ISOLATED *FICUS* TREES AND CONSERVATION IN HUMAN-MODIFIED LANDSCAPES

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VOLUME I

ISOLATED *FICUS* TREES AND CONSERVATION IN HUMAN-MODIFIED LANDSCAPES

Abstract to Chapter 8

ABSTRACT

Isolated *Ficus* trees and conservation in human-modified landscapes

The destruction of tropical forests is the most concerning current threat to biodiversity. Although protected areas have long been used as the primary tool for biodiversity conservation, there is an increasing need to find suitable conservation strategies for the growing area of human-modified land. This thesis addresses three themes that have been identified as the most pressing areas for research in human-modified landscapes: biodiversity conservation beyond protected areas, forest restoration, and the human–environment relationship. By studying the interactions between birds, plants, and people with isolated *Ficus* (Moraceae) trees in Assam, India, this thesis reports several important findings: 1) isolated *Ficus* trees are extraordinarily important to frugivorous bird communities that inhabit human-modified landscapes; 2) the frugivores visiting these isolated trees still sustained the majority of ecological function found in trees close to the forest edge; 3) isolated *Ficus* trees are also exceptionally important feeding sites for insectivorous birds in human-modified landscapes, compared to other trees; 4) *Ficus* trees are better restoration nuclei than other isolated trees; 5) although the sacred status of *Ficus* trees in Assam has a major influence on their abundance and distribution, faith-based values are insufficient in ensuring their conservation. In conclusion, this thesis finds that isolated *Ficus* trees are critically important micro-sites for conservation in human-modified landscapes, the loss of which may lead to avifaunal collapse and a reduction in restoration potential. However, by stressing their ecological and cultural properties, it may be possible to build a strong case for the conservation of isolated *Ficus* trees in Assam and elsewhere.

EXECUTIVE SUMMARY

The extensive loss of forest across the world's tropics and subtropics, coupled with the limited scope for the creation of new protected areas, creates a considerable challenge for the future direction of biodiversity conservation. Considering current socio-economic trends, and continuing declines in biodiversity, new approaches to conservation are needed that offer more affordable solutions. In particular, the proliferation of human-modified landscapes in formerly forested regions means that the conservation community cannot continue to rely on protected areas to reverse deteriorating biodiversity indicators. In an attempt to provide innovative yet achievable pathways to address these concerns, this thesis assesses the efficacy of a novel mechanism to enhance conservation returns in human-modified landscapes.

At a global scale, one genus of fruit tree is consistently reported to hold extraordinary importance for biodiversity in tropical and subtropical forests. *Ficus* (Moraceae, L.) trees, due to their unusual mutualistic relationship with pollinating fig wasps (Agaoninae, Chalcidoidea), produce fruit aseasonally throughout the year. They also produce fruit on an astonishing scale, which is easy to consume, and has high concentrations of scarce nutrients. As a result of these traits and of the large size of many *Ficus* species, *Ficus* trees are a critical resource for a wide range of species and ecosystem functions. For example, despite chronic under-sampling, over 1,274 vertebrate species have been recorded feeding on *Ficus* trees. These frugivorous birds and mammals play an important role in tropical seed dispersal, influencing the distribution and composition of rain forest flora. However, little is known about the strength of this interaction beyond the forest edge, and whether *Ficus* trees can continue to support ecological function independent of forests. This thesis therefore attempts to judge the utility of isolated *Ficus* trees for conservation in human-modified landscapes.

Networks of isolated *Ficus* trees have been reported from numerous human-modified landscapes around the world. One such landscape is the heavily populated, mixed agricultural district of Golaghat in Assam, North-east India. Over the course of five months of fieldwork in a 250 km^2 study area, three prominent conservation themes were investigated in relation to human-modified landscapes: avifauna conservation per se, forest restoration, and human–*Ficus* relationships. Field methods included single-tree bird surveys (127 three-hour early morning surveys), vegetation surveys (207 surveys of plants growing under and around isolated *Ficus* and non-*Ficus* trees), and five months of ethnographic data collection while living in two rural villages. Further data collection efforts included one month measuring 364 historically-collected bird specimens at the British Natural History Museum, and an online survey of 144 *Ficus* experts working around the globe.

In all, the results emphatically indicated that *Ficus* trees were considerably more important than other isolated trees in supporting both frugivorous, and unexpectedly, insectivorous avifaunal assemblages beyond the forest edge. In fact, isolated *Ficus* trees over 30 km from the nearest forest still supported, or at least were visited by birds representing, the majority of bird functional traits found in trees growing in close proximity to forest. Perhaps partly as a consequence, *Ficus* trees also supported higher plant richness, abundance, and density under and around their canopies compared to other isolated trees. *Ficus* trees were therefore argued to be critically important components of this human-modified landscape, both in terms of conserving the composition and function of current avian diversity, and in facilitating vegetation regeneration, and potentially forest restoration, by acting as restoration nuclei. In

addition, the ethnographic work and online expert survey help to inform current debates about the adoption of religious or spiritual beliefs in conservation. By identifying a more practicable approach to trade-offs between doctrinal concerns and economic imperatives than commonly assumed, inhabitants of Golaghat District and beyond were able to justify the felling of *Ficus* trees, despite their sacred status, in cases where they imposed an economic cost or barrier to development. Combined with the geographical variation in religious value attributed to *Ficus* trees that the global survey detected, it may be more prudent to stress other ecological or cultural values when promoting the conservation of *Ficus* trees.

Although population simulation models delivered a promising picture for the future prospects of *Ficus* trees in the study area, isolated *Ficus* tree populations are still sensitive to enhanced adult mortality. Therefore it is important that an awareness of the valuable role *Ficus* trees play in human-modified landscapes is emphasised to relevant conservation strategists and policy makers. In India, the adoption of *Ficus* conservation measures may reinvigorate tired and frequently frustrated conservation efforts, and stimulate further work into *Ficus*–frugivore relationships as satellite tracking technology improves. If further studies could verify that isolated *Ficus* trees play a similar role in other regions, as would be expected given their broad ecological significance in tropical and subtropical forests around the world, it would create a compelling case to focus efforts more closely on conserving *Ficus* trees in human-modified landscapes. The results of this thesis therefore map out a path that offers to deliver real ecological and humanitarian value, and which may be achievable at relatively little cost, by incorporating *Ficus* conservation measures into existing sustainable agriculture frameworks, and emphasising the ecological and cultural benefits that come with preserving *Ficus* trees in human-modified landscapes.

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PREFACE

This thesis attempts to identify a mechanism for effective conservation in human-modified landscapes. In doing so, it investigates the relationships between isolated *Ficus* trees and birds, plants, and people in turn. *Ficus* is the taxonomic name for the genus commonly referred to as fig trees. The edible, or domestic, fig (*F. carica*) that many people are familiar with is one of over 840 members of this genus. Although they share similar reproductive strategies, the figs studied in this thesis have quite different life histories. They are hemi-epiphytic figs, which can grow to enormous sizes, and which are believed to be critically important food resources of fruit eating birds in tropical forests. This thesis seeks to uncover how the relationship between fig trees and frugivorous birds changes in non-forest landscapes, along with the consequences for seed dispersal in deforested habitats, and the potential for tropical forest restoration. In addition, it seeks to discover the nature of human relationships with these impressive trees, and identify conservation strategies that may be coherent within existing cultural and economic frameworks.

This thesis follows the permitted option of presenting a set of at least four empirical chapters, which appear as self-contained journal manuscripts, situated within introductory and discussion chapters. To outline the links between individual chapters, each empirical chapter and appendix is introduced by a brief preface. The thesis itself starts with an introduction to the theoretical context of the work and the research aims. This is followed by a critical survey of the literature that has informed the approach to this research, and an overview of the study area and data collection methods.

The first empirical chapter is Chapter 4, which, along with Chapters 5 and 6, addresses aspects of avifaunal interactions with isolated *Ficus* trees. Chapters 7 investigates the potential of *Ficus* trees to act as forest restoration nuclei, while Chapter 8 looks at the ramifications of this for the communities living in the study area. Looking ahead, the future prospects of isolated *Ficus* tree population densities are modelled in Chapter 9. Chapter 10 takes an ethnographic approach to understanding the relationships between people and *Ficus* in the study area, and so attempts to build on the quantitative survey conducted as part of Appendix 3. Finally, in an effort to identify patterns in the human–*Ficus* relationship at a wider scale, Chapter 11 presents the results of a global survey of *Ficus* values, as reported by experts in 27 countries. Although the initial aim was to produce four empirical chapters, it soon became apparent that some additional angles would have to be investigated to tell the story of isolated *Ficus* trees in human-modified landscapes. This story is developed and discussed in Chapter 12, with a synopsis in Chapter 13.

The literature cited in the empirical chapters is referenced in the Harvard style at the end of each chapter, while the citations made in the Introduction, Literature Review, Methods, and Discussion are referenced in the final reference section on page 441.

Four appendices follow this reference list. The first three make important contributions to this body of work, but are not included as empirical chapters for reasons outlined in the prefaces to each. The fourth contains statements from the collaborators who have co-authored papers submitted as part of this thesis. These letters outline their roles in the formulation of the papers that bear their names, as required by the Examination Regulations.

CHAPTER 1: INTRODUCTION

1.1 Conceptual framework

Habitat destruction, and in particular the conversion of tropical forest to agricultural land, has reorganised ecosystems across the world's tropics (Ellis & Ramankutty, 2008; Gibbs et al., 2010; Laurance et al., 2014). This reorganisation has been accompanied by the fragmentation of animal and plant populations, species extinction, and the deterioration of ecological service provision (Tabarelli et al., 2012; Gibson et al., 2013; Ferraz et al., 2014), to the extent that it is considered to be the most concerning current threat to biodiversity (Newbold et al., 2014). To counter this threat, conservation organisations have endorsed and sponsored the creation of protected areas, where resource use is restricted to safeguard biodiversity (Meir et al., 2004; Butchart et al., 2010). In fact, establishing protected areas has become the main weapon in the conservation armoury (Laurance, 2013). However, dissatisfaction with the use of protected areas is now growing. Questions have been raised over their effectiveness at conserving the species that reside within their boundaries, their suitability for addressing new challenges to conservation, such as the decline in migratory species, and their substantial economic cost, despite only covering a small percentage of the Earth's land area (Brooks et al., 2004; Chape et al., 2005; Ferraro & Pattanayak, 2006; Joppa et al., 2008; Chazdon et al., 2009a; Laurance et al., 2012; Geldmann et al., 2013; Trierweiler et al., 2014). These concerns, combined with growing pressure on land and resources from an increasingly large and wealthy human population (Rands et al., 2010), provide a strong incentive to identify alternative conservation strategies (Martin et al., 2014).

Conservation beyond protected areas, in human-modified landscapes, may achieve a host of environmental and social benefits. By conserving remnants of native vegetation and regulating agricultural practices, production landscapes can still conserve populations of threatened species (Gardner et al., 2009; Tobias et al., 2013), restore connectivity between protected areas (Harvey et al., 2006; Chazdon et al., 2009), provide ecosystem services (Daily et al., 2009; Cardinale et al., 2012), and strengthen human–wildlife bonds by bringing nature closer to people (Folke et al., 2011). The key question is: how can we best conserve species and ecological function in human-modified landscapes?

Isolated trees scattered across human-modified landscapes are believed to be useful tools within this framework (Fischer et al., 2010). In addition to the benefits listed above, they are believed to provide nesting and roosting sites (Manning et al., 2006), which might otherwise be rare in agricultural landscapes (DeMars et al., 2010), regulate nutrient cycles (Barnes et al., 2011), and facilitate forest restoration by attracting seed dispersers and ameliorating environmental conditions to encourage seed germination and seedling survival (Herrera & García, 2009; Chetana & Ganesh, 2012).

One novel approach to this topic centres on the use of *Ficus* trees (Moraceae). The *Ficus* genus includes more than 840 species (www.theplantlist.org; accessed: 07/05/2014), which occur around the world's tropics and subtropics. Their unusual breeding biology, which depends on a mutualistic relationship with pollinating fig wasps (Agaoninae, Chalcidoidea), means that figs produce fruit throughout the year (Kinnaird et al., 1996; Bain et al., 2013; Harrison, 2013). This aseasonal fruiting pattern, combined with the volume, presentation, and unusual mineral concentrations in their fruit, has led several researchers to conclude that *Ficus* trees are "keystone species", playing a disproportionate role in supporting critical forest dynamics (Terborgh, 1986; Lambert & Marshall, 1991; Nason et al., 1998; Dev et al., 2011).

Although the definition of the keystone term, and the difficulty in testing whether species qualify for species status, constrains its application (Mills et al., 1993; Cottee-Jones & Whittaker, 2012), the overwhelming weight of evidence from tropical forest studies indicates that *Ficus* trees are critically important in maintaining the composition of frugivore communities and determining the recruitment patterns of plants in tropical forest ecosystems around the world (Lambert & Marshall, 1991; Corlett, 1998; Korine et al., 2000; Shananhan et al., 2001; Kinnaird & O'Brien, 2005; Harrison, 2006; Carlo et al., 2013).

While *Ficus*–frugivore interactions are well studied in forest ecosystems, changes in the properties of this relationship beyond the forest edge remain poorly quantified (Galindo-González et al., 2000; Eshiamwata et al., 2006; Caughlin et al., 2012). Although mobile, many tropical frugivores are reluctant to cross non-forest habitat (Tobias et al., 2013), which may be sufficient to cause the breakdown of this relationship in human-modified landscapes. The ecological consequences of such a breakdown may include the genetic isolation of frugivore populations in forest fragments, a reduction in seed dispersal and regeneration potential in non-forest habitats, and the local extirpation of *Ficus* trees themselves (Mawdsley et al., 1998; Bleher et al., 2003; Caves et al., 2013). However, if the relationship between *Ficus* trees and frugivores could be conserved in modified landscapes, a host of ecosystem services and species could be supported, offering the prospect of low cost forest restoration, and maintaining the strong cultural ties observed between people and *Ficus* trees in several parts of the world (Wilson & Wilson, 2013).

1.2 Research aims

Considering the concerns described on page 3, this thesis aims to test the efficacy of *Ficus* trees as conservation agents in human-modified landscapes. With this goal in mind, three areas of research were pursued.

1) The importance of isolated *Ficus* trees in conserving bird communities in human-modified landscapes.

Frugivorous birds are important seed dispersers in tropical ecosystems, and as such, play a major role in determining plant composition. However, forest-dependent and large frugivores are particularly vulnerable following deforestation. Therefore, it is important to establish whether isolated *Ficus* trees effectively conserve frugivorous bird assemblages beyond the forest edge, and to address the following questions. To what extent is distance from the nearest forest the overarching driver of bird community composition in isolated *Ficus* trees? Are protected areas required in order to conserve ecological function in human-modified landscapes? Or can the majority of ecological function and seed dispersal capacity be maintained through networks of isolated *Ficus* trees? These questions are addressed in Chapter 4.

Aside from frugivores, the importance of *Ficus* trees to insectivorous birds has never been studied, despite the established importance of *Ficus* trees to their arthropod prey. Considering that insectivorous birds are the largest dietary guild of birds globally, and that they are facing major declines following deforestation, investigating the relationship between isolated *Ficus* trees and insectivore communities may offer critical and novel approaches to insectivore conservation. Chapter 5 assesses the importance of *Ficus* trees for insectivorous birds, and whether they can provide useful micro-sites for insectivore conservation in human-modified landscapes.

Returning to frugivores, many bird species are believed to be largely dependent on *Ficus* food resources, and several others have been identified as key seed dispersers. *Megalaima* barbets, which occur sympatrically throughout the range of the genus, are one such group. Chapter 6 analyses a case study of fruit resource partitioning patterns, ecological redundancy, and seed dispersal effectiveness in human-modified landscapes through the interactions of this group with isolated *Ficus* trees.

2) The potential role isolated *Ficus* trees play in restoring plant communities in human-modified landscapes.

Isolated trees are believed to be important forest restoration sites. Given their size, the abundance of fruit they produce, and their pan-tropical distribution, Chapter 7 investigates whether *Ficus* trees could be particularly effective sites for forest restoration, compared to other isolated trees.

If isolated *Ficus* trees do have value in the conservation of bird and plant communities in human-modified landscapes, it is particularly important that *Ficus* populations in these habitats are safeguarded in the long-term. However, in all landscapes previously studied, isolated trees are projected to experience sharp declines in the next 100 years through high mortality and low recruitment. Chapter 9 projects likely *Ficus* densities in the study area over the next 300 years in an effort to identify measures that could help maintain *Ficus* populations over long time scales.

3) The relationship between people and *Ficus* trees, and how this may influence conservation strategies in human-modified landscapes.

Rural communities in many parts of the developing tropics often have limited economic wealth, and frequently rely on the local provision of ecological goods and services. Chapter 8 examines the human-uses of plant communities growing under

Ficus trees, to determine whether *Ficus* help provide goods and services that are useful to rural human communities.

The persistence of *Ficus* trees in human-modified landscapes around the world is notable, and if they have useful conservation properties, it may be advantageous to understand the economic and cultural reasons behind their survival. Therefore, Chapter 10 considers a local case study of the societal reasons for *Ficus* tree survival in human-modified landscapes, while Chapter 11 makes the first global scale assessment of human beliefs and attitudes towards *Ficus* trees.

1.3 Geographical context

To address these research questions, a network of isolated *Ficus* trees in Assam, North-east India, was studied. Assam has experienced extensive lowland forest clearance, starting with the arrival of British tea planters in the 19th century. In Golaghat District, where fieldwork for this thesis was conducted, the only remaining areas of forest are contained within protected areas. However, isolated *Ficus* trees were a common feature in agricultural and urban areas of the landscape, and so presented a suitable setting in which to analyse their role in conservation biogeography. Furthermore, despite numerous studies investigating the ecological role of *Ficus* trees in forests around the world, none had before been conducted in North-east India, which is a large and ecologically rich region facing a range of pressing conservation concerns (Bhatta, 2011; Horwich et al., 2013; Wilson et al., 2013). Studying *Ficus* trees in this area therefore provided an opportunity to make a novel contribution to the literature from both a theoretical and geographical perspective.

CHAPTER 2: LITERATURE REVIEW

2.1 Flagships, umbrellas, and keystones

In an effort to garner support for particular conservation missions, and build conservation literacy in public domains, conservationists have developed and deployed specialised terminology to communicate ecological concepts (Simberloff, 1998). Three prominent terms, if not buzzwords, are flagship, umbrella, and keystone species (Barua et al., 2011) (Table 2.1). These terms serve as proxies for the conservation of biodiversity in general, and in the case of keystones, have been widely applied to *Ficus* trees. Here, the merits of each of these terms, and the suitability of *Ficus* trees as conservation proxies, shall be considered.

Table 2.1: Definitions and published examples of flagship, umbrella, and keystone species. Definitions are quoted from Heywood (1995), with page numbers in parentheses.

Flagship species	Umbrella species	Keystone species
"Popular charismatic species that serve as symbols and rallying points to stimulate conservation awareness and action" (p. 491).	"Those whose area of occupancy or home range are large enough and whole habitat requirements are wide enough that, if they are given a sufficiently large area for their protection, will bring other species under their protection" (p.490)	"A species whose impact on its community or ecosystem are large and would be greater than would be expected from its relative abundance" (p. 290)
Polar Bear (*Ursus maritimus*)	Spotted Owl (*Strix occidentalis*)	*Ficus* spp.

Flagship species are "charismatic species that serve as symbols and rallying points to stimulate conservation awareness and action" (Heywood, 1995:41). The concept has been used by conservation organisations for decades, although it only started attracting interest in the academic literature in the 1980s (Mittermeier, 1986;

Verrísimo et al., 2011). Species popularly used as flagships include Polar Bears (*Ursus maritimus*), Asian Elephants (*Elephas maximus*), and Golden Lion Tamarins (*Leontopithecus rosalia*) (Dietz et al., 1994; Stirling & Derocher, 2007; Barua et al., 2010). Given the fluidity of the notion of charisma, a handful of other, less iconic species have also been suggested (for example, the Lord Howe Island Stick Insect *Dryococelus australis*) (Lorimer, 2007; Berenbaum, 2008; Barua et al., 2012). While established definitions of flagship species, such as the one given above, do not recognise any significant ecological role, they are often also thought of as *de facto* umbrella species (Caro et al., 2004; Barua et al., 2012).

Controversy surrounds the appropriate method for selecting flagships, and the possible unintended consequences of the promotion of one species as a conservation symbol. Recommended selection methods include various combinations of ecological, phenotypic, cultural, and policy-related traits (Dietz et al., 1994; Bowen-Jones & Entwistle, 2002; Veríssimo et al., 2011; Barua et al., 2011), with recent researchers stressing the importance of applying marketing theory, and ensuring that flagships are selected with a clearly defined, culture-specific audience (Home et al., 2009; Barua et al., 2011). In many cases, however, flagships have been selected on an *ad hoc* basis, with insufficient consideration of the cultural relationship between a proposed flagship species and the target audience (Veríssimo et al., 2014). Even if selected appropriately, the dangers of deploying a flagship species in a conservation initiative include evoking emotions through their metaphorical nature that distort ecological reality (Barua, 2011), having a detrimental impact on the conservation status of non-flagship species (Caro et al., 2004), and undermining future conservation efforts if the flagship species becomes extinct (Simberloff, 1998).

The constituencies flagship species represent can be either geographical (conservation in a particular country, region, or island), ecological (a particular ecosystem or habitat), institutional (a conservation organisation), or biological (a particular taxonomic group) (Veríssimo et al., 2011). The timing of flagship species selection often coincides with the development of a new threat to a species, landscape, or ecosystem. For example, the Giant Panda (*Ailuropoda melanoleuca*) became the logo of the World Wide Fund for Nature as the global conservation movement became established, the African Elephant (*Loxodonta africana*) became a symbol of the anti-poaching movement with the boom in the ivory trade in the 1980s, and images of the Polar Bear are now widely used in the popular media to report concern over climate change (Dietz et al., 1994; Bulte & van Kooten, 1996; Leader-Williams & Dublin, 2000; Blake & Hedges, 2004; Peacock et al., 2011).

Several of the criticisms directed at the use of flagship species also apply to the umbrella species concept. Although umbrella species differ in that the main criterion for their identification is the area required to conserve a population, rather than having characteristics which are likely to raise public interest or sympathy, the assumption that their conservation will ensure the conservation of those other species which occur within the geographical limits of the umbrella species is "a matter of faith rather than research" (Simberloff, 1998:247). One species identified as an umbrella species is the Spotted Owl (*Strix occidentalis*), which requires approximately 800 ha of old-growth forest per breeding pair in the Pacific North-west, USA (Simberloff, 1987; Shrader-Frechette & McCoy, 1993). However, the assumption that conserving the Spotted Owl would also mean the other old growth forest inhabitants were adequately conserved requires careful investigation, as several species may have specific habitat requirements that do not overlap with that of the owl. Like flagships, the use of illconceived umbrella species in conservation campaigns may stimulate perverse management decisions, and may prove to be detrimental to broader conservation goals on longer time-scales (Caro, 2010).

