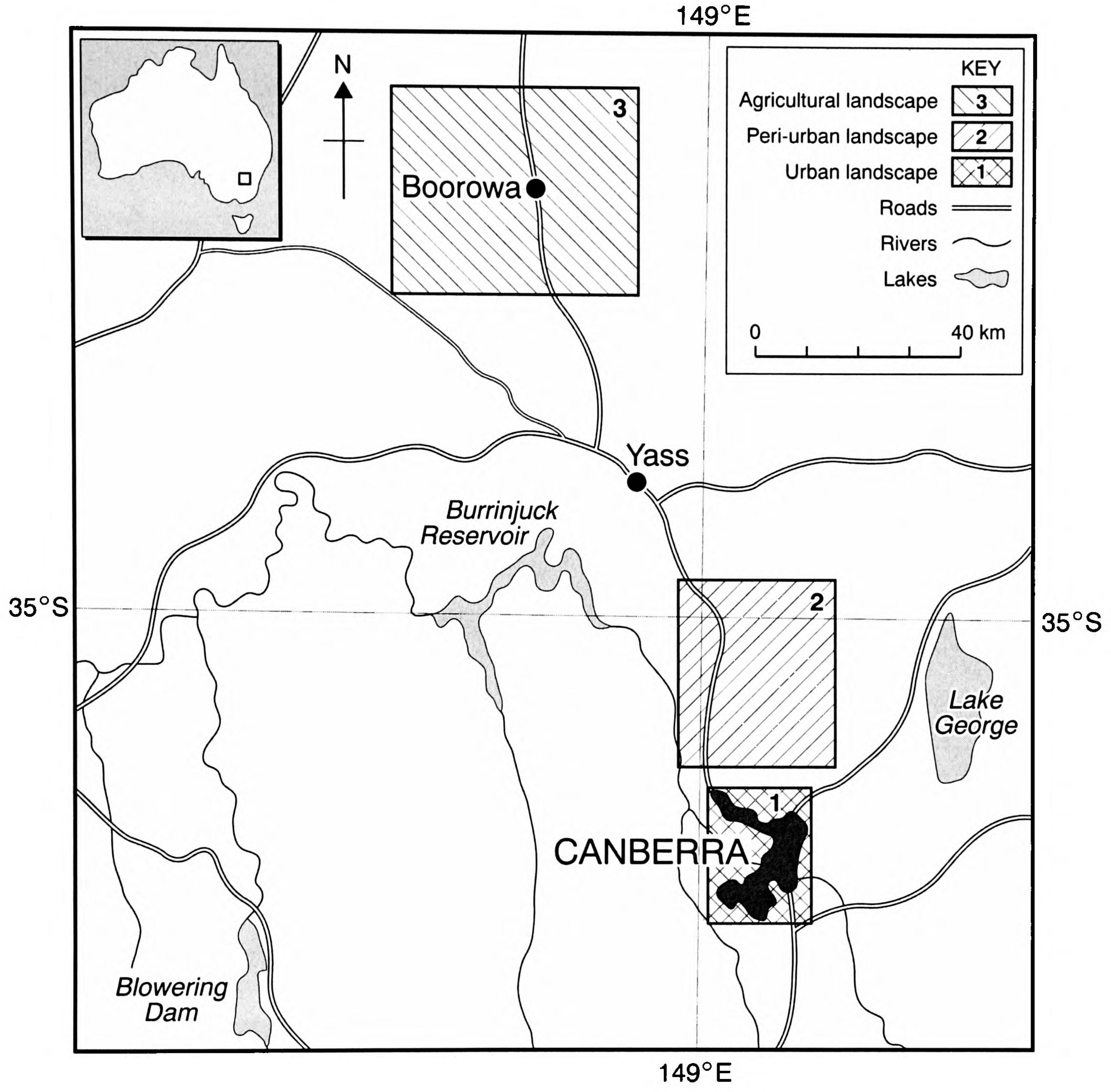
One of the main objectives of this thesis is to assess the effects of habitat fragmentation on birds in the woodlands of southeastern Australia. The aim of this chapter is to describe this region in more detail, and explore the relevant ecological research that has been conducted within these fragmented woodland landscapes.

9.2 The woodlands of southeastern Australia

Figure 9.1 shows that the study area is located within the northern ACT and bordering areas of NSW. Lowlands and forested mountain slopes are the two distinct landforms within the study area. The lowlands are made up of undulating hills and the floodplains of the Murrumbidgee, Molonglo and Boorowa Rivers. The city of Canberra (with a population of approximately 293 000) is the major urban area within the region and is located within the lowlands (ACT Government, 1998). To the immediate south and west of Canberra are forested mountain slopes rising to an altitude of 1900 m. The extent of forested mountains within the study area is insignificant.

The region has a temperate climate that is characterised by hot summers and cold winters, with altitude moderating summer temperatures and lowering winter temperatures. There are five meteorological recording stations located in the study area: Canberra City (35° 27′ S, 149° 12 ′E), Canberra Communications Solar Observatory (35° 30′ S, 149° 00′ E), Acton (35 °31′ S, 149° 2′ E), Duntroon Military College (35° 3′ S, 149° 1′ E), and Canberra Forestry

Figure 9.1 Map of the Australian study area and the three study systems.



(35° 3′ S, 149° 10′ E) (Bureau of Meteorology, 2003). These stations have measured temperature and rainfall for the past 80 years (Bureau of Meteorology, 1999). The monthly mean temperatures at these recording stations range from 10.2°C to 27.7°C in summer and 1.2°C to 12.7°C in winter (Bureau of Meteorology, 2003). The mean annual rainfall from the five recording stations was 632.8 mm, with a range of 600 mm to 800 mm. Moore (1970) argued that these temperature and precipitation patterns have probably remained relatively stable for 6000 years.

The lack of climatic change suited the growth of a diverse array of vegetation within the study area because extremes of temperature and precipitation would have limited the growth of many species found in the area today. The vegetation of Canberra at the time of European settlement has been the subject of numerous studies (summarised in Pryor, 1954; Burbidge and Gray, 1979). These studies demonstrate that the study area did not constitute a distinctive botanical region. The region lies south of the boundary of the Hawkesbury sandstone flora, and north of the sub-alpine region (Chan, 1980). Therefore, some floral elements within the study area display affinities with flora in coastal and western regions and many are at the eastern or western limits of their distribution (for example River Oak (*Casuarina leuhannii*)) (Burbidge and Gray, 1979).

Studies by Pryor (1954), Burbidge and Gray (1979) and Chan (1980) show that three types of vegetation dominated the study area at the time of settlement: (i) dry sclerophyll forest on the less fertile hilltops at altitudes above 600 m; (ii) woodlands on the more fertile slopes below 750 m; and (iii) Kangaroo Grass - Spear Grass (*Themeda triandra - Stipa bigeniculata*) grassland on the plains. These three vegetation types were stratified by the effects of altitude, microclimate and soil properties, forming a continuum from hilltop to plains (Banks and Paton, 1993). This stratification was also influenced by the migration of species in response to past climatic change and the role of Aboriginal land practices. Benson and Redpath (1997) argue that Aboriginal burning practices were particularly important because the frequent burning of vegetation led to the 'opening-up' of the *Eucalyptus* canopy, aiding the development of a complex understorey.

Within the woodland remnants, associations of Yellow Box *Eucalyptus melliodora* and Blakely's Red Gum *E. blakelyi* dominate the tree cover of many remnants on lower slopes and deeper soils, while Red Box *E. polyanthemos*, White Box *E. albens*, Apple Box *E. bridgesiana*, Mealy Bundy *E. nortonii*, Red-spotted Gum *E. mannifera* and Ribbon Gum *E. viminalis* are less common. The drier and steeper slopes are dominated by Red Stringybark *E.*

machorhyncha, Brittle Gum *E. mannifera*, and Scribbly Gum *E. sclerophylla.* The shrub strata are typically comprised of *Bursaria spinosa*, *Cassinia* spp. and *Acacia* spp. The ground layer in relatively undisturbed remnants is dominated by species such as Kangaroo Grass *Themeda triandra* and Spear Grass *Stipa* spp. Degraded woodland remnants contain exotic understorey plants, including blackberries *Rubus* spp., roses *Rosa* spp. and introduced grasses (Hind, 1991; Watson 1999; Freudenberger, 2001). Figure 9.2 gives an example of the vegetation structure of a typical woodland.

9.3 Human landuse practises in the region

When European settlers arrived in the region in the 1820s, they found well-drained and fertile soils along the lower slopes and plains (Pryor, 1954). Pastoralists favoured these areas, so the woodlands that naturally occurred there were cleared by settlers and grazed by cattle and sheep. Some remnants of woodland were left because they were valued as a source of firewood and provided shelter for livestock (Leigh, 1975; Frawley, 1991). The larger trees were removed over time, resulting in an uneven retention of tree species within these remnants (Boland *et al.*, 1984). High grazing pressure within remnants also led to the loss of shrub cover, making room for a ground cover dominated by exotic grasses and herbaceous species (Boland *et al.*, 1984).

The development of Canberra as the federal capital from 1911, and the establishment of *Pinus radiata* plantations in the 1920s, further replaced tracts of native temperate woodland in the study area (Pryor, 1954). As Canberra grew, exotic tree species such as Poplar (*Populus alba*) and Velvet Ash (*Fraxinus velutina*) were introduced (Burbidge and Gray, 1979). Exotic species thrived in the temperate conditions of Canberra. Subsequently exotic tree species were found in every woodland patch studied by Er (1995) within the northern ACT.

Figure 9.2 Mt Majura, Australian Capital Territory: an example of a temperate woodland. *Source*: Watson (1999)

As a result of urbanisation and rural land management practices, woodlands now occur as fragmented remnants. These remnants are found on private land, leased land, nature reserves and urban parks. The establishment of Canberra Nature Park and Majura Firing Range mean that a number of woodland remnants are 'protected'; the Canberra Nature Park consists of 27 reserves with a total area of 5720 ha (ACT Government, 1998). However, the majority of remnants occur on private or agisted land and have no formal legislative protection. The viability of many of these remnants is uncertain, with the impacts of domestic livestock, tree dieback, invasion of weeds and harvesting of timber also threatening their existence (Landsberg *et al.*, 1990; Tidemann, 1997).

9.4 The different woodland landscapes of the region

Based on their dominant matrix characteristics, three different variegated (sensu McIntyre & Hobbs, 1999) woodland landscapes were identified in the region: agricultural, peri-urban and urban. The agricultural woodland landscape is found to the north and west of Canberra. Agriculture, including wool, beef, cereal and some horticultural production, is the dominant land-use. Numerous outbreaks of dryland salinity have been mapped within the catchment, with 1372 ha of salt-affected areas identified within an 83 000 ha mapped area in 1995 (Hayman, 1996).

The peri-urban landscape comprises areas of the northern ACT and bordering areas of New South Wales, and consists of undulating hills and floodplains of the Murrumbidgee and Molonglo Rivers. The landscape covers approximately 150 000 ha. Large portions of this area were cleared for agriculture and only 8% of the temperate woodlands that occurred prior to European settlement are left within the ACT (Environment ACT 1998). Unlike the agricultural landscape, this landscape is not currently fragmented by intense cultivation and annual crops, but instead is modified by grazing, introduced pasture grasses, scattered housing, and selective clearing (e.g. firewood removal) (Figure 9.3). As a consequence, the matrix has many more paddock trees than the agricultural landscape.

The urban landscape is within the realms of the city of Canberra (population 313,000), the major urban centre within the region. This landscape covers approximately 150 000 ha. Within the city, woodland patches make up approximately 10% of the landscape. They remain as parks and hillside reserves surrounded by the urban matrix, which consists mostly of housing and exotic vegetation in gardens and along suburban streets (Figure 9.4).

Figure 9.3 Wallaroo Road, ACT: an example of the agricultural landscape in the study area. Aerial photograph taken from an aeroplane in January 1999. *Source*: Watson (1999)

Figure 9.4 The suburb of Gunghalin, Canberra: an example of the urban landscape in the study area. *Source*: Watson (1999).

9.5 Avifaunal studies in the area

The diversity of canopy and understorey vegetation presents opportunities for a large diversity of woodland and grassland bird species. Every woodland bird species that has been identified within eastern Australia has been recorded within the study area, and all were considered common at the time of European settlement (Taylor and COG, 1992). Many of these species have declined during the past 200 years because of past and present landuse practices (Environment ACT, 1998).

There have been numerous avifaunal studies conducted within the ACT and the surrounding districts of NSW (e.g. Taylor and COG, 1992; Er, 1995; Watson, 1999; Freudenberger, 2001; Watson *et al.* 2001; Watson *et al.* 2003). The Canberra Ornithologists Group's study of the birds within the ACT between 1986 and 1991 is the largest study conducted within woodlands (Taylor and COG, 1992). This study involved over one hundred participants and found that in a five-year period the number of woodland dependent bird species in the region had declined dramatically. The study also predicted that the decline would continue because of on-going woodland habitat alteration. Table 9.1 shows that over half of the bird species considered rare and endangered within the ACT rely on woodland habitat (Taylor and COG, 1992; Er 1995). In response to these findings, Action Plans were implemented for the conservation of the Hooded Robin (*Melanodryas cucullata)*, Superb Parrot (*Polytelis swainsonnii)*, Brown Treecreeper (*Climacteris picumnus)* and Regent Honeyeater (*Xanthomyza phrygia)* (ACT Government, 1998).

The focus of these species-orientated Action Plans is on revegetating smaller woodland remnants (ACT Government, 1998). Therefore, these Action Plans aim to create an interactive conservation network within the ACT, where both large and small remnants play a

Table 9.1 Summary of bird species in the ACT that have disappeared, are presently rare, or declining in numbers. *Sources*: Taylor and COG (1992); Er (1995).

Bird species	**Habitat type**	**Local status**
Emu (*Dromaius novaehollandiae*)	Grassland	Extinct
Brolga (*Grus rubicundas*)	Grassland	Extinct
Australian Bustard (*Ardeotis australis*)	Grassland	Extinct
Glossy Black-Cockatoo (*Calyptorhynchus lathami*)	Casuarina Forest	Rare
Superb Parrot (*Polytelis swainsonnii*)	Woodland	Rare
Brown Treecreeper (*Climacteris picumnus*)	Woodland	Declining
Jacky Winter (*Microeca fascinans*)	Woodland	Declining
Hooded Robin (*Melanodryas cucullata*)	Woodland	Declining
Crested Shrike-tit (*Falcunculus frontatus*)	Forest	Declining
Speckled Warbler (*Chthonicola sagittatas)*	Woodland	Declining
Regent Honeyeater (*Xanthomyza phrygia*)	Woodland	Rare
Painted Honeyeater (*Grantiella picta)*	Riparian Forest	Rare
Yellow-tufted Honeyeater (*Lichenostomus melanops*)	Riparian Forest	Declining
Diamond Firetail (*Stagonopleura guttata*)	Woodland	Declining

part in protecting woodland biodiversity. Unfortunately, the managers who are tasked with implementing these Action Plans do not know the spatial characteristics of woodland remnants that will conserve all of the threatened species within the ACT (Watson, 1999). Therefore, these Action Plans can only rely on broad-scale revegetation programs, using the logic that 'the bigger the remnant the better'. Moreover, they had no idea how different landscapes could be affecting the connectivity within the landscape for woodland birds and hence did not consider planting within the matrix surrounding woodland remnants.

9.6 Conclusion

This chapter has described the woodland landscapes of southeastern Australia and explored the ecological research that has been conducted within them in the past. This chapter therefore sets up the stage for the following two chapters, which are empirical research papers analysing data on the bird communities of these fragmented woodland landscapes. Chapter 10 specifically examines the effects of woodland fragmentation on birds at a regional scale by focusing on six different bird species area-incidence functions and minimum area requirements to determine if they varied within the different woodland landscapes described. Chapter 11 examines the woodland bird community of the same three woodland landscapes and determines how species richness-area and species-richness isolation relationships varied between them. In addition to this, this paper looks at how individual species area-isolation relationships changes in the three landscapes, to ascertain if there is specific species variation between landscape type.

CHAPTER 10

VARIABILITY OF WOODLAND BIRD INCIDENCE FUNCTIONS IN SIMILAR FRAGMENTED LANDSCAPES WITH DIFFERENT LANDSCAPE MATRIXES IN SOUTHEASTERN AUSTRALIA

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10.1 ABSTRACT

Species-area incidence relationships are important tools for analysing how area-sensitive species are affected by habitat loss. Herein, we assess how bird species incidence functions vary among similar fragmented landscapes in the Australian Capital Territory (ACT) and surrounding areas of southeastern Australia. Bird presence/absence data were collected for resident woodland birds in 127 woodland remnants of different sizes in three different fragmented landscapes, termed agricultural, peri-urban and urban woodlands, using an area-search methodology. We assess species-area incidence relationships of six area-sensitive woodland bird species in each of the three landscapes. These landscapes are located within 50 km of each other, have fragments of similar age, size and spatial pattern distribution, similar proportions of woodland cover and experience similar weather conditions. The major distinguishing feature of the three study systems is in the properties of the matrix habitats surrounding woodland remnants. Remnant area was found to explain a significant ($p<0.05$) portion of the deviance in the logistic regressions for three of the six species in all three landscapes, while the other three species were found to be area sensitive in two of the three landscapes. We show that incidence functions within species vary substantially between each landscape system. There was no uniformity in which landscape the species were most area-sensitive, with three species appearing to be most area sensitive in urban landscape and two species most area sensitive in the agricultural landscape. There are many potentially important properties of both woodlands and intervening landscapes that might influence fragment use by particular bird species, such that the correlative exercise undertaken herein cannot resolve causation. However, the variation in form of incidence functions appears most parsimoniously explained as a function of the differing properties of the matrix within which the three sets of woodland fragments are embedded. We therefore endorse previous calls for more attention to be paid to the role of matrix properties in respect of the distribution of animals across fragmented systems.

Keywords

Australia, conservation biology, fragmentation, incidence functions, matrix effects, species-area relationship, woodland birds

10.2 INTRODUCTION

In the past two decades there has been considerable interest in studying the effects of habitat fragmentation on population dynamics, community richness and composition (Connor and McCoy 1979, Gilpin and Hanski 1991). Frequently, this interest is expressed through analysis of the species richness area relationship (SPAR). Whilst the SPAR is one of the longest known general relationships in ecology, there still remains considerable debate about the form of the relationship and how it varies between system types (Williamson et al. 2002, Ovaskainen and Hanski 2003, Scheiner 2003, Tjørve 2003). Underpinning variation in the form of SPARs between systems we should expect to see systematic variations in the form of species-area incidence functions (the relationship between species occurrence in isolates and the area of the isolates) (Lomolino 2000, Ovaskainen and Hanski 2003).

Probably the earliest use of incidence functions as a biogeographic tool was Diamond's (1975) analysis of incidence as a function of richness (rather than area) in New Guinea birds. Since then, incidence functions have been used as a tool in both theoretical and applied biogeographic research, to elucidate effects of area and isolation, and to show that incidence may vary through time and in relation to ecological traits, such as body size (e.g. Hinsley et al. 1995, 1996a, Whittaker 1998, Biedermann 2003). Increasingly, incidence relationships are being used as tools in determining the minimum area requirements of species in fragmented landscapes, and have often influenced species-level management policy (Vickery et al. 1994, Helzer and Jelinski 1999, Davies et al. 2000; Fagan et al. 2001). Surprisingly, how individual species-incidence functions vary between different landscape systems has been less well studied. A few studies have: (i) developed models to simulate the effects of the matrix on movement patterns (e.g. Gustafson and Gardner 1996, Cooper et al. 2002), (ii) tested whether patterns of patch occupancy are consistent with the hypothesis that resistances to inter-patch dispersal differ among matrix types (e.g. Lomolino 1984, 1994, Åberg et al. 1995, Ricketts 2001, Brose 2003, Krauss et al. 2003), and (iii) tested if matrix type was a determinant of change in bird densities (i.e. the matrix quality hypothesis) (Dunning et al. 1992, Norton et al. 2000, Brotons et al. 2003). We are unaware of any studies that have assessed how individual species' area incidence functions change with different landscape context.

Here we test the hypothesis that bird species incidence functions should be broadly consistent in form in similar fragmented landscapes from the same region. Our research was conducted on area-sensitive woodland birds in three fragmented woodland landscapes of southeastern Australia. These landscapes were located within 50 km of each other, contain fragments of similar age, size and spatial pattern distribution, have similar proportions of woodland cover and experience similar climates. As shown below, the major difference in the landscapes appears to be in the properties of the landscape matrix surrounding the woodland remnants.

10.3 MATERIALS AND METHODS

The study region included the northern part of the Australian Capital Territory (ACT) and bordering areas of New South Wales, and consisted of undulating hills and floodplains surrounding the Murrumbidgee River, Molonglo River and Boorowa River catchments (Fig. 9.1). Before European colonization in the early nineteenth century, grasslands and woodlands comprised the dominant vegetation communities (Burbidge and Gray 1970). Since then, these vegetation communities have been altered due to the development of the city of Canberra and agricultural activities. The temperate woodlands in this region are now one of the most fragmented ecosystem types in Australia (Garnett and Cowley 2000).

Based on their dominant matrix characteristics, three different variegated (sensu McIntyre and Hobbs 1999) woodland landscapes were identified in the region: agricultural, peri-urban and urban. The agricultural woodland landscape comprised the Boorowa River catchment, which covers approximately 168 000 ha on the south-west slopes of New South Wales. Agriculture, including wool, beef, cereal and some horticultural production, is the dominant land-use. The catchment has been extensively cleared and only about 7% of it remains under woodland cover. Numerous outbreaks of dryland salinity have been mapped within the catchment, with 1372 ha of salt-affected areas identified within an 83 000 ha mapped area in 1995 (Hayman 1996).

The peri-urban landscape comprised areas of the northern ACT and bordering areas of New South Wales, and consists of undulating hills and floodplains of the Murrumbidgee and Molonglo Rivers. The landscape covers approximately 150 000 ha. Large portions of this area were cleared for agriculture and only 8% of the temperate woodlands that occurred prior to

European settlement are left within the ACT (Environment ACT 1998). Unlike the Boorowa catchment, this landscape is not currently fragmented by intense cultivation and annual crops, but instead is modified by grazing, introduced pasture grasses, scattered housing, and selective clearing (e.g. firewood removal). As a consequence, the matrix has many more paddock trees than the Boorowa catchment (Table 10.1).

The urban landscape is within the realms of the city of Canberra (population 313,000), the major urban centre within the region. This landscape covers approximately 150 000 ha. Within the city, woodland patches make up approximately 10% of the landscape. They remain as parks and hillside reserves surrounded by the urban matrix, which consists mostly of housing and exotic vegetation in gardens and along suburban streets.

The floristic composition of woodland remnants in all three landscapes is very similar. Associations of Yellow Box *Eucalyptus melliodora* and Blakely's Red Gum *E. blakelyi* dominate the tree cover of many remnants on lower slopes and deeper soils, while Red Box *E. polyanthemos*, White Box *E. albens*, Apple Box *E. bridgesiana*, Mealy Bundy *E. nortonii*, Red-spotted Gum *E. mannifera* and Ribbon Gum *E. viminalis* are less common. The drier and steeper slopes are dominated by Red Stringybark *E. machorhyncha*, Brittle Gum *E. mannifera*, and Scribbly Gum *E. sclerophylla*. The shrub strata are typically comprised of *Bursaria spinosa*, *Cassinia* spp. and *Acacia* spp.. The ground layer in relatively undisturbed remnants is dominated by species such as Kangaroo Grass *Themeda triandra* and Spear Grass *Stipa* spp. Degraded woodland remnants contain exotic understorey plants, including blackberries *Rubus* spp., roses *Rosa* spp. and introduced grasses (Hind 1991, Watson 1999, Freudenberger 2001).

We chose these three landscapes because they were in very close proximity to each other, and as such, experience very similar climatic conditions (Bureau of Meteorology 2004). Moreover, each landscape had very similar remnant sizes, spatial pattern distribution and similar proportions of vegetation cover in each landscape. The woodland cover ranged from 7 to 10%, well within the range where fragmentation effects are postulated to occur (Andrén 1994). The modern clearance and modification of all three landscapes started approximately at the beginning of the 20th century and therefore woodland remnants are similarly aged.

10.3.1 Landscape characteristics

The areas and isolation of remnant woodland patches were calculated after screen-digitising their outlines from two SPOT panchromatic satellite images captured on 23 May 1997 (urban and peri-urban landscapes) and 17 April 1997 (agricultural landscape). Surveyed woodland remnant areas ranged from 1 to 1616 ha in the agricultural landscape, 1.1 to 989 ha in the peri-urban landscape and 3.3 to 571 ha in the urban landscape (Table 10.1). An isolation index for each patch was defined as the distance to the nearest remnant >10 ha in size. This form of patch isolation index has been found to be a useful predictor of isolation in woodland birds studies in eastern Australia (Seddon et al. 2001) and in other fragmented landscapes (e.g. van Dorp & Opdam 1987, Delin and Andrén 1999). Woodland remnant isolation values ranged from 10 to 6440 m in the agricultural landscape, 68 to 8700 m in the peri-urban landscape and 40 to 5300 m in the urban landscape (Table 10.1).