A final proxy worth discussing is the keystone species concept. Where umbrella species require large population range sizes to be considered, the determinant of a keystone has proved to be somewhat more fluid. Definitions range from species that "play a critical role in determining community structure" (Jones et al., 1994:380) to "rare species of low abundance in a community but whose removal has drastic effects on many other species in the community" (Krebs, 2009:402). Most definitions, however, centre on the notion that keystone species have a disproportionately large influence on their community relative to either their abundance or biomass. While intuitively appealing, if this is taken to be the definition of a keystone species, it creates considerable problems in testing for the existence of, and therefore identifying, such species. It implies that a threshold value must exist, where the ratio between the abundance of a particular species, and the influence that species has over the rest of the community, can be tested to qualify species for keystone status. Despite Power et al.'s (1996) attempt to devise a "Community Importance Index", no such threshold ratio has been successfully developed, and as a result the term cannot be used in a precise and defensible fashion (Cottee-Jones & Whittaker, 2013).

Despite the shortcomings in the development of the keystone concept, numerous authors have described *Ficus* trees as keystone species (for example: Terborgh, 1986; Lambert & Marshall, 1991; Shanahan et al., 2001; Diaz-Martin et al., 2014). For the reasons outlined above, and elaborated further in Appendix 1, this thesis will not use the term in reference to *Ficus*. It will, however, briefly consider the suitability of

Ficus trees as flagship or umbrella species, in recognition of the way these proxies can raise the profile and conservation value of particular species.

In many parts of the world's tropics, neither flagship species nor any other actions in the conservationists' toolbox have managed to avert the destruction of tropical forests. In their place, new human-modified landscapes have been created, with a range of cultural histories and biogeographic relationships. Here, a human-modified landscape is an area that has lost its pre-existing "natural" vegetation through anthropogenic processes. Typically, these landscapes were once tropical forests that have now been converted to agricultural production, but also include other vegetation types, such as marshland and savanna habitats, and include a wide range of human land-uses, from abandoned mining sites to urban areas. In this way, human-modified landscapes are synonymous with disturbed, human-dominated, and degraded landscapes, and specific forms of human-modified landscapes can be referred to as production, agricultural, or managed landscapes. The term is useful in so far as it captures the key property of many tropical ecosystems: that they have been created through the conversion of forest; but its breadth demands that it be clarified further. For the purposes of this thesis, a human-modified landscape is a rural area that is under agricultural production following deforestation.

2.2 Land-sparing versus land-sharing

The growth in academic concern for human-modified landscapes developed as a component of the land sparing versus land sharing debate (Phalan et al., 2011; Ramankutty & Rhemtulla, 2013). In this fairly crudely constructed dichotomy, policy makers and land managers are presented with two pathways to achieve the greatest conservation returns (Balmford et al., 2005). The first, land sparing, requires that farmers maximise yields through agricultural intensification, which will increase food production to the point where some land is not required, so that it can then be devoted to biodiversity conservation (Fischer et al., 2008). The second, land sharing, involves low intensity farming, permitting biodiversity to co-exist alongside agricultural production (Perfecto & Vandermeer, 2010). While both landscape types exist, to a large extent they represent hypothetical scenarios, and it is unclear how well these academic debates are engaging with land-use decision-making at a practical level (Mattison & Norris, 2005; Ewers et al., 2009). Nonetheless, if conserving species richness was the objective, the weight of evidence indicates that land sparing would be the best general strategy, as many forest-specialist species would struggle to persist in a mixed land-use setting (Manning et al., 2006; Jetz et al., 2007; Edwards et al., 2010; Gibson et al., 2011). However, given growing demand for food and other commodities, the opportunities to spare land are diminishing. Furthermore, there is growing evidence that areas which have already been converted from forest can still support biodiversity. For example, a recent study from Costa Rica indicates that the majority of reptile and amphibian species in the study area were found in anthropogenic habitat types. Small patches of vegetation structures embedded within the agricultural landscape increased the effective forest cover 14-16 times, contributing roughly 95% of the available habitat for forest-dependent species (Mendenhall et al., 2014). While reserves will always be required to conserve some forest-dependent species (Stouffer & Bierregaard, 1995; Laurance et al., 2004; Stouffer et al., 2006), there is growing recognition, and optimism, that diverse agricultural mosaics can also play an important role in biodiversity conservation (Fischer et al., 2006; Mendoza et al., 2014).

2.3 Countryside biogeography

Research into ecological processes and the conservation potential of human-modified landscapes in the tropics has been described as countryside biogeography. Countryside biogeography is the study of the diversity, abundance, conservation, and restoration of species in rural and other human-dominated landscapes (Daily, 1997:105), and has increasingly been studied in the tropics as the area of deforested land has grown. Most studies in tropical countryside biogeography have been conducted in Central America, where the biological potential of coffee plantations, cattle ranches, and mixed agricultural plots has been quantified (Daily et al., 2001; Luck & Daily, 2003; Perfecto et al., 2004; Harvey et al., 2011). These studies indicate that forest species can survive in human-modified landscapes long after deforestation (for a non-Central American example over very long time-scales, see Ranganathan et al., 2008), and that human-modified landscapes may support a small proportion of species in the absence of forests (Daily et al., 2001; Sekercioglu et al., 2007). Importantly, some studies have also demonstrated that forest-specialist species, which are often of higher conservation concern than habitat-generalist, can also persist in largely deforested areas (Bhagwat et al., 2008). With a view to augmenting the area of ecologically valuable habitat, improving connectivity between fragments, and insulating protected areas from anthropogenic influences beyond their boundaries, the influence of several vegetation structures in enhancing biodiversity metrics in human-modified landscapes has been investigated over the last two decades (Daily et al., 2003; Gardner et al., 2007; Chazdon et al., 2009a). They include the conservation of small patches of remnant vegetation, secondary forest plots, live fences, and isolated trees (Harvey & Haber, 1999; Daily et al., 2001; Fischer & Lindenmayer, 2002; Hughes et al., 2002; Luck & Daily, 2003; Harvey et al., 2005; Chacón & Harvey, 2006; Manning et al., 2006; Fischer et al., 2010; Harvey et al., 2011). In an attempt to identify the vegetation structures that are most effective in enhancing biodiversity, the conservation capacity of each will be discussed in turn.

2.3.1 Remnant vegetation

Patches of remnant vegetation, which are commonly thought of as small scale stands of original growth trees that survived clearance, are frequently cited as important habitat for biodiversity in modified landscapes (Daily et al., 2001; Hughes et al., 2002; Daily et al., 2003; Pereira & Daily, 2006; Sodhi et al., 2010; Tobias et al., 2013; Goodale et al., 2014; Mendoza et al., 2014). Landscapes with more original forest cover are likely to support more forest-specialist species and higher forest-specialist abundances (Petit & Petit, 2003). There is also some evidence that even small forest remnants hold high biodiversity value. In their study of mammals in Costa Rica, Daily et al. (2003) compared species richness in five habitat types: extensive forest (227 ha), small remnants surrounded by coffee plantations (<35 ha), small remnants surrounded by pasture (also <35 ha), coffee plantations, and pasture. They found that small remnants surrounded by coffee plantations did not differ in mammal species richness from extensive forest areas, and were richer than other agricultural habitat types. However, they were also richer than small remnants surrounded by pasture, indicating the importance of matrix quality and human-modified habitat management for biodiversity conservation at the landscape scale (Ricketts, 2001). Of the 60 species likely to have occurred in the study area before clearance (40 years earlier), 10% had become locally extinct before the survey. These were the largest members of their families, and are of the most conservation concern, including the Jaguar (*Panthera onca*) and Baird's Tapir (*Tapirus bairdii*), indicating that the processes which created this modified landscape may have already caused the extinction of several forest-specialist mammal species. Therefore, and perhaps unsurprisingly, Mendoza et al. (2014) recommend that any forest surviving in human-modified landscapes be prioritised for conservation.

Secondary forest patches, which are small-scale areas of significantly degraded old-growth forest, or forest that has regenerated since clearance, are widespread in tropical regions (Chazdon et al., 2009b). Available data indicate that they are important for the persistence of biodiversity, and in particular of forest-specialists, in human-modified landscapes (Chazdon et al., 2009a; Goodale et al., 2014). They have been found to hold much higher species richness than, and different species assemblages from, agricultural habitats, and can also hold some forest-specialist species (Mendoza et al., 2014). In the absence of old-growth remnants, secondary forest patches may offer the only habitat for a range of species, and act as critical refugia for forest-dependent species. In a comprehensive assessment of the conservation value of secondary forests, Barlow et al. (2007) analysed the proportion of old growth species found in 14- to 19-year old secondary forest in the Brazilian Amazon, across 15 taxonomic groups. They found secondary forests held 59% of the species recorded in old-growth forests, although responses to habitat modification varied widely across taxa. While these results indicate secondary forests are far from a perfect substitute, the proportion of old-growth species inhabiting them is likely to increase over time, as secondary plots increasingly develop the properties of old-growth stands (Raman et al., 1998; Dunn, 2004; Chazdon et al., 2009b).

2.3.2 Riparian corridors

Linear vegetation features are common in human-modified landscapes, as trees surviving clearance on steep ridge tops, vegetation lining roads, or riparian corridors along streams or other watercourses (Mayfield et al., 2006). Aside from their established influence on water flow and nutrient content (Osborne & Kovacic, 1993; Dosskey et al., 2010), riparian corridors may also be the best linear tree structure for biodiversity conservation (Bennett et al., 2014). Across four landscapes in Central America, riparian corridors had higher species richness and abundances than live fences and pastures with tree cover (Mendoza et al., 2014). When this analysis was restricted to forest-specialists, the relationships were even stronger. In an experimental test of the use of corridors by a forest-specialist bird species, Gillies and St Clair (2008) found the Barred Antshrike (*Thamnophilus doliatus*) to return faster, and with greater success, to their original territories when translocated to an area with a forested riparian corridor as intervening habitat, rather than a tree line or open pasture. While promising, the promotion of riparian corridors as movement facilitators suffers from many of the same data deficiencies as the corridor debate in general (Lindenmayer & Nix, 1993; Beier & Noss, 1998; Bolliger et al., 2014). In this case, the birds were experimentally manipulated, and it is possible that they may not choose to use the corridor under natural conditions. The distance they were translocated was only 0.7–1.9 km (which was also the strongest determinant of return success), and two of the 10 (20%) Antshrikes translocated to a riparian corridor still failed to return to their original territories. If they do not have a major role to play in enhancing connectivity, riparian corridors may still have some value as small-scale habitat patches, and as important modifiers of environmental conditions for aquatic biodiversity. However, given that many countries have regulations enforcing the conservation of trees along waterways for hydrological and erosion-control purposes, and that landowners often conserve them for aesthetic reasons anyway (Sherren et al., 2010), they may continue to persist in human-modified landscapes even in the absence of a clear ecological case.

2.3.3 Live fences

Another linear vegetation structure commonly found in human-modified landscapes is live fences, a term used to describe tree lines, hedgerows, and other vegetation used to demarcate land boundaries. Live fences provide additional habitat, foraging resources, and nest sites for species inhabiting modified landscapes, and act as stepping-stones for forest-specialist species, enhancing connectivity across modified landscapes (Chacón & Harvey, 2006). In a pastoral landscape in Veracruz, Mexico, 54% of the bird species recorded in adjacent forests were found to use live fences (Estrada et al., 2000), while in a similar Nicaraguan landscape, 29 species were found to be using eight live fences (Harvey et al., 2005). While of some demonstrable value to biodiversity, the utility of live fences could be improved through increasing the diversity of plant species used for this purpose, reducing the frequency and severity of pruning, and expanding their use across modified landscapes to enhance structural connectivity (Harvey et al., 2005; Chacón & Harvey, 2006). In Costa Rica, for example, simulations indicate that converting all wooden fences to live fences would double the number of direct connections between forest habitats, and reduce the average distance between tree canopies (Chacón & Harvey, 2006). Further research on live fences, and experimental tests of their ability to enable mobility between forest patches, may add more weight to the argument that they are ecologically important features of human-modified landscapes. However, any future researchers should investigate the chance that live fences may lead to unintended, and perverse, ecological consequences through the provision of more edge habitats (Lindenmayer et al., 2012; Cottee-Jones, 2013). Furthermore, economic trade-offs with landowners have to be taken into account, particularly potential losses to productivity, and the high costs of establishing and maintaining fence lines, before making any policy recommendations (Chan & Daily, 2008).

2.3.4 Scattered trees

One further structure, which in pastoral systems at least, appears to be more attractive to landowners than live fences, is the presence of scattered trees. Scattered trees, which for this analysis are taken to be trees dispersed in human-modified landscapes, are a common feature of cultural and disturbed landscapes around the world (Manning et al., 2006; Gibbons et al., 2008; Harvey et al., 2011). They are synonymous with isolated trees, remnant trees, pasture trees, and paddock trees (Dunn, 2000; Law et al., 2000; Guevara et al., 1986). Scattered trees are believed to deliver a host of benefits to biodiversity in modified ecosystems by augmenting biotic processes (Vesk & MacNally, 2006). At a local scale, they enrich soil nutrient levels, provide hydrological regulation, and stabilise environmental conditions (Manning et al., 2006). They also provide habitat for other plants by providing canopy cover, and for animals which may use scattered trees as a foraging, roosting, or nesting location (Fischer & Lindenmayer, 2002; Sekercioglu et al., 2007; Lindenmayer et al., 2013; Manning et al., 2013; Le Roux et al., 2014). At the landscape scale, scattered trees can make a major contribution to overall tree cover, providing connectivity to enable some animal movements, and softening edge effects on the border of protected areas (Harvey et al., 2006; Medina et al., 2007). There is evidence that they are also useful restoration nuclei, facilitating tree recruitment by attracting seed rain and ameliorating non-forest microenvironments, as will be discussed further below (Slocum, 2001; Guevara et al., 2004; Elgar et al., 2014).

Increasing the density of tree cover in agricultural areas is likely to have benefits for a range of taxa (Mendoza et al., 2014). Precise guidelines for managers were provided by Fischer et al. 2010, who found a threshold relationship between the density of isolated trees and the richness of bird and bat communities in 2 ha Australian paddocks. They found that the marginal value of scattered tress was highest when trees occurred at low density, with a doubling of bird richness in the presence of one tree compared to treeless sites, and a tripling of bat richness with 3–5 trees compared to treeless sites. Further measures to consider include increasing the diversity of tree species in agricultural areas, conserving large old trees for their particular value to biodiversity (Lindenmayer et al., 2013), and promoting natural regeneration (Esquivel et al., 2008; Harvey et al., 2011; Murgueitio et al., 2011). Although little research has looked at the properties that make certain species of isolated tree more effective at conserving biodiversity than others, there is a debate over the utility of native versus non-native scattered trees. Indeed, two studies from East Africa reported contrasting results, with Douglas et al. (2013) arguing that native tree cover had the strongest relationship with forest-dependent bird species richness in agricultural landscapes in Uganda, while Berens et al. (2008) found isolated Guavas (*Psidium guajava*), which are exotic in their Kenyan study area, supported high levels of frugivorous bird richness, which increased the density of seed rain and proportion of late-successional recruits under their canopies.

Like all vegetation structures in human-modified landscapes, isolated trees face the threat of decline with continued agricultural intensification (Gibbons et al., 2008). Aside from elevated mortality through human clearance, they also suffer from low recruitment rates, which threatens their existence in landscapes around the world (Lathrop et al., 1991; Harvey & Haber, 1999; Plieninger et al., 2004; Gibbons et al., 2008; Fischer et al., 2009). High grazing pressure in pastoral landscapes suppresses seedling recruitment, and creates a scenario where the existing mature trees are in effect “the living dead” (sensu Janzen, 1988). Conventional management systems in many areas consists of near-continuous livestock grazing with few rest periods, and in some cases, regular fertiliser application, which also serve to reduce understory growth, compact soils, and increase water sediment loads (Steinfeld et al., 2006; Esquivel et al., 2008; Fischer et al., 2009; Murgueritio et al., 2011; Newton et al., 2013). However, by studying different grazing management practices and quantifying scattered tree recruitment in Australian pastoral landscapes, Fischer et al. (2009) found that fast rotational grazing, where livestock graze particular fields in high-intensity, short-duration periods before being moved onto a different field, did not have a high opportunity cost to the farmer, while also increasing the probability of regeneration by approximately four times. Medium term measures, such as reducing fertiliser application, may also enhance regeneration, along with a range of other ecological processes. It appears that reversing the decline in scattered trees is possible through discussing trade-offs and management decisions with landowners, but in common with any of the above methods for conserving biodiversity in human-modified landscapes, conservationists must have a high degree of confidence that their recommended management actions will be successful to avoid losing credibility with landowners and other partners (Cottee-Jones, 2013).

2.3.5 Evaluation of countryside biogeography conservation structures

In reality, the effectiveness of any of these measures is likely to be dependent on a complex hierarchy of factors that interact at a range of scales across time and space. Furthermore, the efficacy of any one structure is likely to be interdependent on the presence or absence of other vegetation structures at the landscape or even regional scale. The probability of their implementation is also more likely to be determined by socio-economic drivers than by ecological science, limiting the application of these lessons to cases which are the exception rather than the norm (Chan & Daily, 2008). Even in heterogeneous human-modified landscapes, with a range of vegetation structures, some species show little response. In Costa Rica, no significant difference was detected in moth species richness or abundance across four different agricultural regimes (Ricketts, 2001). Indeed, many species recorded in modified habitats appear to show a uniform distribution across non-forest landscapes, exhibiting a high degree of similarity in species composition and relative evenness of diversity among different sites (Daily et al., 2001). In several European agricultural landscapes that have been subject to decades of environmental regulation with the aim of enhancing biodiversity, no discernable improvement has been recorded (Kleijn et al., 2001), especially not with regards to threatened species (Kleijn et al., 2006). These findings undermine the incentive for land managers to engage in trade-offs between productivity and conservation (Chan & Daily, 2008).

Furthermore, the evidence seems to suggest that small forest blocks are far more effective at conserving a higher richness and abundance of species, and in particular forest species (which are often of greater conservation concern) than any configuration of a production landscape. In a study of four Central American landscapes, dispersed trees and live fences consistently had lower richness and abundance than small forest patches (Mendoza et al., 2014). In Daily et al.'s (2001) study of bird assemblages in a Costa Rican tropical countryside landscape, the majority (55%) were only found in forest blocks, with five of the 28 avian families recorded entirely absent from human-modified habitats. Furthermore, the authors believed the proportion of birds only found in forest blocks would have been higher were it not for the extirpation of several forest-specialist species in the 40 year period between forest clearance and their study. Even in cases where a high proportion of species are recorded beyond the forest borders, such as in Veracruz, Mexico, where more than 70% of bird species present in the area were recorded in human-modified habitats (Estrada et al., 1997), they may be declining, or they may still be dependent on local forest blocks (Gilroy et al., 2014). For example, in Ricketts's Costa Rican moth study, agricultural sites within 1 km of the forest fragment had significantly higher richness and abundance than sites further than 3.5 km away (Ricketts, 2001). Evidently, there is no substitute for native forest habitat (Daily et al., 2003; Gibson et al., 2011). But, if we are to reconcile production with conservation, we will have to find the most efficient method of increasing biodiversity value other than setting aside land.

2.4 Tropical forest restoration

Aside from conserving biodiversity on short time scales, suitable strategies are needed to improve vegetation cover, and perhaps even reforest abandoned agricultural land, to improve the conservation potential of human-modified landscapes in the medium to long term. While showing some signs of slowing, the global rate of forest loss is still very high, accounting for an estimated 13 m ha of forest annually between 2005 and 2010 (FAO, 2010). This results in the loss of biodiversity, reduced carbon sequestration, and the loss of local ecosystem services, which are of critical importance to some of the world's most vulnerable people (MEA, 2005; TEEB, 2010). However, the annual net forest loss for the same period was only 5.2 m ha, as natural regeneration and anthropogenic afforestation increased forest cover in 19 countries, including China, India, Russia, and the USA (FAO, 2010). Afforestation has been driven by agricultural land abandonment, which is a prerequisite for natural regeneration, along with large-scale tree planting schemes attempting to stabilise environmental conditions and take advantage of growing incentives through Reduced

Emissions from Deforestation and Degradation (REDD+) finance (Rudel et al., 2005; Nagendra, 2007; Angelsen, 2009).

Policy makers and practitioners seeking to restore forests have a range of strategy options: passive restoration, perching structures, focal trees, applied nucleation, commercial plantations, and mixed native species plantations (Lamb et al., 2005; Chazdon, 2008; Table 2.2). Each of these strategies has advantages and disadvantages that need to be carefully considered on a project-by-project basis, although several overarching themes are broadly relevant to most trade-offs. These include the goals, cost, and scale of the project, and the time it will take between project initiation and forest creation (Catterall et al., 2007; Le et al., 2012; Figure 2.1). Implicit to the goals of the project are a set of broader ecological questions over why a forest is needed, and what forest community is envisaged (Sayer, 2007). Ecological restorations often attempt to recreate the assemblage of plants present before the last anthropogenic clearance, but older baselines, or no baseline at all are also justifiable outlooks (Götmark, 2013), especially as growing concerns over climate change place a greater emphasis on ecological resilience (Willis et al., 2010). Here the trade-offs and ecological challenges surrounding each of these strategies are reviewed, before evaluating their effectiveness with reference to their potential for expansion, the time-scale of regeneration, and the likely resultant community composition.