In order to establish empirically the difference between the three landscapes' matrix compositions, we quantified the amount of tree cover in each of the matrices, as well as amount of human disturbance in terms of houses and roads (Table 10.1, as Kluza et al. 2000). In each landscape we quantified the number of trees in paddocks, numbers of houses, numbers and length of roads, numbers and length of vegetated creeklines, and the number of clump trees (i.e. more than 1 tree together) in 10 randomly placed one km radius circles. We made sure that no circle contained any form of woodland remnant, i.e. they were placed in the matrix surrounding each woodland. All measurements were conducted using the SPOT imagery in the peri-urban and agricultural landscapes. Aerial photographs captured in May

Table 10.1 Summary statistics for woodlands remnants and of matrix variables in each of the three landscapes (mean ±SE). All measurements were conducted using the SPOT imagery captured in May 1997 in the peri-urban and agricultural landscapes. Aerial photographs captured in May 2000 at a spatial resolution of 1:20 000 and SPOT imagery captured in April 1997 were used for the urban landscape. All area measurements are in hectares (ha). Landscape matrix variables are the means of measurements taken from 10 randomly placed one km radius circles in each landscape. Remnant isolation was defined as the distance to the nearest remnant greater than 10 ha in size.

	Agricultural	**Peri-urban**	**Urban**
Number of remnants	55	42	30
Remnant area range (ha)			
Area (min)	1	1	3
Area (max)	892	1616	571
Area (mean)	93 (195.5)	125 (300.2)	181 (155.1)
Area (median)	21	14	22
Remnant isolation range (m)			
Isolation (min)	10	68	40
Isolation (max)	6440	8700	5300
Isolation (mean)	1488	2470	1362
Isolation (median)	870	1271	802
Matrix measures			
Number of houses/ km^2	0.12 (0.23)	0.31 (0.36)	701.2 (73.1)
Number of roads/ km^2	0.4 (0.42)	0.98 (0.62)	48.9 (9.6)
Length (km) of roads/ km^2	0.38 (0.42)	0.62 (0.43)	8.8 (1.5)
Number of trees/ km^2	14.8 (5.6)[a]	30.2 (14.2)[a]	417 (162.3)
Number of clumps/ km^2	0.54 (0.41)	0.35 (0.31)	77.4 (60.1)
Number of vegetated creeks/ km^2	0.28 (0.31)	0.1 (0.15)	0.11 (0.4)
Length (m) of vegetated creeks/ km^2	0.12 (0.15)[b]	0.03 (0.04)[b]	0.18 (0.85)

[a] The means were highly significantly different (t= -3.21, df=18, $p<0.01$).

[b] The means were significantly different (t=2.1, df=18, $p<0.05$).

2000 at a spatial resolution of 1:20,000 were used for the urban landscape. It must be noted that the SPOT imagery had a spatial resolution of 10m, and hence smaller trees and shrubs within the matrix were unlikely to be observed.

10.3.2 Bird census

Bird presence/absence data were collected for all resident woodland birds in 127 woodland remnants of different sizes in the three landscapes. Bird surveys in the urban (n=30) and peri-urban (n=42) landscapes were conducted in March-May 1999 (Watson *et al.* 2001) and those in the agricultural landscape (n=55) were conducted in March 2000 (Freudenberger 2001). In the agricultural landscape, woodland remnants were surveyed using three area-search 30-minute surveys by two experienced field ornithologists (Bibby et al. 1992). In all surveys species occurrence and relative abundance were recorded. In the other two landscapes, woodland remnants were surveyed using three 20-minute surveys by two experienced ornithologists. In these surveys, only species occurrence data were recorded. Species accumulation curves and pilot studies showed that the sampling effort was sufficient to capture accurately bird presence in every remnant. Full details of the census methodology and results of pilot studies are given in Watson (1999) and Freudenberger (2001). Because missing species that are actually present in a patch can distort species-incidence analyses if the errors are related systematically to patch size, we took the further step of comparing our results to studies conducted by the Canberra Ornithologist Group (COG) in 18 large (>20 ha) woodland remnants in the ACT (Taylor and Canberra Ornithologist Group 1992, Barrett et al. 2003). We found exactly the same species presence/absence for all six species under consideration that the COG surveys found, providing further support for the effectiveness and lack of bias of our survey notwithstanding the slight difference in survey duration in the agricultural system.

10.3.3 Analyses

An independent *t*-test was used to assess the difference in means of all the matrix characteristics of three landscapes, after testing the variables for normality using the Kolmogorov-Smirnov test (Dytham 1999, Kinnear and Gray 2000).

We chose to focus our analysis on six known area-sensitive insectivores that vary in foraging behaviour and body size (Garnett et al. 1992, Baker et al. 1997, Watson et al. 2000, Mac Nally and Horrocks 2002, Watson et al. 2003). The presence/absence data for all six species were modelled for each landscape using binomial logistic regressions to determine the relationships between the occurrence of each species and the size of woodland habitat. Incidence functions for all six species were developed using the results of the logistic regression (following Watson et al. 2001, Biedermann 2003). Following Helzer and Jelinksi (1999), an arbitrary incidence value of 50% was used to define the minimum area requirement for each species within each landscape. These statistics were calculated using the statistical package SPSS (Kinnear and Gray 2000).

10.4 RESULTS

Each landscape had similar remnant area and isolation ranges, means and medians suggesting that remnant distribution in the three landscapes was similar (Table 10.1). The properties of the three landscape matrices were clearly different; the agricultural and the peri-urban landscapes being the most similar (Table 10.1). For example, the agricultural matrix had significantly ($p<0.01$) fewer trees than the peri-urban matrix (Table 10.1). Moreover, the agricultural matrix had nearly five times greater length of vegetated creeklines than the peri-urban matrix ($p<0.05$; Table 10.1). The amount of human settlement within the two matrices was also very different with almost double the number of houses and triple the number of roads within the peri-urban landscape than the agricultural matrix (Table 10.1). The urban matrix was very significantly ($p<0.01$; Table 10.1) different to the peri-urban and agricultural landscapes, having a far greater number of houses and trees and far higher road density.

For the full dataset of 127 remnants, remnant area explained a highly significant ($p<0.01$) portion of the deviance in the logistic regression models of each species (Table 10.2). When the models were calculated for each landscape separately, remnant area was found to explain a significant ($p<0.05$) portion of the deviance in the logistic regressions for all three landscapes for three of the six species, namely *Climacteris picumnus*, *Cormobates leucophaeus* and *Chthonicola sagittata.* The other three species were found to be area sensitive in two of the three landscapes (Table 10.2).

There was no general trend or uniformity among the incidence functions, as the six species selected showed varying incidence function patterns across the three landscapes (Fig. 10.1; Table 10.3). *C. sagittata* showed the most uniform pattern but had higher incidences in urban remnants greater than 100 ha than in equivalent surveyed remnants in the other landscapes. *C. picumnus* and *C. leucophaeus* had similar incidence of probability for small and large remnant areas in all three landscapes, but showed varying incidence distribution through the mid range of areas. *Smicrornis brevirostris*, *Eopsaltria australis* and *Acanthiza pusilla* had varying incidences in the mid-range and large range of remnant areas in the landscapes. There was also no uniformity in which landscape the species were most area-sensitive. Three species (*C. picumnus*, *C. leucophaeus*, *E. australis*) appear to be more area sensitive in urban landscape whereas *A. pusilla* and *S. brevirostris* both appear to be more area sensitive in the agricultural landscapes (Fig. 10.1).

10.5 DISCUSSION

For the six selected species, incidence functions vary considerably in form across the three different landscapes in the region. This variation in response is representative of the responses of 20 other species in this system (work in progress). This is an interesting finding because it goes against our initial hypothesises that bird species would have similar incidence functions in similar fragmented landscapes and that similar species would show congruent patterns.

Table 10.2 Summary of mean deviance in individual logistic regression models for six woodland bird species in the woodland remnants in the region of the northern Australian Capital Territory and surrounding areas, calculated for all sites (n=127), and separately for three distinct landscapes: agricultural (n=55), peri-urban (n=42) and urban (n=30). Bird species were categorised based on their body weight and the foraging substrates they exploit (bark, ground, foliage, canopy, air) using Baker *et al.* 1997 (body mass) and Garnett *et al.* 1992 (foraging substrate).

Species	**Body Mass (g)**	**Foraging substrate**	**Mean deviance of logistic regression models**			
			All	**Agricultural**	**Peri-urban**	**Urban**
Brown Treecreeper *Climacteris picumnus*	33	Terrestrial	17.01**	5.5**	7.5**	3.3*
White-throated Treecreeper *Cormobates leucophaeus*	22	Bark	21.5**	3.5*	10.1**	3.3*
Speckled Warbler *Chthonicola sagittata*	14	Terrestrial	17.07**	4.3*	4.5*	4.8*
Brown Thornbill *Acanthiza pusilla*	9	Shrub	10.7**	0.9	6.7**	4.1*
Weebill *Smicrornis brevirostris*	6	Shrub	12.8**	1.3	8.4**	3.4*
Eastern Yellow Robin *Eopsaltria australis*	19	Terrestrial	14.2 **	9.3**	4.1*	0.9

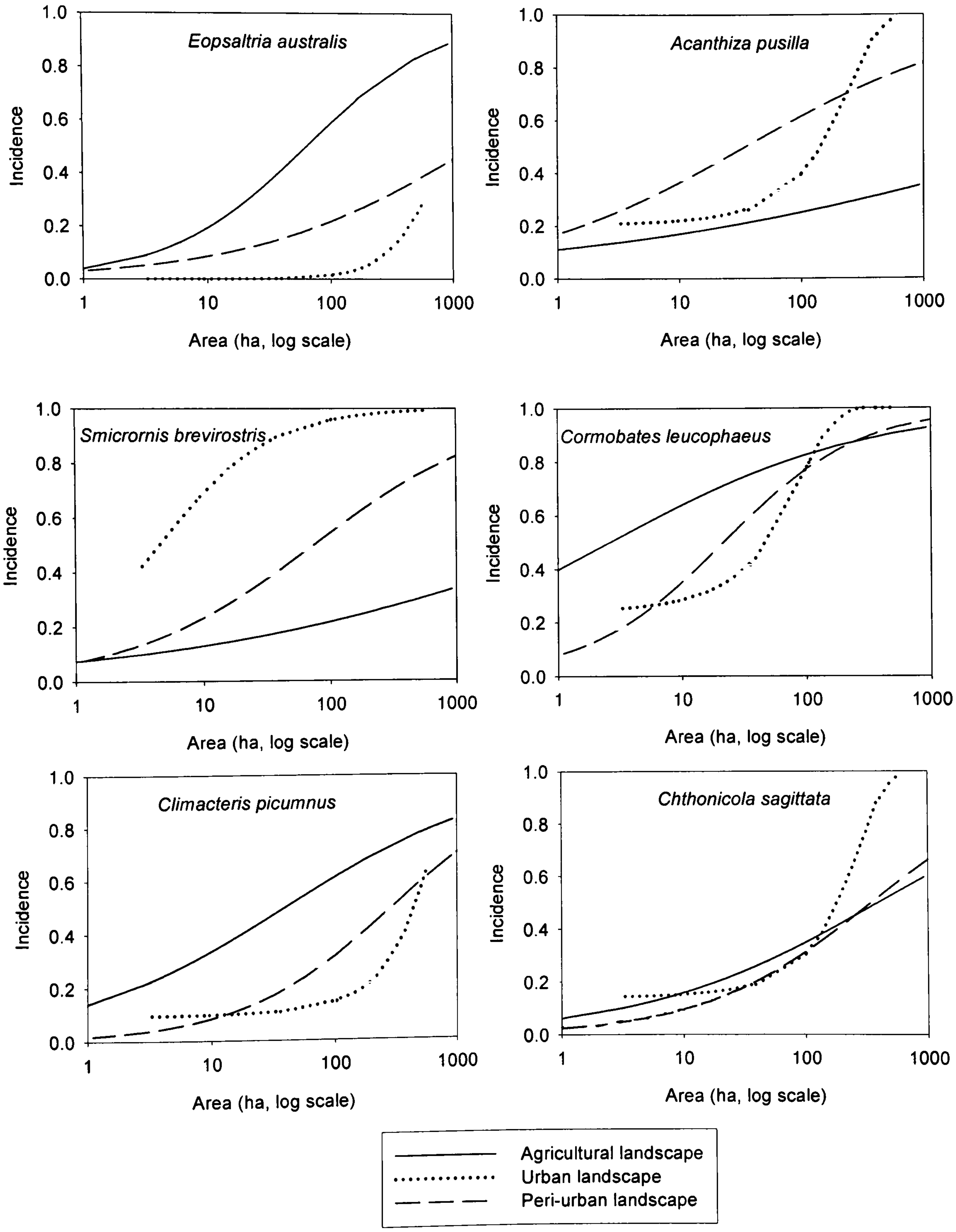
** p <0.01, * p <0.05

Table 10.3 Minimum area (ha) requirements of six woodland bird species in woodland remnants of three landscapes (agricultural, peri-urban, urban). Following Helzer and Jelinski (1999), minimum area requirements were calculated as the area where a species reached 50% probability of occurrence in their individual area-incidence function. Incidence functions were developed from logistic regressions based on the presence/absence data for all six species in each landscape. If a species did not reach 50% probability of occurrence, no minimum area requirement was calculated.

Species	**Species minimum area requirements**		
	Agriculture	**Peri-urban**	**Urban**
Brown Treecreeper *Climacteris picumnus*	40	410	320
White-throated Treecreeper *Cormobates leucophaeus*	3	19	60
Speckled Warbler *Chthonicola sagittata*	390	365	180
Brown Thornbill *Acanthiza pusilla*	-	35	140
Weebill *Smicrornis brevirostris*	-	90	5
Eastern Yellow Robin *Eopsaltria australis*	73	990	-

It has previously been observed that species incidence functions will vary in concert with variations in the population size within the landscape under consideration (Hinsley et al. 1996b), as the probability of a species occurring in a given patch is directly affected by its regional abundance. Species with smaller total landscape populations will have less chance of occurring in both larger and smaller patches (Connor and McCoy 1979). In this study we lack data on regional population sizes of the bird species under consideration and so cannot determine the extent to which our findings are indicative of top-down regional controls on local species incidences or bottom-up patch-region control of population sizes. All our data illustrate is that there are substantial differences in the use of woodlands as a function of area across the three different landscapes. All six species considered are common woodland-restricted birds in the region and are in the core of their overall range (Taylor and Canberra Ornithologists Group 1992, Barrett et al. 2003). Therefore, whilst pre-fragmentation variations in abundance of these species across the region cannot be determined, the

Fig. 10.1 Incidence curves for six area-sensitive woodland species in different landscape matrices in the ACT region of southeastern Australia. The three woodland landscapes surveyed were: agricultural (n=55), peri-urban (n=42) and urban (n=30). Incidence functions were developed using the results of a logistic regression based on the presence/absence of each species in woodland remnants in each landscape. The significance of each logistic regression model is given in Table 10.2.



differences in species-area incidence functions recorded herein appear attributable to habitat fragmentation.

There are a variety of possible reasons why species-area incidence functions may vary between fragmented landscapes. One possibility is that if the spatial pattern and size distribution of woodland remnants are vastly different in each landscape, then species-area incidence function may also be different. However, as previously mentioned, this was not the case in this study because all three landscapes had similar remnant size distribution and spatial pattern (Table 10.1). Moreover, fragmentation of woodland habitats occurred at approximately the same time – the start of the last century- and hence, even though the woodland fragments may not have reached a dynamic equilibrium (MacArthur and Wilson 1967, Diamond 1975, Simberloff 1992, Whittaker 1998), it is reasonable to assume that they are at a similar stage in the process. It is therefore unlikely that the variation we found in individual species incidence functions was due to the range of remnants sizes or because of differences in remnant age in the different landscapes.

Another possible explanation for the variation in species-incidence functions could be that the resources within woodland remnant may be significantly different between the three landscapes; hence, affecting a bird species' ability to occur within them. Studies of woodland habitat complexity in the three landscapes have shown that each landscape has very similar ranges of habitat complexity; as remnant area increases so does the vegetation complexity of the remnant, with area and habitat complexity measures being highly significantly ($p<0.001$) correlated (see Freudenberger 2001, Watson et al. 2001 for more details). Moreover, the woodlands in each of the three landscapes contained very similar floristic communities. Therefore, it is unlikely that different resources within remnants are the reason why species-incidence functions varied in such a marked fashion between landscapes.

A further possibility is that there may be ecologically relevant climatic differences across the three landscapes. Hinsley et al. (1995, 1996b) showed marked year to year variation in incidence functions for particular bird species in severely fragmented woodland remnants in eastern England. These variations were attributed to annual variations in weather conditions affecting the regional population sizes of birds. In our study we have only 'snapshot' survey data. However, all landscapes were very close to each, and fell into the same maximum temperature, minimum temperature and annual rainfall gradient (Bureau of Meteorology 2004). For two of the three landscapes (urban and peri-urban), surveys were conducted during the same period (March – May 1999) while for the agricultural landscape, the bird sampling period was March 2000. Furthermore, for the period two years prior to the bird surveys and during the bird surveys (March 1999 – March 2000), the three landscapes had very similar climatic conditions, varying at most by 2°C in temperature ranges per month throughout this period, and had a very similar rainfall regime. In addition, the three landscapes did not experience severe drought or flooding events during the period 1997-2000 that could have affected the total population size of a bird species differently across our study systems (cf Hinsley et al. 1995, 1996b). This makes it unlikely that the differences in species' incidence functions between the different landscapes are distorted by our sampling the systems at particular points in a temporal dynamic responding to climatic stress. The high similarity between our species lists and those of the COG bird atlas (Barrett et al. 2003) provides further support for this position.

The main difference between the three landscapes is the dominant matrix types. It therefore appears that our findings can be most parsimoniously explained as a function of differences in the properties of the habitat matrix surrounding the woodland remnants. There are a number of factors related to the matrix that could affect the area-sensitivity of a species. Some relate to the way the matrix in which a fragment is embedded influences the edge and internal properties of the fragment. For example, the 'edge-contrast' between remnant and matrix has been shown to be an important predictor for bird diversity within fragmented landscapes

(Stamps et al. 1987; Dale et al. 2000). This is because the edge-contrast governs the micro-climate gradient at the edge of a remnant, which in turn could lead to substantial vegetation changes (including changes in species composition and structure) and biological changes (including increases in predators, nest predators and nest parasites) along the new edge (Robinson et al. 1995, Kapos et al. 1997, Rankin-De Mérona and Hutchings 2001). The agricultural and peri-urban landscapes have far more similar edge contrasts than the urban landscape. This is because the matrix in each case is dominated by fields, albeit with differing numbers of houses, paddock trees and creek lines. In the urban landscape, the matrix is dominated overwhelmingly by housing and roads. Therefore, 'edge-contrast' provides one hypothesis for the observation that *E. australis*, *C. picumnus* and to a lesser extent, *C. leucophaeus*, were extremely area sensitive in the urban landscapes and far less sensitive in the agricultural and peri-urban landscapes (Table 10.3; Fig. 9.1). These species may be affected by urban edge effects such an increase in exotic mesopredators within the remnant (Marzluff and Restani 1999, Marzluff and Ewing 2001). Another possible edge-effect is a loss of food resources (i.e. insects) within woodland remnants in the urban landscapes. Food supply may vary with fragment size as a result of edge effects, because invertebrates, especially surface dwellers, are prone to desiccation and may not survive well in edge habitat, which is often warmer and drier than the forest interior (Matlock 1993, Didham et al. 1996). The urban-woodland edge-contrast may be particularly extreme for this, as the contrast between woodland and suburbia is great. Interestingly, Zanette et al. (2000) suggest food shortages in small remnants as the likely reason for area-sensitivity of *E. australis* in woodland remnants in north-eastern New South Wales.

In addition to the above, the movement of birds between fragments may be strongly influenced by the nature of the landscape matrix, thus influencing the use of fragments by particular species (Stouffer and Bierregaard 1995a, Sisk et al. 1997, Fischer and Lindenmayer 2002a, b, Lindenmayer et al. 2002). Different matrices are home to different exotic species and threatening processes (e.g. predators) that could negatively effect the dispersal capabilities of some species between remnants, to the potential differential impact on indigenous species of that habitat (Andrén 1994, Stouffer and Bieeregaard 1995a, Sisk et al. 1997). In this context, the urban landscape is far more likely to contain exotic species that may threaten woodland bird species (Marzluff and Restani 1999). Moreover, different landscape matrices have different resources within them, and therefore have differential capacity for different species – if a species cannot use the resources of a particular matrix, the population may be dependent on a bigger area within the remnant habitat itself to sustain a population in a fragment (Lindenmayer et al. 2003). Probably of greatest importance is the ability of a matrix to provide connectivity and aid species dispersal through the landscape (Åberg et al. 1995, Ricketts 2001). The capacity for movement among remnant patches (i.e. connectivity) is an important factor in the maintenance of organisms in isolated habitats (Beier and Noss 1998), enabling persistence of possible metapopulations (Opdam 1990, Whittaker 1998, Brose 2003). One candidate species for such an effect in our study system is *C. picumnus*, which was especially affected by remnant area reduction in the urban landscape, raising the hypothesis that the 'hostility' of the urban matrix may prevent successful dispersal. This line of reasoning is supported by Walters et al. (1999) and Cooper et al. (2002), as they argue that this species is affected by disrupted dispersal mechanisms and that loss of remnant connectivity is the primary basis why the species is affected by fragmentation.

In contrast, *S. brevirostris*, was found to be very area-sensitive in the agricultural landscape and sensitive in the peri-urban landscape but not sensitive to remnant area in the urban landscape. This species may be able to better utilise the resources within the urban landscape, particularly the greater tree cover along the streets within the city or the shrubs in suburban gardens. It may be less threatened by urban effects, or alternatively, find dispersing through the agricultural and peri-urban landscapes to be exceedingly difficult compared to the urban landscape, due to the absence of many paddock trees and shrub cover within the matrix (Table 10.1; JW, DF pers. obs.). Therefore, matrix composition may be driving species incidence functions to vary because it is either affecting the total landscape population of each of the three species in different ways (e.g. Hinsley et al. 1996b) and/or it is affecting how species are occupying patches of different sizes in different ways (e.g. Lomolino and Smith, 2003).

We stress that much of this is speculation; we are unable to show causation for why species-incidence functions vary between the three fragmented landscapes and we do not claim to have established that the patterns shown herein for a particular landscape, e.g. the urban system, are general for these species in all urban systems. However, by identifying these variations we believe that our results have wide implications. As ecologists and land managers improve their understanding of the environmental problems associated with habitat loss and fragmentation, major efforts are being made to identify minimum areas for sensitive species, and to use these data to identify areas that should be conserved or restored (Saunders *et al.* 1993). As a consequence, many approaches in conservation biology, in particular modelling (e.g. With, 2002), and restoration ecology (e.g. Lambeck 1997; Brooker et al. 2002), are currently being used either to explain how species generally react to habitat loss or to determine appropriate restoration programmes in fragmented landscapes. While these approaches are laudable, the results from this study suggest that there is a danger in trivialising the species-area relationship. Our results clearly demonstrate that the same bird species react differently to remnant area in fragmented landscapes of the same region with different landscape matrices, and that the habitat/non-habitat paradigm these theories and models are based on (and, until recently, dominated the fragmentation literature), broke down in ways that were, in their detail, unexpected.

Moreover, the search for general biogeographic patterns such as body-size and area-incidence relationships (e.g. Biedermann 2003), or general biogeographic theories that explain species presence in fragmented landscapes (e.g. Lomolino 2001, Watson 2002) may be problematic as we show that: (i) species with the same body weight have very different area requirements across the three different types of landscape of the same region (Table 10.2, 10.3); (ii) the same species are not following any form of general pattern in similar fragmented landscapes of different matrix context (Fig. 10.1) and (iii) similar species did not show congruent incidence patterns in the three landscapes (Fig. 10.1). We argue for caution in the use of any species-based model of fragmentation that does not examine the consistency of responses across different fragmented landscapes. Although identifying broad general biogeographic patterns can be useful to guide conservation planning in fragmented landscapes, the assumption that a particular species will respond to reduction in remnant area in the same way from place to place and irrespective of context, needs to be questioned on the basis of this empirical evidence. Overlooking processes such as differential responses to disturbance regimes that underpin species diversity and influence species distribution patterns may lead to the creation of too broad a framework or theory, and ultimately flawed conservation strategies (Lindenmayer and Franklin 2002, Lomolino and Smith 2003; MacDonald and Kirkpatrick 2003).

To conclude, there are many potentially important properties of both woodlands and intervening landscapes that might influence fragment use by particular bird species, such that the correlative exercise undertaken herein cannot resolve causation. However, the variation in form of incidence functions appears most parsimoniously explained as a function of the differing properties of the matrix within which the three sets of woodland fragments are embedded. We hope this research will provide some initial hypotheses for future research examining the effects of fragmentation on biodiversity. Moreover, we encourage future research that examines how different species utilise the matrix surrounding fragmented habitats in order to determine if it is matrix issues that are causing species-area relationships to vary from landscape to landscape; and if so, if it is edge-contrast or connectivity within the matrix that are making species more area-sensitive in different fragmented landscapes.

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CHAPTER 11

BIRD COMMUNITY RESPONSES TO FRAGMENTATION: HOW CONSISTENT ARE THEY ACROSS LANDSCAPES?

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11.1 ABSTRACT

Aim The woodland ecosystems of southeastern Australia have been extensively disturbed by agriculture and urbanization. Herein, the occurrence of birds in woodland remnants in three distinct landscapes was analysed to examine the effects of different types of landscape matrices on species richness vs. area and species richness vs. isolation relationships and individual species responses to woodland fragmentation.

Location The study system comprised three distinct woodland landscapes of the northern Australian Capital Territory and bordering areas of New South Wales. These landscapes (termed agricultural, peri-urban and urban) are located within 50 km of each other, have remnant fragments of similar age, size, isolation, woodland cover, elevation and climates. The major distinguishing feature of the three landscapes was the properties of the habitats surrounding the numerous woodland remnants.

Methods Bird surveys, using an area-search methodology, were conducted in 1999 and 2000 in 127 remnants in the three landscapes to determine bird species presence/absence. Each remnant was characterised by measures of remnant area, isolation and habitat complexity. To characterise differences between each landscape, we conducted an analysis of the amount of tree cover and human disturbance in each landscape using SPOT imagery and aerial photographs. Linear regressions of woodland-dependent species richness vs. remnant area and remnant isolation for the three different landscapes were calculated to see if there were any apparent differences. Binomial logistic regressions were used to determine the relationships between the occurrence of each species and the size and isolation of woodland habitat, in each landscape.

Results All the landscapes displayed a significant ($p<0.01$) species vs. area relationship, but the slope of the urban relationship was significantly greater than those of the other landscapes. In contrast, only the agricultural landscape displayed a significant ($p<0.01$) species richness vs. isolation relationship. When individual species were investigated, we found: (i) species that were apparently insensitive to reduction in remnant area and increase in isolation across all landscapes, (ii) species that were absent in small remnants in all landscapes, (iii) species that were absent in small remnants in all landscapes and also absent in isolated remnants in the agricultural landscape, (iv) species that were absent in isolated remnants in the agricultural landscape and, (v) species that were absent in small remnants in the urban landscape. Threshold values (50% probability of occurrence) for area and isolation for individual species were highly variable across the three landscapes.

Main conclusions These results indicate that woodland bird communities have a varying response to habitat fragmentation in different landscapes. Whilst we cannot be sure how representative our chosen landscapes are of other similarly composed landscapes, these results suggest that type of landscape matrix may have a considerable influence on how bird species are affected by woodland fragmentation in the region. For instance, the properties of a

matrix may influence both the resources available in the landscape as a whole for different bird species, and the connectivity (dispersal of birds), between woodland remnants. We encourage further research that examines these hypotheses and argue that the management of the matrix should be included in conservation strategies for fragmented landscapes.

11.2 INTRODUCTION

Human activities, such as forest clearance and the expansion of agricultural land, have exacerbated the natural fragmentation of landscapes (Andrén, 1994). In the past two decades there has been increasing interest in studying the effects of anthropogenic habitat fragmentation on the spatial dynamics of populations and communities. In particular, the effects of reducing the size of habitat patches (area effects), increasing the distance between occupied patches (dispersal effects), and the creation of habitat edges on patches (edge effects) have dominated the conservation literature (reviewed in Saunders *et al.*, 1991; Turner, 1996; Debinski & Holt, 2000). Many studies have demonstrated that these three processes have been detrimental to indigenous biodiversity throughout the world.

One important aspect of habitat fragmentation, the creation of a different (often human dominated) matrix that surrounds habitat fragments and its impacts on animal communities that inhabit habitat fragments, has been less well studied (Lindenmayer & Franklin, 2002 but see Åberg *et al.*, 1995; Malcolm, 1997; Ås, 1999; Brotons *et al.*, 2003; Murphy & Lovett-Doust, 2004). We suggest that the role of the matrix has been given insufficient attention, perhaps as a result of the dominance of MacArthur & Wilson's (1967) equilibrium theory of island biogeography, and the related concepts of rescue effects (Brown & Kodric-Brown, 1977), nestedness (Patterson & Atmar, 1986), and metapopulation dynamics (Levins, 1968; Hanski & Gilpin, 1991), as theoretical frameworks in many fragmentation-related studies (Lomolino & Smith, 2003). This body of work is based on the concept of populations inhabiting suitable habitat patches and being surrounded by non-suitable habitat (Doak & Mill, 1994; Whittaker, 1998; Ricketts, 2001).

In the present paper, we present a within-region analysis of three bird data sets, all collected recently in different fragmented woodland landscapes in and around Canberra, in southeastern Australia. Each of the three data sets was taken from 'variegated' (sensu McIntyre & Hobbs, 1999) landscapes that have distinctly different landscape contexts (i.e. different matrices). We defined these landscapes as: 'agricultural', 'peri-urban' and 'urban'. The landscapes are otherwise very similar, as modern clearance and modification occurred approximately at the start of the 20th century, and each landscape has analogous remnant size and spatial pattern distributions (Freudenberger, 2001; Watson *et al.*, 2001). We show below that the major difference in the landscapes appears to be in the properties of the landscape matrix surrounding the woodland remnants. For this reason, and because of the close proximity of the landscapes to each other (thus negating a climate effect), we were able to assess how woodland bird communities respond to habitat fragmentation in landscapes of substantially different matrix compositions.

Our first aim was to determine if bird species richness-area and species richness-isolation relationships differed in fragmented woodland remnants in the three landscapes. We hypothesized that there would be different species richness-area and species richness-isolation relationships between each of the three landscapes, for a number of reasons. Firstly, the 'edge-contrast' between remnant and matrix has been shown to be an important predictor for bird diversity within fragmented landscapes (Watson *et al.*, 2004). Edge-contrast governs the micro-climate gradient at the edge of a remnant, which in turn could lead to substantial vegetation changes including changes in floristic composition and structure (Kapos *et al.*, 1997; Rankin-De Mérona & Hutchings, 2001). Edge effects can also cause increases in predators, nest predators and nest parasites along the new edge (Robinson *et al.*, 1995). Secondly, different matrices have different resources within them, and therefore have differential capacity for different species – if a species cannot use the resources of a particular matrix, remnant patches may have to be larger to support the species (Cook *et al.*, 2002; Lindenmayer *et al.*, 2003). Thirdly, the contrast between fragments and matrix may determine the degree of isolation a local population experiences, because the properties of a landscape matrix may affect the ability of individuals to move through it, which will influence population persistence in fragmented landscapes (Stouffer & Bieeregaard, 1995a,b; Sisk *et al.*, 1997; Gascon *et al.*, 1999; Renjifo, 1999; Wethered & Lawes, 2003). All these factors affect the distribution of species in fragmented landscapes, and all may potentially change if matrix composition differs.

Our second aim was to determine which species were sensitive to area loss and patch isolation in each landscape, and whether they were affected in the same way in all three landscapes. We did this by taking a species-level approach and classifying the species response to the five biologically realistic outcomes for how a species may react to remnant area and isolation (Lomolino, 1984, 1986; Lawlor, 1998; Watson, 2003). These are: random, minimum area, maximum isolation, non-compensatory area vs. island, and compensatory patterns (Fig. 2.2). We investigated if these patterns of distribution were consistent for individual species in all three landscapes.

11.3 MATERIALS AND METHODS

11.3.1 Study area

The study area included the northern part of the Australian Capital Territory (ACT) and bordering areas of New South Wales, and consisted of undulating hills and floodplains surrounding the Murrumbidgee, Molonglo and Boorowa River catchments (Fig. 9.1). Before European colonization in the early nineteenth century, grasslands and woodlands comprised the dominant vegetation communities (Burbidge & Gray, 1970). Since then, these vegetation communities have been largely cleared of native vegetation due to the development of the city of Canberra and agricultural activities including cultivation for crops and introduction of exotic pasture grasses and legumes. The temperate woodlands in this region are now one of the most fragmented ecosystem types in Australia (Garnett & Cowley, 2000).

The 'agricultural' woodland landscape comprised the Boorowa River catchment, which covers approximately 168 000 ha on the south-west slopes of New South Wales. Agriculture, including wool, beef, cereal and some horticultural production, is the dominant land-use. The catchment has been extensively cleared and only about 7% of it remains under woodland cover in patches at least 1 ha in size. Numerous outbreaks of dryland salinity have been mapped within the catchment, with 1372 ha of salt-affected areas identified within an 83, 000 ha mapped area in 1995 (Hayman, 1996).

The 'peri-urban' landscape comprises 150 000 ha of the northern ACT and bordering areas of New South Wales, and consists of undulating hills and floodplains of the Murrumbidgee and Molonglo Rivers. This landscape is not characterized by intense cultivation and annual crops, but instead has been modified by the establishment of introduced pastures, grazing by livestock, urbanization, and selective clearing (e.g. firewood removal). The establishment of small (<50 ha) 'hobby' farms over the past 50 years has been the dominant form of urbanization in this landscape. It still has about double the number of scattered trees in fields compared to the agricultural landscape of the Boorowa catchment, but many more roads and houses.

The urban landscape is within the realms of the city of Canberra, the major urban centre within the region (population 313 000). This landscape covers approximately 150 000 ha. Within the city, woodland patches remain as parks and hillside reserves surrounded by the urban matrix, which is dominated by housing, roads and a diversity of native and exotic vegetation in gardens and along suburban streets.

The floristic composition of woodland remnants in all three landscapes is very similar. Associations of Yellow Box *Eucalyptus melliodora* Schauer and Blakely's Red Gum *E. blakelyi* Maiden dominate the tree cover of many remnants on lower slopes and deeper soils, while Red Box *E. polyanthemos* Schauer, White Box *E. albens* Miquel, Apple Box *E.*

bridgesiana Baker, Mealy Bundy *E. nortonii* Blakely, and Ribbon Gum *E. viminalis* Hook are less common. The drier and steeper slopes are dominated by Red Stringybark *E. macrorhyncha* Bentham, Brittle Gum *E. mannifera* Mudie, and Scribbly Gum *E. sclerophylla* Blakely. The shrub strata are typically comprised of *Bursaria spinosa* Cavanilles, *Cassinia* spp. and *Acacia* spp. The ground layer in relatively undisturbed remnants is dominated by species such as Kangaroo Grass *Themeda triandra* Forsskal and Spear Grass *Stipa* spp. Degraded woodland remnants contain exotic understorey plants, including blackberries *Rubus* spp., roses *Rosa* spp. and introduced grasses (Hind, 1991; Watson, 1999; Freudenberger, 2001).

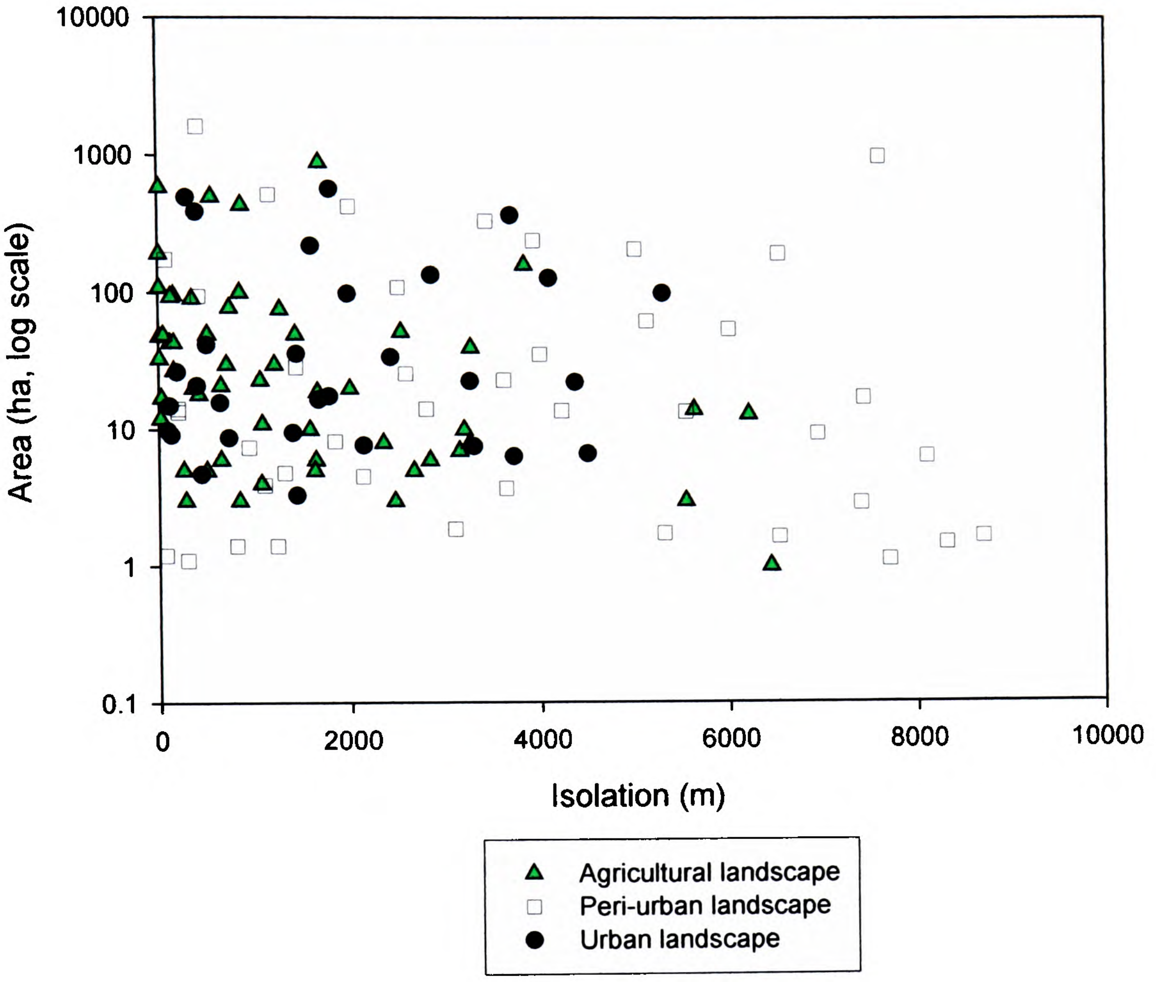
We chose these three landscapes not only for their different landscape matrix composition but because they were in close proximity to each other, and as such, experience very similar climatic conditions (Bureau of Meteorology, 2004). Moreover, each landscape had similar remnant size, spatial pattern distribution and similar proportions of vegetation cover in each landscape (Table 11.1; Fig. 11.1, 11.2). The woodland cover ranged from 7 to 10%, well within the range where fragmentation effects are postulated to occur (Andrén, 1994). The extensive clearance and modification of all three landscapes by Europeans started approximately at the start of the 20th century and the woodland remnants have similar ages since fragmentation.

11.3.2 Field Methods

Bird presence/absence data were collected in 127 woodland remnants of different sizes in the three landscapes. Bird surveys in the urban (n = 30) and peri-urban (n=42) landscapes were conducted during March-May 1999 and bird surveys in the rural landscape (n=55) were conducted in March 2000. For the period two years prior to the bird surveys and during the bird surveys (March 1999 – March 2000), the three landscapes had very similar climatic conditions, varying at most by 2°C in temperature ranges per month throughout this period, and had a very similar rainfall regime. In addition, the three landscapes did not experience

Figure 11.1 The distribution of surveyed remnants in terms of their size and isolation in agricultural, peri-urban and urban landscapes in southeastern Australia.

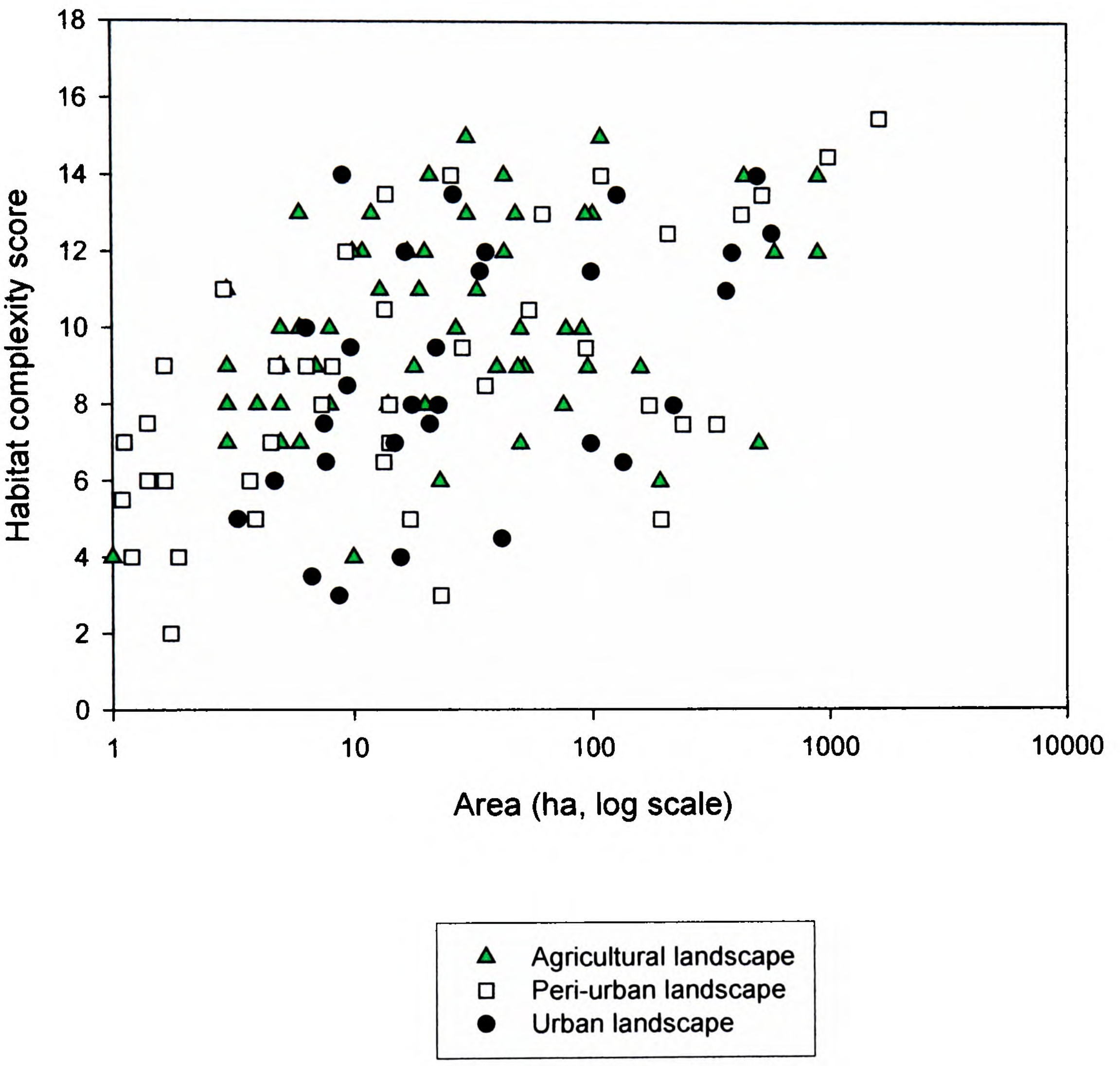
Remnant area and isolation were independent of each other (urban $F_{1,28} = 0.26$, P=0.61, r^2=0.01; peri-urban $F_{1,40}$= 0.48, P=0.4, r^2=0.01; agricultural $F_{1,53}$= 0.73, P=0.39, r^2= 0.02).



severe drought or flooding events during the period 1997-2000 that could have affected the total population size of a bird species in one or more of the landscapes (cf. Hinsley *et al.*, 1995, 1996b).

In the agricultural landscape, woodland remnants were surveyed using three area-search 30-minute surveys by two experienced field ornithologists (Bibby *et al.*, 1992). In these surveys species occurrence and relative abundance were recorded. In the other two landscapes, woodland remnants were surveyed using three 20-minute surveys by two experienced ornithologists. In these surveys, only species occurrence data were recorded. Species

Figure 11.2 Area (A) and habitat complexity scores (HCS) of the surveyed remnants in the agricultural, peri-urban and urban landscapes. Remnant area and habitat complexity were correlated with each other (urban $F_{1,28} = 7.1$, $P<0.01$, $r^2=0.21$, $HCS = 8.1 + 1.41\log(A)$; peri-urban $F_{1,40} = 14.5$, $P<0.01$, $r^2=0.27$, $HCS = 5.8 + 2.2\log(A)$; agricultural $F_{1,53} = 3.12$, $P<0.01$, $r^2= 0.12$, $HCS = 5.2 + 2.4\log(A)$).



accumulation curves and pilot studies showed that the sampling effort was sufficient to capture accurately bird presence in every remnant. Full details of the census methodology and results of pilot studies are given in Watson (1999) and Freudenberger (2001). Because missing species that are actually present in a patch can distort species-incidence analyses if the errors are related systematically to patch size, we took the further step of comparing our results to studies conducted by the Canberra Ornithologist Group (COG) in 18 large (>20 ha) woodland remnants in the ACT (Taylor & Canberra Ornithologist Group, 1992; Barrett *et al.*,

Table 11.1 Components of the avifaunal habitat complexity score (HCS), measured in 1 ha quadrats in woodland remnants (Source: Watson, 1999; Freudenberger, 2001).

Canopy layer. Estimated percentage foliage cover of trees >4 m high.
Tall shrub layer. Estimated percentage foliage cover of shrubs 2-4 m high.
Low shrub layer. Estimated percentage foliage cover of shrubs 0.5-2 m high.
Ground layer. Estimated percentage foliage cover of flora <0.5 m high.
Logs and fallen branches. Estimated percentage of ground covered by logs and fallen branches.
Litter layer. Estimated percentage of ground covered by dead leaves, sticks and twigs.

Habitat Complexity Score	0	1	2	3
Canopy layer	0-10%	10-20%	20-50%	> 50%
Tall shrub layer	0-10%	10-20%	20-50%	> 50%
Low shrub layer	0-10%	10-20%	20-50%	> 50%
Ground layer	0-10%	10-40%	40-70%	> 70%
Logs and fallen branches	0-10%	10-40%	40-70%	> 70%
Litter layer	0-10%	10-40%	40-70%	> 70%

2003). We found the same species presence/absence that the COG surveys found, providing further support for the effectiveness and lack of bias of our survey. This makes it unlikely that the differences in species' incidence functions between the different landscapes are distorted by either survey bias or our sampling the systems at particular points in a temporal dynamic responding to climatic stress.

11.3.3 Patch characteristics

A rapid appraisal procedure was used to measure the structural complexity of vegetation in the 127 remnants surveyed for birds. Habitat complexity was recorded using randomly placed quadrats of 100 m x 100 m. After conducting a pilot study using habitat complexity accumulation curves per quadrat, it was found that two quadrats were required to represent variation in habitat heterogeneity in remnants sized between 2 and 10 ha, three quadrats for remnants of 10-50 ha, four quadrats for remnants of 50-100 ha and five quadrats for remnants greater than 100 ha (Watson, 1999). For each remnant, a mean habitat complexity score (HCS), modified from that described by Catling and Burt (1995), was derived on the basis of six attributes (Table 11.1). Resources relevant to birds and encompassed by these attributes included: nectivorous food supply; nesting sites and shelter from predators in the shrub layer; grass seeds in the ground layer; and invertebrate food in the litter layer. Each habitat attribute was rated on a scale of 0 to 3, and the scores for the six attributes were summed to calculate a HCS for each quadrat. Scores <5 were typically obtained from woodland remnants with sparse shrub and ground layers, few logs and fallen branches, and not much litter. A HCS >10 described structurally complex woodlands in which most habitat components were given a medium to high score.

The area of each remnant woodland patch was calculated after screen-digitising their outlines from a SPOT panchromatic satellite image captured on 23 May 1997 (urban and peri-urban landscapes) and 17 April 1997 (agricultural landscape). We derived an isolation index for each patch as the distance to the nearest remnant >10 ha in size. This form of patch isolation index has been found to be a useful predictor of 'effective isolation' in woodland birds studies in eastern Australia (Seddon *et al.*, 2001) and in other fragmented landscapes (e.g. van Dorp & Opdam, 1987, Delin & Andrén, 1999). The range of patch area and isolation values for each landscape is found in Table 10.1 and shown in Figures 11.1 and 11.2

11.3.4 Matrix characteristics

To quantify some ecologically relevant properties of each landscape, we estimated the tree cover and the amount of human disturbance in terms of houses and roads (Kluza *et al.*, 2000, Table 10.1). In detail, for each landscape we quantified the number of trees in paddocks, numbers of houses, numbers and length of roads, numbers and length of vegetated creeklines, and the number of trees in clumps (i.e. more than 1 tree together) in 10 randomly placed circles of one km radius. We made sure that no circle contained any form of woodland remnant, i.e. they were placed in the matrix surrounding each woodland. All measurements were conducted using the SPOT imagery in the peri-urban and agricultural landscapes. Aerial photographs captured in May 2000 at a spatial resolution of 1:20,000 were used for the urban landscape. The SPOT imagery had a spatial resolution of 10 m, hence smaller trees and shrubs within the matrix were unlikely to be detected, but they were in any case rarely found during field surveys.

11.3.5 Analysis

The species-level analyses were restricted to species that are resident and breed only in woodland habitat because summer migratory species were leaving the study area and winter migratory species were arriving during the early autumn surveys. These species were defined *a priori* 'resident woodland birds' following the classifications of Taylor and Canberra Ornithologists Group (1992), Robinson and Traill (1996) and Watson *et al.* (2003). Those birds that occurred in fewer than five woodland remnants in any landscape were also excluded from the analyses because the logistic regression modelling technique could not pick up any area or isolation pattern for these species statistically. All statistics were calculated using SPSS version 11.5 (Kinnear & Gray, 2000).

Resident woodland bird species were further categorized by their body mass, foraging niche (insectivore, nectivore, or granivore) and the foraging substrates they exploit (bark, ground, foliage, canopy, or air) in order to examine the effects of the different matrices on functional groups of avifauna. Bird species were classified into these groups using data in Baker *et al.* 1997 (body mass) and Garnett *et al.* 1992 (foraging guilds and substrates).

As the matrix data captured were multi-variate, a principal components analysis (PCA) was used to analyze and highlight the difference in the matrix characteristics of the three different landscapes. The seven matrix measures described in Table 10.1 were entered into the PCA as environmental variables. The PCA was conducted in Community Analysis Package (CAP) software (Pisces Conservation, 2002).