Strategy name	**Definition**	**Advantages**	**Disadvantages**
Passive restoration	The abandonment of land to allow natural succession processes to take place.	Low cost (potentially free) No human legacy of plant selection	Can be very slow May not work at all May produce non-analogue communities May not hold large-seeded species
Artificial perches	The use of man-made structures to entice avian frugivores to land and deposit seeds in open habitats.	Fast and low cost way of increasing dispersal in open habitats	Unlikely to increase recruitment as it does not address seedling survival problems
Focal tree	The conservation of remnant, isolated, or scattered trees and the area around them.	Low cost Fast No human legacy of plant selection	Only works where remnant trees exist Mixed evidence of expansion May not hold large-seeded species
Applied nucleation	Planting small areas ("islands") with selected plant species, which will then spread and coalesce with other islands.	Possibly cheaper than plantations Works in landscapes without focal trees May be better for biodiversity than plantations	Management costs may be high Mixed evidence of expansion May not hold large-seeded species Human legacy of plant selection Moderate speed
Commercial plantation	Planting large areas with fast growing trees. The trees used are often non-native and often planted in monocultures.	Relatively low cost per tree Easy to manage	Moderate speed Can have very poor biodiversity outcomes Human legacy of plant selection May not hold large-seeded species
Mixed native species plantation	Large-scale planting of selected native tree species.	Relatively low cost per tree Can have better biodiversity outcomes than commercial plantations	Moderate speed Human legacy of plant selection May not hold large-seeded species

Table 2.2: Definitions of the six major ecological restoration strategies with summaries of their advantages and disadvantages.

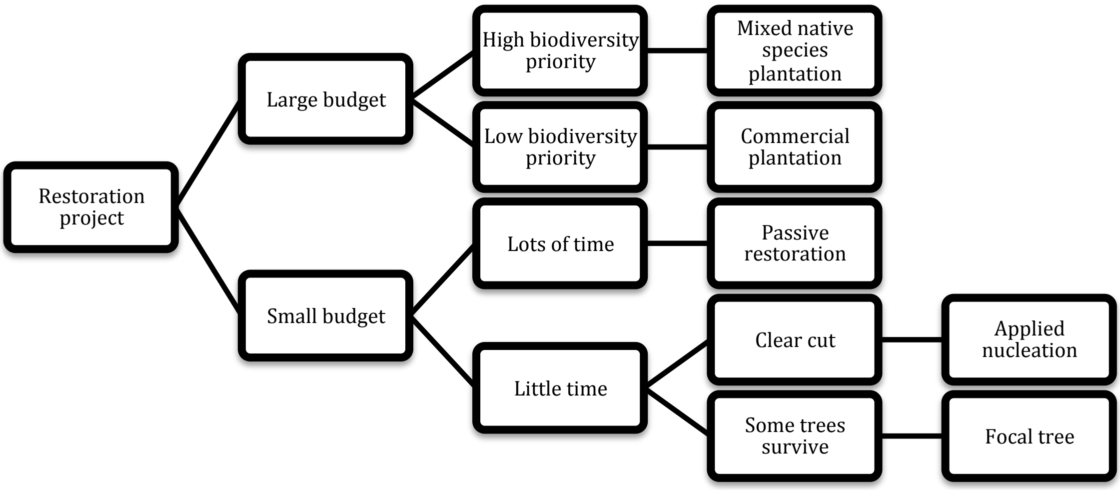

Figure 2.1: A decision tree for ecological restoration practitioners.

2.4.1 Passive restoration

In suitable environmental conditions, natural afforestation describes the replacement of other habitat types by forest in the process of succession (Clements, 1916). Theoretically, if a deforested area were abandoned, in time it would revert to forest through passive restoration (Zahawi & Augspurger, 1999; Aide et al., 2000; Corbin & Holl, 2012). Passive restoration has two major advantages: 1) it is low cost, although usually it requires the exclusion of grazers through fencing (Chazdon, 2003); and 2) it minimises the scope for human intervention to distort the final community composition, as all seeds are sourced naturally from the surrounding landscape (Wijdeven & Kuzee, 2000). This helps avoid difficult questions over ecological baselines, and if the original seed bank and dispersal mechanisms are still intact, should produce analogue forests (Lamb et al., 2005; Letcher & Chazdon, 2009). For example, 40 years after pasture abandonment in depopulated agricultural landscapes of Puerto Rico, naturally regenerating secondary forests had similar stem densities, basal areas, above ground biomass, and species richness as neighbouring old growth forests (Aide et al., 2000). However, exotic species were abundant in these new forests, and only five of the top ten most common old growth tree species were found in more than 50% of secondary forests after 77 years of regrowth. This suggests non-native species and dispersal barriers can influence passive restoration (Holl et al., 2000), particularly if the area has been deforested for a long time, for example, decades instead of years, and if the intervening land-use has been fairly intensive (Wijdeven & Kuzee, 2000; Lamb et al., 2005).

Frugivorous birds and bats are major seed dispersal agents in forest and early-successional ecosystems (Daily & Erhlich, 1996; Zimmerman et al., 2000). In deforested areas, however, the lack of perching structures may reduce the flow of bird-dispersed seeds (Graham & Page, 2012; Heelemann et al., 2012; Leighton & Holl, 2013), and a lack of feeding or roosting sites may deter bats (Kelm et al., 2008; Bianconi et al., 2012).

If a seed does overcome the dispersal barrier, it will be more vulnerable to predation, and faces a high chance of mortality through desiccation from exposure to direct sunlight and high temperatures (Cole, 2009). The soil substrate is also an important determinant of the likelihood of germination. Although different plant species vary in their requirements, many forest dependent plant species are more likely to germinate in moist, aerated conditions with a medium loam texture (Schmidt, 2007). Compact soils, or soils with a hard crust, reduce the chances of successful germination, especially in small-seeded species (Hartmann et al., 1997).

Should it germinate, competition with ruderal grasses, in particular, may crowd out tree seedlings (Holl et al., 2000), while also reducing soil nitrogen levels (Rhoades et al., 1998). Even in situations where seedlings do manage to grow through grass layers, the high light intensity in open habitats may actually lead to photoinhibition and water stress in forest-adapted species (Loik & Holl, 1999; dos Santos et al., 2006; Holl et al., 2011), thus reducing survival. In fact, a study in Costa Rica found that seeds arriving in an abandoned pasture had just a 0.1% chance of surviving over an 18-month period (Holl, 2002a).

These different climatic and nutrient cycling regimes in disturbed sites may delay the start of succession, which can either make passive restoration a very slow process (Lamb et al., 2005), or trap the disturbed community in an alternative open habitat stable state (Suding & Hobbs, 2009). Should invasive or exotic species prevent the natural re-colonisation of native forest species, another legacy of disturbance may be the creation of non-analogue communities that are heavily dominated by non-native species (Aide et al., 2000; Franklin et al., 2000; Chazdon, 2003; Grau et al., 2003; Hooper et al., 2005; Franklin, 2007). Here, human perturbations may distort the developing assemblage more than alternative active restoration approaches, while the low cost of passive restoration must be balanced against the often long time lags on the path to natural recovery.

2.4.2 Perching structures

One method of overcoming the seed dispersal barrier is to attract frugivorous birds into deforested areas using artificial perching structures. This system uses man-made frames with cross bars designed to encourage birds to land on them (Holl et al., 2000), and has been successfully demonstrated to increase seed rain in temperate (McClanahan & Wolfe, 1993), savanna (Heelemann et al., 2012), and tropical landscapes (Holl, 1998; Graham & Page, 2012). While these increases in seed rain are promising, studies that incorporated seedling establishment rates demonstrated that perching structures did not enhance recruitment (Holl, 1998; Reid & Holl, 2013). This is likely because perches do not help ameliorate the other threats facing seeds once they arrive at a restoration site, including high light conditions and competition with grasses (Reid & Holl, 2013).

2.4.3 Focal trees

Given the problems of limited seed dispersal and establishment in passive restoration, and the low establishment rates recorded with artificial perches, alternative strategies that take advantage of existing ecological structures have been investigated. Focal trees, which are synonymous with isolated or scattered trees, can overcome both of these limitations (Manning et al., 2006). Through their interaction with birds and bats, which are major seed dispersal agents in forested and deforested ecosystems in the tropics (Daily & Erhlich, 1996; Zimmerman et al., 2000), they may increase the flow of seeds into disturbed areas and act as recruitment foci (Guevara & Labrode, 1993; Galindo-González et al., 2000; Slocum & Horvitz, 2000; Hooper et al., 2005). Birds are attracted to them for use as perches, for cover to avoid predators, and as stepping-stones when crossing open patches of habitat (Graham, 2001; Fischer & Lindenmayer, 2002; Eshiamwata et al., 2006). Birds also show a behavioural trend towards defecating while perched, and especially just prior to taking flight (Charles-Dominique, 1986; Pausas et al., 2006; Reid & Holl, 2013), so any seeds a bird may be carrying are more likely to be dispersed under focal trees than in open areas (Herrera & García, 2009). Indeed, the number of animal dispersed seeds falling under focal trees can be comparable to that of intact forests, and two orders of magnitude higher than open habitats (Holl et al., 2000).

As with artificial perches, higher seed rain is of no use in restoration if the dispersed seeds do not survive (Reid & Holl, 2013). Fortunately, focal trees help create the right environmental conditions for forest seeds to germinate and grow. They ameliorate the local microclimatic conditions, providing shade and higher humidity, both of which mimic conditions under a forest canopy (Mistry, 2000; Eldridge & Freudenberger, 2005; Manning et al., 2006). These conditions also deter grasses, which prefer open, high light environments, and which can be major competitors with forest seedlings (Holl 1999).

Focal trees also act as "fertility islands", altering the soil nutrient balance through higher leaf fall (which has been reported to be 20 times higher under focal trees than in open pasture; Loik & Holl, 1999), bird droppings, and in some cases fallen fruit, all of which decompose and supply nutrients beneath the canopy (Toh et al., 1999; Prober et al., 2002; Tiessen et al., 2003). Perhaps then, it is no surprise that seedlings planted under focal trees have been reported to grow significantly faster than those planted in open habitats (Loik & Holl, 1999). In a test where livestock grazers were excluded beneath the canopies of five focal trees in Mexican pastures, Guevara et al. (2004) found not only that sapling communities grew very quickly, but that they held a high proportion of late-successional, large-seeded tree species (further details below). Beyond experimental tests, focal trees have been reported to hold higher sapling species richness and stem densities than open habitats in Cameroon (Carrière et al., 2002a), Mexico (Guevara et al., 1992), Costa Rica (Schlawin & Zahawi, 2008), and Spain (Pausas et al., 2006). In a study in Northern Spain, Herrera and García (2009) argued that some thorny focal trees might further facilitate secondary succession by deterring grazers, thus acting as nurse plants for saplings. It appears that even without conservation interventions, focal trees can play a role in accelerating natural succession using seeds dispersed from local plant communities. If isolated trees are actively conserved, and grazers are excluded from the area around them, they may offer a low cost and relatively fast opportunity to restore forests that are supported by surviving dispersal agents.

Given that focal trees contribute by attracting seed dispersers and facilitating seedling growth, the trees which are favoured most by frugivores, and the trees which provide the best shade and nutrient conditions, are likely to be the most effective recruitment nuclei (Hooper et al., 2005, but see Carrière et al., 2002b). Slocum's (2001) comparative work on four different tree types in Neotropical pastures is one of the few studies to test this hypothesis. He selected four focal tree types: 1) *Ficus* trees (Moraceae), which are fleshy fruited and cast a deep shade; 2) *Pentaclethra macroloba* (Fabaceae), which have explosively dispersed seeds and a deep shade; 3) *Cecropia* trees (Cecropiaceae), which are fleshy fruited with sparse shade; and 4) *Cordia alliodora* (Boraginaceae), which have wind dispersed seeds and sparse shade. As fleshy-fruited trees should be more attractive to frugivores, they should have higher densities of seed rain. In this system, after four months of data collection, the results supported the hypothesis, with *Ficus* trees receiving 16 species of seed at a rate of 90 seeds/m^2 per month; *Cecropia* receiving 13 species at 108 seeds/m^2 per month; *Pentaclethra* receiving 13 species at 51 seeds/m^2 per month; and *Cordia* receiving 10 species at 50 seeds/m^2 per month (Slocum & Horvitz, 2000). The higher seed rain densities were combined with greater shade levels, so that *Ficus* trees had the highest density and richness of animal-dispersed recruits, followed by *Cecropia*, *Pentaclethra*, and then *Cordia* (Slocum, 2001). This suggests that high shade, fleshy-fruited tree types, such as *Ficus* species, should be more effective restoration foci than other tree types (Kuaraksa & Elliott, 2013).

However, Slocum also observed that the focal trees with more open canopies had faster-growing recruits, and were beginning to form islands of fast-growing shrubs.

Ficus, on the other hand, had slow growing recruits that were not expanding out into the surrounding pasture. Slocum concluded that *Ficus* trees may not be as effective recruitment foci as the other tree types, but may be more important in later seres of succession due to the higher diversity of species growing under them. It is also worth emphasising that Slocum's study was conducted in Central American pastures, where a Neotropical lineage of *Ficus* was studied. Given the taxonomic differences between New and Old World *Ficus* groups (Berg, 1989), it is unclear how well these results translate into Old World, or particularly Indian, contexts.

Concerns about the growth rates of recruits under *Ficus* trees are tempered, however, by Guevara et al. (2004). In an experimental study of five *Ficus* trees in Mexican pastures, Guevara et al. enclosed the areas beneath the canopy with barbed wire to exclude livestock grazing. After three years, a dense, tall (4–5 m) understory had developed, comprised of 95 species of plant, 68% of which had seeds larger than 3 mm. Furthermore, there is evidence that *Ficus* trees promote nucleation. In their study of 30 isolated *Ficus* trees and 20 isolated *Nectandra ambigens* (Lauraceae) trees, Guevara et al. (1992) found slightly higher mean richness and densities in the perimeter of focal trees (richness per quadrat, mean±SD= 11.2±3.4; stem density/m^2= 0.3±0.4) compared to open pasture (richness per quadrat, mean±SD= 10.6±3.6; stem density/m^2= 0.2±0.3), although these differences were non-significant.

2.4.4 Applied nucleation

In situations where focal trees are absent, planting small tree islands may also reduce barriers to seed dispersal and establishment (Corbin & Holl, 2012). By planting clumps of fast growing trees, carefully designed restoration plantings can mimic the nucleated pattern of succession that occurs around focal trees (Yarranton & Morrison, 1974). Once a nucleus of regenerating vegetation has established, seed rain is likely to increase as frugivorous birds and mammals begin to visit the site (Cabral et al., 2003), while the vegetation itself may also capture wind blown seeds (Franks, 2003; but see Robinson & Handel, 2000 who found no evidence of this). The abiotic conditions may stabilise, allowing seedlings to successfully establish and out-compete grasses (Holl, 2002b; Zahawi & Augspurger, 2006). Theoretically a nucleus will spread outwards and meet the boundaries of other nuclei over time, creating a heterogeneous mosaic of plant ages. This should help counter one of the major criticisms of plantation-led restoration attempts (see below), and create a community with a broad age structure and greater habitat complexity (Lundholm, 2009).

In comparing the effectiveness of applied nucleation versus passive restoration, several experimental tests in Neotropical pastures (Zahawi & Augspurger, 2006; Cole et al., 2010), Mediterranean farmland (Rey Benayas et al., 2008), and temperate woodland (Robinson & Handel, 2000) have found a consistent pattern of higher sapling and seed rain richness and densities in 2–13 year old nuclei than neighbouring control treatments undergoing passive restoration. There has not, however, been a consistent trend in the relationship between the distance from a forest and seed rain. Biogeographic theory suggests that sites at greater distances from forests, which are assumed to be the major seed sources in a landscape, should receive lower rates of seed rain than nuclei closer to forests. In their five-year study at a six hectare abandoned landfill site in New Jersey, USA, Robinson and Handel created 16 clusters of native trees and shrubs. They discovered a higher rate of bird-dispersed seed rain at clusters closer to forest resources on the edge of their study site, supporting an earlier finding from a different site in Staten Island, New York (Mattei & Handel, 1997). These results are supported by Parrotta and Knowles' (2001) work on restoration plantations, where a strong distance effect was detected in zoochorous tree sapling recruits over 1 km, with higher abundance and species richness in plantations within 640 m of old-growth forest. However, restoration nuclei studies in Honduras (Zahawi & Augspurger, 2006) and Costa Rica (Cole et al., 2010) failed to find any correlation between distance and seed rain rates. Corbin and Holl (2012) suggest that this may be a result of the shorter experiment lengths in these studies, as nuclei were not sufficiently tall to attract forest dwelling frugivores. This argument is supported by Robinson and Handel (2000), who found that taller clusters had higher sapling recruitment rates. However, no results of the relationship between height and seed rain itself are presented, so this may actually be due to taller nuclei creating better conditions for seedling growth. An alternative explanation is presented by Zahawi and Augspurger (2006), who suggest that the frugivorous birds acting as dispersal vectors are not dependent on, or even frequent visitors to, forests; but instead are species which inhabit human-modified landscapes.

The bird assemblages reported by Zahawi and Augspurger, and from other Neotropical pastures, are chiefly composed of disturbed-habitat “generalists” rather than forest “specialists” (Petit & Petit, 2003), and so lend support to this argument. If this is the case, even in areas with widespread disturbance, that are devoid of forested seed source populations, seed dispersal processes are still functional, albeit with different agents of dispersal. While this may be good news for those seeking to restore landscapes that have suffered large-scale deforestation, there are two important issues to consider. Firstly, would nuclei have to act as seed sources themselves, making the composition of species planted very important for long-term forest assemblages? And secondly, would this exclude large-seeded forest species? These trees are often low-density late-successional species in intact forests, which support and are dispersed by specialist frugivores, and therefore may struggle to establish in disturbed habitats restored using applied nucleation (Babweteera & Brown, 2009).

In addressing the first concern, in their New Jersey study system, Robinson and Handel (2000) found their experimental plantings did not serve well as recruitment sources. Of the 26 sapling species recorded, an encouraging 22 were not species planted in the original clusters, further emphasising the continuing function of dispersal in this disturbed landscape. However, 93% of recruits were drawn from just five tree species, only one of which was originally planted in the clusters. Such a scenario would be helpful if the immigrant sapling species were forest species, but if the seeds are being sourced in deforested landscapes by generalist birds, the likelihood is that they are open habitat or even non-native species. Indeed this was the case in Cole et al.'s (2010) Costa Rican experimental plots, where the most commonly dispersed tree seeds were from species of edge, roadside, or fallow field habitats. In a close reflection of Robinson and Handel's sapling data, five early successional tree species accounted for 99.3% of zoochorous seed rain in Cole et al.'s plots, and of the 146 tree species recorded in neighbouring forests, only 11 of these were recorded in the seed rain traps.

In addressing the second concern, Cole et al.'s (2010) seed rain results may also be useful. In their analysis of seed rain in experimental plots over one and a half years, they recorded 251,768 seeds, of which only 0.4% were large-seeded, forest tree species. This reflects Zahawi and Augspurger's results, where "trees dispersed into islands were predominantly early-successional species" (2006:471), and indeed this is supported by a host of other disturbed landscape seed rain studies (Ingle, 2003; Martinez-Garza & Howe, 2003; Dosch et al., 2007). Set against this, however, the dispersal of large-seeded species, even in intact forests, is a comparatively rare event

(Babweteera & Brown, 2010). Furthermore, when large-seeds do arrive, they grow shoots significantly faster than small seeded species in shaded conditions, and are able to maintain the resulting height advantage (Leishman & Westoby, 1994). Therefore, if restoration nuclei are able to attract specialist dispersers as they grow, they may eventually be able to support large-seeded species as well. In a study of secondary forest stands in Mexico, del Castillo and Pérez Ríos (2008) presented some evidence to support this theory, reporting an increase in zoochorous and late-successional seed rain densities with stand age.

Other assumptions with the theory of applied nucleation are also worth exploring. One of the key assumed benefits of applied nuclei is the variation in vegetation age they create, leading to greater species diversity than plantation approaches. However, in a study of the environmental heterogeneity–species diversity relationship, Holl et al. (2013) found sapling species density, richness, and diversity to be equivalent in early-successional plantations and applied nuclei. While this trend may change as plantations and nuclei age, it does underline the lack of evidence for one of the key presumed advantages of applied nucleation.

A second key assumption in the effectiveness of applied nucleation is their ability to expand and merge with other nuclei. If frugivores are mainly depositing seeds under perches, nucleation may only occur as vegetation grows outwards, creating perches over and shading open habitat. In a comparison between two-year old planted tree islands and their 1 m perimeters, Zahawi and Augspurger (2006) found no significant difference in the density of seed rain, or in sapling species richness and density, although the islands did have a higher sapling stem density. This suggests that a nucleation pattern may commence from a very early stage. However, in a similar study looking at seed rain, Cole et al. (2010) found seed rain densities were lower at 2 m, 4 m, and 8 m beyond tree islands than within them, which is consistent with drops in zoochorous seed rain densities found beyond the borders of forests (Cubiña & Aide, 2001). The low levels of seed rain reported beyond the tree islands, along with this difference in results, may be a consequence of greater distances between the tree island and seed trap, which suggests nucleation may indeed only occur beneath overhanging branches (Zahawi et al., 2013). To date, studies of the expansion of tree islands give no clear message as to the length of time it takes for the nucleation process to begin.

An important consideration in applied nucleation design is how large should nuclei be? Biogeographic theory suggests that larger tree islands should obtain higher species richness through the area effect (Whittaker & Fernández-Palacios, 2007). In relation to restoration nuclei, this effect may be enhanced as frugivorous birds are preferentially attracted to larger tree islands, thus increasing seed dispersal rates (Fink et al., 2009). Certainly Zahawi and Augspurger (2006) found higher zoochorous and anemochorous seed rain densities in larger tree islands, along with higher sapling species richness. In a four-year study of tree recruits in Costa Rican restoration nuclei, Zahawi et al. (2013) found a positive relationship between island size and animal-dispersed sapling density. Large islands (12x12 m) held significantly greater zoochorous sapling densities than small islands (4x4 m), while medium sized islands (8x8 m) did not differ from either. Working in the same study site two years earlier, and using the same tree islands, Cole et al. (2010) found a different relationship between area and seed rain. They found large and medium islands received significantly greater densities of zoochorous seed rain than small islands, indicating a threshold effect in attracting frugivorous dispersers. Here, seed rain and sapling densities showed different area relationships in the same system, which seems to suggest that animal dispersed saplings are struggling to grow in medium-sized islands. No explanation for this phenomenon was given; instead a guideline following Rey-Benayas et al.'s (2008) suggestion of 100 m^2 as the ideal size of an effective restoration nucleus was provided.

Several of the concerns surrounding applied nucleation, including their ability to nucleate, host large-seeded species, and act as seed sources, along with questions over the plant selection legacy, their ideal size, the diversity of the communities they can support, will hopefully be resolved as experimental treatments mature. Other strategies, such as plantations, have been used for a sufficient length of time to allow us to answer some of those questions.

2.4.5 Commercial plantations

Commonly used in temperate systems, plantations of trees in uniform rows have also been widely used to restore forests in the tropics (Lamb, 1998; Wang et al., 2012; Pawson et al., 2013). Although labour intensive, plantations have proved popular due to their relatively low costs per planted tree, and have been used on large-scales (Parrotta & Knowles, 2001). Indeed an estimated 30% of the world's 4,000,000,000 ha of forest are designated as production forests (FAO, 2010), and as an illustration of their growing popularity, India and China have almost doubled the area of land managed as plantation forests between 1990 and 2010 (from 5,700,000 ha to 10,200,000 ha, and 41,900,000 ha to 77,200,000 ha, respectively), while Peru and Uruguay have roughly quadrupled the size of their plantations (from 263,000 ha to 993,000 ha, and 201,000 ha to 978,000 ha, respectively) (FAO, 2010). The use of non-native tree species is common in these plantations, with 27% of China's and 13% of India's planted forest area composed of exotic species (FAO, 2010).

Plantations can overcome seed dispersal and establishment barriers by having fast growing native or non-native tree species (Lamb, 1998; Nájera & Simonetti, 2010; Zahawi et al., 2013), thereby attracting avian frugivores and mimicking forest understory conditions as quickly as possible (Parrotta et al., 1997). In a long-term study, Lima and Vieira (2013) analysed the vegetation growing in five native monoculture plantations, 35 years after establishment. They found high stem densities and high species richness (range: 70–91, depending on the plantation tree type), although all plantations had significantly lower richness than the reference forest. Commercial plantations with this single-species "monoculture" approach are very popular in forestry and other production landscapes (Bonner et al., 2013). However, they are usually considered to have poor biodiversity, hydrological, and nutrient cycling properties (Lamb et al., 2005; Piotto, 2008; Sang et al., 2013; Sprenger et al., 2013). While the trees selected usually offer faster initial growth rates, they do not encourage the development of dense understories (especially if they are non-native), and are vulnerable to early canopy die-back (Parrotta, 1995; Parrotta, 1999). This makes monoculture plantations especially vulnerable to reinvasion by grasses and the outbreak of fire, both of which would arrest succession (Nepstad et al., 1991; Aide et al., 1996; Parrotta & Knowles, 2001).

2.4.6 Mixed native species plantations

Mixed native species plantations, with nursery grown seedlings, have been demonstrated to have higher species richness, closer community similarity to old-growth forests, and greater longevity than other plantation systems (Parrotta & Knowles, 2001). While some studies have also documented strong nutrient cycling results, the situation with regards to carbon sequestration and storage is slightly complicated. In a synthesis of 81 studies reporting 400 plantation and naturally reforested sites, Marín-Spinotta and Sharma (2012) found climate to be a more important predictor of soil carbon stocks than reforestation treatment, age of stand, or land-use prior to reforestation, with similar soil carbon stocks in secondary forests, plantations, and reference forests. In comparisons between monocultures and plantations with two intercropped species, Bini et al. (2013) recorded stronger microbial action in intercropped plantations, indicating a positive relationship between tree diversity and biogeochemical cycling, improving soil chemistry and soil biology indicators. Therefore, while climate seems to be a more important driver of soil carbon stocks than forest type, a higher diversity of trees is likely to improve nutrient cycling in a restoration treatment.

Although escaping several of the drawbacks of monoculture plantations, mixed native species plantations have also been criticised for being too homogeneous (Piotto et al., 2008). They typically have trees of similar ages, uniform vegetation heights, and limited compositional diversity – along with a strong human legacy in species selection (Corbin & Holl, 2012). It follows, therefore, that young plantations may not be able to attract the number or diversity of frugivores that carefully designed tree islands might, thereby reducing the density and richness of seed rain and sapling recruits (Zahawi et al., 2013).

Turning first to seed rain, Cole et al. (2010) compared seed rain densities in plantation and restoration nuclei treatments, but found no significant difference in seed rain densities or species richness after one and a half years of growth. There were also no significant differences when the analysis was restricted to zoochorous species. With regards to sapling recruitment, Zahawi et al. (2013) found a similar pattern to Cole et al. (2010). Sapling recruitment rates in plantation and restoration nuclei treatments were equivalent after four years of growth, even though only 20% of the area in the restoration island treatments was planted. After three years, Holl et al. (2011) surveyed the planted saplings in the two treatment types at the same site as Zahawi et al. (2013), and found plantations had higher growth and survival rates compared to the restoration islands. However, the improved performance of plantations was offset by the relative costs of the treatments: plantations cost three to four times as much as restoration islands. Therefore restoration nuclei, which are also comparable to plantations in attracting seed rain and inducing sapling growth, may offer a more cost effective strategy.

This is especially important when the scale of the task is considered. Plantations are expensive, with the cost of the first 2–3 years of seedling growth and labour estimated to range from US$400–3,000 per hectare (Corbin & Holl, 2012). Which, according to Corbin and Holl's calculations, would place the cost of reforesting the 27.2 million hectares of tropical forest lost between 2000–2005 at US$10–82 billion (Corbin & Holl, 2012). However, in their comparison of growth rates in plantations and restoration islands, Holl et al. (2011) commented that organising the irregular configuration of restoration nuclei, along with clearing grasses competing with the saplings, was more difficult than establishing and maintaining a plantation. As these problems arose with experienced assistants, and if large tracts of deforested lands are to be restored, management and maintenance costs may be significantly lower in plantations compared to restoration islands. Although not as critical as it is in nucleation approaches, further studies are also needed to determine whether plantations can expand beyond their planted area, and at what rate.

2.4.7 Evaluation of restoration strategies

In evaluating the appropriateness of these strategies for a particular restoration project, issues surrounding their ability to expand, the time-scale of growth, and community composition need to be considered. Turning first to the use of focal trees and applied nucleation, a key assumption is that over time, the nuclei, whether isolated trees or planted saplings, will expand outwards, eventually meeting the borders of other expanding nuclei. However, evidence for this process occurring in experimental tests is very scarce. Only one study has documented high levels of seed rain in the perimeter of restoration nuclei (Zahawi & Augspurger, 2006), while two have found greatly reduced levels (Cole et al., 2010; Zahawi et al., 2013). This is unsurprising as most seed rain falls beneath perches rather than in the open (Holl, 1998), suggesting that nucleation may be a very slow process indeed.

A second concern with restoration techniques surrounds their cost-effectiveness over longer time-scales. While experimental tests clearly demonstrate focal trees, applied nucleation, and plantations accelerate restoration versus passive restoration over a length of 1.5–13 years, will they make a significant difference when viewed on a 100 year time-scale? Or will the slow rate of nucleation and secondary succession make the initial advantage negligible? In systems where the community is trapped in a stable open habitat state, restoration treatments will clearly have a role in accelerating succession regardless of time-scale, but in systems where passive restoration is possible, it may be more cost-effective to let succession take place without intervention (Letcher & Chazdon, 2009). After all, tropical forests have been disturbed by humans for millennia (Willis et al., 2004), and yet appear to show remarkable resilience and capacity for natural restoration (Jones & Schmitz, 2009).

Fostering the growth of late-successional, large-seeded tree species is a major concern for all restoration treatments. In the studies reviewed, large-seeded species are under-represented in applied nucleation and plantation approaches, although preliminary findings suggest that more large seeds arrive in the seed rain of plantations than restoration islands (Holl et al., 2013). Large-seeded plants perform very poorly when planted in open conditions, and even after 10 years of plantation growth, large-seeded plants were poorly represented in Brazilian mine restoration sites (Knowles & Parrotta, 1995; Parrotta & Knowles, 2001). Their absence in restoration nuclei prompted Cole et al. (2011) to suggest that enrichment planting may be necessary to overcome their persistent dispersal difficulties, while Parrotta and Knowles suggest creating habitat features targeted at attracting large-bodied frugivores into plantation landscapes. Regardless of the strategy used, an enrichment approach where large-seeded trees are directly planted into c.10-year-old restoration treatments may be the best solution. Fortunately, Parrotta and Knowles report that large-seeded species are the easiest to handle and cultivate from a nursery management perspective, which should help reduce the costs of this tactic.

Due to limited information and resources, both plantation and applied nucleation approaches can only plant a small subset of the species originally present at a restoration site. These species are often “framework species”, which are usually a mixture of fast growing, fruit bearing, and nitrogen fixing species (Elliott et al., 2003; Wydhayagarn et al., 2009). As the treatment develops into forest, it will carry this legacy of anthropogenic intervention, in terms of species assembly (Silver et al., 2004), composition (Barbier et al., 2008), and nutrient cycling (Celentano et al., 2011), which may continue to influence ecosystem function over long time-scales. Therefore “restoration” may not be restoring the original forest ecosystems at all, but creating novel, non-analogue ecosystems with a strong human fingerprint (Hobbs et al., 2006; Suding, 2011). In many cases, however, it is impossible to restore ecosystems to their pre-disturbance configurations, especially given the limited knowledge of many undisturbed tropical forests, which in any case may have already experienced centuries of human modification (Gillson & Willis, 2004; Willis & Birks, 2006; Jones & Schimtz, 2009; Suding, 2011). Furthermore, the communities that are planted by studying the recent past may not be able to respond to changes in the future. With the threat of fast climate change over the coming century (IPCC, 2013), communities that are created by means of natural ecological drivers may be more resilient to environmental fluctuations (Willis et al., 2010). Therefore, it may be wise to try to restore ecological function as the first priority, and secondarily to play as little a role as possible in influencing species composition (beyond perhaps the removal of non-native and invasive species). If these principles are adopted, the use of focal trees appears to be the most attractive option.

2.5 *Ficus* biology and ecology

One of the focal tree types studied by Slocum (2001) and Guevara et al. (2004) was the genus *Ficus*. *Ficus* are important components of tropical floras, with a pantropical distribution in all major habitats: coastlines, swamps, riparian, lowland, montane, closed forest, and human-modified landscapes (Berg, 1989). This may not be surprising given the genus contains an estimated 700–900 species (840 are currently recognised by the Royal Botanic Gardens at Kew, www.theplantlist.org; accessed: 07/05/2014), which display a wide range of life strategies. These include species that grow as shrubs, climbers, epiphytes, hemi-epiphytes, and free-standing trees (Basset et al., 1997). Indeed, the *Ficus* genus has been described as one of the most diverse plant genera in the world (Chaudhary et al., 2012), to the extent that no single growth form can be described as typical (Berg, 1989). While it is unusual for such a disparate range of growth forms to be included in a single genus, one unique taxonomic feature is common to all species: the syconium.

This highly specialised inflorescence is a receptacle internally lined with many minute flowers, and enclosed by a fleshy wall with a tiny bract-lined ostiole (Harrison, 2013). Syconia are the site of reproductive interactions between the *Ficus* plant and pollinating wasps (Agaoninae, Chalcidoidea), many of which are believed to be specific to individual species of fig in a close mutualistic system (Herre et al., 2008; although many non-pollinating and non-host specific species are also known, see: Marussich & Machado, 2007; Jandér & Herre, 2010; McLeish et al., 2010; Cruaud et al., 2011; Al-Beidh et al., 2012). This relationship between figs and their pollinators is believed to be at least 75 million years old (Cruaud et al., 2010), and depends on at least one individual fig within a population producing receptive florets for female fig wasps to pollinate within 1–3 days of leaving their natal syconia (Kjellberg et al., 1988; Compton et al., 2000; Harrison, 2003; Jevanandem et al., 2013). After pollination the syconia grow and change colour, until they form edible "fruit", which are an important food resource for frugivorous birds and mammals (Shanahan et al., 2001).

2.5.1 The importance of *Ficus* characteristics to frugivores

The close link between fig wasp life cycles and *Ficus* phenology means that, across a population, *Ficus* produce fruit throughout the year. This is unusual among plants, which typically display seasonal peaks in fruit production linked to fluxes in light, temperature, the availability of nutrients, and precipitation (Chapman et al., 2005; Polansky & Boesch, 2013). The aseasonal availability of *Ficus* crops, therefore, is argued to provide a critical resource for frugivorous organisms during times of general fruit scarcity (Leighton & Leighton, 1983; Terborgh, 1986; Price, 2004). In forest on Sulawesi, Indonesia, for example, Kinnaird et al. (1996) found the fig community to exhibit an asynchronous fruiting phenology, with no recurrent annual pattern, where figs were available in all months of the year. Similar results have been reported from lowland Malaysia, where *Ficus* crops were available in every month of a three-year study, with 126 individual trees fruiting 427 times (Lambert & Marshall, 1991). The recognition that specialist frugivores were, to some degree, reliant on *Ficus* crops outside the main fruiting season in Cocha Cashu, Peru, was the first time *Ficus* plants were described as ecological keystones (Terborgh, 1986). Ambiguity surrounding the scientific use of this term may make it more pragmatic to describe *Ficus* plants simply as critically important (Cottee-Jones & Whittaker, 2013; see Appendix 1), but there are nonetheless several other reasons why the role *Ficus* plants play in supporting tropical frugivory may merit special attention.

Hemi-epiphytic and free-standing *Ficus* trees can grow to very large sizes. In a study in Karnatake, India, Dhanya et al. found the average diameter at breast height for ten *F. benghalensis* trees to be 1.88 m, with an average crown height of 15 m, and an average crown diameter of 20 m (Dhanya et al., 2013). However, there are reports in non-peer reviewed sources of individual *Ficus* trees reaching enormous sizes, with one *F. benghalensis* in the Acharya Jagadish Chandra Bose Indian Botanical Gardens at Calcutta said to have a canopy area that covers 8 ha (www.bgci.org/garden; accessed: 12/05/2014). The large size of *Ficus* trees, combined with the density of syconia on their branches, means that they can produce extremely large crops. In a forest in Malaysia, Lambert and Marshall (1991) estimated the crop of one *F. caulocarpa* to hold 250,000 fruits, while Kinnaird et al. (1996) recorded a range of crop sizes from 100,000 to 1,000,000 fruits per tree in large strangling species such as

F. virens. Clearly *Ficus* crop size varies between species, but there is also evidence that it varies between fruiting events on individual trees. In a monitoring study in Kibale Forest, Uganda, Chapman et al. (1992) recorded the fruit crops of a single *F. brachylepis* over successive fruiting events. They found substantial variation in crop size, from 30,480 in 1987, to 7,399 in 1988, and 12,494 in 1989. Furthermore, in the year with the smallest crop size (1988), the size of the individual fruits were also reduced, so that the difference in fruit biomass was even more pronounced than fruit crop size (from 1146 kg in 1987, to 56 kg in 1988, and 472 kg in 1989; Chapman et al., 1992).

Despite this variation, *Ficus* plants generally have relatively short intervals between fruiting events, compared to other plants, and so are considered to be reliable sources of fruit (Lambert & Marshall, 1991). In their study of *Ficus* phenology in Malaysia, Lambert and Marshall (1991) found a range of fruiting intervals across species, although only 11 of the 29 species (38%) had average fruiting intervals that exceeded one year. Indeed the most abundant species, *F. delosyce*, had a mean fruiting interval of only 4.2 months, with a range of 1–8 months over 37 individuals. The regular supply of *Ficus* fruit, with individual trees fruiting repeatedly within a year, may be an important characteristic in the relationship between *Ficus* plants and frugivores. In this way, supply may interact with the temporal variation in *Ficus* fruiting phenologies to increase the likelihood of *Ficus* fruit being available all year round, as previous studies have found to be the case, which may lead to some frugivores developing a dependency on figs. Evidence for this can be found in a range of bird species that specialise in eating figs, including species of *Megalaima* barbet, *Treron* green pigeons, Asian hornbills (Bucerotidae), the Vulterine Parrot (*Psittrichas fulgidus*), Crinckle-collared Manucode (*Manucodia chalybata*), Common Koel

(*Eudynamis scolopacea*), Channel-billed Cuckoo (*Scythops novaehollandiae*), and the Figbird (*Sphecotheres vieilloti*). Further evidence of specialisation, if not dependence on figs, can be found in studies of specific Asian hornbills. In Sulawesi, Kinnaird et al. (1996) discovered that the local Red-knobbed Hornbill (*Aceros cassidix*) population fluctuated in line with *Ficus* fruit availability over two years, while feeding surveys in Sumatra found that the Helmeted Hornbill (*Buceros vigil*) fed almost exclusively on figs (comprising 98.6% of feeding records; Hadiprakarsa & Kinnaird, 2004).

Another characteristic that may make *Ficus* fruit particularly attractive to frugivores is the nutrient content of the fruit. *Ficus* fruit do not contain particularly high protein, carbohydrate, or lipid content compared to other tropical fruit (Concklin & Wrangham, 1994; O'Brien et al., 1998), leading to conclusions that *Ficus* fruit had low nutritional value (Bronstein & Hoffmann, 1987; Kunz & Diaz, 1995). However, *Ficus* fruit does contain high levels of calcium, with a particularly high calcium to phosphorus ratio (which is a measure of calcium availability). Furthermore, although different species of *Ficus* show considerable variation in nutritional properties, *Ficus* fruit can contain high levels of amino acids, potassium, magnesium, and sodium (Wendeln et al., 2000). One comparative study, which analysed nutrient content in fig and non-fig fruit from Belize, Uganda, and Indonesia, found fig calcium levels were, on average, 3.2 times higher than other fruits, with calcium to phosphorus ratios 3.7 times higher (O'Brien et al., 1998). These calcium levels are believed to be important for bone growth in birds and mammals, and eggshell development in birds (O'Brien et al., 1998). Another study in Panama found *Ficus* fruit had greater nutritional value than other common forest fruit, and that average nutritional value did not differ significantly between large and small *Ficus* fruit sizes (Wendeln et al., 2000). Despite these results, Bravo et al. (2012) argue that the reason frugivorous bats (which specialise on *Ficus* fruit in the Neotropics) frequent soil licks is to supplement their diet with sodium obtained through geophagy. Marshall et al. (2012) also note the low overall nutritional value of figs, together with their year-round availability, when describing them as “fallback foods”, which are foods of relatively low quality that are consumed during periods of low overall food availability. They cite research from Kalimantan, Indonesia, where *Ficus* consumption by Bornean White-bearded Gibbons (*Hylobates albibarbis*) varies from 0% to 75% of monthly feeding observations, with lower proportions of *Ficus* consumption during periods of higher overall fruit availability (Marshall & Leighton, 2006). As such, *Ficus* fruit may be critically important in helping frugivores survive resource bottlenecks, indicating that they may exert a disproportionately large influence on species composition, or even morphological and sociological evolution (Marshall et al., 2012).

A final attribute of *Ficus* fruit that may enhance their attractiveness to frugivores is the relative ease of handling and consuming individual fruits. When ripe, *Ficus* fruits have soft exocarps, they are small seeded, and can be either bitten while still attached to the stem, or plucked from the stem with ease by even small birds and mammals (Foster, 1987; Korine et al., 2000; Levey & del Rio, 2001; Tello, 2003). This, combined with the large crop sizes of many *Ficus* trees, has led some researchers to describe *Ficus* fruit as the “fast foods of the forest” (Kinnaird & O’Brien, 2005:155).

2.5.2 The strength of the *Ficus*–frugivore relationship

Given the interdependencies between many of these *Ficus* characteristics, it is hard to disentangle the property that best explains the strength of their relationship with frugivores. The range of relationships between different *Ficus* species and frugivores across the world’s tropics, and the variety of terms used to describe them, have received traction in academic debates (Power et al., 1996; Herre et al., 2008; Marshall et al., 2012). There is very little dissent, however, from the fundamental assertion that *Ficus* plants are critically important resources for frugivorous assemblages in tropical forests (Lambert, 1989; Kinnaird et al., 1996; Kirika et al., 2008a). In a review of the literature available on vertebrate frugivores' consumption of figs, Shanahan and colleagues found that at least 1,274 bird and mammal species, representing 523 genera and 92 families, are known to eat figs (Shanahan et al., 2001). Several avian families showed a strong affinity for figs, including the Columbidae, Psittacidae, Pycnonotidae, Bucerotidae, Sturnidae, Megalaimidae, and Lybiidae. They found that 125 of the 310 species of pigeon and dove (Columbidae), and 64 of the 148 species of starling and myna (Sturnidae) had been recorded feeding on figs (40.3% and 43.2% respectively, although these percentages would be higher if birds that did not occur in the tropics were excluded from the calculations). Furthermore, hundreds of frugivorous birds and mammals have been recorded feeding on some individual *Ficus* species (such as *F. microcarpa*), suggesting that *Ficus* plants may be dietary components of a large number of frugivores.

2.5.3 The relationship between *Ficus* and frugivorous bats

Aside from birds, frugivorous bats are also known to be important *Ficus* seed dispersers, and to exhibit some degree of dietary reliance on *Ficus* fruit (Shanahan et al., 2001). In Old World fruit bats (Pteropodidae), *Ficus* fruit has been recorded in the diet of at least 47 species across 20 genera (Shanahan et al., 2001). Studies in West Africa and South-east Asia have documented a high proportion of *Ficus* fruit in the diet of particular fruit bat species: over 88% of *Hypsignathus monstrosus* oral and faecal samples in Gabon contained *Ficus* seeds (Gautier-Hion & Michaloud, 1989), and 90% of *Cynopterus sphinx* faeces on Anak Kratakau contained *Ficus* seeds

(Shilton et al., 1999). In South Africa, radio-tagged fruit bats displayed movement patterns that largely reflected the distribution of ripe *F. sycomorus* in Kruger National Park, suggesting some degree of dependence on the availability of *Ficus* fruit (Bonaccorso et al., 2014). In the New World, at least 35 species in 16 genera of Neotropical fruit bat are known to eat *Ficus* fruit (Shanahan et al., 2001). In Peru, *Ficus* seeds were the most frequently recorded seeds in the faeces of *Artibeus* bats, and were recorded throughout the year (Romo, 1996), while in Saldaña-Vázquez (2014) found that *Carollia*, *Sturnira*, and *Artibeus* bats specialised on *Ficus* fruit across the Neotropics.

There is considerable variation in fruit characteristics within *Ficus*, which has encouraged some authors to classify major fruit presentation syndromes depending on the relationship between the *Ficus* species and its main seed dispersers. For example, figs which are primarily dispersed by birds are described as tending to have small (approximately 8 mm diameter), odorless, colourful fruit that grows amongst the leaf foliage, whereas figs which are primarily dispersed by mammals are characterised by having large (approximately 20 mm diameter), dull in colouration, odorous fruit that is presented on stems that protrude from major tree branches (van der Pijl, 1982; Marshall, 1985; Lambert, 1989; Whittaker & Jones, 1994; Hodgkison et al., 2003). Whether these two categories are distinct in practice is a question addressed by Appendix 2, which compares the abundance and richness of bird communities observed visiting a “mammal-dispersed” *Ficus* species, *F. racemosa*, with those of “bird-dispersed” *F. religiosa* and *F. benghalensis*. In summary, the results indicate that *F. racemosa* is considerably less attractive to frugivorous birds than the other species, and so this species was excluded from the bird surveys conducted as part of this thesis.