Linear regressions of woodland-dependent species richness vs. remnant area and remnant isolation for the three different landscapes were calculated to test if there were differences between them. Linear regressions of log-species on log-area and log-species on log-isolation for the three landscapes were plotted and compared for accuracy of fit to untransformed or semi-log plots. Species-log area and species-isolation regressions fitted best. The slope of each regression in each landscape was thus compared, using the methodology described in Zar (1996: 292-294). This method uses a *t*-test in a fashion analogous to that of testing for differences between two populations. The test statistic is

$$t = \frac{b_1 - b_2}{S_{b_1 - b_2}} \quad (1)$$

where the variables b_1 and b_2 are the regression coefficients and Sb_1-b_2 is the standard error of the difference between the regression coefficients.

As patterns of spatial autocorrelation in data can influence results in these types of regression analysis, we conducted a spatial autocorrelation analysis in all three landscapes using SAAP 4.3 software (Wartenberg, 1989; Diniz-Filho *et al.*, 2003; Hawkins & Pausas, 2004). To evaluate the adequacy of the landscape regression models we generated spatial correlograms at 8 distance classes of the raw woodland species richness data in all three landscapes, using Moran's *I* coefficients (Legendre, 1993).

A three-step procedure was used to determine if individual species had significant relationships between remnant area, isolation or both (i.e. Fig. 2.2), and if these relationships varied between the three landscapes. First, presence/absence data for all resident woodland-dependent species were modelled statistically using binomial logistic regressions to determine the relationships between the occurrence of each species and the size and isolation of woodland habitat, in each landscape. Second, if a species was found to have a significant ($p<0.05$) relationship with area or isolation, a logistic regression equation was calculated to determine 'threshold' area and isolation sensitivities at an arbitrary 50% probability of occurrence, following the procedure and rationale of Aberg *et al.* (1995) and Helzer and Jelinksi (1999). If both remnant area and isolation were found to be significant in explaining the presence/absence of a species in a landscape, a step-wise logistic regression model (following Aberg *et al.*, 1995) was used to determine the strength of each variable in explaining the species distribution. A new variable in the step-wise analysis was created to distinguish between compensatory effects and the block pattern (Fig. 2.2; following Lomolino, 1986). This variable equalled '1' when the habitat coordinate was within the block formed by the area and isolation minimum requirements and '0' when it was outside the region. This new 'block' variable was used in a step-wise regression analysis with area and isolation to test whether the 'block' variable best accounted for the observed pattern. If the block variable was a better fit than the other two variables (i.e. area and isolation), we assumed the species had a block pattern but if the former variable had a better fit, we assumed the species had a compensatory effect pattern. This technique was used to determine each species' pattern of distribution across the three landscapes.

11.4 RESULTS

11.4.1 Patch and landscape characteristics

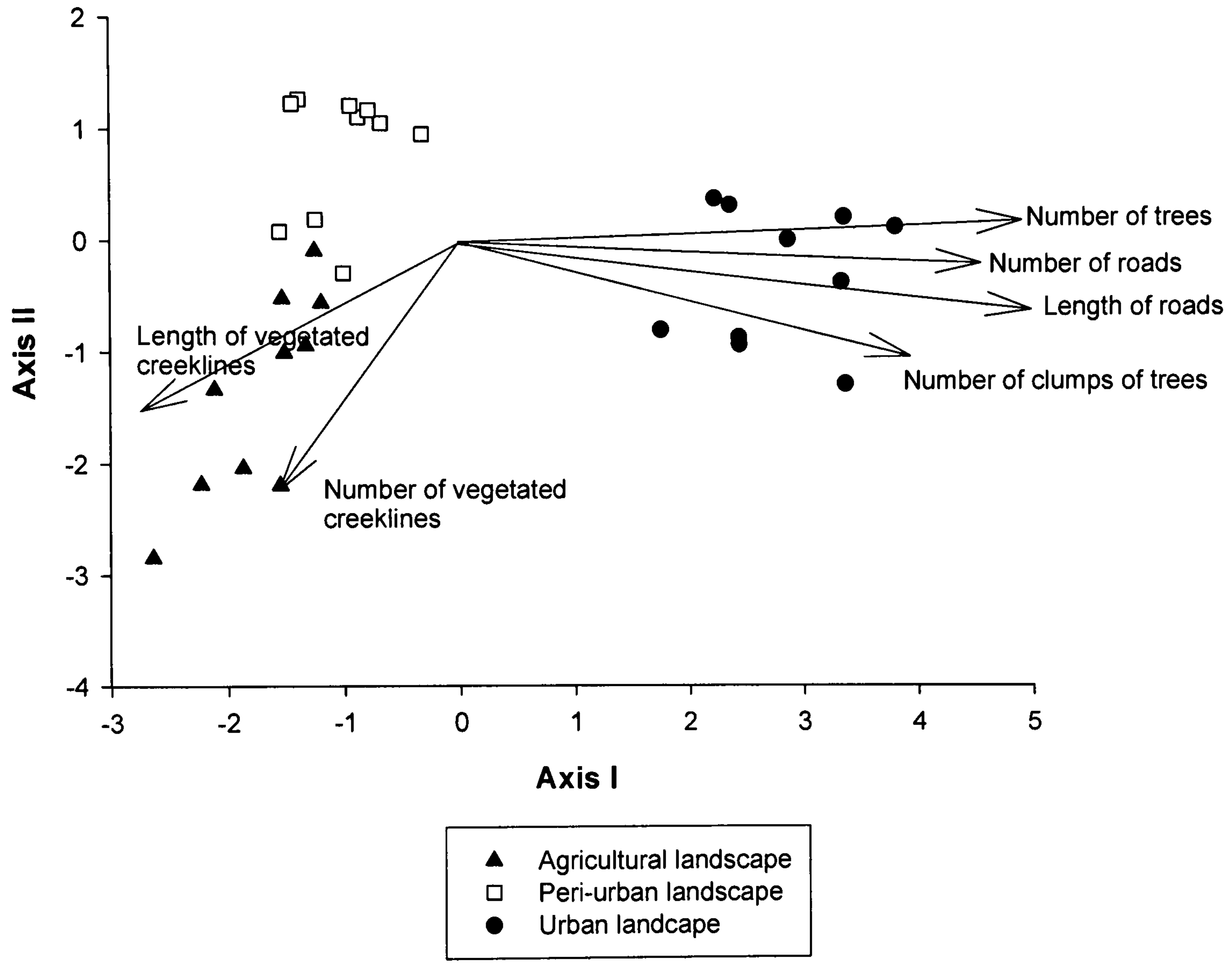
Each landscape had similar remnant area and isolation ranges, means and medians, suggesting that remnant distribution in the three landscapes was comparable (in all cases, well within an order of magnitude, Table 10.1). Remnant area and remnant isolation were independent of each other in all three landscapes (Fig. 11.1). There was a significant linear relationship between the log of remnant patch area and habitat complexity (condition) of the patch in all three landscapes (Fig. 11.2), indicating that small remnant patches, regardless of landscape, tended to have simpler habitat structure and larger remnant patches had more complex habitat structure.

The characteristics of the three landscape matrices were quite different. The agricultural matrix had fewer trees and nearly five times greater length of vegetated creeklines than the peri-urban matrix (Table 10.1). The amount of human settlement within the two matrices was also different with almost double the number of houses and triple the number of roads within the peri-urban landscape than the agricultural matrix. The urban matrix had a far greater number of houses, trees and road density than the other two landscapes. Two PCs accounted for 84.2% of the variation in matrix structure between the three landscapes. The first component separated the surveyed matrix circles on both the density (per km^2) of man-made objects (e.g. houses and roads) and the density of trees and clumps of trees (Fig. 11.3). The second component separated the surveyed matrix circles on the density of creeks and length of creek lines within the matrix sample. This ordination clearly showed that there were differences in matrix composition among three different landscapes. Predictably, there was overlap between the peri-urban and agricultural landscapes and no overlap between these landscapes and the urban landscape.

11.4.2 Avifauna of the region

In total, 130 bird species were identified within woodland remnants in the three landscapes: 115 in the agricultural landscape, 95 species in the peri-urban landscape and 90 in the Canberra urban landscape. The three landscapes had proportionally similar numbers of resident woodland species, with 54 species recorded from woodlands in the agricultural landscape, and the peri-urban and urban landscapes each having 43 species. Eleven woodland-dependent species were found only in the agricultural landscape (Black-chinned Honeyeater *Melithreptus gularis* Gould, Chestnut-rumped Heathwren *Hylacola pyrrhopygia* Mathews, Common Bronzewing *Phaps chalcoptera* Latham, Grey-crowned Babbler *Pomatostomus temporalis* Vigors & Horsfield, Little Friarbird *Philemon citreogularis* Gould,

Figure 11.3 Ordination diagram of the first two axes of principle components analysis for matrix environmental variables in three fragmented woodland landscapes in southeastern Australia. Axis I and II accounted for 62% and 22% of the variance in the environmental data. Arrows represent directions of greatest change of environmental variables. See Table 10.1 for definitions of environmental variables.



Painted Button-quail *Turnix varia* Mathews, Peaceful Dove *Geopelia striata* Rand, Red-capped Robin *Petroica goodenovii* Mathews, Superb Parrot *Polytelis swainsonii* Mathews, White-browed Woodswallow *Artamus superciliosus* Gould, Striped Honeyeater *Plectorhyncha lanceolata* Gould). This may, in part be due to the greater sampling effort (n=55 woodlands) in the agricultural landscape compared to the peri-urban (n=42) and the urban (n=30) landscapes. Twenty-seven woodland dependent species were found in more than 5 remnants in all three landscapes (Table 11.2). These species were used to develop individual logistic regression models of occurrence as a function of remnant area and isolation.

11.4.3 Species richness

For each landscape, we found no significant spatial autocorrelation between woodland remnant species richness and the location of the remnants. There was a significant ($p<0.0001$) relationship between resident woodland species richness and log remnant area in each of the three landscapes (Fig. 11.4). The tightest species-area relationship, with the greatest slope, was found in the urban landscape. The slopes of the urban and peri-urban regressions ($t=2.42$, df=68, $p<0.005$) and the urban and agricultural regressions ($t=2.95$, df=80, $p<0.0025$) were significantly different, but the slopes of the peri-urban and agricultural regressions ($t=0.87$, df=92, $p>0.10$) were not. When remnant isolation was considered, we found that there was a significant ($p<0.01$) relationship between remnant isolation and resident woodland species richness only in the agricultural landscape (Fig. 11.5). These results suggest that the urban matrix has a different and greater effect on the species-area relationship than the two other matrices and that the agricultural matrix appears to have an influence on species sensitivity to isolation, whereas the other two matrices do not.

11.4.4 Individual species responses

Of the 27 species analysed, remnant area explained a significant ($p<0.05$) portion of the deviance in the presence/absence logistic models of 16 resident woodland species, in one or more landscape (Table 11.2). Ten species were found to be area sensitive in all three landscapes, while two species were area-sensitive in the agricultural and peri-urban landscapes, and four species were found to be area-sensitive only in the urban landscape (Table 11.2). Remnant isolation explained a significant ($p<0.05$) portion of the deviance in the presence/absence logistic models of 10 woodland resident species, but only in the agricultural system (Table 11.2). Eight resident woodland species were affected neither by remnant area nor isolation in any of the landscapes.

Figure 11. 4 Woodland bird species richness (SP) vs. log area (A) regressions for woodland patches in a) agricultural landscape, b) peri-urban landscape and c) urban landscapes [urban $F_{1,\ 28} = 50.4$, $P < .0001$, $r^2=0.64$, $SP = 0.37 + 8.95 \log(A)$; peri-urban $F_{1,40}= 46.4$, $P<0.0001$, $r^2=0.53$, $SP = 5.3 + 5.5 \log(A)$; agricultural $F_{1,53}= 21.7$, $P<0.0001$, $r^2= 0.54$ $SP = 8.9 + 4.11\log(A)$].

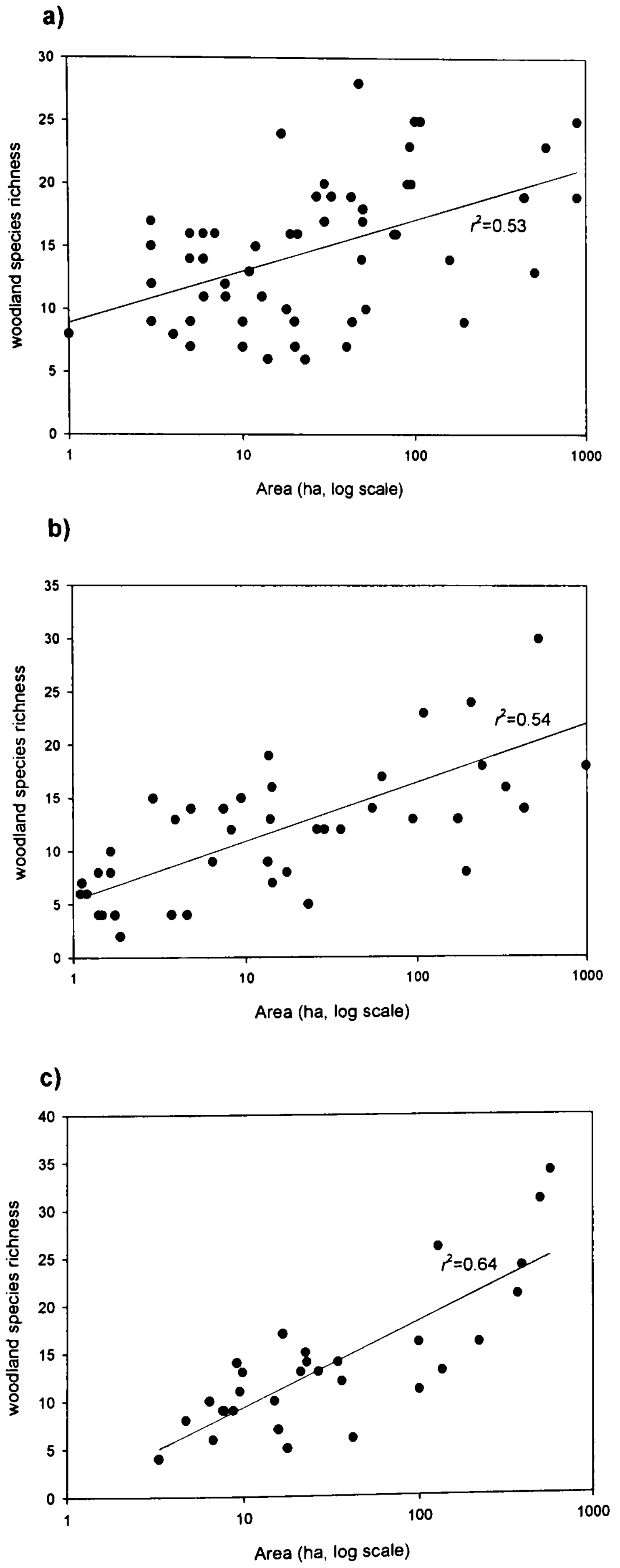
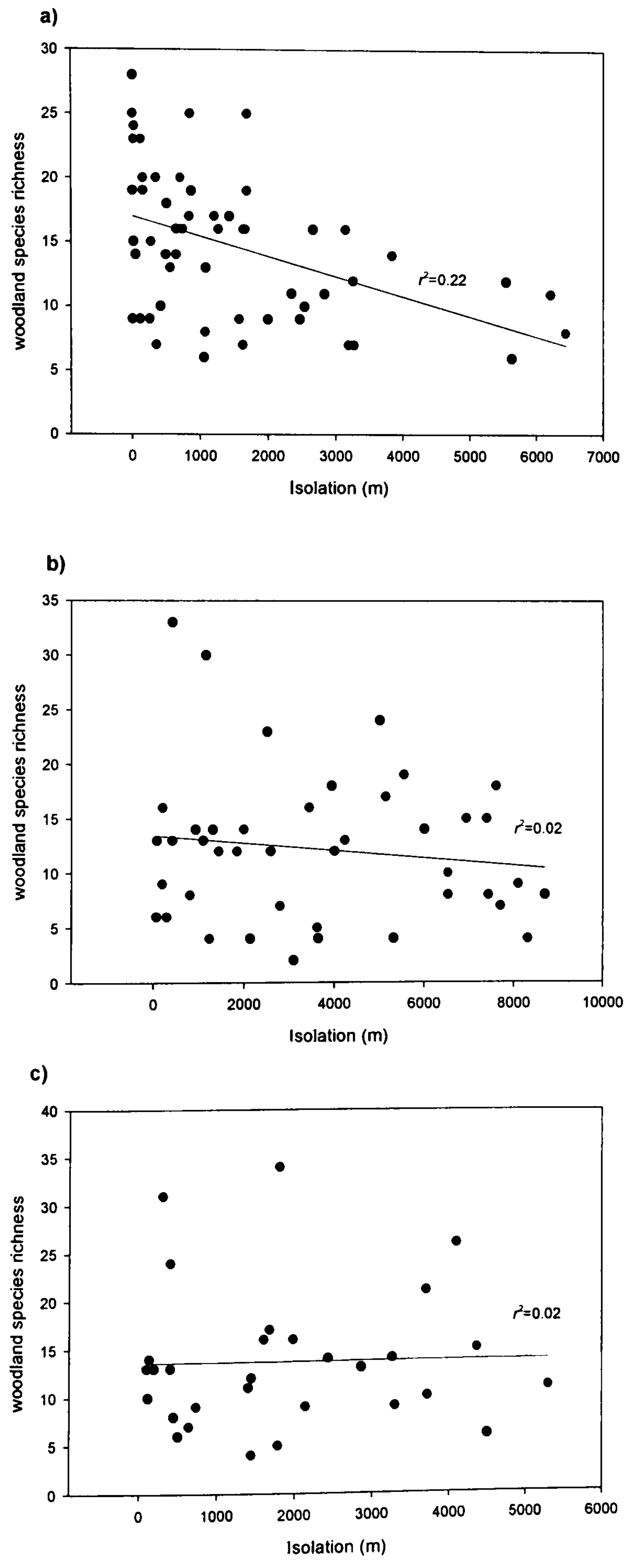


Figure 11.5 Woodland bird species richness (SP) vs. isolation (I) regressions for woodland patches in a) agricultural landscape, b) peri-urban landscape and c) urban landscapes. Remnant isolation was calculated as the distance to the nearest remnant equal to or greater than 10 ha in size. Only the agricultural landscape species-isolation regression was significant [(agricultural $F_{1,53} = 15.1$, $P<0.001$, $r^2 = 0.22$, $SP = 16.97 - 1.54\ (I)$; urban ($F_{1,28} = 0.03$, $P=0.95$, $r^2 = 0.01$; peri-urban $F_{1,40}=0.76$, $P=0.38$, $r^2=0.02$)].



Using the results of the logistic analyses, we identified six broad patterns of sensitivity to remnant area and/or isolation in the three landscapes (Table 11.2). The largest group (n=8) was of species considered 'tolerant', as they occurred in most or all remnant sizes, irrespective of degree of isolation. A second group of four species was found to be area sensitive in all three landscapes, but not sensitive to isolation in any landscape. A further four species were area-sensitive only in the urban landscape and not sensitive to isolation in any landscape. Two species were found to be area-sensitive in peri-urban and agricultural landscapes but not in urban landscapes, with one of these species (Brown Thornbill *Acanthiza pusilla*) appearing to be sensitive to isolation in the agricultural landscapes.

Six species were significantly ($p<0.01$) affected by remnant area and isolation in the agricultural landscape (Table 11.2). All six species were found to have a compensatory effect between area and isolation (e.g. Eastern Yellow Robin *Eopsaltria australis* Shaw; Fig. 11.6) and no species displayed a 'block' pattern (Fig. 2.2). Another group comprising three species were sensitive only to isolation in the agricultural landscape and were not area-sensitive in any landscape (Table 11.2).

The 'threshold' values, defined as the area/isolation where 50 % probability of occurrence is reached, for area-sensitive species ranged from 5 ha (Weebill *Smicrornis brevirostris* Gould in urban landscapes) to 990 ha (Eastern Yellow Robin *E. australis* in peri-urban landscapes). Many species found to be area-sensitive in all three landscapes were found to have markedly different threshold values in each landscape (Table 11.3). For example, the Brown Treecreeper *Climacteris picumnus* Temminck had a threshold of 40 ha in the agricultural landscape, 320 ha in the urban landscape and 410 ha in the peri-urban landscape. The Eastern Yellow Robin *E. australis* was equally variable its threshold; 73 ha in the agricultural landscape, 101 ha in urban landscape and 990 ha in the peri-urban landscape (Table 11.3).

Figure 11.6 Area-isolation plots for Eastern Yellow Robin *Eopsaltria australis* in three fragmented woodland landscapes [a) agricultural, b) peri-urban, c) urban] in southeastern Australia. Open circles are unoccupied remnants, while closed circles represent remnants in which the species occurs. This species displayed a minimum area pattern in urban and peri-urban landscapes and a compensatory pattern in the agricultural landscape (see Fig. 2.2). The dashed lines represent the arbitrary species threshold where above the filled line the probability of occurrence is > 50%. Thresholds were determined using a logistic regression equation following Aberg *et al.* (1995), Helzer and Jelinksi (1999).

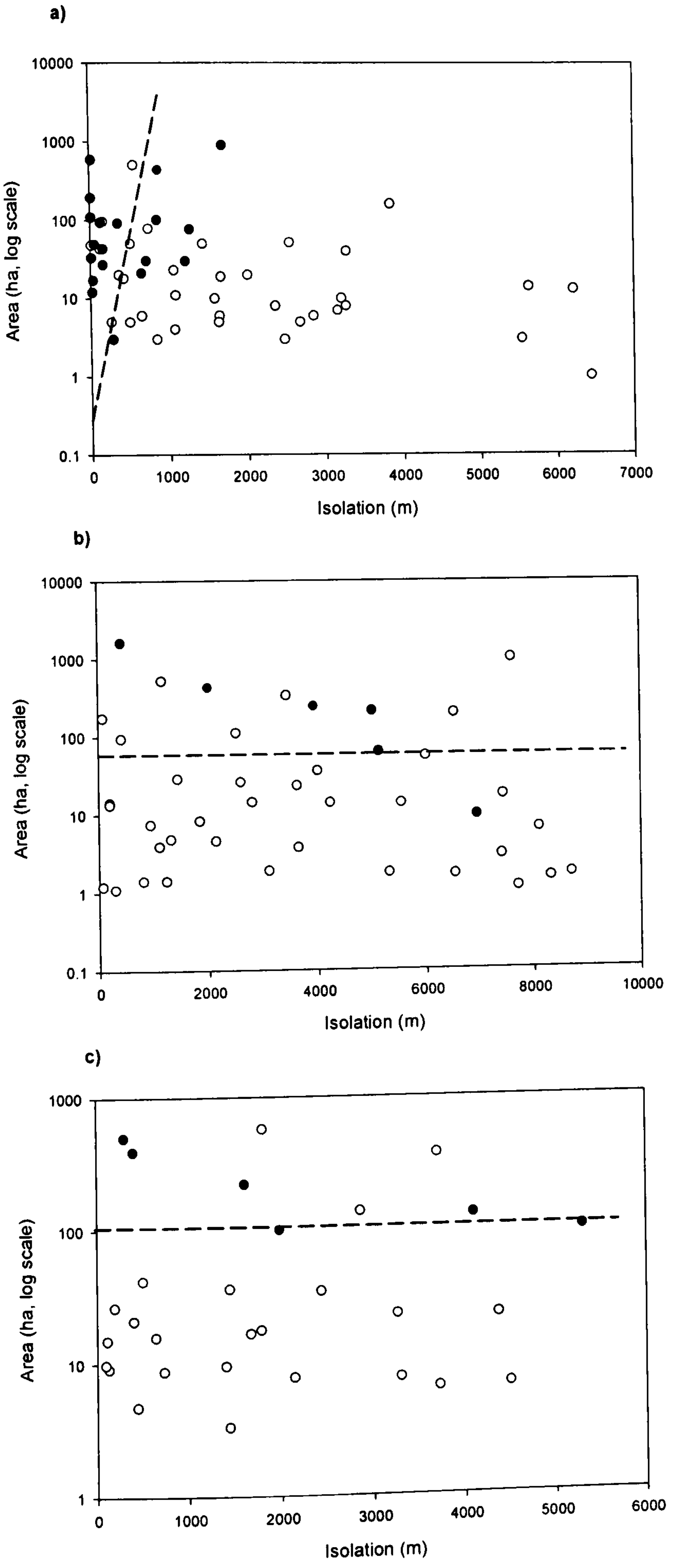


Table 11.2 Mean deviance in individual-area and individual-isolation logistic regression models for resident woodland bird species in woodland remnants of three distinct landscapes: agricultural (n=55), peri-urban (n=42) and urban (n=30) in the region of the northern Australian Capital Territory and surrounding areas of New South Wales. Birds have been categorised into four groups, based on their sensitivity to remnant area and remnant isolation. Bird species were categorised based on their body mass, foraging niche (insectivore, nectivore, granivore) and the foraging substrates (bark, ground, foliage, canopy, air) using Baker *et al.* (1997) (body mass) and Garnett *et al.* (1992) (foraging guilds and substrates). *$p<0.05$, **$p<0.01$

Bird name and category				**Agricultural**		**Peri-urban**		**Urban**	
	Body size (g)	Foraging substrate	Foraging habit	Area	Isolation	Area	Isolation	Area	Isolation
Non-sensitive species									
Crimson Rosella *Platycercus elegans*	53	canopy	granivore	0.7	2.9	0.3	2.1	2.7	1.2
Striated Pardalote *Pardalotus striatus*	11	shrub	insectivore	0.3	0.4	0.4	1.4	0.7	0.2
Yellow-rumped Thornbill *Acanthiza chrysorrhoa*	9	shrub	insectivore	1.3	0.2	0.3	0.6	2.2	1.7
Restless Flycatcher *Myiagra inquieta*	20	sallying	insectivore	0.3	1.5	0.2	0.7	1.3	0.2
Mistletoebird *Dicaeum hirundinaceum*	9	canopy	nectivore	1.1	0.3	0.9	1.2	2.1	0.9
Noisy Friarbird *Philemon corniculatus*	115	canopy	nectivore	2.8	0.2	1.2	0.9	1.3	0.3
Noisy Miner *Manorina melanocephala*	58	canopy	insectivore	1.5	1.2	0.4	0.5	1.1	0.1
Dusky Woodswallow *Artamus cyanopterus*	35	aerial	insectivore	0.1	0.8	0.3	0.6	1.2	0.9
Sensitive to remnant area in all landscapes									
Brown Treecreeper *Climacteris picumnus*	33	terrestrial	insectivore	5.5**	2.6	7.5**	2.1	3.3*	2.3
Speckled Warbler *Chthonicola sagittata*	14	terrestrial	insectivore	4.3*	1.7	4.5*	1.1	4.8*	0.3
Striated Thornbill *Acanthiza nana*	6	shrub	insectivore	5.5*	3.1	3.2*	1.2	3.4*	0.24
Brown-headed Honeyeater *Melithreptus brevirostris*	14	canopy	nectivore	6.8**	1.5	4.3*	1.3	5.1**	0.7

Table 11.2 cont.