A key question, that applies to bats as much as it does to birds, is how successfully frugivores facilitate seed dispersal. *Ficus* seeds ingested by fruit bats have been demonstrated to survive and germinate with similar success to control seeds, indicating the even small seeds remain viable after consumption by bats (Helbig-Bonitz et al., 2014). For most frugivorous bats, gut passage times are believed to be short, given the short length of their guts and the large intake of food when feeding (Wolton et al., 1982). As a result, most seeds are likely to be excreted within one hour of consumption. The distance over which seeds are dispersed is therefore likely to be short, although there is considerable variation depending on the ranging distances of the fruit bat species (Whittaker & Jones, 1994). For example, *Dyacopterus spadiceus* of Malaysia flies long distances high above the canopy between roost sites and fruit trees (Hodgkison et al., 2003), *Pteropus vampyrus* is considered to have a nightly range of 70 km (Dammerman, 1948), while *Epomophorus crypturus* has been recorded to cover 13.90 km in one night in South Africa (Bonaccorso et al., 2014). Further studies in Indonesia indicate that some species, at least, may retain seeds in their gut for much longer times that otherwise believed, with gut retention times of greater than 12 hours recorded for viable *Ficus* seeds in captured *C. sphinx* (Shilton et al., 1999). Furthermore, because bats do not fly by visiting a series of perches, they may provide a more homogenous seed rain by defecating in flights (Hodgkison et al., 2003). In addition, by flying above the canopy, large fruit bats may also benefit the dispersal of epiphytic and strangler *Ficus* species, as these seeds may have a greater chance of being intercepted by vegetation when defecated than alternative modes of dispersal (Hodgkison et al., 2003). Fruit bats have also been observed to carry intact fruit from fruit trees to feeding perches in other trees prior to consumption, which increases dispersal distances irrespective of gut passage times, and which has been observed to occur over distances of 0.25 km (Phua & Corlett, 1989; Funakoshi & Zubaid, 1997). Given these characteristics, it is therefore unsurprising that fruit bats have been identified as important seed dispersers in human-modified landscapes, and indeed the tolerance of several species to habitat alteration is argued to further augment their utility in forest restoration (Shilton & Whittaker, 2010; Helbig-Bonitz et al., 2014). However, a recent study of forest restoration in Mexico found that fruit bats mainly dispersed pioneer tree and shrub species to slowly regenerating grassy areas, and no late successional species were dispersed by bats in the 76-month study (de la Peña-Domene et al., 2014). Further work monitoring bat seed dispersal, particularly with reference to *Ficus* dispersal in human-modified landscapes, may be helpful in determining the role played by frugivorous bats.

2.5.4 The *Ficus*–frugivore relationship around the world

More generally, the importance of *Ficus* plants to communities of tropical forest frugivores has been demonstrated around the world. In the Neotropics, Terborgh found primates in Peru to be reliant on figs during periods of general fruit scarcity (Terborgh, 1986), while Tello (2003) recorded 44 diurnal vertebrates eating figs from a single fruiting tree. Wendeln et al. (2000) and Korine et al. (2000) reported a high diversity of birds and bats feeding at *Ficus* trees in Panama, Bronstein and Hoffmann (1987) record 26 species of bird feeding at a single species of *Ficus* (*F. pertusa*), while in Venezuela Walther (2000) recorded 20 species of bird feeding at one individual *Ficus*.

The message is somewhat mixed in West Africa, where Gautier-Hion and Michaloud (1989) found figs to occur in low densities, and to be rare in the stomach contents of seven monkey species caught by hunters in Makokou Forest, Gabon. Examining 19 hornbill and turaco gizzards, the authors found only one contained *Ficus* seeds, although another study in the same forest found that figs were a major component in the diet of large frugivorous bats (Bradbury, 1981). The lack of *Ficus* records in hornbill stomach contents is surprising when compared to results from elsewhere in West Africa. In Cameroon for example, Breitwisch (1983) recorded four hornbill species feeding at a single *Ficus* vine over 58 hours of observation. In the same country, Whitney et al. (1998) found *Ficus* to be an important component in the diets of three *Ceratogymna* hornbills, although the trees most commonly frequented by the hornbills were in the same families as those reported to be major sites of frugivory by Gautier-Hion and Michaloud. Until the paucity of records from West Africa is augmented by further studies of the *Ficus*-frugivore relationships, it is unclear whether the relationship between frugivores and *Ficus* trees is as strong as it has been found to be elsewhere. Other records in Africa suggest that the relationship between *Ficus* plants and frugivores is as strong as on other continents. In South Africa, for example, *Ficus thonningii* attracted the higher numbers of animal frugivores than other fruiting trees (Bleher et al., 2003), while in Kenya, 36 frugivores visited the same *Ficus* species over 400 hours of observation in Kakamega Forest (Kirika et al., 2008a). At a broader scale of analysis, Kissling et al. (2007) tested the variation in avian frugivore species richness against *Ficus* species richness, contemporary climate conditions, energy flux, and habitat heterogeneity across sub-Saharan Africa. They found that *Ficus* species richness had the strongest direct effect on avian frugivore richness, even after controlling for confounding environmental variables and spatial autocorrelation.

In Asia there is strong evidence from studies focusing on hornbills (Leighton & Leighton 1983; Kinnaird et al., 1996; Hadiprakarsa & Kinnaird, 2004) as well as forest frugivores in general (Lambert, 1989; Lambert & Marshall, 1991; Walker,

2007) that *Ficus* plants are very important in supporting frugivore assemblages. For example, Lambert (1989) recorded 60 bird species feeding at 29 *Ficus* species in lowland Malaysia, while in Khao Yai National Park, Thailand, two of the four hornbill species present consumed more *Ficus* fruit (measured in grams per day) than all other species of fruit summed together (Poonswad et al., 1998). In New Guinea, 16% of visits to a *F. obliqua* were made by birds of paradise (Beehler & Dumbacher, 1996), and figs comprised the largest proportion of the diet of several species (Frith & Beehler, 1998). The evidence from studies in Asia, supported by those in Africa and the Neotropics, suggest that *Ficus* plants may be major components in the diets of frugivores at a global scale. Furthermore, the richness of frugivorous species recorded feeding at *Ficus* plants implies that a range of seed dispersal functions is likely to exist (discussed further below).

Although the importance of *Ficus* plants for tropical ecosystems is well established in forest landscapes, their interactions with frugivores in human-modified landscapes are poorly known. In fact, interactions between fruit producing plants and frugivores of any kind in human-modified landscapes remain "a critical frontier in ecology" (Tscharntke et al., 2008:947), while the factors that influence bird visitation rates to isolated trees are also still debated (Sheldon & Nadkarni, 2013). Given that *Ficus* seeds are well suited to germinating in disturbed substrates, which are commonly found in human-modified landscapes, isolated *Ficus* trees may be particularly useful conservation structures in areas with poor soil quality. However, many pressing issues concerning the conservation of the *Ficus*–frugivore relationship in human-modified landscapes remain poorly understood. Key questions include: what is the conservation value of specific types of tree (Douglas et al., 2013; Mendoza et al., 2014)? Do frugivores still require forest blocks, and just commute to isolated *Ficus* trees, or can they survive in modified landscapes independently (Daily et al., 2001; Sekercioglu et al., 2007)? Does the distance from the isolated tree to the nearest forest have an effect on spatial scales that exceed two kilometres (Luck & Daily, 2003; Eshiamwata et al., 2006; Lasky & Keitt, 2012; Sheldon & Nadkarni, 2013)? How does the intensity of land-use in modified landscapes affect the movement of frugivores (Luck & Daily, 2003; McConkey et al., 2011; Watling et al., 2011)? And how does the reaction of forest-dependent frugivores differ to habitat-generalists in response to the previous questions (Gillies et al., 2011; McConkey et al., 2011; Menke et al., 2012; Neuschulz et al., 2012)? It is important to close this knowledge gap both to identify viable conservation strategies at the species level in human-modified landscapes, and also to conserve the important ecological functions that may be provided by frugivores (Tscharntke et al., 2008; Chazdon et al., 2009a; McConkey et al., 2011; Sekercioglu, 2012; Bregman et al., 2014; Deikumah et al., 2014).

It is also worth considering how the answers to these questions may change over space. Deep divisions in the phylogenetic relationships between New and Old World *Ficus*, fruit bats, and frugivorous birds suggest that results from *Ficus*–frugivore studies may vary depending on the geographical location of the field site, and that patterns in this relationship may differ at a range of spatial scales. These issues are particularly concerning considering the imbalance of study effort across the world.

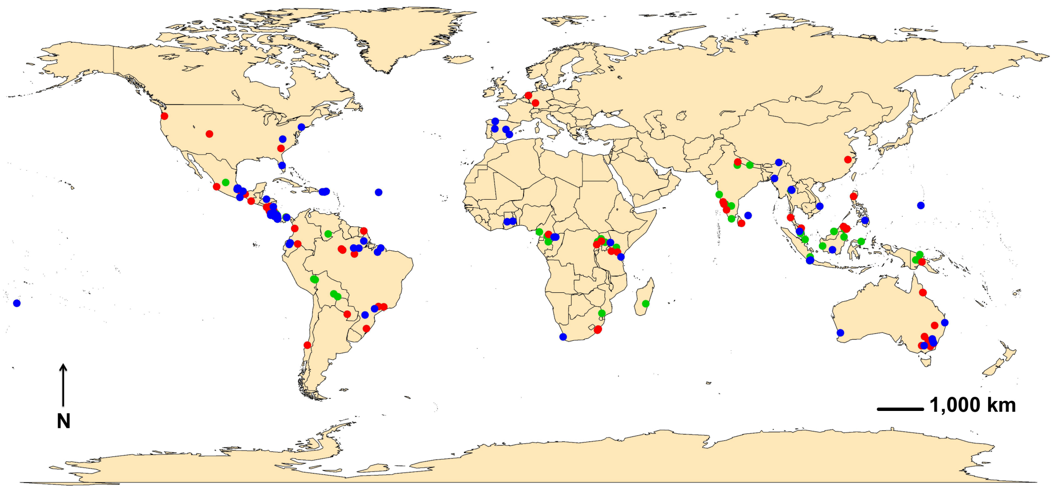

Figure 2.2: Map of study sites reported in the literature review. All studies that were cited in the literature review, and that conducted field work at a specific site, were grouped as studies concerning *Ficus* ecology, conservation in human-modified landscapes, or ecological restoration. They were then mapped with green dots representing studies of *Ficus* ecology, red for conservation in human-modified landscapes, and blue for ecological restoration. Studies that did not fit into one of these categories, or which did not investigate a specific research site, were excluded.

Although certainly not comprehensive, Figure 2.2 shows the locations of the studies cited in this literature review, which acts as a fairly broad sample of published *Ficus*, frugivory, and human-modified landscape studies. Here, the suggestion is that several "conservation blindspots" exist, where the research effort in this field of conservation science has been relatively poor. Despite a particularly high effort to find relevant studies from Assam and India, one of the noticeable blindspots in the figure is the area where field work for this thesis was conducted.

2.6 Birds as mobile links

Among frugivores, birds are the best-studied class of organisms (Sekercioglu, 2006). The mobility of many species, and the distances they can travel, may also make them integral to the function of human-modified landscapes (Sekercioglu et al., 2004).

Indeed, these characteristics led Gilbert to describe frugivorous birds as key "mobile links" which sustain the dispersal of plants seeds (Gilbert, 1980:19). Their role in seed dispersal has been recognised for a long time, with Charles Darwin observing that birds were "highly effective agents in the transportation of seeds" (Darwin, 1859:431), and Alfred Russel Wallace commenting that "birds are undoubtedly important agents in the dispersal of plants over wide spaces" (Wallace, 1880:79). In fact, seed dispersal is thought to be critical in maintaining the plant diversity observed today, and may have facilitated the dominance of angiosperms in the tropics (Tiffney & Mazer, 1995; Schupp et al., 2002; Terborgh et al., 2011).

Seed dispersal is thought to benefit plants in three ways: 1) by facilitating the escape from density-dependent mortality caused by pathogens and competition under the parent plant; 2) by increasing the chance of colonising a new site that may be suitable for establishment and survival; and 3) by transporting seeds to specific sites that are favourable for plant growth (Janzen, 1970; Connell, 1971; Howe & Smallwood, 1982; Wenny, 2001; Howe & Miriti, 2004; Terborgh et al., 2011). Birds, by consuming fruit and grain, moving over moderate to large distances quickly, and defecating viable seeds, act as important genetic linkers, and determine the location and probability of seedling survival, thereby influencing the distribution and abundance of plants (Wenny, 2001). As such, seed dispersal may be the most important ecological service delivered by birds (Sekercioglu, 2006:19).

Ecological services are defined as the benefits that humans obtain from ecosystems (MEA, 2005), which in terms of seed dispersal, would mean the role birds play in dispersing seeds has material benefits for humans. These benefits would largely derive from the goods that can be harvested following the natural recruitment of plants, but may also involve aesthetic or spiritual returns. Ecosystem function is a related concept, whereby the collective interactions of biota maintain the structure of ecological processes and the provision of services (Schwartz et al., 2000). Therefore, by dispersing seeds, birds can play an important role in maintaining the function of an ecosystem, which may also increase the resilience of an ecosystem to disturbance (Wenny et al., 2011). The destruction of forest is a widespread form of disturbance in tropical regions, which presents a major threat to the continued provision of seed dispersal services (Levey et al., 2005; Kirika et al., 2008b; Babweteera & Brown, 2009; Helbig-Bonitz et al., 2014). Within this ecosystem function framework, the continued provision of seed dispersal services by birds would indicate a degree of resilience in formerly forested systems. So how have seed dispersal patterns changed following deforestation in human-modified landscapes?

Seed dispersal can be very resilient; persisting even in highly modified urban environments (Markus & Hall, 2004). In fact, it continues to have a major influence on plant species persistence and diversity (Sansevero et al., 2011; Rey & Alcántara, 2014), while also driving regeneration when disturbance is reduced or ceases (McConkey et al., 2011; García & Martínez, 2012). However, some characteristics of the function are altered through changes in habitat, and subsequent changes in avian disperser abundance, diversity, and behaviour (Markl et al., 2012). A bird does not have to be extinct or even endangered for its dispersal services to decline (McConkey et al., 2011), even small reductions in the abundance of common species may lead to the decline of important seed dispersal functions (Sekercioglu, 2006).

Replacing forest with human-modified landscapes, and the reductions in forest area that such a process entails, has provided evidence on how the volume of seeds dispersed declines in modified landscapes. In Tanzania, reductions in frugivore populations in small forest remnants led to a three-fold decrease in the number of seedlings of 31 species of animal-dispersed trees, compared to wind- or gravity-dispersed species (Cordeiro & Howe, 2001). In Amazonia, seedling establishment of *Heliconia acuminate* was found to be 1.5 to 6 times higher in continuous forest than in small (1 ha or 10 ha) forest remnants (Bruna et al., 2002). The decline in seed dispersal in open sites is even more dramatic. In an experimental test, Cole et al. (2010) recorded the zoochorous seed rain received by open sites compared to two-year old regeneration tree plantations in Costa Rica. They found plantations received an average of 266±65 seeds/m^2/year, compared to just 87±13 in open sites.

In the Cole et al. study, the reduced seed rain only told half the story. The key facet of seed dispersal is whether it is effective or not, which requires that seeds are delivered to sites with amenable conditions for both germination and growth (as discussed in Section 2.4 above). Schupp et al. (2010) describe this as dispersal effectiveness, as determined by both the quantity and quality of seed rain. Here the number of adult plants produced by the activities of a disperser is the best measure of seed disperser effectiveness, as calculated by considering the number of visits a frugivore makes to the parent plant, the number of seeds dispersed per visit, the probability that a seed is still viable after consumption by the frugivore, and the probability that a seed will germinate and reach maturity after deposition (Schupp et al., 2010). There is little conservation managers can do to manipulate the first three components, but there is scope to increase the chances of seed germination and survival.

Once again, conserving existing vegetation in the landscape appears to be the best method of improving germination and seedling survival rates. This conclusion, along with the potential need to control rodent populations or grazing-intensity, has been discussed in Section 2.4.7 above, although the results of some further studies are worth reporting. Prioritizing the conservation of existing vegetation may help increase directed dispersal, where seeds are transported and deposited at sites with favourable growth conditions (Wenny, 2001). Bird movement patterns are rarely random, and particularly in human-modified landscapes, frugivores may seek particular habitat structures, such as isolated trees. To illustrate the process, an example of directed dispersal from intact forest can be found in Wenny and Levey's (1998) study of avian frugivory in Costa Rica. They found that the Three-wattled Bellbird (*Procnias tricarunculata*) preferred to fly to particular song perches in the canopy, over 40 m from the parent tree, where recruitment success was significantly higher due to a reduction in fungus-induced seed mortality. Further evidence of directional dispersal over long distances (150–700 m) was gathered by Carlo et al. (2013). In their study, the seeds of two fleshy-fruited trees were tracked using stable isotope nitrogen enrichment in a heterogeneous landscape in northern Spain. Their results revealed that long-distance seed dispersal was dependent on existing templates of vegetation structure, as frugivorous birds deposited seeds at greater distances and in greater numbers in habitats with more fleshy-fruited trees. In open areas of human-modified landscapes, seeds falling under isolated trees are likely to have a substantially higher chance of germinating due to the amelioration of environmental conditions found away from such structures (Reid & Holl, 2013). Therefore, the conservation of isolated trees may be a major way conservation managers can increase the effectiveness of seed dispersal.

In cases where no more gains can be made through the conservation of existing vegetation, management actions that improve the connectivity of the landscape may be useful in improving seed dispersal. Levey et al. (2005) analysed the movements and seed dispersal behaviours of wintering Eastern Bluebirds (*Sialia sialis*) in an experimentally manipulated savanna landscape. They placed seed traps in the centre of wooded patches that were isolated in the savanna, and in patches that were connected to other woodland. They found the chances of a seed falling into a seed trap from a connected patch were 37% higher than in an isolated patch. They argue that the benefits of increasing connectivity exceed the benefits of providing addition habitat (as all their patches were equal in size), and that these synergies can improve plant recruitment within the directed dispersal framework.

2.6.1 Large frugivores in human-modified landscapes

While these studies indicate useful strategies to conserve seed dispersal services in human-modified habitats, one major challenge that is common in this landscape configuration remains unresolved. Large-gaped avian frugivores (with gape widths ≥12 mm), which also tend to have larger body sizes, are particularly important mobile links as they can consume and disperse large seeds (Lundberg & Moberg, 2003; Galetti et al., 2013). Large-seeded plants are also typically late successional, forest interior species, which depend on (often specialised) mutualistic relationships with large frugivores for dispersal. For example, in the mountains of New Guinea, Dwarf Cassowaries (*Casuarius bennetti*) preferentially disperse the large seeds of the rare canopy tree *Aglaia* aff. *flavida* uphill from the parent tree (Mack, 1997). The absence of Dwarf Cassowaries would lead to reduced genetic exchange and fragmented populations as the tree would only be able to disperse downhill.

In human-modified landscapes, several studies have found that large frugivores are rare or absent compared to their abundance or occurrence in continuous forest. In their study of a fragmented forest landscape in Queensland, Australia, Moran et al. (2004) found that large-gaped frugivores were less abundant beyond continuous forest, where small-gaped species with mixed diets were the most abundant guild. In a similarly fragmented landscape in the Brazilian Atlantic forest ecoregion, Galetti et al.

(2013) studied palm seed size in 22 fragments. They found that the palms in defaunated fragments, which had lost their large-gaped avian frugivores following regional deforestation, were producing smaller seed than the palms in fragments where toucans and large cotingas persisted. They argued that the reduction in seed size may have negative consequences for palm recruitment, as smaller seeds are more vulnerable to desiccation and produce smaller seedlings, which may reduce the fitness of the population (Galetti et al., 2013). The prospects of similar alterations to population dynamics in other ecosystems are considerable (Wright et al., 2007), as the loss of large frugivores appears to be deterministic rather than random (Owens & Bennett, 2000; Zavaleta & Hulvey, 2004).

There are several reasons for the deterministic decline of large frugivores in fragmented forests and non-forest landscapes. First, as they are larger species, they tend to have larger home ranges than smaller birds. This, combined with the need to travel long distances to find the fruit of large-seeded species, means they are more vulnerable to habitat change (Velho et al., 2012; Española et al., 2013; Vidal et al., 2014). Secondly, the life histories of large birds are characterised by long life spans, small clutch sizes, relatively infrequent breeding, and low population densities (Wotton & Kelly, 2012). These characteristics make them more sensitive to increases in adult mortality, and further reduce their resilience to land-use change. Finally, large species, including the Dwarf Cassowary described above, are more likely to be hunted by humans than smaller-bodied species, which increases adult mortality (Peres & Palacios, 2007; Terborgh, 2013; Vidal et al., 2013). The synergistic combination of these three vulnerabilities has led to widespread defaunation in human-modified landscapes, reducing the primary dispersal of large-seeded plant species (Wotton & Kelly, 2011; Traveset et al., 2012; Kurten, 2013). Although some of the losses incurred through decreased dispersal by large frugivores are offset by lower seed predation, the net effect of this process is to produce plant communities with consistently lower species richness, higher species dominance, and lower diversity (Traveset et al., 2012; Kurten, 2013).

The negative consequences of the loss of large frugivores, combined with the difficulty of creating protected areas large enough to encompass the home ranges of a functionally viable population (McConkey et al., 2011), increase the need to identify strategies that may enhance their conservation in human-modified landscapes. One method that may help support large frugivore populations in human-modified landscapes is the conservation of isolated *Ficus* trees. Their large crop sizes, along with other factors described above, make them attractive food sources to the largest frugivorous birds in Asia at least (Kinnaird et al., 1996; Poonswad et al., 1998; Kannan & James, 1999; Kitamura, 2011), along with a host of smaller bird species.

2.6.2 A *Ficus*–insectivore relationship?

Aside from supporting frugivores, *Ficus* trees may also help achieve additional conservation and ecosystem service provision goals in human-modified landscapes. Pest control services carried out by insectivorous birds provide an important means of reducing crop damage caused by insects in agricultural areas (Perfecto et al., 2004). With large insect assemblages associated with *Ficus* trees, they may be able to help support insectivorous bird species, which may then also prey on insects that cause crop damage.

The abundance and richness of invertebrates on *Ficus* trees is believed to be very high (Basset et al., 1997). Despite chronic undersampling, Basset et al. (1997) found published records of 1,875 arthropod species feeding on *Ficus*, and hypothesised that the actual number of species feeding on *Ficus* is probably much higher (Basset & Novotny, 1999). In fact, in their review, Basset et al. only found records of arthropods feeding on 286 species of *Ficus*, which is a fraction of overall *Ficus* species richness, and records of pollinating wasps (many of which are host specific), for one-third of all *Ficus* species. Despite the paucity of records, it seems likely that *Ficus* plants are utilised by a great diversity of arthropod species, and given the size of *Ficus* trees and their crops, in all likelihood a vast number of individuals.

The likely size of invertebrate assemblages on *Ficus* plants is perhaps unsurprising considering the mutualistic relationship between *Ficus* plants and Agaoninae fig wasps, along with the large quantity of fruit produced by *Ficus* plants, and the complex bark topography of *Ficus* trees. Together, these *Ficus* properties provide the foundations for a diverse invertebrate food web, which may also act as an important resource for insectivorous birds. For instance, the arrival of potentially millions of fig wasps at a large *Ficus* tree during its receptive stage may provide a large food resource for a range of insectivores, particularly as the wasps fly diurnally (Compton et al., 2000; Harrison, 2003; Bain et al., 2013).

There is some evidence that these wasps are also an important food resource for other invertebrates. In her study of fig wasp mortality in Costa Rica, Bronstein found that wasps were predated at all stages of their life cycle (Bronstein, 1988). Wasps arriving to oviposit at syconia were predated by ants, moth and weevil larvae destroyed wasps as they developed within syconia, a staphylinid beetle predated adult wasps before they left the syconia, and dragonflies consumed wasps as they flew away from the syconia (Bronstein, 1988; Harrison, 2013). The role of ants in fig wasp predation was investigated further through Harrison's (2013) study of ant–fig wasp interactions in Malaysia. He found that *Philidris* ants patrolled the syconia of *F. schwarzii*, capturing fig wasps as they landed. However, the ants were considerably more successful at catching non-pollinating wasps, which are more vulnerable as they oviposit using extended ovipositors through the syconia wall, rather than entering the syconia like pollinating wasps do. When experimentally removed, Harrison discovered that syconia with no guard ants became so heavily attacked by non-pollinating wasps that many were aborted. In their review of ants on figs, Bain et al. (2013) found that ants have been recorded on approximately 11% of *Ficus* species, where they regularly predated both pollinating and parasitic fig wasps. The wealth of examples suggested that the *Ficus*–pollinator and pollinator–ant interactions may form the basis of a complex biotic system of mutualisms, which may support a range of other arthropod populations (Bain et al., 2013).

Aside from fig wasps, many invertebrates exploit *Ficus* syconia as sources of food. These include phytophagous parasitic fig wasps, some of which gall the fig flowers in the absence of wasp larvae, along with many hemipterans (Hemiptera), flies and fruit flies (Diptera), nematodes (Nematoda), and beetles (Coleoptera) which feed internally on syconia (Basset et al., 1997; Bain et al., 2013). Some of these species specialise in feeding on *Ficus* syconia, including 35 African species of *Curculio* (Curculionidae) and *C. bicruciatus* from Australia (Perrin, 1992). Within Diptera, some African *Lissocephala* species specialise in breeding inside *Ficus* syconia, while others feed on the yeast in decaying fruit (Basset et al., 1997). There are also records of hemipterans and fruit-piercing moths (Noctuidae) feeding on the surface of syconia, which would provide a ready prey source to other arthropods and gleaning birds.

There are also records of sap-sucking and leaf-chewing insects inhabiting *Ficus* plants, and while they may form an important invertebrate food resource, there is no evidence that these species are more numerous on *Ficus* than other trees of similar size (although many are host-specific). One final feature of *Ficus*–invertebrate interactions worth considering, however, is the abundance and richness of arthropods living on and in the bark of *Ficus* trees. Due to their strangling life history, many species of *Ficus* tree have very complex bark topography. This creates a multitude of hollows and recesses in which insects can nest, shelter, and feed (Basset & Novotny, 1999). A strangling life history and the proliferation of aerial roots also creates a higher surface area than would otherwise be expected from a tree of equivalent size, creating more habitat for stem and wood boring invertebrates. These include lepidopteran species of *Scalmatica* and *Trachytyla* (Tineidae) that bore into aerial roots, and many Coleoptera from Cerambycidae, Buprestidae, and Bostrichidae that bore into the soft and easily rotted *Ficus* wood (Basset et al., 1997).

Given the size and diversity of insect assemblages inhabiting *Ficus* trees, it seems plausible that they might be important foraging sites for insectivorous birds. For example, Harrison notes that it is "a common sight" to see swifts hunting above large fig trees when the female wasps are emerging (Harrison, 2013:89), and one study of swift stomach contents in Panama found over 80% of their diet was composed of fig wasps (Hespenheide, 1975). Fig wasps may also be important prey items for migratory Neotropical warblers, as Bronstein observed 11 insectivorous bird species, primarily warblers, gleaning fig wasps as they left the syconia (Bronstein, 1988). Despite this, the importance of the link between *Ficus* trees and insectivores has never been studied in forested or human-modified landscapes. If an important *Ficus*–insectivore relationship is established, the presence of *Ficus* trees in human-modified landscapes may contribute towards the conservation of insectivores, which often exhibit dramatic declines beyond intact forest, as well as providing pest control services to farmers (Stouffer & Bierregaard, 1995; Canaday, 1997; Perfecto et al., 2004). This, combined with their potential role in supporting frugivore assemblages, may make them important ecological components in human-modified landscapes.

2.7 Functional diversity

Investigations into the structure of ecological assemblages across space and time have expanded from taxonomic measures of diversity (such as species richness) to incorporate phylogenetic, and more recently, functional measures of diversity (Petchey et al., 2007; Mouchet et al., 2010). As the functional characteristics of species vary, so too do the functional roles performed by assemblages (McGill et al., 2006). By using trait information to define a species' ecological role within a community, a small number or even a single continuous metric can be produced, permitting an assessment of functional redundancy and structured turnover in assemblages across environmental gradients (Edwards et al., 2013; Luck et al., 2013).

Several different definitions and measures of functional diversity have been proposed (Díaz & Cabido, 2001; Tilman, 2001; Tesfaye et al., 2003; Mason et al., 2005; Cornwell et al., 2006; Petchey & Gaston, 2006; Villéger et al., 2008; Laliberté & Legendre, 2010; Mouchet et al., 2010). This thesis follows Villéger et al.'s (2008) definition of functional diversity as the distribution of functional traits within multidimensional niche space (Villéger et al., 2008:2290). This definition reflects the progress that has been made in functional diversity analyses, away from functional group studies (which results in the loss of information and the imposition of a discrete structure on continuous functional differences), and towards measures that focus on traits measured on a continuous scale (Petchey & Gaston, 2006; Villéger et al., 2008). However, there is still a lack of consensus concerning the best index to measure functional diversity (Mouchet et al., 2010). Petchey and Gaston's (2002) "FD" index is popular, as it is a continuous rather than categorical measure, and measures diversity at all hierarchical scales simultaneously. However, it can only be used for presence/absence data, rather than abundance data, and so loses potentially useful information. Despite this, many functional diversity studies only have presence/absence information, and so it remains widely used. Mason et al. (2005) argue that functional diversity cannot be summarised by a single number, and recommend quantifying three independent components: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). An additional measure, proposed by Laliberté and Legendre (2010), is functional dispersion (FDis). This index, which calculates the mean distance in multidimensional trait space of individual species to the centroid of all species, has some advantages over the Mason et al. (2005) framework (Laliberté & Legendre, 2010). Unlike FRic, it can be weighted by abundance, and unlike FEve and FDiv, it can estimate the dispersion of species in trait space (Laliberté & Legendre, 2010). Furthermore, it is not as sensitive to outliers as FRic, and it only requires a minimum of two species in an assemblage, rather than three (as in the Mason et al. framework), which is useful when analysing species-poor assemblages.

Recent research using functional diversity measures has focused on community assembly, ecological redundancy, and niche filtering (Mouchet et al., 2010; Luck et al., 2013). Somewhat reminiscent of Diamond's (1975) assembly rules, several researchers have tested the role of functional trait distributions in the structure of ecological communities (Petchey et al., 2007; Flynn et al., 2009; Mouchet et al., 2010). Here, if species assemblages are composed of random sets of species, their functional diversity will be randomly distributed. A non-random distribution may indicate that processes such as environmental filtering may be influencing the structure of communities (Petchey et al., 2007). Furthermore, the comparison of null model expectations to functional diversity scores in disturbed environments may indicate whether functionally redundant (the loss of a species has little effect on functional diversity) or unique species are lost first following a disturbance, or whether functional traits are lost at random (Flynn et al., 2009).

Using two continuous and 16 binary scale trait measures, and presence/absence data from two national British Trust for Ornithology surveys separated by 20 years, Petchey et al. (2007) applied the Petchey and Gaston (2002) FD index to real and null bird assemblages. They found that the change in functional diversity was, on average, proportional to the change in species richness over 20 years. They also found that functional diversity was lower than expected by chance, with co-occurring species holding more similar functional traits than random sets of the same number of species. Assuming that the measured trait differences are ecologically meaningful, the absence of functional redundancy in British bird communities suggests that natural systems may not be buffered against disturbance by ecological redundancy.

A second major area of research has been the response of assemblages to ecological disturbance. In a heavily modified palm oil plantation landscape in Borneo, Edwards et al. (2013) calculated Petchey and Gaston's (2002) FD for birds in primary forest, logged forest, and palm oil plantations. They found that the functional diversity of bird assemblages in primary forest and logged forest were similar, but palm oil plantation assemblages exhibited substantially lower levels of functional diversity. The consequences of land-use change for the functional diversity of bird assemblages were also investigated by Flynn et al. (2009). They assembled 20 studies from temperate and tropical regions of the New World and categorised species across five traits, before calculating FD (Petchey & Gaston, 2002). When comparing their synthetic dataset to random null simulations, they found that functional diversity was lower than random in 41% of agricultural landscapes, and 29% of semi-natural landscapes. In fact, not a single study recorded a higher functional diversity score than the null model expectations, and a consistent decline in observed FD scores was reported from natural, to semi-natural, and finally agricultural landscapes.

These studies demonstrate the way functional diversity calculations can be used to uncover patterns of community assemblage, and to understand the relationship between land-use change, species richness declines, and the loss of functional traits (Luck et al., 2013). However, further work remains to be done in assessing why these losses occur, and what can be done to better conserve functional diversity in human-modified landscapes (Edwards et al., 2013). In particular, the evaluation of different conservation opportunities, such as isolated tree conservation, has yet to be studied in relation to functional diversity.

2.8 Social values and *Ficus* trees

Even after extensive deforestation, isolated *Ficus* trees are reported to survive in many human-modified landscapes around the world. In India, they persist in urban and rural areas (Sitaramam et al., 2009; Caughlin et al., 2012), in Nepal they are commonly found in production landscapes (Kumar & Bussmann, 2006), in Kenya they occur in agricultural regions despite very high human population densities (Eshiamwata et al., 2006), and in Madagascar they are scattered across human-modified landscapes (Martin et al., 2009). In Central America, isolated *Ficus* trees are also reported to grow in numerous pasture landscapes in Mexico (Guevara et al., 1992; 2004; Galindo-González et al., 2000; 2004; Serrato et al., 2004) and Costa Rica (Bronstein, 1988; Sillett et al., 1995; Harvey & Haber, 1999; Holl, 1999; Slocum, 2001).

2.8.1 Economic uses of *Ficus* trees

The persistence of isolated *Ficus* trees in these human-modified landscapes is somewhat surprising, as *Ficus* trees are not reported to have many economic benefits. The nature of their strangling behaviour means that hemi-epiphytic figs do not produce good timber, and their wood is also reported by some to burn poorly (Bhatt & Tomar, 2002; Tabuti et al., 2003, but see Agea et al., 2010). In a survey of farmer uses of isolated trees in Costa Rican pastures, Harvey and Haber (1999) found that of the six *Ficus* species present, only two had uses that the farmers benefitted from. These two species were used as fence posts, were part of live fences, and were harvested for firewood. No *Ficus* trees were useful as timber (which was the most important human-use cited), or as fodder for cattle. Even for the uses they did have, over one-third of the 190 species identified in the pastures were harvested for firewood, and one-fifth were used as fence posts, so it is unclear how damaging the loss of *Ficus* trees from this landscape would be for local farmers. Given the size of the genus, perhaps it is unsurprising that there are exceptions. Of the six *Ficus* species recorded in Bolivian forestry concessions, one, the free-standing *F. boliviana*, produced commercial-grade timber. Unlike many *Ficus* species, *F. bolivana* usually grows with relatively straight stems, and can be used to make doors, furniture, sawn wood, and plywood (CFB, 2010). However, the wood of *Ficus* trees is relatively soft, and requires extensive drying and fumigation to increase its durability in tropical climates. As this treatment is expensive, most forestry companies export it to temperate markets in North America and Europe (Felton et al., 2013). Ecological concerns have been expressed over the harvesting of this species in Bolivia (Felton et al., 2013), although current harvest estimates are below the legal limit. In fact, in a study of *F. boliviana* harvest rates in a humid forest in Bolivia, the high occurrence of extremely large buttresses (up to 4 m DBH, which are difficult to cut), low stem forks, heart rot, hollows, and termite colonies meant that only 13% of standing *F. boliviana* trees above the legal minimum diameter for harvesting had good form and condition (Fredericksen et al., 1999).

Although not a major human food resource globally, the widely cultivated *F. carica* is very popular in the Middle East, with over 1 million tons of dried fig produced annually, almost half of which come from Turkey and Egypt (FAO, 2013). There is also evidence that figs were cultivated before cereals by prehistoric humans (Gibbons, 2006; Kislev et al., 2006). Today, a variety of figs are eaten in North-east India (Chhetri, 2010), Nepal (Uprety et al., 2010), Tanzania (Smith et al., 1996), Uganda (Ipulet, 2007), China (Shi et al., 2014), and Australia (Cane, 1987), although it is unclear whether they are ever more than a minor dietary component in these places.

Unlike in Costa Rica, *Ficus* trees are valued as useful providers of animal fodder in Cameroon, Nepal, and India (Kunwar & Bussmann, 2006; Focho et al., 2009; Chhetri, 2010; Uprety et al., 2010; Kumar et al., 2011), with some estimates suggesting they may even provide 40–50% of the animal feed in Nepal (Pandey, 1982). Other widespread human-uses of figs include the production of barkcloth and traditional medicine. Barkcloth is a stiff paper-like fabric that is produced by beating sodden sheets of bark from the outer layer of a *Ficus* tree’s trunk. The practice appears to have developed independently in three separate areas of the world (Central America, East Africa, and South-east Asia), and is at least 1,400 years old (Peters et al., 1987; Aragon, 1990; Wilson & Wilson, 2013). The production of barkcloth was certainly historically important in Mexico and Indonesia at least, and has been listed by UNESCO as a representative of “intangible cultural heritage” in Uganda. However, with the development of, and widespread access to, cheaper substitute materials, the practice is now declining (Aragon, 1990).

Reports of figs being used to produce traditional medicines are even more wide-ranging, with different parts of figs used to treat a huge variety of ailments. For example, the white latex of *F. insipida* and *F. maxima* in Peru, and *F. doliaria* and *F. clusiifoli* in Brazil, are used to treat intestinal parasites (Mors & Rizzini, 1966; Bourdy et al., 2000). Vomiting and diarrhoea are treated in Bangladesh and Ethiopia by chewing the roots of *F. benghalensis* and *F. thonningii* respectively (Anisuzzaman et al., 2007; Teklehaymanot & Giday, 2007), while in India, the ethnomedical uses of figs range from treating constipation to lung disease and bladder infections (Kumar et al., 2011). In their review of prehistoric and medieval uses of figs, Lansky et al. identified a consistent pattern in the use of *Ficus* parts to treat inflammations, and also hypothesise that *Ficus* compounds may have useful anticancer properties (Lansky et al., 2008). While further research into the potential use of *Ficus* in medicine may be warranted, the wealth of ethnomedical reports on *Ficus* utility also betrays a problem. Namely, there is huge inconsistency in the type of ailments that can be treated in one place, and by one *Ficus* species, as well as inconsistency in the parts of the plant used, and how to prepare and administer the treatment (see Lansky et al., 2008; Kumar et al., 2011). Furthermore, reporting that two species of *Ficus* in different parts of the world are used by local people to treat the same illness does not inherently strengthen the case for the treatment's effectiveness. They are still just as likely to be invalid in each local context, and often involve different *Ficus* species, preparation, and administration. Reading accounts of ethnomedicinal treatments that discuss a wide range of plants in a given region points to a second concern. The illnesses treated by applying *Ficus*-based medicine can, in all cases investigated, also be treated by medicine derived from other plants (Dutta, 2006; Kadavul & Dixit, 2009). Finally, the use of *Ficus* in ethnomedicine is likely to have declined, and to continue to decline, with increasing urbanisation in tropical countries, coupled with the spread of modern medicine (Kala et al., 2006; Bowen et al., 2011).

2.8.2 Cultural uses of *Ficus* trees

Although economic uses of *Ficus* are very limited in terms of the provision of timber, limited in the provision of human food and livestock fodder, and declining in the manufacture of materials and supply of medical products, they appear to have important cultural and religious standing in many societies and faiths. One fairly widespread use of *Ficus* trees is marking important geographical features. In Fundong, Cameroon, *Ficus* trees are traditionally used to demarcate land boundaries (Focho et al., 2009), where they are also planted to confirm gifts of farmland (Gaultier, 1996). Fig trees are also reported to mark agricultural land boundaries in Kenya (K. Böhning-Gaese *pers. comms.*) and Madagascar (Martin et al., 2009). As with ethnomedical uses of *Ficus*, however, it is not clear whether these uses are unique to *Ficus*, or substitutable with other species. In studies that focus on *Ficus* trees, the use of other species to mark boundaries may be overlooked, and there is evidence that other trees in sub-Saharan Africa are used as landmarks, such as the baobab (*Adansonia digitata*) in South-western Mali (Duvall, 2007).

The most widely reported cultural role *Ficus* trees have is as sites of worship, with a range of local faiths and world religions holding particular species of *Ficus*, or individual trees, as sacred or holy. Evidence for the importance of *Ficus* trees to local faiths can be found in numerous examples from Africa and Southern Asia. In Kenya, *F. thonningii* is the medium through which the prayers of the A-Kikuyu people ascend to their God (Beech, 1913). In the Moshi area of Tanzania, every chief must have a *F. thonningii* tree to pray under, while in neighbouring Arusha, people place offerings of grass or flowers at the base of *F. sycomorus* in return for blessings from God (Hines & Eckman, 1993). In the Bamileke region of Cameroon, figs are sites of family worship (Gaultier, 1996), and in Burundi and Rwanda, figs are places to worship ancestral spirits (Niyonkuru, 1995). Indeed, in these countries, figs were historically planted at the burial sites of kings (Chrétien & Mworoha, 1970; Niyonkuru, 1995). The association between figs and gods, spirits, or ancestors appears to be the basis for taboos and social norms prohibiting the felling of *Ficus* trees (Anthwal et al., 2010). In southern China, where the Dia and Jinuo ethnic groups revere *F. altissima*, the cutting of large figs is taboo (Long & Zhou, 2001; Huabin, 2003). In Kalimantan, Indonesia, the Iban prohibit the cutting of figs as they are the homes of spirits or demons (Horowitz, 1998), a belief that is also held by the Bina tribesmen of West Papua (Lyons, 1921).

Figs also have a prominent role in several world faiths. Indeed, the frequent appearance of figs as sacred or holy trees is striking (Wilson & Wilson, 2013). In Islamic and Jewish traditions, the forbidden fruit from the Garden of Eden is commonly understood to be a fig rather than an apple, a belief that was followed by Byzantine and Italian artists, including Michelangelo, whose 1510 painting of the Sistine Chapel seems to depict the tree of knowledge as a fig (Wilson & Wilson, 2013). In Hindu tradition, *F. benghalensis* features regularly as a holy tree, and *F. benghalensis* is one of the trees that can be planted to avoid going to hell (Jain & Kapoor, 2007). For Buddhists, *F. religiosa* is the most holy tree, as it was under a *F. religiosa* that the Buddha received enlightenment (Kunwar & Bussmann, 2006). Indeed, the geographical distribution of *F. religiosa* has been argued to parallel that of

Buddhism, possibly a result of Buddhist monks transplanting it as they moved eastwards (Kosambi, 2005).

Although the wealth of examples of human-uses of *Ficus* suggest they hold considerable value, it is hard to evaluate the importance of fig trees to people. The core problem is that the evidence has been gathered through a multitude of ethnographic and other studies, where a range of tree species may not have been rigorously compared, and where methodologies have varied considerably across space and time. It is therefore difficult to determine whether figs are sufficiently important animal fodder sources that they are irreplaceable in Nepal, or whether farmers would be disadvantaged by the loss of figs as sources of fence posts in Costa Rica. Furthermore, changing technology, new cultural influences, and shifting demographic patterns may be diminishing the values people hold for figs over time. A study which gathered information on human values and attitudes towards figs, with a consistent methodology that was replicated over a large spatial scale, would provide data to assess the importance of figs versus other trees, and act as a baseline to test for future changes in these values over time.

In the absence of such an analysis, it is still worth remarking on the astonishing occurrence of so many associations between belief systems and figs, especially considering the size of the geographical area they encompass. It appears that in many societies, their high cultural standing may compensate for the low economic value of figs. The impressive size and complex structures figs form may provide the basis for their sacred value. Observers have remarked upon the beauty of large *Ficus* trees, and older figs also give an incredible sense of antiquity (Sitaramam et al., 2009). In this fashion, perhaps the sacred value of *Ficus* trees is a further iteration of the values people from all cultures hold towards large old trees? In Western Europe, oaks

(*Quercus* spp.) and yews (*Taxus baccata*) are often held in high regard, and in some cases have ancient links to religion, as exemplified by the proliferation of yews in British graveyards (Palmer, 2012), and the supposed link between oaks and the religious ceremonies of the Druids (Matthews & Matthews, 2002). Another interesting feature of *Ficus* values is the paucity of reports of figs holding any religious significance in the Neotropics. This is especially conspicuous considering the weight of examples from Africa and Asia, but it is not clear whether this is some form of sampling artifact, or an accurate reflection of the lack of sacred value in Central and South American *Ficus* trees. If it is an accurate reflection, it may be worth considering whether the taxonomic split between New and Old World *Ficus* trees provides a viable explanation for this difference? Even if a better appreciation of the distribution of cultural value towards figs could be gained, understanding the relationship between economic and social values remains a challenge. Efforts to conserve *Ficus* trees will have to remain sympathetic to local values (Berkes et al., 2000; Martin et al., 2009), but if conservation arguments are situated too closely with traditional belief systems, they may face difficulties in the dynamic tensions between changing economic and cultural forces.