Sensitive to remnant area and isolation only in the agricultural landscape									
White-throated Treecreeper *Cormobates leucophaeus*	22	bark	insectivore	3.5*	9.6**	8.3**	1.3	3.3**	0.6
Buff-rumped Thornbill *Acanthiza reguloides*	8	shrub	insectivore	6.8*	6.7**	10.1**	2.1	7.3**	2.3
Eastern Spinebill *Acanthorhyncus tenuirostris*	11	shrub	nectivore	3.9*	3.8*	4.1*	0.7	4.2*	0.5
Little Wattlebird *Anthochaera carunculata*	110	canopy	nectivore	9.6**	7.1**	4.1**	2.9	5.6**	0.4
Eastern Yellow Robin *Eopsaltria australis*	19	ground	insectivore	9.3**	8.1**	4.1*	1.6	5.1**	0.4
White-winged Chough *Corcorax melanorhamphos*	358	terrestrial	insectivore	3.5*	6.8**	7.7**	2.9	8.8**	0.1
Sensitive to isolation only in the agricultural landscape									
Striated Thornbill *Acanthiza lineata*	7	shrub	insectivore	0.2	5.6**	1.1	2.3	0.5	1.4
White-eared Honeyeater *Lichenostomus leucotis*	20	shrub	insectivore	1.8	6.4**	2.1	1.8	0.9	0.8
Fuscous Honeyeater *Lichenostomus fuscus*	17	canopy	nectivore	3.1	4.7*	2.2	2.3	0.1	1.5
Sensitive to area only in the urban landscape									
Crested Pigeon *Ocyphaps lophotes*	210	terrestrial	granivore	0.2	0.3	1.1	0.1	5.9**	0.4
Eastern Rosella *Platycercus eximius*	99	canopy	nectivore	1.2	2.7	0.9	1.5	7.4**	3.1
Jacky Winter *Microeca fascinans*	14	terrestrial	insectivore	0.2	1.7	1.4	0.2	3.8*	0.1
Brown Shrike-thrush *Colluricincla harmonica*	63	shrub	insectivore	0.5	0.1	2.3	2.1	8.5**	0.1
Sensitive to isolation in the agricultural landscape and area in peri-urban and agricultural landscapes									
Brown Thornbill *Acanthiza pusilla*	9	shrub	insectivore	0.9	6.4**	6.7**	0.3	4.1*	0.9
Sensitive to area in peri-urban and agricultural landscapes									
Weebill *Smicrornis brevirostris*	6	shrub	insectivore	0.9	0.5	8.4**	0.2	3.4*	0.1

Table 11.3 'Threshold' area (ha) and isolation (m) values of bird species in woodland remnants of three landscapes (agricultural, peri-urban, urban). Following Helzer and Jelinski (1999), threshold values were defined as the area or the isolation measure where a species reached 50% probability of occurrence in their individual area and isolation incidence functions. Incidence functions were developed from logistic regressions based on the presence/absence data for all six species in each landscape. If a species did not reach 50% probability of occurrence within the limits of the data, no minimum area requirement was calculated.

Bird name and category	**Agricultural**		**Peri-urban**		**Urban**	
	Area	Isolation	Area	Isolation	Area	Isolation
Sensitive to remnant area						
Climacteris picumnus	40	-	410	-	320	-
Chthonicola sagittata	390	-	365	-	180	-
Acanthiza nana	40	-	30	-	35	-
Melithreptus brevirostris	160	-	40	-	45	-
Sensitive to remnant area and isolation in agricultural landscapes						
Cormobates leucophaeus	3	2600	19	-	60	-
Acanthiza reguloides	18	1640	13	-	41	-
Acanthorhyncus tenuirostris	580	450	310	-	410	-
Anthrochaera carunculata	40	780	35	-	45	-
Eopsaltria australis	73	560	990	-	101	-
Corcorax melanorhamphos	190	260	209	-	105	-
Sensitive to isolation in the agricultural landscape						
Acanthiza lineate	-	1270	-	-		-
Lichenostomus leucotis	-	200	-	-		-
Lichenostomus fuscus	-	230	-	-		-
Sensitive to area in the urban landscape						
Microeca fascinans	-	-	-	-	140	-
Colluricincla harmonica	-	-	-	-	200	-
Ocyphaps lophotes	-	-	-	-	40	-
Platycercus eximius	-	-	-	-	35	-
Sensitive to isolation in agricultural landscapes and area in peri-urban and rural landscapes						
Acanthiza pusilla	-	-	35	-	140	-
Sensitive to area in peri-urban and rural landscapes						
Smicrornis brevirostris	-	-	90	-	5	-

Woodland dependent birds were significantly affected by remnant isolation in only the agricultural landscape. The isolation threshold values (50% probability of occurrence) varied from 200 - 2600 m between species, with the White-throated Treecreeper *Cormobates leucophaeus* Latham having the largest threshold distance (Table 11.3).

11.5 DISCUSSION

Whilst this study comprises a large sample effort, with 127 woodlands enumerated, we have no replication of landscapes. We therefore cannot claim that the relationships described herein are characteristic for each landscape type, e.g., that the species-incidence relationships reported for Canberra would be repeated for other urban landscapes in eastern Australia. However, we have shown that resident woodland bird species differed in their response to remnant patch size and isolation across the three contrasting landscapes. Whilst it is important to acknowledge that there might be ecologically relevant differences in the properties of the woodland remnants that were not quantified in our study, it appears unlikely that intrinsic properties of the remnants could account for the pronounced differences in species incidences. This is because the spatial pattern, size distribution, level of disturbance to habitat, and floristic composition of woodland remnants were similar in all three landscapes (Fig. 11.1, 11.2; Table 10.1; Watson, 1999; Freudenberger, 2001). Moreover, each landscape experiences a similar climate due its proximity to each other and similar altitude (Bureau of Meteorology, 2004). We therefore consider that the variation in species' relationships with remnant area and isolation are most parsimoniously explained as a function of differences in the properties of the landscape matrix surrounding the woodland remnants.

It was beyond this study to discern the reasons why species had varying area-sensitivity and isolation-sensitivity responses in these landscapes, but there are a number of plausible hypotheses for how the condition of the matrix could affect bird distribution within woodland remnants. Firstly, different matrix conditions will affect the 'edge-contrast' between woodland remnant and matrix, which will change many edge and internal properties of a woodland fragment. This is because the 'edge-contrast' governs the micro-climate gradient at the edge of a remnant, which in turn could lead to substantial vegetation changes (including changes in species composition and structure) and biological changes (including increases in predators, nest predators and nest parasites and changes in food resources) along the new edge (Robinson *et al.*, 1995; Kapos *et al.*, 1997; Zanette *et al.*, 2000; Rankin-De Mérona & Hutchings, 2001). This could change the rates of nest predation, nest parasitism or inter-specific competition within woodland remnants, as well as the availability of food and resources, all of which will affect a bird species area-sensitivity (Ambuel & Temple, 1983; Wilcove 1985; Soulé *et al.*, 1988; Robinson, 1992; Burke & Nol, 1998; Grey *et al.*, 1998; Crooks & Soulé 1999). Secondly, different landscape matrices have different resources within them, and therefore have differential capacity for different species – if a species cannot use the resources of a particular matrix, the population may be dependent on a bigger area within the remnant habitat itself to sustain a population in a fragment (Lindenmayer *et al.*, 2003).

This variation in individual species responses underpins the differences in species-area relationships between the three landscapes (Fig. 11.4). Wethered and Lawes (2003) report a similar matrix-effect for birds in the Afromontane Mistbelt of South Africa, as they found a strong species-area effect in forest patches surrounded by grassland but no effect for forest patches surrounded by commercial plantation matrix. They concluded that commercial plantations may increase the likelihood of movements of birds into small native forest patches. We found that the urban landscape had the steepest slope (i.e. had the greatest area effect). In addition to threats mentioned above, bird populations in small urban woodland remnants may be threatened by factors such as (i) greater competition with exotics such as European Starlings *Sturnus vulgaris* Linnaeus (Kerpez & Smith, 1990), (ii) exposure to larger populations of predators such as domestic cats (Marzluff & Restani, 1999), and (iii) heightened disturbance and mortality from human activity (Knight & Gutzwiller, 1995; Evans, 1998). However, it is not the case that the urban landscape was the most 'hostile' (sensu Watson, 2002) matrix for all species. Rather, trends in area-sensitivity were shown to be species-specific and not landscape-specific (Tables 10.2 and 10.3).

Woodland-dependent species richness was significantly ($p<0.01$) correlated with remnant isolation only in the agricultural landscape (Fig. 11.5), within which we found 10 individual species that were statistically sensitive to remnant isolation (Table 10.2). This may be due to a lack of connectivity within the agricultural landscape matrix as there are fewer paddock trees within the matrix and therefore the remnants are acting more like true islands. Alternatively, or additionally, the agricultural matrix may be home to different alien species and threatening processes (e.g. predators), which could impact the dispersal capabilities of some species between remnants (Andrén, 1994; Stouffer & Bieergaard, 1995b; Sisk *et al.*, 1997). Interestingly, we found that seven species were sensitive to area and isolation in the agricultural landscapes, with all species displaying a compensatory effect (as Fig. 2.1e.). That is, these species occurred in small remnants only if they were weakly isolated. This pattern has been described in insular mammals in the Thousand Islands region of New York (Lomolino, 1986) but was not found in resident bird communities in humid pine-oak forest fragments in Oaxaca, southern Mexico (Watson, 2002).

11.5.1 The role of the matrix in conservation biology and ecological theory

How matrix characteristics influence changes in bird species richness in small forest patches is not well known. The matrix may influence ecological functions within small patches (Estades & Temple, 1999, Fischer & Lindenmayer 2002a) by determining the likelihood of successful movement of birds between forest fragments (Stouffer & Bierregaard, 1995b, Sisk *et al.*, 1997; Fisher & Lindenmayer, 2002a, b; Lindenmayer *et al.*, 2002). By exploring the effect of remnant area and remnant isolation on individual woodland species in different landscapes, we have highlighted that it is not a simple matter of measuring matrix (cf Watson, 2002) hostility but a complex, often counter-intuitive, interaction between individual species and matrix type.

Numerous approaches in conservation biology, from theoretical modelling (e.g. Lindenmayer & Lacy, 1995; With, 2002) to practically oriented ecology (e.g. Lambeck, 1997; Brooker *et al.*, 2002) have been used to explore and explain how species react to habitat loss and fragmentation. Many of these models or approaches ignore matrix characteristics as an explanatory factor. The results in this study suggest that there is a danger of over generalising and thus trivialising species-area and species-isolation relationships. Our results indicate that the structure, composition and disturbance regimes of the matrix may strongly influence both the area-sensitivity and/or dispersal behaviour of a bird species in highly fragmented landscapes. If the matrix properties are considered in metapopulation modelling, for example, the projections of the survival probability may be incorrect, as these values may not necessarily predict the immigration rates into patches (Tischendorf *et al.*, 2003). Landscape matrices cannot be assumed to be a hostile 'sea' of non-habitat. For some species the matrix may be habitat most of the time (Manning *et al.*, 2004), while for other species a 50 m gap between patches of forests may be a sufficient barrier to dispersal (Brooker & Brooker, 1997, 2001).

Furthermore, the search for general biogeographic patterns such as body-size and area-incidence relationships (e.g. Bierdermann, 2003), or general biogeographic theories that explain species presence in fragmented landscapes (e.g. Lomolino, 2000; Watson 2002) may be problematic when landscape context is considered. For example, we showed that species with the same mass may have very different probability of occurrences (Table 11.3) in landscapes with different matrices surrounding remnants, thereby confounding the general pattern suggested by Bierdermann (2003). This finding goes against other studies that have shown that body mass is correlated with minimum patch size (e.g. Leck, 1979; Beier *et al.*, 2002) and is inconsistent with the hypothesis that if home range size scales to body mass, area-sensitive birds will be absent from patches smaller than a few home ranges (Stratford & Stouffer, 1999). In our study area, some small bodied birds may have relatively higher minimum patch size requirements because they may be more susceptible to small environmental perturbations (Johst & Brandl, 1997, Gaston & Blackburn, 2000), which will occur with more frequency in small remnants.

Lomolino's (2000) species-based theory of insular zoogeography employs the concept of 'immigration filters' to show the impacts of the matrix on area-isolation relationships of species. In our study we do not find a common response to matrix condition. Rather, species area vs. isolation relationships can change considerably across landscapes with markedly different matrices, but similarly fragmented remnants. While identifying broad general biogeographic patterns can be useful to guide conservation planning in fragmented landscapes, the assumption that species or functional groups will conform to remnant area reduction and remnant isolation in a consistent fashion, needs to be re-addressed on the basis of this empirical evidence. Overlooking processes such as differential responses to matrix conditions could lead to the creation of too broad a framework or theory, and perhaps ultimately poor conservation strategies (Lindenmayer & Franklin, 2002; Lomolino & Smith, 2003; MacDonald & Kirkpatrick, 2003).

11.5.3 Conservation implications

Perhaps the clearest finding in this study in terms of bird conservation in the region is the large number of resident woodland species (in particular small insectivorous species) that were found to be area-sensitive in all landscapes. This area-effect in resident woodland bird species is now well documented in Australia (e.g. Saunders, 1993; Zanette *et al.*, 2000; Major *et al.*, 2001; Mac Nally & Horrocks, 2002; Watson *et al.*, 2003). The majority of these studies argue that conservation strategies should protect larger woodland remnants, buffer and rehabilitate small woodland remnants and create habitat corridors. We agree that this is a logical starting point, but this and other recent work leads us to suggest that small patches and appropriate matrix management can be valuable components of a conservation strategy (Margules & Pressey, 2000; Fischer & Lindenmayer 2002). In fact at the scale involved in our system, corridors may not be required for many bird species if matrix conditions allow for adequate dispersal and colonisation. Small patches, isolated trees or urban street trees in the matrix may serve as 'stepping stones' and thus facilitate movement through the landscape; especially in the agricultural landscape where some bird species are affected by remnant isolation (Potter, 1990; Fisher & Lindenmayer, 2002a,b). The matrix habitats may also contain resources that are rare in the landscape or absent from larger patches (Zimmerman & Bierregaard, 1986). Moreover, it is likely that small patches have other ecologically desirable functions –for example, they may stabilise soils, reduce salinity and provide habitat for less area-sensitive species like small reptiles and invertebrates (summarised in Fisher & Lindenmayer, 2002). Therefore, our findings are consistent with research encouraging a more multi-faceted conservation approach than typifies earlier work viewing woodland fragments as islands in an essentially hostile sea of non-habitat. We strongly encourage conservation programmes that maintain woodland vegetation within the matrix habitats, especially agricultural environments where paddock trees are rare and declining (Ozolins *et al.*, 2001; Gibbons & Boak, 2001).

11.5.4 Conclusion

Protecting biodiversity in fragmented landscapes will require substantial conservation and ecosystem restoration efforts (Young, 2000; Lindenmayer *et al.*, 2002). In the past, these efforts have focussed on either creating corridors or buffering remnant areas to make them bigger (Marzluff & Ewing, 2001). Our study strongly suggests that landscape matrix characteristics play an important role in determining how individual species respond to processes associated with habitat fragmentation. Species cannot be assumed to respond in a consistent fashion across landscapes because fragmentation processes appear to interact with matrix conditions to produce highly individualistic responses. Indeed, it is noteworthy how substantial the variation in form of incidence functions and critical areas for patch occupation is for some of our study species. With this paper we hope to stimulate further research and discussion concerning the factors controlling such variation and how to develop approaches for landscape conservation in fragmented landscapes that incorporate matrix management. To assist conservation and restoration efforts, more research is needed on how the matrix affects animal distributions in fragmented landscapes; especially how different taxa disperse through different landscapes.

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CHAPTER 12

CONCLUSION

12.1 Introduction

This thesis has investigated the effects of habitat fragmentation on birds at three spatial scales (patch, landscape and regional) in two different case study areas and ascertained whether it is appropriate to use island theory to derive appropriate conservation plans within these study systems. To achieve these aims, I outlined seven objectives within the Introduction chapter (section 1.4). Separate chapters and papers have addressed the first five objectives while the discussions sections of all the research chapters have jointly addressed the last two objectives. This chapter aims to synthesise the main conclusions presented in the papers that make up the core of this thesis, under headings relating to the seven objectives of the research. As the seventh objective is aimed at discussing the theoretical implications of the research conducted in both case study systems, this chapter focuses on this objective in more depth. The chapter ends by discussing the limitations of this research and suggests directions for future research in both study areas and for habitat fragmentation-related research in general.

In summary, this thesis has shown that bird species distributions in the fragmented littoral forests of southeastern Madagascar are driven not just by regional and landscape-scale factors such as remnant area and the geographic location of a forest remnant, but also by local influences such as vegetation complexity and proximity to remnant edge. It also has shown that woodland bird distribution in different fragmented landscapes in southeastern Australia appears to be affected not just by remnant area and isolation, but also by the composition of the surrounding matrix habitat. These findings have important consequences for conservation in the two regions and significant implications for theoreticians, researchers and modellers who still base fragmentation research on the paradigms of island theory. Scale-dependent processes associated with habitat fragmentation such as local habitat complexity, the shape of a remnant, and the nature of the matrix surrounding a habitat island, must be given greater attention if any predictive general theory is to be produced on the effects of habitat fragmentation on biodiversity.

12.2 Objective 1: Review the effects of habitat fragmentation on birds and examine theory that has been used in habitat fragmentation studies

Chapter 2 provided a review of the effects of habitat fragmentation on birds and also a review of the theories that have been used as a basis for previous habitat fragmentation studies. In this chapter, I show that the development of MacArthur and Wilson's (1963, 1967) ETIB was, in essence, the start of fragmentation research. This original theory led to the development of other ideas on how to assess the effects of fragmentation on biodiversity, all based on the island-habitat fragment analogy. These 'island theories' have been the basis of the study conducted on the effects of habitat fragmentation on biota and I argue that now (even with the growth of landscape ecology), island theory is still playing a central role in both the development of conservation guidelines and the determination of future predictions of species loss, in fragmented landscapes. Two relatively modern examples of the continued development of island theory are Lomolino's (2000a) species-based theory and Watson's (2002) conceptual framework for studying species composition in habitat fragments. These are both based on the island-habitat patch ideals and provide evidence that island theory is still the basis of modern fragmentation research. As a consequence, I used this review of the fragmentation theory literature as justification to assess the role of island theory in the empirical case studies conducted in Madagascar and Australia.

By reviewing the past fragmentation literature that have focussed on the effects of fragmentation on bird diversity, I showed that it is essential to consider the fragmentation process at the local, landscape and regional scales. I found that there are very few general trends among the many fragmented systems that have been studied, with many systems showing case-specific tendencies. This review therefore justified the need to consider the effects of habitat fragmentation at different spatial scales in the Madagascan and Australian case studies.

12.3 Objective 2: Determine an appropriate way to conduct a rapid bird census in the littoral forests of southeastern Madagascar

Chapter 4 contributed to the debate on the application of rapid assessment bird methodologies (i.e. MacKinnon lists and point counts) in little-studied ecosystems. It did this by comparing a species-rich system (cloud forests in Ecuador) and, for the tropics, a species-poor system (littoral forests in Madagascar). Specifically, Chapter 4 shows that both MacKinnon lists and point counts were suitable in the Madagascan littoral forests as bird species-accumulation and species-estimation curves plateau (Figures 4.1 and 4.2) for both survey methodologies. Therefore, the use of either bird methodology was satisfactory in capturing the total species richness within each littoral forest remnant surveyed, with the MacKinnon List technique being more time-effective in data entry than the point counts (Tables 4.1, 4.4). However, it was also shown that data collected by each bird census method reflected different patterns of relative abundance among the five most abundant species in the littoral forest system (Table 4.2), with MacKinnon list data showing a bias towards solitary and territorial species and against monospecific flocking species relative to the point count data. As a consequence of this bias, MacKinnon list data fail to reflect accurately the structure of communities as quantified by an index of community evenness.

I (along with the other authors on this paper) proposed a hybrid rapid assessment methodology that capitalises on the strengths of both techniques while compensating for their weaknesses. I used this hybrid technique when assessing the effects of patch and landscape fragmentation on birds in the littoral forests, by using point counts to determine individual species abundances and using both point count data and MacKinnon Lists to ascertain total species richness in each remnant.

12.4 Objective 3: Determine which bird species inhabit the littoral forests of southeastern Madagascar, and how these species compositions compare to other forested habitats in the region

Chapter 5 described the bird communities that inhabit the littoral forests of southeastern Madagascar and determined whether these communities differed from the bird communities of other forested habitats in the region. The analysis conducted in this chapter, in particular the NMDS ordination (Figure 5.2) and ANOSIMs (Table 5.4), showed that the littoral forests contained a unique bird assemblage compared to the other forested habitats in the region. The analyses also showed that the Petriky littoral forest sub-type was different to the Mandena and Ste-Luce sub-types. The species accumulation curves (Figure 5.1) highlighted the fact that the habitats immediately surrounding littoral forest remnants were depauperate of bird species (a result that was also shown in the edge analysis, Chapter 6). The similiarity indices (Table 5.2 and 5.3) and ANOSIM analysis (Table 5.4) showed that geographic location of littoral forest remnants had an important role in determining what bird species occurred within them, with the large northern remnants having similar bird communities to nearby humid forest whilst the most southern remnant had a bird community that resembled those of nearby spiny forest habitats.

The research in this paper showed that eleven bird species that have been previously described as being habitat-restricted endemics to either spiny forests or humid forests, were found in littoral forest remnants. These results suggest that littoral forest remnants may play an important transitional role between the two other major natural forest habitats (spiny forest and humid forest) of southeastern Madagascar, which serve to highlight the national importance of these forests and the need to prioritise their conservation.

12.5 Objective 4: Examine how fragmentation of littoral forests affect bird diversity at the local and landscape scales

This objective was met by two chapters, Chapter 6 and 7. Chapter 6 focussed on the effects of habitat fragmentation on birds at the patch scale in the littoral forests. Prior to conducting this patch-scale analysis, I determined which species were forest-dependent and which were generalist by conducting bird surveys in littoral forest and surrounding non-forest (matrix) habitats, (Appendix 3). The results of these surveys showed that the matrix habitats had very different bird communities to the littoral forests (Figure 6.3; Table 6.2). Forty species out of a total of 74 were not found in non-littoral forest habitats and were hence classified as forest-dependent. When abundances at edge sites were compared with core sites, it was found that littoral forest core habitats had significantly ($p<0.01$) more bird species than forest edge and matrix habitats. Moreover, thirty-one (68%) forest dependent species were found to be edge-sensitive with forest edge sites having fewer species, and a higher representation of common species than forest interior sites. To determine if species were affected by patch-scale fragmentation, I used step-wise regressions to ascertain which aspects of vegetation structure were affecting bird abundance and distribution across the two littoral forest patches. The distributions of nine edge-sensitive species were significantly ($p<0.01$) affected by changes in habitat complexity and vegetation vertical structure in core or edge point counts (Tables 6.4 and 6.5).

Chapter 7 focused on the landscape-scale effects of habitat fragmentation in littoral forests by assessing the effects of landscape metric variables (see Table 7.1) on the distribution of birds in the Ste-Luce and Mandena littoral forests. This was achieved by using Canonical Correspondence Analysis (CCA), step-wise regressions and binomial logistic regressions. Bird species richness and forest-dependent bird species richness were significantly ($p<0.01$) explained by remnant area (Figure 7.1), with 22 forest-dependent species having significant relationships with remnant area. Minimum area requirements for area-sensitive species ranged from 15 to 150 ha, with the majority of species having area requirements > 30 ha (Appendix 4). The distribution of four forest-dependent species also appeared to be related to remnant shape where remnant area was less than 100 ha (Figure 7.3). A surprising finding was that bird species richness or individual bird species abundance was not affected by any measure of isolation or landscape complexity.

12.6 Objective 5: Examine how fragmentation of Australian woodland influences bird distributions at a regional scale

Chapters 10 and 11 assessed the effect of habitat fragmentation on Australian woodland birds at a regional scale by assessing the differences in response of bird species in three distinct woodland landscapes. Chapter 10 specifically focussed on six area-sensitive species to determine how their bird species area-incidence functions and minimum area requirements varied within the different woodland landscapes. The incidence function analyses (Figure 10.1) showed there was no uniformity in which landscape the six species were most area-sensitive, with three species appearing to be most area sensitive in the urban landscape and two species most area sensitive in the agricultural landscape. Remnant area was found to explain a significant ($p<0.05$) portion of the deviance in the logistic regressions for three of the six species in all three landscapes, while the other three species were found to be area sensitive in two of the three landscapes (Table 10.2). The variation in form of incidence functions appears most parsimoniously explained as a function of the differing properties of the matrix within which the three sets of woodland fragments are embedded.

Chapter 11 examined the woodland bird community of the same three woodland landscapes and determined if species richness-area and species-richness isolation relationships varied between them. In addition to this, the paper looked at how individual species area-isolation relationships change in the same three landscapes described above. All the landscapes displayed a significant (p<0.01) species vs. area relationship, but the slope of the urban relationship was significantly greater than those of the other landscapes (Figure 11.3). In contrast, only the agricultural landscape displayed a significant (p<0.01) species richness vs. isolation relationship (Figure 11.4). When individual species were investigated, we found a number of distinct response groups: (i) species that were apparently insensitive to reduction in remnant area and increase in isolation across all landscapes, (ii) species that were absent in small remnants in all landscapes, (iii) species that were absent in small remnants in all landscapes and also absent in isolated remnants in the agricultural landscape, (iv) species that were absent in isolated remnants in the agricultural landscape and (v) species that were absent in small remnants in the urban landscape (Table 11.2).

These results indicate that woodland bird communities have a varying response to habitat fragmentation in different landscapes. Whilst I cannot be sure how representative our chosen landscapes are of other similarly composed landscapes, these results suggest that landscape matrix type may have a considerable influence on how bird species are affected by woodland fragmentation in the region.

12.7 Objective 6: Determine the conservation implications of this research in both regions

The results of this research show that the bird communities of southeastern Madagascar are threatened by habitat fragmentation at both the local and landscape scales. At the patch-scale, 31 species were found to be edge-sensitive, and nine species were sensitive to changes in habitat complexity and vegetation structure. At the landscape scale, the distributions of 20 species were significantly related to remnant size, and four species related to remnant shape. In Chapter 8, I argue that a multi-faceted approach to conservation of these forests must be incorporated. Conservation recommendations include: (i) as much littoral forest be formally protected as possible in each of three sub-types, (ii) preserving the largest littoral forest remnants should be the priority, (iii) efforts should be made towards restoring the native vegetation in and around remnants, and (iv) efforts should be made to make the smaller remnants more compact.

The Australian regional case studies (Chapters 10 and 11) indicated that the composition of the landscape matrix might be an important component in determining the distribution of bird species within woodland remnants. It must be noted that these analyses only highlighted bird community patterns and could not reveal underlying casual mechanisms. Moreover, the results described in Chapters 10 and 11 do not show that a certain matrix type is more detrimental to the woodland bird community than another, as there seems to be a species-specific response to different matrix conditions. However, the results of Chapter 11 in particular do indicate that remnant isolation may be an issue when the landscape matrix lacks paddock trees (which provide connectivity) as some species were significantly affected by remnant isolation in the agricultural landscapes. The urban landscape appeared to contain more area-sensitive species, with the smaller urban woodland remnants being relatively species poor compared to the similar size remnants in the other landscapes.

These results are important when bird conservation in the region is considered. There is a growing concern that Australian woodland biodiversity will not withstand the pressures of human-induced habitat fragmentation (Barrett *et al.*, 1994; Ford *et al.*, 2001). As little as five percent of Australia's former temperate woodlands is protected within Australia's nature reserve system. The possibility of acquiring more agricultural and urban land for conservation purposes is slim due to financial and political reasons (Ford and Barrett, 1995; Binning, 1998). With only a fraction of the woodland biodiversity that existed prior to clearance protected in Australia's reserve system, it is now clear that conservation of much of the original woodland biota now depends on maintaining woodland remnant vegetation outside of the present reserve system. Woodland management strategies are now looking to develop a viable network of residual habitats extending beyond the formal reserve system (Brooker and

Margules, 1996; Binning, 1998). The results of the present research show that large woodland remnants are essential in the conservation of woodland birds in the region. However, I encourage woodland restoration ecologists and land managers in eastern Australia to not only increase the size of woodland remnants but also to actively increase the amount of vegetation in the matrix surrounding woodland remnants, especially in the agricultural landscapes north of Canberra. Furthermore, whilst the analyses reported herein are not informative on these points, I encourage designing woodland buffers that reduce penetration of undesirable agents from the matrix, maintaining natural vegetation, deadwood and other nesting structures within woodland fragments via revegetation, while also actively managing introduced mammal populations in remnants and growing native trees and shrubs in the matrix to make it more like woodland remnants.

12.8 Objective 7: Determine the theoretical implications of this research

12.8.1 The theoretical implications of the Madagascan littoral forest case study

The strong relationship between species richness and littoral forest fragment area conformed to an important prerequisite of MacArthur and Wilson's (1967) ETIB: the existence of a significant SPAR. The z-value (z=0.34) obtained for the littoral forests was extremely high, and actually beyond Rosenzweig's (1995) claimed range of $0.1<z<0.3$ for sample-area SPARs. This high z value is due to the very low species richness in small (<10 ha) littoral forest remnants. It is possible that the high z-value calculated in the littoral forests could be indicative of the fact that the littoral forests may have been fragmented for a long period of time (potentially thousands of years). If so, the littoral forest remnants may have reached an equilibrium that is more similar to archipelagic islands than a recently fragmented terrestrial system. This may be a fragmented system that has paid its extinction debt.

The few bird species within the small littoral forests remnants (especially the small number of forest-dependent species where n=0 or 1 in all remnants < 10 ha) suggests that species loss (i.e. relaxation) has occurred, and that these remnants have reached a new, species-poor equilibrium. Furthermore, the absence of observations of even a small number of forest-dependent species within these remnants show that they are not acting as sink habitats for littoral forest-depending bird communities, as they are simply not occurring within the remnants. More rigorous auto-ecological studies are needed to test this. As there are no base-line data on the species richness of these littoral forests before fragmentation, it is impossible to determine the extent of species loss in these forests.

Although there was a strong SPAR for the littoral forest bird communities, the results of the littoral forest study were not consistent with ETIB or any of the descendent island theories (i.e. Lomolino's (2000a) species-based theory or Diamond's (1975a) assembly rules), as these theories predict that habitat isolation will play an important role in determining richness on habitat 'islands'. In the littoral forests, no isolation effect on bird species richness was identified. There are several possible explanations for the relative lack of importance of isolation in our data. For instance, it may be that the bird species found in the study area are so mobile that they are not affected by isolation to the extent that other taxa are, and as such, immigration limitation may not be an issue (Margules *et al.*, 1982; Ambuel & Temple, 1983). Those species that are not highly mobile may be able to disperse through the landscape matrix, again removing an isolation effect (Andrianarimisa *et al.*, 2000; Renjifo, 2001). As the dispersal capabilities of Madagascan birds are unknown, it is impossible to resolve this issue. The lack of an isolation effect in this study may not in fact be generalisable to Madagascan birds, as it may reflect the relatively limited range of isolation in the present study (cf. Whittaker, 2000).

In summary, bird diversity patterns in the littoral forest landscape were not related to isolation and landscape composition patterns but were instead related to area, edge and habitat structural patterns. As both landscape context and remnant isolation were found not to play a significant role in determining species presence within the littoral forest remnants, theories that utilise these components in determining the presence of birds in habitat fragments (e.g. MacArthur and Wilson, 1967; Lomolino, 2000a; Watson, 2002) are not applicable for bird conservation in the littoral forest landscape. Furthermore, as edge-effects, remnant shape and habitat complexity all played a role in explaining the distribution of a number of species, I argue that simply using the SPAR as the sole basis of a conservation strategy in this system is inappropriate.

12.8.2 The theoretical implications of the Australian woodland case study system

The three fragmented Australian woodland landscapes gave a unique opportunity to assess the suitability of the '*habitat patch - hostile matrix*' model of habitat fragmentation, which is the basic premise of MacArthur and Wilson's (1967) ETIB and its descendent theories. The habitat patch - hostile matrix model assumes that the matrix habitat is comprised of 'a sea of hostility' and that habitat dependent species will only occur in the island habitat and utilise resources from it. Therefore (all other things being equal) landscapes with different matrix properties should have similar species-area and species-isolation (SPIR) relationships, according to this theory. The empirical papers of Chapter 10 and 11 examined this particular hypothesis.

In the three Australian woodland landscapes, there was a strong SPAR relationship between bird species richness and woodland remnant area, which conformed to an important aspect of MacArthur and Wilson's (1967) ETIB. Moreover, the z-values for the three landscapes (agricultural z=0.20, peri-urban z=0.21 and urban z=0.25) were each within the range of Rosenzweig's (1995) sample-area SPARs. However, the slopes of the urban and peri-urban regressions and the urban and agricultural regressions were significantly ($P<0.05$) different to each other (Chapter 11). When woodland remnant isolation was considered, there was only a significant (p<0.001) relationship between remnant isolation and resident woodland species richness in the agricultural landscape. These results indicate that the properties of the landscape matrix were important in governing SPARs and SPIRs in the three landscapes.

The differences in SPARs and SPIRs in the three landscapes were the result of variation of minimum area and minimum isolation needs of individual bird species (see Chapter 11 for more details). The results highlighted in Chapter 10 and 11 suggest that the urban matrix has a different and greater influence on species-area relationships in woodland remnants than the two other matrices, and that the agricultural matrix appears to have an influence on species sensitivity to isolation, whereas the other two matrices do not. The relatively high *z* value for the urban landscapes was due to a relatively lower species richness in small (<10 ha) urban woodland remnants. These urban woodland remnants probably have additional 'threats' compared with the other two landscapes, such as greater competition with exotics like European Starling *Sturnus vulgaris* (Kerpez and Smith, 1990), greater exposure to larger populations of predators, such as domestic cats (Marzluff and Restani, 1999), and heightened disturbance and mortality from human activity (Knight and Gutzwiller, 1995; Evans, 1998). These additional threats may contribute to the low species richness in small urban remnants.

Even though causality could not be proven in this research, it appears that differences in SPARs and SPIRs can be most parsimoniously explained as a function of differences in the properties of the habitat matrix surrounding the woodland remnants. This means that the premise of *habitat patch - hostile matrix* (the basis of nearly all island theory) in this system is inappropriate. By exploring the effects of remnant area and remnant isolation on individual woodland species in different Australian landscapes, I have highlighted that it is not a simple matter of measuring matrix hostility (cf Watson, 2002) but a complex, often counter-intuitive, interaction between individual species and matrix type. This has important implications for those researchers working within the island paradigm in fragmentation research. My results indicate that the structure and composition regimes of the matrix may strongly influence the area-sensitivity and/or dispersal behaviours of bird species in highly fragmented landscapes.

12.8.3 The theoretical implications of these case study systems

The importance of considering the landscape matrix

The contribution of the matrix to patterns of species diversity and the response of individual species and species assemblages to landscape change are not taken into account in the original ETIB and many of its descendent theories (e.g. nestedness, assembly rules, metapopulation theory- see Chapter 2). One feature that distinguishes terrestrial habitat fragmentation from the *habitat patch- hostile matrix* model is that the landscape matrix may, for some species, actually be hospitable to varying degrees. In this case the matrix should have a strong influence on the between-patch processes of dispersal and colonisation, as well as the within-patch processes of extinction, population growth and density dependence. The assumption in island theory that properties of the matrix are unimportant is probably only true for terrestrial organisms inhabiting true islands. This situation sits at one extreme of a continuum extending from situations such as these true islands, where the marine matrix is completely inhospitable and quite homogenous (Gilpin and Diamond, 1980), through the metapopulation landscape where discrete habitat is conceived of as separated by a homogenous matrix that is not suitable for colonisation but is also not fatal to dispersers (Ims and Yoccoz, 1997), and finally to continuous habitat in which the matrix nature is almost indistinguishable from the patch (Vandermeer and Carvajal, 2000).

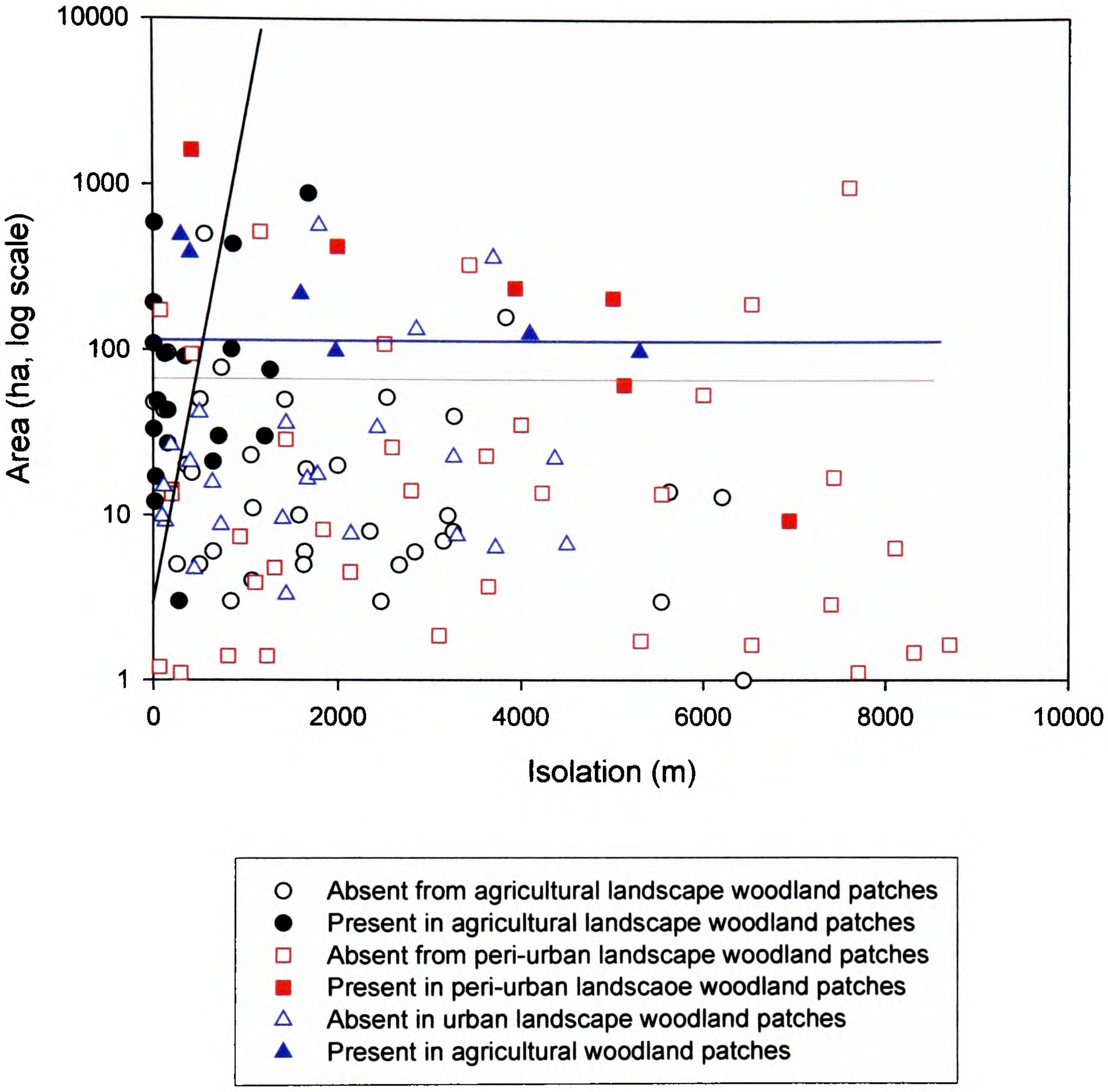
D.M. Watson (2002) tried to overcome this 'matrix' problem inherent in mainland applications of island theory by suggesting that the matrix can have different contrasts (i.e. high contrast and low contrast), and therefore having different effects on the species living in the fragmented habitats (Figure 2.5). Even though this is an improvement on the theory, I argue that this remains over-simplified. With only two matrix contrasts ('low' and 'high'), Watson (2002) ignores the fragmentation continuum mentioned above. As the Australian analysis in this thesis shows (Chapters 10 and 11), bird species do not all perceive the matrix in the same way. Some species will better utilise the resources or find higher connectivity within the matrix habitat, and as such, there is no uniform response. By over-simplifying the characteristics of matrix, there is a chance that the subtleties of benefits and costs that a particular matrix could provide may be over-looked.

Lomolino's (2000a) species-based theory of insular zoogeography also attempts to overcome these matrix dilemmas by introducing the concept of 'immigration filters'. These filters show the impacts of different matrices on individual species' area-isolation relationships. While the properties of the matrix will clearly affect the immigration ability of species between remnants, this may be a simplification of the effect the matrix can have on the distribution of species in fragmented landscapes. Lomolino's (2000a) sole example to support the 'immigration filter' was Åberg *et al.*'s (1995) study of one area-sensitive species in two different fragmented landscapes in Scandinavia. The Australian case studies conducted in this thesis (of which many area-sensitive bird species in three different fragmented landscapes were assessed) show no general trends of species (or functional groups) that would support Lomolino's (2000a) general theoretical response to matrix condition. Rather, individual species area-isolation relationships were shown to vary considerably across the three landscapes (e.g. Figure 12.1). The results of this thesis would suggest that Lomolino's (2000a) insular distribution of focal species is probably more appropriately drawn as in Figure 12.2.

Habitat fragmentation is a complex, multi-scalar process

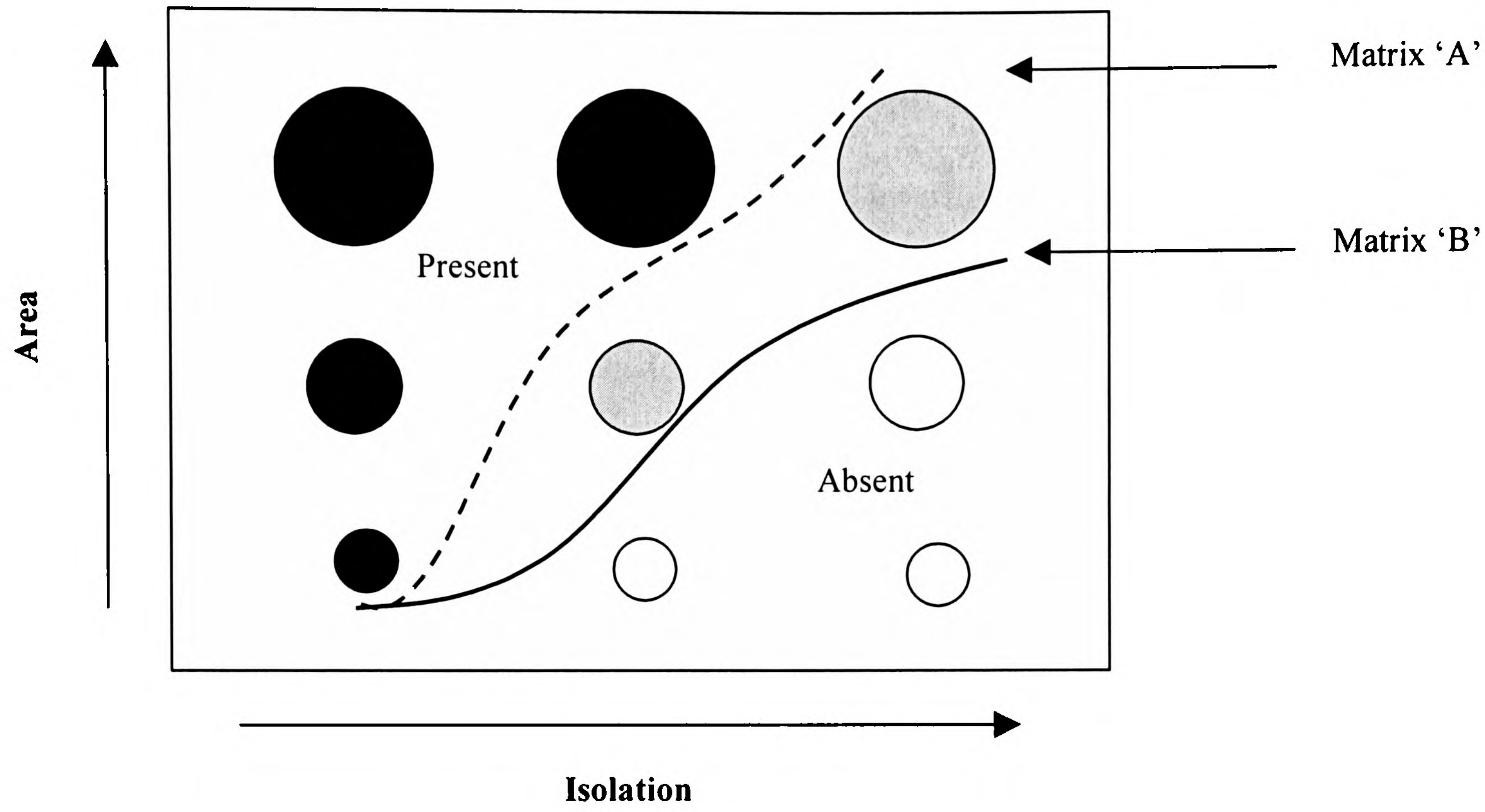
The results of the Madagascan case study highlight that within-patch effects (such as habitat complexity and juxtaposition to remnant edge) and landscape effects (such as remnant shape) can each demonstrate statistically significant effects on bird species distribution within a

Figure 12.1 Area-isolation plots for Eastern Yellow Robin (*Eopsaltria australis*) in three fragmented woodland landscapes (agricultural, peri-urban and urban), redrawn from the figure presented in Chapter 11. This species displayed a minimum area pattern in urban and peri-urban landscapes and a compensatory pattern in the agricultural landscape. The coloured lines represent the arbitrary species threshold where above the filled the probability of occurrence is > 50% in each landscape (see Chapter 11 for further details).



fragmented landscape. A number of species inhabiting the littoral forests (e.g. Madagascar cisticola, Madagascar brush warbler) were found only in areas with high amount of low shrub cover within a patch, and distributions were not explained by landscape variables such as remnant area. Many species were both area-sensitive at the landscape-scale and edge-sensitive at the patch-scale, indicating that they only occurred in core habitats in large remnants. However, several species (e.g. long-billed green-sunbird) were found to be

Figure 12.2 My attempt at redefining Lomolino's (2000a) insular distribution of focal species (dark symbols indicate presence, open circles indicate absence of a focal species), highlighting the effect of the matrix on both immigration abilities and minimum area requirements. The grey remnants and dashed line indicate that a species would inhabit these remnants when in a landscape with matrix composition 'A' but would not in matrix composition 'B'.



area-sensitive at the landscape scale but occurred at similar relative abundances near the edge of remnants. The local habitat influence on patch and landscape dynamics was consistent among a number of species, and highlights that a general theory cannot simply overlook these complex processes.

Fragmented landscapes are more complex than current island theory allow. Although the SPAR was shown to be highly significant in predicting the presence of bird species in habitat fragments in all the landscapes studied in this thesis, it did not account for all the variation shown by bird species presence in habitat remnants. Such variation matters, particularly when attempting to predict the response of species to landscape modification. As mentioned in the literature review (Chapter 2), a number of researchers (e.g. McIntyre and Hobbs, 1999; Manning *et al.*, 2004) have been developing different approaches in viewing fragmented landscapes away from the island-habitat analogy. In these models, the level and scale are determined by characteristics of the organism or ecological system of interest and the questions asked. The focus of this approach is on the mechanisms by which the spatial structure of the environment influences phenomena of conservation value such as populations or biodiversity. The scales on which these mechanisms are expressed (and thus the 'landscape') therefore will differ for different kinds of organisms. I believe this is a step forward, and will provide the best way to derive insights about how spatial texture and configuration of landscapes can influence ecological systems and their dynamics. If most conservation issues are indeed ultimately tied to human land use, the importance of such an understanding should be obvious. However, the question remains how to utilise such an approach in fragmented and little-studied systems? Can a general theory encapsulate this complexity?

A possible solution: a scale-oriented framework for conducting fragmentation studies

It is unreasonable to assume that habitat fragmentation will subside as long as humans dominate the earth. This thesis has shown that a theory based on the tenets of ETIB or any of its descendent theories, will probably not be able to guide land managers into making responsible conservation decisions in under-studied fragmented landscapes. This is not to say that the development of a general theory is irrelevant; however, as landowners are seeking conservation solutions within fragmented landscapes, it is necessary to conduct research that will guide appropriate decisions and not simply rely on island theory that suggests that (i) 'bigger is better', (ii) landscape-scale processes are the only processes driving species presence in fragmented landscapes, and (iii) that the contribution of matrix habitat on species persistence is irrelevant. This thesis has shown that a number of things must be considered when conducting research on the effects of fragmentation on biodiversity, especially if there is little knowledge of biodiversity within the landscape:

(1) For a particular landscape under investigation, it is necessary to identify the alteration state in the sense that different states can be functionally different and may need to be investigated differently. For example, in the Australian landscapes research in Chapters 10 and 11, the *habitat patch-hostile matrix* model could not be utilised to describe any landscape.

(2) It is important not to assume that a human-oriented assessment of the alteration state is the same as that which will be experienced by other organisms. For example, in the littoral forests remnants researched in this thesis, some forest-dependent bird species persisted in areas with little vegetation structure. Areas of little vegetation structure are often considered degraded by ecologists but were optimal (or at least acceptable) areas for these forest-dependent species.