2.9 The decline in isolated trees

The need to configure appropriate conservation arguments for *Ficus* trees may also be urgent, as isolated *Ficus* populations appear to be vulnerable to decline in human-modified landscapes. In many human-modified landscapes around the world, isolated trees face a regeneration crisis, where high mortality coupled with low recruitment are predicted to cause major population decreases (Manning et al., 2006; Gibbons et al., 2008; Fischer et al., 2010). In Australian agricultural landscapes, isolated trees on farms are predicted to decline by two-thirds by 2100, and simulation models have predicted the loss of mature isolated trees from four landscapes around the world within 90–180 years under current management (Gibbons et al., 2008). Reasons for these declines include natural senescence (Gibbons & Boak, 2002; Sherren et al., 2010), early mortality through elevated nutrient loads (Landsberg et al., 1990), salinity (Kimber, 1981), desiccation (Laurance et al., 2000), soil compaction (Yates & Hobbs, 1997), human clearance (Freudenberger & Ozolins, 2000; Ozolins et al., 2001), disease (Brasier, 2001) or low recruitment (Harvey & Haber, 1999; Pulido et al., 2001; Hanspach et al., 2011), which is often a function of the same problems driving early mortality, with the addition of high grazing pressure and competition with ruderal grasses (Holl et al., 2000).

In addressing the isolated tree recruitment crisis, several studies have recommended increasing recruitment rates (Harvey & Haber, 1999; Plieninger et al., 2004; Vesk & Dorrough, 2006; Le Roux et al., 2014). While improving recruitment is certainly a major issue, it must be accompanied by reducing mortality in mature trees (Gibbons et al., 2008). In the absence of management strategies that address both issues, isolated trees in human landscapes may in fact be the fast-disappearing "living dead" (sensu Janzen, 1988; Manning et al., 2006; Harvey et al., 2011).

Along with the threats faced by isolated trees in general, isolated *Ficus* trees have some further ecological challenges. Unlike other isolated trees, *Ficus* species are dependent on pollinating fig wasps for reproduction (Bronstein et al., 1990). In monoecious species of *Ficus*, at least one tree must be receptive to fig wasps at any given time, within a sustainable population (Compton et al., 1994). To estimate the minimum viable population size required for a 99% chance of figs persisting over 1,000 years, Anstett et al. (1997) modelled fig–fig wasp mutualistic population dynamics. Depending on the degree of seasonality, they estimated that a population of

170–2,000 *Ficus* trees might be required. For some of the larger hemi-epiphytic species, this has led to concerns that very large forest reserves are needed if *Ficus* trees cannot survive in human-modified landscapes (Mawdsley et al., 1998; Walker, 2007). Furthermore, these estimates suggest that even for species that can persist in deforested areas, some *Ficus* species may have very large minimum viable population thresholds.

2.10 Synopsis

Ficus species have several unique biological characteristics, which also serve to make them uniquely important in many tropical forest ecosystems. Their relationship with fig wasps means that, within a viable population, *Ficus* fruit is available year-round. The number of fig wasps required to provide a good probability of successfully dispersing, finding, and pollinating a receptive fig requires low-density *Ficus* trees to produce very large fruit crops. And the hemi-epiphytic growth strategy of many species demands that *Ficus* seeds are dispersed by arboreal or volant frugivores, to provide a good chance of a seed arriving in a place suitable for germination (Hodgkison et al., 2003). Together, these properties make figs critically important to the composition and distribution of organisms in tropical forests. However, despite widespread deforestation, which is expected to test the strength of the relationship between figs and frugivores, the persistence of fig–frugivore interactions in human-modified tropical landscapes has not been adequately examined. The consequences of a substantial deterioration in this relationship include not only the lower abundance and richness of frugivores, but also a linked decline in seed dispersal and plant regeneration in deforested habitats. The decline of figs in human-modified landscapes also threatens to sever bonds between figs and humans, which may have negative cultural and spiritual implications, as well as reducing the availability of subsistence resources and traditional medicines for impoverished rural communities in developing countries. This thesis seeks to examine these issues, and in doing so, identify strategies that may help to mitigate the threats that isolated *Ficus* trees face.

CHAPTER 3: METHODS

3.1 Field site

Field data for this thesis were collected between October 2012 and June 2013 in the Golaghat District of Assam, North-east India. The seven states of North-east India are biologically and culturally distinct from Peninsular India, and have substantially lower levels of economic development (Dikshit & Dikshit, 2014). The region is over 250,000 km^2, and accounts for 7.75% of India's land area (GOI, 2011). Over 45 million people live in this area (3.7% of India's total population), with more than two-thirds of these people residing in Assam (31 million), which is also the largest state in the North-east (78,000 km^2).

The geography of the state is dominated by the Brahmaputra River, which runs from east to west through the state for 700 km, surrounded on both sides by a flat lowland valley. The Himalayan Mountains flank Assam's northern borders, with the Karbi and North Cachar Hills to the south. The valley soils are chiefly comprised of Pleistocene alluvial sediments, which overlie a variety of mostly sedimentary strata (including hard sandstone, loose sands, sandy clays, shales, coal seams, and limestone), some of which originate from Gondwana (Fox, 1934; GSI, 2011).

The climate is subtropical with a pronounced monsoon season from May to August. Mean annual rainfall is amongst the highest in the world, with a range of 1,500–4,300 mm in different parts of the state, and an overall average of 2,900 mm (GSI, 2011). The majority of precipitation (c. 76%) falls during the monsoon season. The temperature ranges 4–19°C during the winter months (November to February) and 26–37°C during the summer (May to August), which is also accompanied by very high humidity (with a daily range of 55 to 95%).

The study site was a ≈250 km^2 area bounded by the Western Range of Kaziranga National Park at N26 34.394 E93 15.433, the city of Jorhat at N26 46.198 E94 12.678, and the town of Golaghat at N26 27.819 E93 54.978. To the north, the study area is bordered by the Brahmaputra River, which runs from the eastern Himalayas to the Bay of Bengal. Aside from Kaziranga National Park, additional protected areas in the locality are Panbari Forest Reserve (N26 37.025 E93 30.963), at the foot of the Karbi Hills, and Nambor Wildlife Sanctuary (N26 28.769 E93 48.687) south of Golaghat. Fewer than 10 small patches (≤1 ha) of secondary forest persist in the intervening landscape, although there is extensive low-quality forest covering the Karbi Hills, south of the western end of the study area. This forest is dominated by bamboo (Bambuseae spp.) with numerous stumps providing evidence of tree felling.

With the exception of these sites, the study area was largely deforested following the commercialisation of tea production around 1840 (Shrivastava & Heinen, 2007). An agricultural mosaic of rice paddies, tea estates, and village home gardens has now replaced the sub-tropical moist lowland forest that formerly existed in the lowland flood plains. The population density of Golaghat District is high by global standards, with 302 people/km^2, although this is below both the state (397/km^2) and national (382/km^2) averages (GOI, 2011). Rice cultivation is the largest occupation in the District, with 28% of the working population listing rice cultivation as their primary occupation. The rice paddies are owned by small-holder rice farmers, who sell the majority of their harvest to local markets (Barua et al., *in prep*). Rice farmers also maintain small gardens around their homes, where they grow subsistence crops such as banana (*Musa* spp.), mango (*Mangifera indica*), and jack fruit (*Artocarpus heterophyllus*). Some farmers also supplement their income by selling cash crops (particularly betel nut *Areca catechu*), cow's milk, or poultry. Another major land-use in the District is tea cultivation, with several major commercial tea estates, and numerous smaller, locally owned tea gardens. Five per cent of the population work as tea estate labourers, who are descendants from indentured labourers brought from the Peninsular states of Orissa and Jharkand to work in the Assamese tea estates by the East India Company in the 19th century (Hazarika, 2012).

The tea estate labourers are commonly referred to as the “tea-tribe”, and form one of the many social groups that inhabit Golaghat District. Other major groups include the Ahom, Karbi hill tribes, Mising river tribes, Nepali and Bangladeshi immigrants. Immigration and tribal tensions have been a concern for some time, with episodes of major political unrest in the 1980s (Hazarika, 1994), and continuing demands for greater autonomy among several local ethnic groups within Assam. The dominant social group are the Ahom, who are the largest by number, and have a higher standard of living than other tribal groups. They mainly live in the lowlands of the Brahmaputra River valley, are Hindu, and speak Assamese, which is the primary language in the District and in Assam.

This area was selected as the study site for this thesis for three reasons. First, it had numerous fig trees. In order to investigate patterns of frugivory with a large dataset, it was important to find a site with a high number of *Ficus* trees, to increase the chances of at least one being in fruit each day of the survey season. While conducting fieldwork as part of an undergraduate dissertation in 2009, the abundance of *Ficus* trees in the landscape was noted, which made this area an attractive location. Secondly, the forest in the area had almost been completely cleared, with only a few remnants surviving in discrete protected areas. Importantly, there was very little secondary forest, or other habitat features, that may have supported forest-specialist frugivores. This helped simplify isolation measurements from *Ficus* trees to the nearest forest, as few other habitat features, which may compromise the accuracy of the measurements, existed (Prugh et al., 2008). Finally, following the undergraduate dissertation fieldwork, experience working at the field site, and in identifying the local fauna and flora, had already been gained, helping to improve the accuracy of the field data collected for this thesis.

3.2 Ecological data collection

The field site was visited twice, from October to December 2012 and April to July 2013. Six drivers, six professional bird guides, and two botanists we employed over the course of the two field seasons. The team was based at three different locations over the course of the fieldwork (Wild Grass Eco Lodge, Komargoan village, and Rajabari village) to reduce journey times to *Ficus* trees in different parts of the study area.

3.2.1 Mapping *Ficus* trees

To gather information on isolated *Ficus* tree locations, we thoroughly searched the landscape for mature *Ficus* trees. Although they are not representative of the *Ficus* genus in general, we confined our search to large, hemi-epiphytic and free-standing species. We were particularly interested in these species, as previous studies in intact forests had indicated that they played especially important ecological roles (Terborgh, 1986; Shanahan et al., 2001), which we sought to test in different landscape contexts. Several smaller *Ficus* species that grow as vines, epiphytes, and shrubs were therefore excluded from the study, the largest of which was *F. assamica*, which can grow to a height of 7 m as an adult.

Searches were carried out on foot, by car, by bicycle, and on one occasion, by elephant. We marked all mature *Ficus* trees with a GPSmap 62s device, typically accurate to ≤ 5 m in the open habitats the *Ficus* trees were situated in. In total, 1,857 *Ficus* trees were located, and as the landscape was quite open, we conservatively estimate that this represents ≥ 80% of the *Ficus* trees in the study area. The most common *Ficus* species encountered were *F. religiosa* and *F. benghalensis*, followed by *F. rumphii*, *F. microcarpa*, *F. racemosa*, *F. assamica*, and *F. benjamina*.

Each afternoon, we checked the marked trees in a given area to monitor fruit ripeness. Although indicators of ripeness varied for each species, useful pointers were fruit size (*Ficus* fruit is larger when ripe), fruit colour (the fruit of the species in the study darkened from light green to orange for *F. benghalensis*, black for *F. religiosa*, and red for *F. rumphii* when ripe), the presence of soft fallen fruit under the crown, and the presence of frugivorous birds during the afternoon. If a *Ficus* tree produced ripe fruit during either field season, we surveyed the birds visiting it once, as described in Section 3.2.6 below.

To estimate the density of *Ficus* trees in the landscape, we uploaded the *Ficus* locations into ArcGIS 10.2.1 (ESRI, 2014), and overlaid them on Landsat 8 satellite images of the study area. After placing 1 km^2 grids over the study area, we identified 202 grids where our survey effort had been comprehensive (in which we conservatively estimate that ≥ 90% of the mature *Ficus* trees were discovered). For these grids, we recorded the dominant land-use, and counted the number of mature *Ficus* trees growing in each. We averaged the densities of *Ficus* trees in these grids to estimate the overall mean density of mature trees per km^2 in the study area.

3.2.2 Focal trees

Aside from *Ficus* trees, we also searched the landscape for two categories of non-*Ficus* tree: large trees and fruit bearing trees. To randomly select trees in these categories, we drove or walked for 500 m and mapped the three largest non-*Ficus* trees in the area at each stop. For a tree to qualify as a large tree, it had to have a minimum circumference at breast height over 1 m, and could not be in fruit. If a fruiting tree was present, we made a special note of it and estimated when the fruit would be ripe. If a tree bore ripe fruit during the field season, we would classify it as a "fruit tree" and survey it at peak fruit ripeness. In all cases, mapped trees had to be a minimum of 30 m from the nearest *Ficus*, large, or fruit tree to minimise the chance of other measured trees influencing the results of the vegetation surveys. We mapped 104 of these non-*Ficus* "focal trees" as part of the study (Vogel & Janson, 2007).

We measured all *Ficus* trees that produced fruit during the survey, along with 41 other randomly selected non-fruiting *Ficus* trees and all 104 non-*Ficus* focal trees. We recorded the species of each of these 207 focal trees and measured the diameter at breast height (DBH) with a tape measure, estimated the maximum tree height with a clinometer, and estimated the canopy area by measuring the canopy diameter at ground level along two axes, and then calculating the area using the formula for an ellipse. In cases where trees had multiple support trunks, we only measured the largest stem. We also recorded the grazing intensity of the area under the canopy by consulting local landowners and observing grazing damage. Although wild Asian Elephant (*Elephas maximus*) and several species of deer (Cervidae) inhabited the area, the overwhelming majority of grazing pressure came from domestic animals, and in particular, goats and cattle. We ranked grazing intensity using a three point scale where 0 is very little evidence of grazing; 1 is some livestock occasionally graze the site; and 2 is large numbers of livestock frequently graze the site. The human land-use of the area under the canopy was also recorded from observations using a similar three point scale (where 0 is very little human land-use; 1 is some human land-use, such as a village home garden or livestock grazing area; and 2 is intense human land-use, in cases where a road, house, or paddy field are present under the canopy). Finally, the land tenure at each focal tree's growing location was recorded as being under either private or public ownership, which was determined through consultation with nearby households. Although these categorisations were fairly broad, this method allowed us to assess the state of the human–environment relationship surrounding focal trees in categories that were appropriate for the research questions at hand (Gomez & Jones, 2010).

3.2.3 Vegetation census

To collect data on the plant communities growing under focal trees, we identified, counted, and measured the heights of all plants that were 20–200 cm tall. This included all trees, shrubs, vines, and forbs, but excluded grasses and ferns (which were often impractically numerous to measure). We surveyed the plant communities at focal trees in two zones: those growing directly under the crown, which we were careful to delimit the extent of, and those growing in a 5 m radius of the crown. Recording the plants in this "expansion zone" is important when trying to determine the ability of an ecological feature to act as a restoration nucleus, although previous studies that have used this approach have only surveyed plants in a 1 m radius (Zahawi & Augspurger, 2006). For statistical analysis, we computed the densities of plants growing in each zone to control for any area effect (Blake & Karr, 1987).

While in the field, we recorded the local name and plant-uses for all species encountered. The local plant-uses were originally provided by our field botanists, and then were cross-checked at a meeting with community leaders at the end of the data collection period. In this meeting the type of plant, different local names, and range of human-uses were elicited in a focus group format (Secor, 2010). The scientific names of the plants recorded were then identified through collaboration with botanists from the Plant Diversity, Systematics and Herbarium Division of India's CSIR-National Botanical Research Institute. Sources used to establish plant taxonomies included Kanjilal et al. (1934–1940), Bora and Kumar (2003), and Sarma et al. (2010). Further research on the human-uses of the plants identified was conducted with the aid of regional plant use publications (Dutta, 2006; Laloo et al., 2006), which produced six major groups: high-grade timber, low-grade timber, firewood, human food, livestock fodder, and medicinal resources. All plants recorded were then categorised into these groups, and plants with multiple uses were placed in several groups.

3.2.4 Seed rain sampling

To sample the density and variety of seeds falling under focal trees, we measured the seed rain under 35 fruiting *Ficus* trees, 10 other fruiting trees, and 10 large trees. This system provided a control group for seed rain under random large trees, and also allowed us to compare the seed rain under fruiting trees from different genera to *Ficus* trees. Seed rain experiments have been conducted by other researchers under isolated trees, restoration plantations, forest regrowth, open habitats and closed forests using a range of trap construction techniques (Cole et al., 2010; Reid & Holl, 2013; Zahawi et al., 2013). We adapted Cole et al.'s (2010) seed trap design using the resources that were available at our field site. We cut a fine (0.5×0.5 mm) mosquito mesh net into 60 cm long squares, and tied each corner to a one metre tall bamboo pole using twine, so that the final length of each side was 50 cm (giving a total area of 0.25 cm^2). A height of one meter was selected to keep the traps above the ground to avoid predation and flooding. A stone was placed in the centre of the traps to prevent wind inverting the net.

In all cases, one seed trap was placed 4 m from the trunk of the focal tree. For large *Ficus* trees, a second seed trap was placed 8 m from the trunk. In eight cases, seed traps were also placed 4 m beyond the edge of the crown of *Ficus* trees to quantify the amount of seed rain falling just beyond the crown perimeter. The material caught in seed traps was collected once every 3–4 days. Leaf litter and twigs that fell into the traps were carefully brushed to collect seeds before being discarded. The material was dried in plastic bottles over several days, and then sorted by species and counted using a hand-held 10× magnifying lens. Seeds were classed as being either zoochorous or anemochorous by morphology. Traps that were damaged by humans, livestock, or, in one case, wild elephants, were excluded from analysis.

3.2.5 *Ficus* sapling transects

To estimate *Ficus* recruitment rates, we ran 10 km transects through each of the three dominant land-use types in our study area: tea estates, paddy fields, and village home gardens. Transects were conducted from the back of a slow moving open-top jeep, with two observers spotting *Ficus* recruits growing either on the ground or epiphytically on trees or buildings. This technique allowed us to survey large areas for *Ficus* recruits, which often occurred in low densities, or were absent from some landscapes. Recruits were defined as young trees between 20 cm and 10 m tall. The species, distance along transect, and perpendicular distance from the transect line were measured (using a 50 m tape measure) and recorded for all recruits. In 62.37% of cases, the recruit was growing high up in a host tree, and so the height (from the rooting point to the highest branch tip) had to be estimated. We estimated the density of *Ficus* recruits in the three land-use types with the DISTANCE program (Version

6.0; Thomas et al., 2010), using 5% right truncation and the minimum Akaike's Information Criterion to select the model with the best fit (Burnham & Anderson, 2002).

3.2.6 Bird surveys

The *Ficus* species in this study usually produced a large ripe fruit crop for 3–7 days. During this period we would conduct one bird survey per tree. Single-tree surveys are increasingly used in ecological studies (e.g. Luck & Daily, 2003; Berens et al., 2008; Breitbach et al., 2010), and can provide detailed results for the target taxa. We selected survey trees by monitoring fruit ripeness each afternoon, as described above. The field team then reached the survey tree before first light the following morning. We often found high numbers of fruit bats (*Pteropus giganteus*) feeding at *Ficus* trees at this time, but these, and other diurnal mammals, were not analysed as part of this study. The fruit bats were difficult to record in low light conditions without specialist equipment (Lumsden & Bennett, 2005), and we only recorded diurnal mammals visiting *Ficus* trees on seven occasions, and so they were excluded from the rest of the study. Surveys commenced at first light (which ranged from 04:20–05:20 depending on the season) and continued for three hours. Previous fieldwork in the study area had demonstrated that few new species were added by repeat surveys, and that three hours was the optimum length of time to record bird assemblages before activity decreased as the sun rose (Cottee-Jones & Whittaker, *in review*). Surveys were only conducted in fair weather conditions. If the weather deteriorated during the survey period, the survey was abandoned and attempted again on the following day. During each survey, an observer would watch the tree from a concealed position with a good view, typically about 20 m from the trunk. Each individual bird that landed in the tree was recorded, including the time, direction, and distance of arrival. The distance of arrival was crudely estimated in three categories: ‘short’ for birds flying from perches within 50 m of the tree, ‘long’ for birds flying in from over the horizon, and ‘medium’ for any distance in between. The time, direction, and distance of departure were also recorded. Birds that made repeated visits to and from the tree were recorded with an asterisk to avoid double counting. In situations where too many birds were arriving and leaving the tree to count accurately, the highest number of birds recorded in any one instance was used for analysis.

Aside from surveying the birds visiting *Ficus* trees, we also surveyed the birds visiting 33 fruit trees and 31 large trees using the same protocols. These surveys were designed to compare insectivore communities, and so to control for the presence or absence of migratory species, all surveys were conducted during the same season. To gather a sufficiently large data set in one season, six professional bird guides from Kaziranga National Park, who have had extensive training and experience in scientific data collection, surveyed fruit and large trees in different parts of Golaghat District. As deforestation in the study area occurred over 150 years ago, and was largely uniform in timing, differential rates of matrix assemblage relaxation were not considered to have an effect on bird communities in the study area (Komar, 2006).

3.2.7 Bird trait data collection

To examine the functional diversity of bird assemblages visiting isolated *Ficus*, fruit, and large trees, we collected trait data on all species recorded during the bird surveys. We defined a “trait” as a measurable aspect of an organism that determines its interaction with the environment (Flynn et al., 2009). We were interested in the foraging and dispersal capacity of frugivorous and insectivorous birds, so we collected data on traits associated with dietary guild, forest-dependence, locomotive behaviour, dispersal ability, gape size, bill structure, and body size (Schoener, 1965;

Miles & Ricklefs, 1984; Derryberry et al., 2011; Claramunt et al., 2012).

Species were classified according to their primary dietary guild (frugivore, nectivore, insectivore, granivore, or carnivore; omnivores were classified according to their main food type, and were not included in any further analyses on insectivorous birds as they may have been attracted to *Ficus* and fruit trees by the fruit present) and forest-dependence (forest-dependent, habitat-generalist, matrix-specialist) following ornithological sources (del Hoyo et al., 1992–2002; 2003–2011).

For the other traits, we preferred to use morphological measurements that corresponded to a trait rather than categorisations extracted from the literature or our field experience. One of the main advantages of this approach was the creation of continuous scale datasets, which improved our ability to analyse differences between species at a finer scale. It also removes the subjectivity of classification techniques, and is replicable.