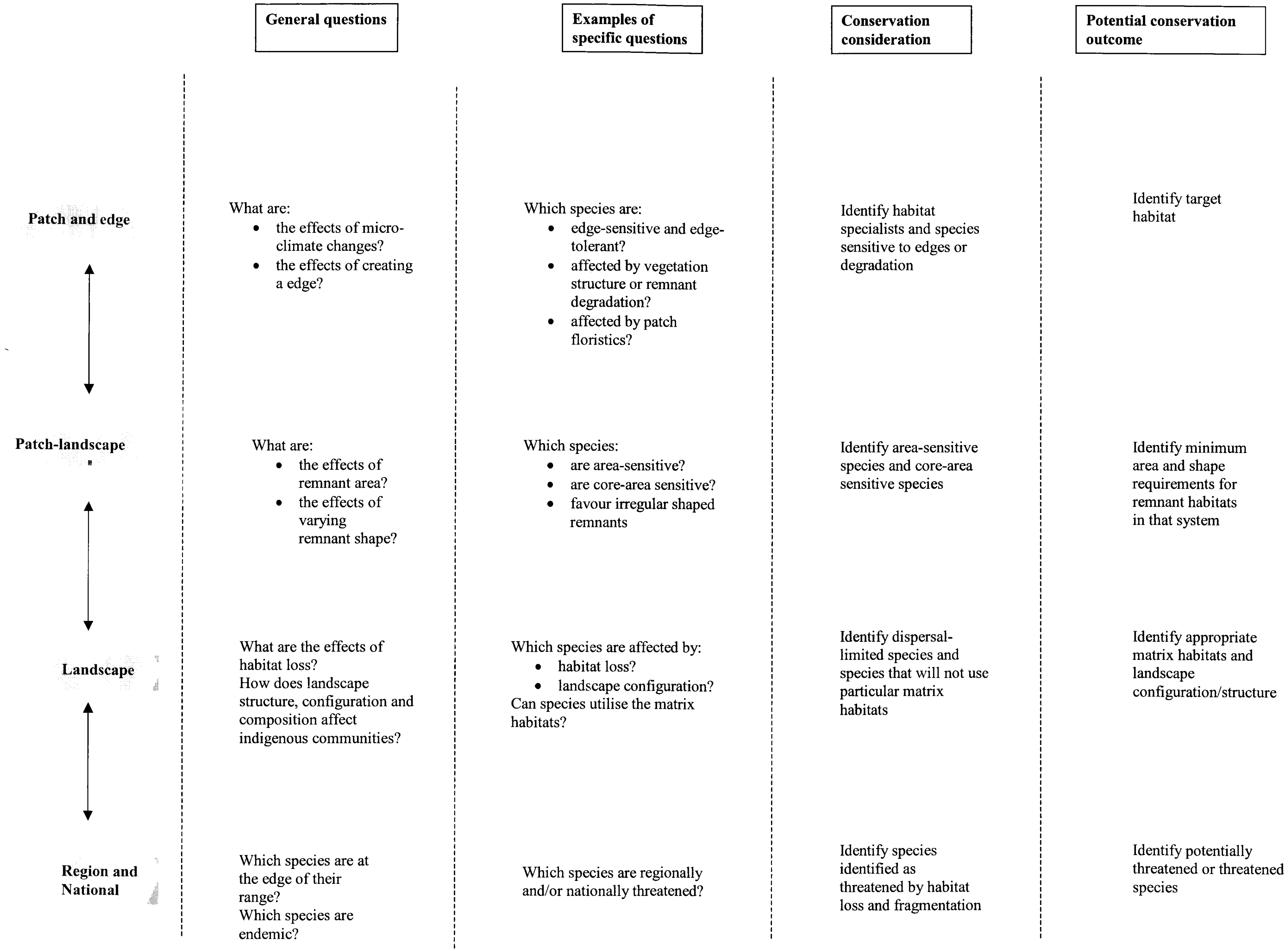
(3) Even in an apparently strongly fragmented landscape (as perceived by humans), the matrix cannot simply be assumed to be non-habitat or impermeable to all species. As shown in the Australian analyses, matrix conditions may even be as important in determining the survival of some species than factors that are traditionally examined, such as fragment size and isolation.

(4) Species-specific responses are important. All the empirical papers written in this thesis highlight the fact that species have different responses to habitat fragmentation. Some species in the littoral forests were solely edge-sensitive; some were area-sensitive while others were non-sensitive. Moreover, when species were found to be area-sensitive, they were found to have vastly different minimum area requirements.

(5) The processes of fragmentation are complex and multi-scalar. The results from this thesis indicate that the processes associated with fragmentation are interlinked and overlap at a number of scales. In practice, ecological studies tend to treat scale

> simplistically, prefacing it variously with patch-, landscape-, local-, regional-, small-, medium-, large-, fine-, individual-, population-, or habitat -, for example, and rarely with reference to whether the scale is based on biological properties of the organisms, physical properties of the landscape or some interaction of the two. Clearly, relevant spatial scale is species specific. Different species perceive the landscape at different scales, and even related species respond to processes operating at different spatial scales. The creation of a forest edge, for instance, is primarily a landscape structural change, but it will affect habitat suitability (a patch process) as well as immigration of individuals (a landscape and regional process). Thus, edge effects lie in a grey zone between local mechanisms that operate in the community living within a fragment, and large-scale processes related to the ensemble of local communities connected by dispersal. As such, edge effects deal with species interactions at local, landscape and regional scales simultaneously.

I argue that a multiple scale approach that specifically looks at the processes and effects of fragmentation on the taxa of interest will be the first useful step in generating appropriate conservation guidelines for a particular fragmented system. Figure 12.3 is an example of a flowchart of questions that shows how a multiple-scale approach to fragmentation research could be used in generating information that can aid land managers. It is in the form of a hierarchical approach, with each scale linking with the one below and above to give a balanced view of how fragmentation is affecting a particular ecosystem. I believe this form of approach could be employed in a study of the effects of fragmentation on biodiversity as it incorporates the five points outlined above.



	General questions	Examples of specific questions	Conservation consideration	Potential conservation outcome
Patch and edge	What are: • the effects of micro-climate changes? • the effects of creating a edge?	Which species are: • edge-sensitive and edge-tolerant? • affected by vegetation structure or remnant degradation? • affected by patch floristics?	Identify habitat specialists and species sensitive to edges or degradation	Identify target habitat
Patch-landscape	What are: • the effects of remnant area? • the effects of varying remnant shape?	Which species: • are area-sensitive? • are core-area sensitive? • favour irregular shaped remnants	Identify area-sensitive species and core-area sensitive species	Identify minimum area and shape requirements for remnant habitats in that system
Landscape	What are the effects of habitat loss? How does landscape structure, configuration and composition affect indigenous communities?	Which species are affected by: • habitat loss? • landscape configuration? Can species utilise the matrix habitats?	Identify dispersal-limited species and species that will not use particular matrix habitats	Identify appropriate matrix habitats and landscape configuration/structure
Region and National	Which species are at the edge of their range? Which species are endemic?	Which species are regionally and/or nationally threatened?	Identify species identified as threatened by habitat loss and fragmentation	Identify potentially threatened or threatened species

Figure 12.3 An example of a flowchart of questions that shows how a multiple-scale approach to fragmentation research could be used in generating information that can aid land managers.

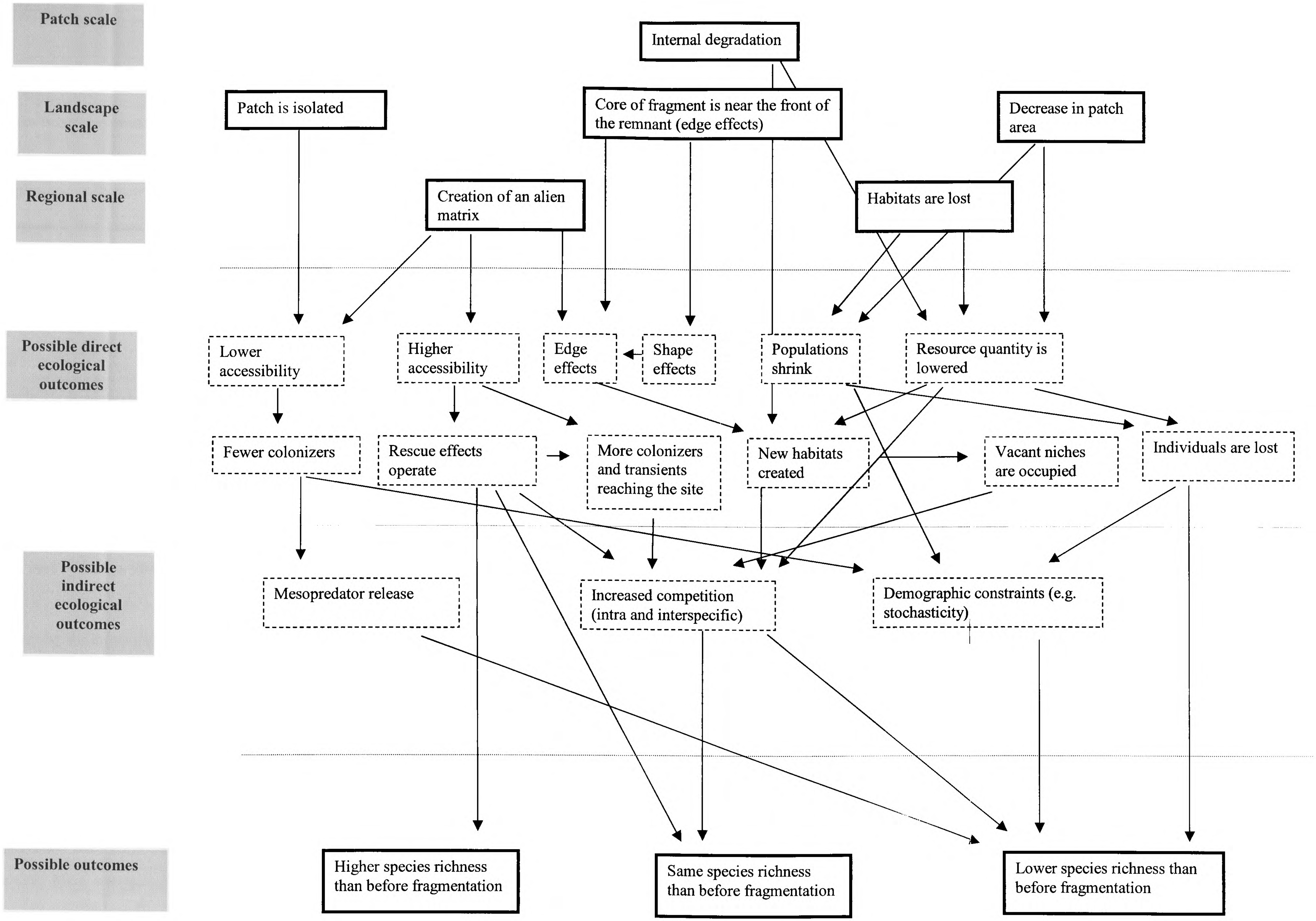


Figure 12.4 Examples of possible outcomes to species richness following a habitat fragmentation event.
The diagram shows some of ecological processes that will determine species richness upon a fragmentation event, highlighting the complex relationship between spatial scale and ecological process. It breaks the ecological outcomes into 'direct' and 'indirect' processes on the basis that indirect processes are ones that occur only after the direct responses occur, i.e. they are indirectly related to habitat fragmentation per se. Any general theory that aims to predict the impacts of fragmentation on species richness needs to take into account this amount of complexity.

I also argue that this type of spatial hierarchal approach is also an important way forward in the development of a general theory that will better explain the effects of forest loss and fragmentation on biota. Clearly, resource availability (such as food, nesting materials, etc) at the local scale will be the start to determining the presence of a bird species in habitat fragments. Factors such as the distance to habitat edges and internal habitat heterogeneity will also mean that bird species abundances will vary within a remnant habitat. At the landscape scale, the size, shape and isolation of remnant habitat will also effect the distribution of some bird species, as some species will need larger territories to survive, while others need a specific amount of core habitat area away from a remnant edge to persist. At the regional scale, certain species will be need to be close to other habitats to move to when food resources are exhausted in habitat remnants and therefore the 'hostility' of the surrounding matrix habitat will become important. Other species will utilise the matrix habitat for food and nesting resources, and therefore the properties of the matrix habitat will become important. There are clearly many other reasons why fragmentation may influence biota at the different scales described in this thesis, and I believe that the only way that a theory may be able to capture the complex processes is to be scale-oriented (Figure 12.4).

12.9 Limitations of this thesis' findings and directions for future research

12.9.1 The general limitations for the use in bird research

Birds appear to meet some but not all of the broad-brush criteria proposed for identifying suitable biodiversity indicators (Pearson and Cassola, 1992; Kremen *et al.*, 1993; Caro and O'Doherty, 1999). Flight means that birds disperse quite readily, and consequently have relatively large distributional ranges. Hence, their biogeography is more coarse-grained than that of many other groups, so that area priorities for birds may fail to capture adequately the biodiversity of taxa exhibiting higher spatial turnover. It has been shown that at global and continental scales, there is often reasonable agreement in the relative richness of large areas for birds and different taxa (Pearson and Cassola, 1992). However, at the regional scales, congruence in species is typically weaker, and at fine scales, it can break down all together (summarised in Norris and Pain, 2002). Although birds are high on the food chain, they are not going to be representative for how all taxa experience fragmentation of their habitat. I encourage future research that examines how different taxa are affected by processes associated with landscape fragmentation at different scales in the same case study areas.

12.9.2 Limitations of the research conducted in the Madagascar case study and future research directions

Although I was able to demonstrate that a large number of species' distributions had significant relationships with landscape components such as remnant area and habitat complexity, the research had some limitations. Firstly, the study has addressed only the pattern of bird distribution across the landscape and has not provided any new data on process. For example, I was unable to assess for what purpose habitat patches (in particular small patches) were used by various bird species, and if their usage changed through space and time. The presence of birds in a particular remnant does not mean that the sub-population is viable, nor does it mean that the particular remnant is making a positive contribution to the metapopulation (Donovan *et al.*, 1995). Some remnants could be acting as population sinks which accommodate birds produced in source remnants but which may not contribute new individuals to the metapopulation (Hinsley *et al.*, 1999). Research has shown that small remnants (or those remnants with large edge-to-interior ratios) may produce relatively few individuals and that such remnants are less preferred by adult birds (Major *et al.*, 1999a,b) and as such, are population sinks. I was unable to determine if small littoral forest remnants were acting as a sink. More auto-ecological studies should be conducted to understand minimum viable populations. These data will be necessary considering the future mining plans.

To assess further the value of the matrix habitats surrounding littoral forest remnants, it would be valuable to design an experiment on the value of patches in different matrices and collect more detailed information on not only how they use habitat patches but also the surrounding environment. This is because it has been shown elsewhere that bird species can often respond to fragmented landscapes as a gradient of remaining habitat and condition (Lindenmayer *et al.*, 2003). However, due to the low numbers of littoral forest patches that are left and the limited number of landscapes they now occur in, such an experiment may be very difficult to conduct. Perhaps a more suitable method is to determine how different bird species utilize the matrix between smaller littoral forest remnants, and which matrix habitats are suitable for species dispersing through them (following Ramanamanjato and Ganzhorn's (2001) on small mammals in littoral forests). This work would directly apply to the reforestation guidelines suggested in this research, as it would assess the possible effects of creating natural buffer zones around littoral forest remnants while also examining how corridors linking remaining forest fragments affect bird communities within the landscape.

I was unable to assess the full impacts of hunting on native bird species in the littoral forests. The local people of all three littoral forest sub-regions hunt large birds and mammals in the forests for food, and some species of lemur (e.g. *Eulemur collaris* and *Pteropus rufus*) have been identified as potentially locally threatened by this (Bollen, 2003). I have been told by a number of local people, and have seen evidence, that a number of terrestrial birds are trapped using snares, arrows or catapults. These include both fruit pigeon species, both vasa parrots, Madagascar bulbul, and blue and giant coua. Bollen (2003) describes similar observations. Clearly any appropriate bird conservation program in the littoral forests must have information on what bird species are threatened by hunting.

12.9.3 Limitations of the research conducted in the Australian case study and future research directions

The Australian case study was able to show and highlight different distribution patterns of woodland birds in three similarly fragmented landscapes but I was not able to show the causation for why these patterns differed. The most parsimonious explanation for why patterns changed in different landscapes was because of the differing matrix properties between the three landscapes. There is only circumstantial evidence that the edge-contrast or the biological and physical properties of the matrix are changing how bird communities inhabit woodland fragments. However, my research provides some important initial hypotheses for any future research examining the effects of fragmentation on biodiversity in the region. I also encourage ecological research in other fragmented landscapes to see if the findings in species distributions among different landscapes itself has generality.

The difficulty with these types of hypotheses is that it is extremely difficult to try and determine causality between process and effect. There are a number of large landscape experiments being conducted so that the prior states can be measured and subsequent changes can be monitored directly; a famous example of this type of research is the Biological Dynamics of Forest Fragments Project (formerly Minimum Critical Size of Ecosystems Study) currently being conducted in the Manaus region of Brazil (summarised in Bierregaard *et al.*, 2001). However, these experiments have not actively sought out how different landscape matrix compositions affect the biodiversity in fragmented landscapes and I believe that a fragmentation research experiment should be set up for this purpose.

12.10 Conclusion

The research has contributed significantly both to practical and theoretical biogeography. Firstly, it has contributed to place-based understandings of avian biogeography. In Madagascar, it is the first attempt to understand the effects of fragmentation on birds at a local and landscape scale and the first time thorough surveys have been conducted in what is a seriously threatened ecosystem: the littoral forests of southeastern Madagascar. It therefore contributes by describing what species occur within the forests, but also provides an understanding of how future changes to the forests may affect individual bird groups and the bird community as a whole. This is particularly pertinent for conservation policies, given the imminent development of mining in southeastern Madagascar. In the Australian case study, it is (to my knowledge) the first time a regional perspective has been placed on the effects of habitats fragmentation on woodland birds and the first study conducted that assesses the relative effects of different landscape matrices on any form of biota. This research showed that the composition of the matrix in which woodland remnants are embedded plays an important role in determining bird species presence within the remnants. This has important ramifications for current woodland revegetation schemes being conducted in the region.

Secondly, this research has contributed to the ecological theory being utilised to describe and forecast the effects of fragmentation on birds. I have shown that island theory is still the dominant theoretical paradigm being utilised in fragmentation research. The tenets of island theory were not suitable for both case study systems I studied in this system. I propose a multi-scale approach for researching and predicting the effects of habitat fragmentation, especially in systems that are under-studied. Although I argue there is a role for a general theory in fragmentation research, I urge for caution if simplicity and generality is in mind, as I show in this thesis that habitat fragmentation is a multi-scalar, complex process whose effects on biota could be over-simplified if an island-habitat analogy is the sole theoretical framework utilised.

Appendix 1. Journal authorship statements for all co-authored papers

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Statement for inclusion with James Watson's thesis

I declare that the manuscripts presented as chapters 5, 6, 7, 10 and 11 within this thesis, for which I am co-author, are substantially the work of the co-author, James Watson, and that my role has been limited to supervisory input and comments on drafts.

Robert J Whittaker

14th July 2004

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Statement for inclusion with James Watson's thesis

19 July 2004

I declare that the manuscripts presented as chapters 10 and 11 within this thesis, for which I am co-author, are substantially the work of the co-author, James Watson, and that my role has been limited to supervisory input and comments of drafts.

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Statement for inclusion with James Watson's and Niall O'Dea's theses

12 July 2004

We declare that the manuscript entitled 'Rapid assessment in conservation research: a critique of avifaunal assessment techniques illustrated by Ecuadorian and Madagascan case study data' (*Diversity and Distributions*, **10**, 55-63) is the work of both James Watson and Niall O'Dea. James came up with the initial idea of developing a research paper to test the two bird methodologies utilised in the littoral forests of Madagascar and the cloud forests of Ecuador but this workload was unequal. Both authors had input in the analytical and writing-up stages in the manuscript. However, Niall conducted the majority of the work in producing the manuscript as he took primary responsibility for writing the manuscript (reflected in his primary authorship), and developed the analytical techniques that were used to test the bird methodologies against each other in each of the study areas. He conducted the half of the analysis concerning the Ecuadorian data set, while James conducted the half concerning the Madagascar data set. James also helped with the development and write-up of the manuscript.

Niall O'Dea **James Watson** **Dr. R. J. Whittaker**

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Statement for inclusion with James Watson's thesis

16th July 2004

I declare that the manuscripts presented as chapters 5, 6, 7 and 10 within this thesis, for which I am co-author, are substantially the work of the co-author, James Watson, and that my role has been limited to supervisory input and comments of drafts.

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Appendix 2. Bird species distribution among the forest habitats found within the Madagascan study area.

Sources for status and endemicity were Langrand (1990), Goodman *et al.* (1997) and Morris and Hawkins (1998). The bird species lists for non-littoral forest habitats were lumped for all sites within each habitat class. See Chapter 5 for details for the bird methodologies employed.

ST describes the status of the bird ((1) resident, (2) local migrant, including species breeding in or near the study area but not present all year and (3) local migrant, present over winter but not breeding in the area).

EN describes the endemicity of the bird: (M) endemic to Madagascar, (R) regional endemic to Madagascar, Comoros and Mascarenes, (A) African endemic, (C) cosmopolitan, (I) Introduced.

X identifies that bird species were found in Ste-Luce (**S**) remnants, Mandena (**M**) remnants, Petriky (**P1**) remnant, Anakapoky spiny forest (**SP**), Farafara lowland humid forest (**RF**), *Melaleuca* forest (**MF**), *Eucalyptus* plantations (**EU**), *Erica* grassland (**ER**) and Marikage swamp habitats (**MK**).

δ indicates species found in littoral forest remnants by this study but not by Goodman et al. (1997).

Bird species	ST	EN	S6	S7	S8	S9	S10	S15	S16	M2	M3	M4	M5	M6	M9	P1	SP	RF	MF	EU	ER	MK
Little Bittern *Ixobrychus minutus*	3	C																				X
Black-crowned Night Heron *Nycticorax nycticorax*	1	C																				X
Sqaucco Heron *Ardeola ralloides*	1	C																				X
Great Egret *Egretta alba*	1	C															X					
Purple Heron *Ardea purpurea*	1	C						X	X													X
Grey Heron *Ardea cinerea*	1	C			X																	X
Madagascar Wood Rail *Canirallus kioloides δ*	1	M	X		X	X			X									X				X
White-throated Rail *Dryolimnas cuvieri*	1	R	X	X		X		X	X	X	X							X				X
Purple Moorhen *Porhyrio porphyrio*	1	C																				X
Greater Painted Snipe *Rostratula benghalensis*	3	C																				X
Madagascar Pratincole *Glareola ocularis*	2	M																			X	X
Kittlitz's Plover *Charadrius pecuarius*	1	A																			X	X
Madagascar Snipe *Gallinago macrodactyla*	1	M																				X
Madagascar Crested Ibis *Lophotibis cristata*	1	M	X	X		X												X				
White-faced Whistling Duck *Dendrocygna viduata*	I	C																				X
Meller's Duck *Anas melleri*	1	M																				X
Red-billed Teal *Anas erythrorhyncha*	1	A																				X
Madagascar Cuckoo-Falcon *Aviceda madagascariensis δ*	1	M	X					X		X												
Yellow-billed Kite *Milvus aegyptius*	1	C	X	X		X	X	X	X		X	X					X	X	X	X	X	
Madagascar Harrier-Hawk *Polyboroides radiatus*	1	M	X	X		X	X			X	X		X			X	X	X				
Madagascar Sparrowhawk *Accipter madagascariensis δ*	1	M	X			X												X				
France's Sparrowhawk *Accipter francesii*	1	R	X			X	X	X	X	X						X	X	X	X	X		X

Bird species	ST	EN	S6	S7	S8	S9	S10	S15	S16	M2	M3	M4	M5	M6	M9	P1	SP	RF	MF	EU	ER	MK
Henst's Goshawk *Accipter henstii δ*	I	M		X														X				
Madagascar Buzzard *Buteo brachypterus*	1	M	X	X	X	X	X	X		X	X	X			X	X	X	X	X	X	X	
Madagascar Kestrel *Falco newtoni*	1	R							X							X	X	X			X	
Banded Kestrel *Faclo zoniventris*	1	M															X					
Eleonora's Falcon *Falco eleonorae*	3	C								X												
Sooty Falcon *Falco concolor*	3	C			X											X					X	X
Peregrine Falcon *Falco peregrinus*	1	C																			X	
Madagascar Partridge *Margaroperdix madagascarensis*	1	M	X	X			X	X				X				X	X	X				
Helmeted Guineafowl *Numida meleagris*	1	A	X	X		X				X			X	X		X		X		X	X	
Brown Mesite *Mesitornis unicolor*	1	M																X				
Madagascar Flufftail *Sarothrura insularis δ*	1	M		X		X		X	X	X								X				
Madagascar Buttonquail *Turnix nigricollis*	1	M			X								X			X	X				X	
Madagascar Sandgrouse *Pterocles personatus*	1	M															X					
Madagascar Turtle-Dove *Streptopelia picturata*	1	R	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Namaqua Dove *Oena capensis*	1	A			X											X	X				X	
Madagascar Green Pigeon *Treron australis*	1	R	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X		
Madagascar Blue Pigeon *Alectroenas madagascariensis*	1	M	X	X	X	X		X		X						X		X				
Lesser Vasa Parrot *Coracopsis nigra*	1	R	X	X	X	X	X	X	X	X	X	X			X	X	X	X				
Greater Vasa Parrot *Coracopsis vasa δ*	1	R	X	X	X											X	X	X				
Gray-headed Lovebird *Agapornis cana*	1	M	X	X				X		X	X					X	X	X				
Madagascar Lesser Cuckoo *Cuculus rochii δ*	2	M	X	X												X	X	X		X		
Red-fronted Coua *Coua reynaudii δ*	1	M		X		X												X				
Running Coua *Coua cursor*	1	M															X					
Red-capped Coua *Coua ruficeps*	1	M															X					
Blue Coua *Coua caerulea*	1	M		X	X	X	X	X		X								X				
Crested Coua *Coua cristata*	I	M														X	X					
Giant Coua *Coua gigas*	1	M	X	X	X	X		X	X	X	X	X				X	X					
Madagascar Coucal *Centrpus toulou*	1	R	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X
Madagascar Scops Owl *Otus rutilus*	1	R			X	X											X	X	X			
Madagascar Long-eared Owl *Asio madagascariensis*	I	M				X																
White-browed Owl *Ninox superciliaris*	1	M														X	X					
Madagascar Nightjar *Caprimulgus madagascariensis*	1	R				X		X		X	X			X		X	X	X			X	
Malagasy Spine-tailed Swift *Zoonavena grandidieri δ*	1	R	X	X	X		X			X	X	X		X		X		X				

Bird species	ST	EN	S6	S7	S8	S9	S10	S15	S16	M2	M3	M4	M5	M6	M9	P1	SP	RF	MF	EU	ER	MK
African Palm Swift *Cypsiurus parvus*	1	A	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X			
Alpine Swift *Apus melba*	1	C	X		X	X		X	X	X		X	X	X	X	X	X	X	X	X	X	X
African Black Swift *Apus barbatus*	1	A				X											X			X		
Malagasy Kingfisher *Alcedo vintsioides*	1	R	X	X	X	X	X	X	X	X	X		X			X		X	X			
Madagascar Pygmy Kingfisher *Ispidina madagascariensis*	1	M				X				X						X	X	X				
Madagascar Bee-eater *Merops superciliosus*	1	A	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X
Broad-billed Roller *Eurystomus glaucurus*	2	A	X	X	X	X	X	X	X	X	X	X	X			X	X	X				X
Scaly Ground Roller *Brachypteracias squamiger*	1	M																X				
Cuckoo-Roller *Leptosomus discolor*	1	R	X			X		X								X		X				
Hoopoe *Upupa epops*	1	C		X	X	X			X	X	X	X				X	X		X			
Velvet Asity *Philepitta castanea*	1	M																X				
Madagascar Bush Lark *Mirafra hova*	1	M			X	X				X	X		X	X	X					X	X	
Brown-throated Sand Martin *Riparia paludicola δ*	1	C			X												X	X				
Mascarene Martin *Phedina borbonica δ*	2	R	X				X			X		X	X	X				X		X		
Madagascar Wagtail *Motacilla flaviventris*	1	M	X		X	X	X	X	X	X	X	X	X		X	X	X	X	X	X		
Ashy Cuckoo-Shrike *Coracina cinerea*	1	R	X	X	X	X		X	X	X						X	X	X				
Long-billed Greenbul Phyllastrephus madagascariensis	1	M																X				
Madagascar Bulbul *Hypsipetes madagascariensis*	1	A	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Madagascar Magpie-Robin *Copsychus albospecularis*	I	M		X		X										X	X	X				
Stonechat *Saxicola torquata*	I	A																			X	
Lantz's Brush-Warbler *Nesillas lantzii*	I	M														X	X					
Madagascar Brush-Warbler *Nesillas typica*	1	M	X	X		X		X		X	X	X						X				
Madagascar Cisticola *Cisticola cherina*	1	M	X	X		X	X	X		X	X	X	X	X		X	X		X		X	X
Common Newtonia *Newtonia brunneicauda*	1	M	X	X	X	X	X	X	X	X	X	X	X			X	X	X				
Archbold's Newtonia *Newtonia archboldi δ*	1	M	X	X	X	X											X					
Common Jery *Neomixis tenella*	I	M	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		
Green Jery *Neomixis viridis δ*	1	M			X	X												X				
Stripe-throated Jery *Neomixis striatigula δ*	1	M	X	X	X	X	X	X	X	X		X				X	X	X	X			
Madagascar Paradise Flycatcher *Terpsiphone mutata*	1	R	X	X	X	X		X		X	X					X	X	X				
White-throated Oxylabes *Oxylabes madagascariensis*	1	M																X				
Crossley's Babbler *Mystacornis crossleyi*	1	M																X				
Souminga Sunbird *Nectarinia souimanga*	1	R	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X
Long-billed Green-Sunbird *Nectarinia notata*	1	R	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X				

Bird species	ST	EN	S6	S7	S8	S9	S10	S15	S16	M2	M3	M4	M5	M6	M9	P1	SP	RF	MF	EU	ER	MK
Madagascar White-Eye *Zosterops maderaspatana*	1	R	X	X	X	X		X		X	X	X		X	X			X				
Chabert's Vanga *Leptopterus chabert δ*	1	M			X	X		X								X	X	X	X	X		
Hook-billed Vanga *Vanga curvirostris*	1	M	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X			
Lafresnaye's Vanga *Xenopirostris xenopirostris*	1	M															X					
Pollen's Vanga *Xenopirostris polleni*	1	M																X				
Blue Vanga *Cyanolanius madagascarinus*	1	R		X	X	X				X	X							X				
Rufous Vanga *Schetba rufa δ*	1	M				X										X		X				
White-headed Vanga *Leptopterus viridis*	1	M														X	X	X				
Red-tailed Vanga *Calicalicus madagascariensis*	1	M																X				
Nuthatch Vanga *Hyposiita corallirostris*	1	M																X				
Tylas Vanga *Tylas eduardi δ*	1	M				X												X				
Sickle-billed Vanga *Falculea palliata*	1	M															X					
Crested Drongo *Dicrurus forficatus*	1	R	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Pied Crow *Corvus albus*	1	A	X		X	X		X		X	X	X	X	X	X	X	X	X	X	X	X	X
Madagascar Starling *Hartlaubius auratus*	1	M		X		X	X	X	X							X	X	X				
Common Myna *Acridotheres tristis*	1	I			X	X							X	X		X			X	X	X	
Nelicourvi Weaver *Ploceus nelicourvi*	1	M																X				
Sakalava Weaver *Ploceus sakalava*	1	M															X					
Madagascar Red Fody *Foudia madagascariensis*	1	M	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	
Forest Fody *Foudia omissa*	1	M	X		X	X				X								X				
Madagascar Mannikan *Lonchura nana*	1	M				X		X				X	X			X		X			X	

Appendix 3 Relative abundance and habitat landscape element association of bird species identified in point count stations in the fragmented littoral forests of southeastern Madagascar

Relative abundance and habitat landscape element association of species identified in point count stations in three landscape elements (littoral forest core (n=20), littoral forest edge (n=20) and matrix habitat (n=20)).

Species were placed in the following categories: forest edge-avoider (FA), forest edge-tolerant (F), forest edge-preferer (FE), matrix species (M) and ubiquitous species (U) on their detection and relative abundance in each landscape element (core, edge and matrix).

Predominate foraging substrate is delineated into Terrestrial (T), Shrub (S), Canopy (C), Aerial (A) and Sallying Insectivore (Sa).

Predominate foraging guild is delineated into Carnivore, Insectivore, Nectivore and Granivore.

Relative abundance was calculated as the mean individual birds per point count.

The *t*-value is the value of a paired *t* test comparing the mean abundance of individual bird species within edge point counts and core point counts. Only species found in both landscape elements were tested. * p<0.01, ** p<0.05.

Bird species, by group	**Foraging guild**	**Foraging substrate**	**Core**	**Edge**	**Matrix**	***t*-value**
			Relative abundance	**Relative abundance**	**Relative abundance**	
Edge-tolerant species						
Henst's Goshawk *Accipter henstii*	C	A	0.05	0.05	0	0
Madagascar Partridge *Margaroperdix madagascarensis*	G	T	0.15	0.15	0	-0.61
Forest Fody *Foudia omissa*	G	C	0.1	0.1	0	0
Hoopoe *Upupa epops*	I	T	0.18	0.18	0	-1
Mascarene Martin *Phedina borbonica*	I	A	0.05	0.05	0	0
Madagascar Swamp-Warbler *Acrocephalus newtoni*	I	S	0.05	0.05	0	0
Madagascar Brush-Warbler *Nesillas typica*	I	S	0.25	0.28	0	0.33
Stripe-throated Jery *Neomixis striatigula*	1	C	0.35	0.1	0	-0.9
Common Jery *Neomixis tenella*	I	C	1.45	1	0	-0.5
Long-billed Green-Sunbird *Nectarinia notata*	N	C	0.63	0.1	0	0.67

Bird species, by group	Foraging guild	Foraging substrate	Core	Edge	Matrix	*t*-value
			Relative abundance	Relative abundance	Relative abundance	
Edge-avoiding species						
Madagascar Harrier-Hawk *Polyboroides radiatus*	C	A	0.13	0	0	-
Madagascar Long-eared Owl *Asio madagascariensis*	C	C	0.03	0	0	-
Madagascar Green Pigeon *Treron australis*	F	C	0.43	0.28	0	-2.03*
Madagascar Blue Pigeon *Alectroenas madagascariensis*	F	C	0.35	0	0	-
Lesser Vasa Parrot *Coracopsis nigra*	F	C	0.98	0.2	0	-4.48**
Greater Vasa Parrot *Coracopsis vasa*	F	C	0.18	0	0	-
Gray-headed Lovebird *Agapornis cana*	F	C	0.18	0	0	-
Madagascar Starling *Hartlaubius auratus*	F	C	0.13	0	0	-
Madagascar Wood Rail *Canirallus kioloids*	I	T	0.05	0	0	-
White-throated Rail *Dryolimnas cuvieri*	I	T	0.15	0	0	-
Madagascar Crested Ibis *Lophotibis cristata*	I	T	0.18	0	0	-
Madagascar Flufftail *Sarothrura insularis*	1	T	0.23	0	0	-
Madagascar Lesser Cuckoo *Cuculus rochii*	I	C	0.03	0	0	-
Red-fronted Coua *Coua reynaudii*	I	T	0.08	0	0	-
Blue Coua *Coua caerulea*	I	C	0.43	0.08	0	-3.56**
Giant Coua *Coua gigas*	I	T	0.13	0	0	-
Madagascar Pygmy Kingfisher *Ispidina madagascariensis*	I	S	0.1	0	0	-
Cuckoo-Roller *Leptosomus discolor*	I	C	0.08	0	0	-
Ashy Cuckoo-Shrike *Coracina cinerea*	I	C	0.4	0.08	0	-3.19**
Madagascar Magpie-Robin *Copsychus albospecularis*	I	C	0.28	0	0	-
Common Newtonia *Newtonia brunneicauda*	I	C	0.3	0.13	0	-0.21*
Archbold's Newtonia *Newtonia archboldi*	I	C	0.23	0	0	-
Green Jery *Neomixis viridis*	I	C	0.18	0	0	-
Madagascar Paradise Flycatcher *Terpsiphone mutata*	I	S	0.43	0	0	-
Madagascar White-Eye *Zosterops maderaspatana*	I	C	0.15	0.08	0	-1.371

Bird species, by group	Foraging guild	Foraging substrate	Core	Edge	Matrix	*t*-value
			Relative abundance	Relative abundance	Relative abundance	
Chabert's Vanga *Leptopterus chabert*	I	C	0.1	0	0	-
Hook-billed Vanga *Vanga curvirostris*	I	C	1.03	0.25	0	-5.49**
Blue Vanga *Cyanolanius madagascarinus*	I	C	0.1	0	0	-
Rufous Vanga *Schetba rufa*	I	C	0.03	0	0	-
Red-tailed Vanga *Calicalicus madagascariensis*	I	C	0.03	0	0	-
Tylas Vanga *Tylas eduardi*	I	C	0.15	0	0	-
Edge-preferring species						
France's Sparrowhawk *Accipter francesii*	C	A	0.03	0.13	0	2.18*
Malagasy Kingfisher *Alcedo vintsioides*	C	C	0.05	0.25	0	2.85**
Broad-billed Roller *Eurystomus glaucurus*	I	Sa	0.03	0.13	0	2.85**
Madagascar Wagtail *Motacilla flaviventris*	I	T	0.05	0.23	0	2.21*
Matrix species						
Sooty Falcon *Falco concolor*	C	A	0	0	0.05	-
Peregrine Falcon *Falco peregrinus*	C	A	0	0	0.05	-
Madagascar Buttonquail *Turnix nigricollis*	G	T	0	0.15	0.1	-
Namaqua Dove *Oena capensis*	G	T	0	0.25	0.15	-
Madagascar Mannikan *Lonchura nana*	G	T	0	0.25	0.15	-
Madagascar Pratincole *Glareola ocularis*	I	T	0	0	0.15	-
Kittlitz's Plover *Charadrius pecuarius*	I	T	0	0	0.1	-
Madagascar Bush Lark *Mirafra hova*	I	T	0	0.2	0.18	-
Stonechat *Saxicola torquata*	I	S	0	0	0.33	-
Pied Crow *Corvus albus*	I	T	0	0.55	0.45	-
Common Myna *Acridotheres tristis*	I	T	0	1.03	0.45	-
Ubiquitous species						
Yellow-billed Kite *Milvus aegyptius*	C	A	0.1	0.28	0.23	1.2

Bird species, by group	Foraging guild	Foraging substrate	Core	Edge	Matrix	*t*-value
			Relative abundance	Relative abundance	Relative abundance	
Madagascar Buzzard *Buteo brachypterus*	C	A	0.2	0.15	0.1	0.31
Madagascar Kestrel *Falco newtoni*	C	A	0.2	0.15	0.1	0.31
Helmeted Guineafowl *Numida meleagris*	G	T	0.2	0	0.13	-
Madagascar Turtle-Dove *Streptopelia picturata*	G	T	0.55	1.43	0.18	0.81
Madagascar Red Fody *Foudia madagascariensis*	G	C	0.43	0.52	0.45	0.57
Madagascar Coucal *Centrpus toulou*	I	S	1.05	1.03	0.2	-1.45
Madagascar Nightjar *Caprimulgus madagascariensis*	I	A	0.1	0.08	0.05	0.57
Malagasy Spine-tailed Swift *Zoonavena grandidieri*	I	A	0.4	0.5	0.3	0.62
African Palm Swift *Cypsiurus parvus*	I	A	0.3	0.6	0.3	0
Alpine Swift *Apus melba*	I	A	0.6	0.13	0.23	-1.37
African Black Swift *Apus barbatus*	I	A	0.3	0.1	0.1	-1
Madagascar Bee-eater *Merops superciliosus*	I	A	0.8	1.1	0.48	1.33
Brown-throated Sand Martin *Riparia paludicola*	I	A	0.03	0.03	0.02	0
Madagascar Bulbul *Hypsipetes madagascariensis*	I	S	1.4	1.68	1.3	0
Madagascar Cisticola *Cisticola cherina*	I	S	0.4	0.53	0.55	1.43
Crested Drongo *Dicrurus forficatus*	1	Sa	0.18	0.33	0.23	1.14
Souminga Sunbird *Nectarinia souimanga*	N	C	0.95	1.65	0.55	0

Appendix 4. Summary of mean deviance in individual logistic regression models, species codes, guild association and minimum area requirements for 54 non-rare bird species found in littoral forest remnants.

Landscape structural metrics are remnant area (AR), shape index (SI), distance to large remnant (DR), distance to source (DS), patch density (PD), edge density (ED), Distance to nearest remnant (DNR) and area of nearest remnant (ANR). See Table 7.1 for how landscape metrics were calculated.

Species were classified on their habitat association (forest dependent (F) or matrix-tolerant (M)) following Watson et al (in press b).

Predominate foraging guild is delineated into Carnivire (C), Insectivore (I), Nectivore (N), and Granivore (G).

Predominate foraging substrate is delineated into Ground (G), Shrub (S), Canopy (C), Aerial (A) and Sallying Insectivore (Sa).

Guild association and weight was determined using species accounts in Langrand (1990), Egushi *et al.* (1993), Wilmé (1996), Goodman *et al.* (1997), Morris & Hawkins (1998), Ravokatra *et al.* (2003) and Wilmé and Goodman (2003).

Bird species < 20 g were defined as 'small' (S), between 20-100 g as 'medium' (M) and > 100 g as 'large' (following Watson *et al.* 2003).

Minimum area requirements for all area-sensitive were determined using incidence functions calculated from the logistic regressions models. An incidence of 50% in the logistic model was used to define the minimum area. * $p < 0.05$, ** $p < 0.01$

Name	Species code	Habitat association	Foraging guild	Foraging substrate	Weight	Minimum Area (ha)	Landscape structural metrics							
							AR	SI	DR	DS	PD	ED	DNR	ANR
Madagascar Wood Rail *Canirallus kioloides*	mawo	F	I	G	L	-	2.83	1.08	1.24	2.65	2.6	3.43	0.85	3.07
Madagascar Crested Ibis *Lophotibis cristata*	maci	F	I	G	L	150	17.32**	9.29*	0.001	0.001	0.148	3.03	3.27	1.89
Yellow-billed Kite *Milvus aegyptius*	ybki	M	C	A	L	-	0.91	1.12	2.1	0.04	0.02	0.12	1.45	2.31
Madagascar Harrier-Hawk *Polyboroides radiatus*	mahh	F	C	A	L	30	10.36**	1.91	0.101	0.122	0.544	0.928	1.67	4.78
France's Sparrowhawk *Accipiter francesii*	frsp	M	C	A	L	-	0.09	1.71	2.12	0.71	1.41	1.3	2.1	0.01
Madagascar Buzzard *Buteo brachypterus*	mabu	M	C	A	L	-	0.01	1.21	2.1	0.01	0.07	0.13	0.89	0.07
Madagascar Kestrel *Falco newtoni*	make	M	C	A	L	-	1.71	1.21	0.01	1.97	1.21	1.1	0.01	0.02
Madagascar Partridge *Margaroperdix madagascarensis*	mapa	M	G	G	L	-	2.54	2.4	1.11	1.43	2.1	0.73	1.21	1.71
Helmeted Guineafowl *Numida meleagris*	hegf	M	G	G	L	-	1.71	2.1	0.01	0.7	1.12	2.12	0.91	1.12

Name	Species code	Habitat association	Foraging guild	Foraging substrate	Weight	Minimum Area (ha)	Landscape structural metrics							
							AR	SI	DR	DS	PD	ED	DNR	ANR
Madagascar Flufftail *Sarothrura insularis*	maft	F	I	G	M	40	7.13*	2.77	0.79	2.26	1.31	0.17	0.15	3.58
Madagascar Buttonquail *Turnix nigricollis*	mabq	M	G	G	M	-	2.11	0.31	0.01	0.61	1.72	0.01	0.78	1.15
Madagascar Turtle-Dove *Streptopelia picturata*	matd	M	G	G	L	-	1.13	0.42	1.41	0.69	2.12	2.98	0.07	1.02
Namaqua Dove *Oena capensis*	nado	M	G	G	L	-	0.71	1.21	1.37	3.21	2.71	0.42	0.19	1.41
Madagascar Green Pigeon *Treron australis*	magp	F	F	C	L	20	25.61**	2.81	0.01	0.07	3.1	0.01	0.88	2.45
Madagascar Blue Pigeon *Alectroenas madagascariensis*	mabp	F	F	C	L	25	24.91**	17.34**	0.63	3.16	2.71	2.78	0.05	1.04
Lesser Vasa Parrot *Coracopsis nigra*	lvpa	F	F	C	L	20	32.72**	15.54**	0.05	0.86	0.05	0.86	0.19	3.32
Gray-headed Lovebird *Agapornis cana*	ghlb	F	F	C	M	-	5.44	5.61	1.57	3.79	0.05	1.98	2.87	0.091
Blue Coua *Coua caerulea*	blco	F	I	C	L	25	9.39*	9.56*	3.77	4.58	1.11	5.22	0.03	0.836
Giant Coua *Coua gigas*	gico	F	I	G	L	35	38.19**	15.93**	0.29	1.67	0.301	7.15	0.04	3.22
Madagascar Coucal *Centropus toulou*	maco	M	I	S	L	-	1.14	1.91	3.12	0.65	2.3	4.2	1.21	2.33
Madagascar Nightjar *Caprimulgus madagascariensis*	mani	M	I	A	M	-	0.67	2.02	3.11	0.03	0.57	1.12	2.71	0.51
African Palm Swift *Cypsiurus parvus*	apsw	M	I	A	M	-	4.22	2.51	0.81	1.43	1.24	2.13	0.81	0.62
African Black Swift *Apus barbatus*	absw	M	I	A	M	-	1.71	2.95	0.63	0.91	2.13	3.41	1.29	0.01
Malagasy Kingfisher *Alcedo vintsioides*	maki	M	C	C	L	-	0.98	1.78	0.62	0.67	7.81	6.42	2.11	2.32
Madagascar Pygmy Kingfisher *Ispidina madagascariensis*	mapk	F	I	S	S	150	21.23**	22.31**	0.006	2.4	0.541	2.86	0.3	0.15
Madagascar Bee-eater *Merops superciliosus*	mabe	M	I	A	M	-	4.56	4.98	0.91	3.12	3.1	2.45	2.12	2.87
Broad-billed Roller *Eurystomus glaucurus*	bbro	F	I	Sa	L	15	33.83**	20.03**	0.4	1.31	0.408	4.47	0.36	2.1
Cuckoo-Roller *Leptosomus discolor*	curo	F	I	C	L	25	11.32**	7.82**	1.45	5.92	2.3	1.86	1.26	2.21
Hoopoe *Upupa epops*	hoop	F	I	G	L	35	8.85*	5.81	0.18	0.62	0.55	1.53	1.31	0.94
Madagascar Bush Lark *Mirafra hova*	mabl	M	I	G	M	-	0.32	2.12	0.13	3.12	2.34	4.76	4.24	2.98
Mascarene Martin *Phedina borbonica*	mamt	M	I	A	S	-	4.32	3.71	0.22	1.11	2.19	3.12	0.81	0.35
Madagascar Wagtail *Motacilla flaviventris*	mawa	M	I	G	M	-	0.21	1.43	0.07	2.66	3.98	0.91	2.34	1.16

Name	Species code	Habitat association	Foraging guild	Foraging substrate	Weight	Minimum Area (ha)	Landscape structural metrics							
							AR	SI	DR	DS	PD	ED	DNR	ANR
Ashy Cuckoo-Shrike *Coracina cineria*	ascs	F	I	C	M	50	22.75**	19.54**	0.25	5.09	3.44	2.1	0.05	1.67
Madagascar Magpie-Robin *Copsychus albospecularis*	mamr	F	I	S	M	110	11.45**	7.76	2.06	3.1	1.25	3.61	0.05	0.87
Madagascar Bulbul *Hypsipetes madagascariensis*	mabb	M	I	C	M	-	5.34	3.45	1.02	0.89	2.17	3.12	0.23	2.33
Madagascar Brush-Warbler *Nesillas typica*	mabw	F	I	S	S	-	4.42	7.6	0.54	0.65	0.22	2.92	0.83	3.11
Madagascar Cisticola *Cisticola cherina*	maci	M	I	S	S	-	4.21	3.51	3.12	0.76	2.11	1.76	0.46	0.98
Common Newtonia *Newtonia brunneicauda*	cone	F	I	C	S	35	28.81**	17.05**	0.59	1.27	0.11	3.39	0.214	1.97
Archbold's Newtonia *Newtonia archboldi*	arne	F	I	C	S	150	16.96**	18.56**	1.66	7.55	2.92	5.91	1.05	2.21
Common Jery *Neomixis tenella*	coje	M	I	C	S	-	7.54	2.34	1.32	1.98	2.87	4.21	1.07	3.12
Stripe-throated Jery *Neomixis striatigula*	stje	F	I	C	S	35	21.22**	18.28**	0.35	4.1	0.87	6.78	0.49	1.68
Madagascar Paradise Flycatcher *Terpsiphone mutata*	mapf	F	I	S	S	25	29.28**	2.1	0.23	2.18	1.01	7.44	0.18	2.62
Souiminga Sunbird *Nectarinia souimanga*	sosu	M	N	C	S	-	4.97	3.67	3.12	0.98	2.3	4.1	1.12	0.81
Long-billed Green-Sunbird *Nectarinia notata*	lbgs	F	N	C	S	15	21.45**	3.2	0.43	0.17	0.43	0.17	0.37	2.97
Madagascar White-Eye *Zosterops maderaspatana*	mawe	F	I	C	S	15	13.88**	18.03*	0.36	0.2	0.1	1.72	4.32	2.12
Chabert's Vanga *Leptopterus chabert*	chva	F	I	C	M	-	5.81	6.6	0.47	7.2	7.4	3.21	3.21	0.98
Hook-billed Vanga *Vanga curvirostris*	hbva	F	I	C	M	15	32.12**	3.7	0.12	0.34	0.23	6.5	1.98	0.76
Blue Vanga *Cyanolanius madagascarinus*	blva	F	I	C	M	-	6.43	5.03	0.11	0.33	0.01	1.49	2.03	2.12
Tylas Vanga *Tylas eduardi*	tyva	F	I	C	M	150	10.42**	3.35	1.26	6.36	0.38	2.26	0.01	4.12
Crested Drongo *Dicrurus forficatus*	crdr	M	I	Sa	M	-	2.76	3.12	2.13	0.97	0.21	2.12	0.98	1.12
Pied Crow *Corvus albus*	pecr	M	I	G	L	-	2.34	0.76	2.13	0.98	0.17	0.87	1.12	0.91
Madagascar Starling *Hartlaubius auratus*	mast	F	F	C	M	-	5.09	3.4	0.03	4.98	2.12	4.57	3.12	1.52
Common Myna *Acridotheres tristis*	comy	M	I	G	M	-	3.21	2.51	0.02	2.11	0.11	0.98	0.78	0.71
Madagascar Red Fody *Foudia madagascariensis*	marf	M	G	C	S	-	0.98	0.7	0.56	1.12	2.01	0.79	3.03	1.87

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