To obtain morphological measurements, we collaborated with the Edward Grey Institute of Field Ornithology from the University of Oxford's Zoology Department. The Edward Grey Institute is currently running a project to measure all the passerine birds in the world, and so we were trained by, and joined their measuring team, and contributed the measurements obtained for this study to their global dataset. Measurements were made of specimens held at the British Natural History Museum's ornithological collections in Tring, Hertfordshire. The avifauna of Assam are very well represented in these collection, with numerous specimen series collected during the colonial era in the vicinity of, or in, Golaghat District. We were therefore able to measure specimens of the local subspecies for each bird species recorded, and in almost all cases it was possible to measure specimens collected within 150 km of the study area.

In accordance with Edward Grey Institute protocols (Pigot & Tobias, 2013), we measured four specimens of each species (two adult males and two adult females). The measurements taken were: culmen length (from the base of the skull to the tip of the bill), bill length from nares (from the anterior edge of the nares to the tip of the bill), bill width (the width of the bill at the anterior of the nares), bill depth (the depth of the bill at the anterior of the nares), gape width, tarsus length (the length from the inner bend of the tibiotarsal articulation to the base of the toes, where the scalation pattern changes), wing chord (from the bend in the wing to the unflattened longest primary), Kipp's Distance (the distance from the longest primary to the first secondary; Kipp, 1959), and tail length (to the tip of the longest retrix; Sutherland et al., 2004). To obtain these measurements, we used 150 mm outside diameter dial callipers (accurate to 0.1 mm), wing rulers (20 cm, 50 cm, and 1 m), and tail rulers (accurate to 0.5 mm) from Porzana Ltd.

As weight data for birds are often variable (Clark, 1979), we preferred to measure body size through a principal components analysis (PCA). We initially conducted a pair of PCA analyses, one for locomotive ability (with input measurements of tail length, wing chord, and tarsus length) and one for bill shape (with bill depth, width, and length from nares) using oblique rotation with Kaiser stopping criterion extraction (eigenvalues > 1). Each of these PCAs produced two components. In both cases, the first related to size, while the second components were taken as indices for locomotive ability and bill shape, respectively. To produce one index for body size, we ran an additional PCA using the first components from the original analyses (Trisos et al., *in press*). To create an index for dispersal ability that standardises for bird size, we calculated the hand-wing index (Claramunt et al., 2012), which is a surrogate for flight performance, migratory behaviour, and natal dispersion in birds.

3.2.8 Functional diversity index selection and computation

To analyse the functional diversity of bird assemblages visiting isolated trees, we had to select and compute a functional diversity measure that best suited our data set. We decided to follow Laliberté and Legendre's functional dispersion (FDis) index to measure functional diversity in our dataset (Laliberté & Legendre, 2010). This represents the spread of the species in quantitative trait space by calculating a multidimensional index of the mean distance of an individual species to the centroid of all species in the community (Laliberté & Legendre, 2010). A major advantage of FDis over other measures, such as FRic, FEve, and FDiv (Mason et al., 2005; Villéger et al., 2008; Mouchet et al., 2010; Whittaker et al., 2014) is that it can be calculated for communities composed of only two species, rather than a minimum of three. As several of our fruit and large tree surveys only recorded two species of insectivorous bird, this lower threshold helped conserve the size of our original data set. FDis is also unaffected by changes in species richness, so was suitable for assessing changing community assemblages along environmental gradients (Mason et al., 2013). Our data were also unusual in that we had information on abundance for all species and surveys, which is typically lacking in functional diversity studies (Ding et al., 2013; Luck et al., 2013). In fact, many functional diversity indices work with only presence/absence data, and do not take species abundances into consideration (for example: Petchey et al., 2007; Flynn et al., 2009; Edwards et al., 2013). However, the FDis index can be weighted by abundance, which allowed us to keep a higher level of detail, and therefore precision, in our functional diversity analyses.

In calculating botanical functional diversity, plant trait data are often weighted to account for the greater importance of certain traits over others. In the absence of strong ecological reasons to assign weights to particular bird traits, we followed other studies of avian functional diversity and used an unweighted trait matrix (Petchey & Gaston, 2006). All traits were standardised to have a mean of zero and a standard deviation of one (Mouchet et al., 2008). As our trait data were measured on a continuous scale, rather than classified into nominal groups, a species–species uncorrected distance matrix was computed. A principal co-ordinates analysis (PCoA) was performed after the distance matrix was corrected for negative eigenvalues (Anderson, 2006; Laliberté & Shipley, 2013). Negative eigenvalues cannot be represented in Euclidean space, and so were corrected following Anderson (2006) to avoid introducing a bias to the functional dispersion estimates (Legendre & Anderson, 1999). These corrected PCoA axes were used to calculate the functional dispersion scores for frugivores and insectivores separately for our isolated trees (Laliberté & Shipley, 2013).

3.3 Ethnographic data collection

To gain a deeper understanding of social relationships between local people and isolated *Ficus* trees in the study area, participant observation and open-ended interviews were conducted. This form of first-hand ethnographic research, where information is gathered informally through observation, participation, and questioning over an extended period of time, is widely used in anthropology and human geography (Hammersley, 1984; Hammersley & Atkinson, 2007). This was considered to be the most appropriate approach to address the aims of this section of the research, as ethnographic analyses place an emphasis on exploring the nature of a social phenomenon rather than testing hypotheses about it, and is well suited to working with unstructured data (Reeves et al., 2008). Furthermore, these techniques can also be employed in situations where there are a small number of cases (Reeves et al., 2008). Given the lack of in-depth research on this topic, an ethnographic method promised to develop the exploration of local beliefs and attitudes towards *Ficus* trees beyond the quantitative social survey results of Barua et al. (*in prep*, see Appendix 3).

The ethnographic observations centred on the experience of living in the nearby villages of Komargoan and Rajabari for three months. In Komargoan, the field team resided with a rice farming family in a recently constructed brick house with a temporary tin roof. Their wealth was typical of the households in the area. They earned money from farming a moderate area of rice paddies, and otherwise produced milk, eggs, and fruit in their home garden for subsistence. We gained access to the household as our driver's aunt lived in a neighbouring house. Over the course of our stay, I became integrated with family life by learning Assamese, to the extent that the head of the household was addressed as "pa" (uncle), his wife "ma" (aunt), and a boy who lived next door addressed me as "elder brother". In Rajabari, I stayed with a slightly wealthier family, the head of which worked for the state oil refinery. I met the head of this household while playing football for the Rajabari Sports Association, their village team. This, combined with further efforts to learn Assamese, provided access to the household, which consisted of the parents, two teenage daughters and one teenage son. These households provided the foundations from which I met and interacted with members of the village communities. As the socio-economic context of the field locations mirrored the environment described in Section 3.1 above, this sample of Assamese communities was appropriate to develop an understanding of the dominant views the local Ahom community held towards *Ficus* trees. During this time, I cooked, cleaned, and helped with tasks around the house, as well as eating and socialising with the household and neighbours in the villages. This "deep hanging-out" (Geertz, 1998:69) allowed me to build up a rapport with the community, and to uncover the suppressed perspectives towards *Ficu*s trees, that were hard to garner from conversations with informants who were more overtly aware of my position as a foreign scientist.

A key site of social interaction in the Assamese village is the reception room, especially while drinking tea, and this was the setting for the majority of conversations. Over the course of the study period, discussions were held with members of the community in Assamese, English, and in Assamese through a translator (who was a native Assamese and fluent English speaker). In cases where a translator was needed, the translator had been trained in the importance of providing an accurate and detailed account of the exchange, and discussions of how questions should be framed were held both before and after those meetings where translation was necessary (Maranhão, 2003). Although the use of a translator increased the formality of some discussions, most of these interactions were still informal and conversational, which enabled me to ask questions in a naturalistic manner.

During the exchanges with members of the local community, several assumptions were considered. First, that a person's behaviour is inextricably linked to the meaning that a situation has. Second, that a person's contributions and behaviour change depending on their interactions with others. Third, that a person's behaviour and beliefs can only be fully understood in the broader context of social organisation and culture (Schatzman & Strauss, 1973). These fundamentals replaced positivist concerns of numerical measurement and replication for this part of the fieldwork. Instead, emphasis was placed on understanding the positionality of the researcher, with constant attention devoted to reflexive appraisals of the research experience (Mackenzie, 1994). In this case, my position as a Caucasian foreigner, the first whom some of the local community had ever seen let alone interacted with, may have helped elicit more social interactions than would have otherwise occurred. When informed of the purpose of the research, namely the scientific study of *Ficus* trees, participants may have moderated their responses to certain questions or ideas. Despite this, participants seemed to make very open and candid contributions to conversations that covered topics that may have been sensitive, such as deforestation and belief systems. An additional concern was my position as a male in a society very deeply and firmly structured along male and female divisions in expected behaviour, education, and employment. As a result, some members of the community, and some potentially important discourses, may have been difficult to access beyond the homestay households.

To augment the information gathered during casual exchanges, we also conducted a series of 12 interviews with key informants who may have been able to offer some additional in-depth insights (Hammersley & Atkinson, 2007). These interviews were still informal, and asked open-ended, unstructured questions. Interviewees included women who lived next to *Ficus* trees, village elders, priests, and tea estate managers. Interviews lasted between 40 minutes to one hour and were transcribed by hand.

I adopted an inductive thematic approach to data analysis, in which meanings and key issues emerged from the data through the careful analysis of all records. Several sources of data were used to generate a more comprehensive understanding of the emerging themes, including observations, conversations, and interviews.

3.4 Online survey

To assess the geographical variation in values held towards *Ficus* trees, we conducted an online survey. Limitations to time and funding precluded administering surveys similar to Barua et al. (*in prep*) in a range of countries around the world. Instead, we identified experts who had conducted fieldwork in rural areas with *Ficus* trees, and sought to gain an overview of the attitudes held by the communities they had worked in. Synthesising the opinions of experts through expert elicitation is a technique that has been recognised for several decades in social science and risk assessment (O'Hagan et al., 2006; Donlan et al., 2010). In data-poor scenarios, expert elicitation is becoming increasingly useful in guiding decision-making in the conservation sector (Martin et al., 2005; Halpern et al., 2007). We sought to apply these techniques to questions concerning the human–*Ficus* relationship by surveying *Ficus* experts around the world.

To conduct this survey, we first selected 10 countries or regions (herein collectively referred to as regions) in the American, African, and Asia-Pacific tropics that we were interested in investigating. They were: India, China, The Philippines, South-east Asia (Indonesia, Malaysia, Brunei), Papua New Guinea, East Africa (Uganda, Tanzania, Kenya, Ethiopia), Madagascar, Mexico, Central America (Panama, Costa Rica), and Brazil. For each region, we aimed to gather a minimum of 10 completed questionnaires as a threshold for inclusion in the analysis. We achieved this in all cases except for Madagascar. Before retaining this country in the study, we conducted a saturation test (following Laurance et al., 2012) to determine how much new information was provided by each additional questionnaire.

We identified experts in each of these regions who had worked in rural field sites with *Ficus* trees, and who may be familiar with the local uses and attitudes towards these trees. These experts were identified by searching the literature, discussions with *Ficus* "gatekeepers", and gatekeepers of tropical ecology and ethnobotany interest groups. To search the literature, we used combinations of keywords including *Ficus*, ethnobotany, ethnopharmacy, ecology, and country names in Google Scholar. We searched all records first, and then limited our search to work published after 2010 to increase the likelihood of identifying an expert with a recent interest in the topic and an accurate email address. To avoid selecting clusters of like-minded experts, we only invited one author from each peer-reviewed paper to participate in the survey. Each expert was invited by a personalised email to participate in the study. In return for completing a questionnaire, experts were offered the option of inclusion as co-authors in any publication using their results.

We prepared a questionnaire that was sufficiently general to be appropriate to administer in a range of contexts. The questionnaire comprised 36 short-answer questions, which covered topics on the economic, environmental, and cultural attitudes towards *Ficus* trees (see Supporting information in Chapter 11). The questions were multiple-response, with each respondent asked to select an answer on a five point-scale. In addition, each question had an "unsure" option to avoid diluting high-confidence, accurate responses with low-confidence, guessed responses (O'Hagan et al., 2006; Laurance et al., 2013). In a further attempt to reduce the chance of low-confidence responses affecting the accuracy of the results, respondents were asked to evaluate the accuracy of their responses by rating their confidence in the answers provided. Responses with a low-confidence rating were excluded from analysis. Respondents were given the option of anonymity, which 9.72% elected to accept. At the start of the questionnaire, each respondent was asked to name a particular study area they had worked in, and confine their answers to that area.

Questionnaire responses were coded and then tested for normality. In cases where the assumptions of parametric tests were met, differences in outcome variables were tested with one-way analysis of variance tests (ANOVA), combined with follow-up post hoc tests where necessary. In situations were the coded data did not conform to a normal distribution, non-parametric chi-squared, Kruskal-Wallis, and Mann-Whitney

U tests were performed (Field, 2009). In addition, a PCA was used to reduce the dimensions of the 13 questions relating to values attributed to *Ficus* trees down to underlying factors, and a reliability analysis was conducted to assess the suitability of the questionnaire design.

3.5 Data organisation for analysis

Details of the statistical methods followed, programs used, and the justification of techniques are provided in each of the relevant empirical chapters. The present section seeks to clarify the way the field data were divided and organised for analysis.

To augment the 62 surveys of frugivore visits to *Ficus* trees collected for Chapter 4, we combined these data with 60 surveys conducted by Barua et al. (*in prep*; Appendix 3). The Barua et al. surveys were conducted by the same field team, using the same survey techniques, and the same data recording protocols as the survey work undertaken from October 2012 to July 2013. The Barua et al. dataset was collected from September 2009 to August 2010, and mainly surveyed *Ficus* trees in close proximity to forested protected areas (72% of trees were within 2.5 km of the nearest protected area, and none were further than 8 km). There were no changes in land-use between the collection of the two datasets in the study area. The only difference between the two datasets was that the field team focused on frugivores, and did not record insectivorous birds, in the Barua et al. dataset.

The frugivore and insectivore analyses (Chapters 4 and 5) compared bird assemblages recorded in *Ficus* trees to fruit and large trees. The trees included in these two categories overlapped with the trees that were measured as part of the sapling and seed rain surveys undertaken for Chapters 7 and 8.

The *Ficus* population model that was used in Chapter 9 was adapted from a model built by Gibbons et al. (2008), and used in Gibbons et al. (2010) and Le Roux et al. (2014). To parameterise this model, we gathered data on the density of mature *Ficus* trees per km^2 in the study area (as described in Section 3.2.1 above), estimated *Ficus* growth rates (from data gathered by Dhanya et al., 2013), mortality rates (following the formula provided by Le Roux et al., 2014), recruitment rates (as described in Section 3.2.5 above), and maximum age. Further details on how these estimates were used to parameterise the model are provided in Chapter 9.

CHAPTER 4:

Are protected areas required to maintain functional diversity in human-modified landscapes?

4.1 Preface

This chapter is the first empirical chapter, and addresses the key concern underpinning the argument presented in this dissertation. Although *Ficus* trees are known to be an important food resource for frugivorous birds, the nature of changes to this relationship beyond forest habitats has been overlooked. This chapter therefore investigates the interactions between frugivorous bird communities and isolated *Ficus* trees in a human-modified landscape, and assesses the implications of these dynamics for seed dispersal, a critical ecological function.

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The co-author contributions were as follows. Conceived and designed the study: HEWC-J, MB. Conducted the data collection: HEWC-J, MB, JT, TPB. Analysed the data: HEWC-J, TJM, TPB. Wrote the paper: HEWC-J, TJM, RJW. Further details of the co-author contributions and their consent to the use of this material in this thesis are provided in Appendix 4.

This chapter has been accepted with revisions at PLoS ONE.

4.2 Abstract

The conversion of forest to agriculture across the world's tropics, and the limited space for protected areas, has increased the need to identify effective conservation strategies in human-modified landscapes. Isolated trees are believed to conserve elements of ecological structure, providing micro-sites for conservation in matrix landscapes, and facilitating seed dispersal and forest restoration. Here we investigate the role of isolated *Ficus* trees, which are of critical importance to tropical forest ecosystems, in conserving frugivore composition and function in a human-modified landscape in Assam, India. We surveyed the frugivorous birds feeding at 122 isolated *Ficus* trees, 33 fruit trees, and 31 large trees across a range of 32 km from the nearest intact forest. We found that *Ficus* trees attracted richer and more abundant assemblages of frugivores than the other tree categories. However, incidence function estimates revealed that forest-dependent species decreased dramatically within the first kilometre of the forest edge. Despite this, species richness and functional diversity remained consistent across the human-modified landscape, as habitat-generalists replaced forest-dependent frugivores, and accounted for most of the ecological function found in *Ficus* trees near the forest edge. We recommend that isolated *Ficus* trees are awarded greater conservation status, and suggest that their conservation can support networks of ecologically functional frugivorous bird communities.

Keywords Assam, canonical correspondence analysis, *Ficus*, frugivory, functional dispersion, incidence functions, India, isolated trees, quantile regression, tropical countryside biogeography

4.3 Introduction

Agricultural conversion is a major driver of tropical forest destruction worldwide (Geist & Lambin, 2002; Gibbs et al., 2010), to the extent that tropical agriculture now accounts for 13.3 m ha, an increase of 3% over the last decade (FAO, 2014). With limited scope for the addition of new protected areas in many tropical regions (Harvey & González Villalobos, 2007), one of the major challenges in tropical conservation is devising strategies that can effectively conserve biodiversity in human-modified production landscapes (Daily et al., 2001; Chazdon et al., 2009).

Several studies have documented species loss and compositional shifts following the conversion of forest to agriculture (Edwards et al., 2011; Styring et al., 2011; Senior et al., 2013; Wilcove et al., 2013). For birds, insectivorous species are often lost from human-modified landscapes (Tscharntke et al., 2008), while forest-dependent species and large-bodied frugivores, which are particularly vulnerable to hunting (Vidal et al., 2013), rarely venture beyond the forest edge (Marsden et al., 2006; Watling et al., 2011). The functional implications of these changes are less clear, however (Gardner et al., 2009; Edwards et al., 2013). Critical ecosystem functions, such as pollination and seed dispersal, may still persist with a depauperate assemblage of species (Perfecto et al., 2004; Van Bael et al., 2008). Indeed in some human-modified landscapes, the frugivore–fruit tree relationship seems to be sufficiently intact to conserve seed dispersal mechanisms through networks of isolated trees (Luck & Daily, 2003; Guevara et al., 2004; Eshiamwata et al., 2006; Douglas et al., 2013). Furthermore, isolated trees are argued to provide a range of other ecological benefits, including nesting and roosting sites, enhanced soil fertility, and sites for forest restoration, making them a potentially important biodiversity conservation agent in these landscapes (Manning et al., 2006; Lindenmayer et al., 2013).

In intact tropical forests, *Ficus* (Moraceae) trees are consistently identified as critically important ecological actors (Leighton & Leighton, 1983; Terborgh, 1986; Lambert & Marshall, 1991; Shanahan et al., 2001). Their large crop size, aseasonal fruiting pattern, and nutritional composition make them a key resource for frugivores around the world's tropics (O'Brien et al., 1998; Kinnaird et al., 1999; Wendeln et al., 2000). Although usually studied in forest ecosystems, networks of isolated *Ficus* trees persist in many human-modified landscapes (Slocum, 2001; Guevara et al., 2004; Eshiamwata et al., 2006; Caughlin et al., 2012). However, little work has been done to assess the status of the *Ficus*–frugivore relationship beyond the forest edge. Key questions, such as whether frugivores commute to fruiting trees from forest habitats, or independently reside in human-modified landscapes, remain unanswered (Sekercioglu et al., 2007; Chazdon et al., 2009). Furthermore, few studies have explicitly considered agricultural habitats as a conduit for the movement of seeds and frugivores, especially at the landscape scale (Tscharntke et al., 2008; McConkey et al., 2012; Helbig-Bonitz et al., 2013). The lack of research on *Ficus*–frugivore interactions in human-modified landscapes is particularly concerning as the area required to support populations of the more sparsely distributed *Ficus* species over the long-term are likely to exceed the size of all but the largest protected areas (Mawdsley et al., 1998; Walker, 2007). Indeed the *Ficus*–frugivore relationship may only be sustainable, both within and beyond protected areas, through effective conservation in human-modified landscapes.

From a functional perspective, if the *Ficus*–frugivore relationship was dependent on protected areas, functional diversity would be expected to decline monotonically in relation to species loss as environmental conditions become increasingly unfavourable (Flynn et al., 2009). However, if frugivore assemblages in *Ficus* trees are composed of random subsets of those species that occur across the landscape, then their functional diversity will be randomly distributed. On the other hand, if environmental filtering influences assemblage composition, we can expect a non-random distribution of functional diversity. Furthermore, the relationship between the decline in functional diversity and the decline in species richness should reveal the structure of species turnover. If species richness declines at a faster rate than functional diversity, functionally redundant species are lost first (functionally redundant species being those with traits shared with other species in the assemblage; Flynn et al., 2009). If species richness declines at the same rate as functional diversity, the assemblages are subject to random turnover, where no traits are particularly vulnerable to structural loss. Finally, where species richness declines at a slower rate than functional diversity, functionally unique species are lost first, indicating that rare traits are more vulnerable to loss through structured turnover, as hypothesised above.

To test the capacity of isolated *Ficus* trees to conserve the *Ficus*-frugivore relationship in human-modified landscapes, we examined three hypotheses. First, given the importance of *Ficus* trees to birds in intact forests, we hypothesise that isolated *Ficus* trees will have a higher abundance and diversity of frugivorous birds than other types of isolated tree. Second, in determining the composition of assemblages at isolated *Ficus* trees, we posit that the distance of a *Ficus* tree from the nearest forest will have the strongest influence on frugivore assemblages. Finally, we hypothesise that functionally unique frugivore species are more vulnerable to extirpation in human-modified landscapes, and so will be lost first from isolated *Ficus* trees.

4.4 Methods

4.4.1 Study area

Our study was conducted in the Golaghat District of Assam, North-east India (Figure 4.1). This region's original moist subtropical forest was largely cleared following the local commercialisation of tea production around 1840 (Shrivastava & Heinen, 2007). The study area of ≈250 km^2 extends between Kaziranga National Park (N26 34.394 E93 15.433), the town of Golaghat (N26 27.819 E93 54.978), and Jorhat (N26 46.198 E94 12.678). Aside from Kaziranga National Park, additional protected areas in the study area were Panbari Forest Reserve (N26 37.025 E93 30.963), at the foot of the Karbi Hills, and Nambor Wildlife Sanctuary (N26 28.769 E93 48.687) south of Golaghat.

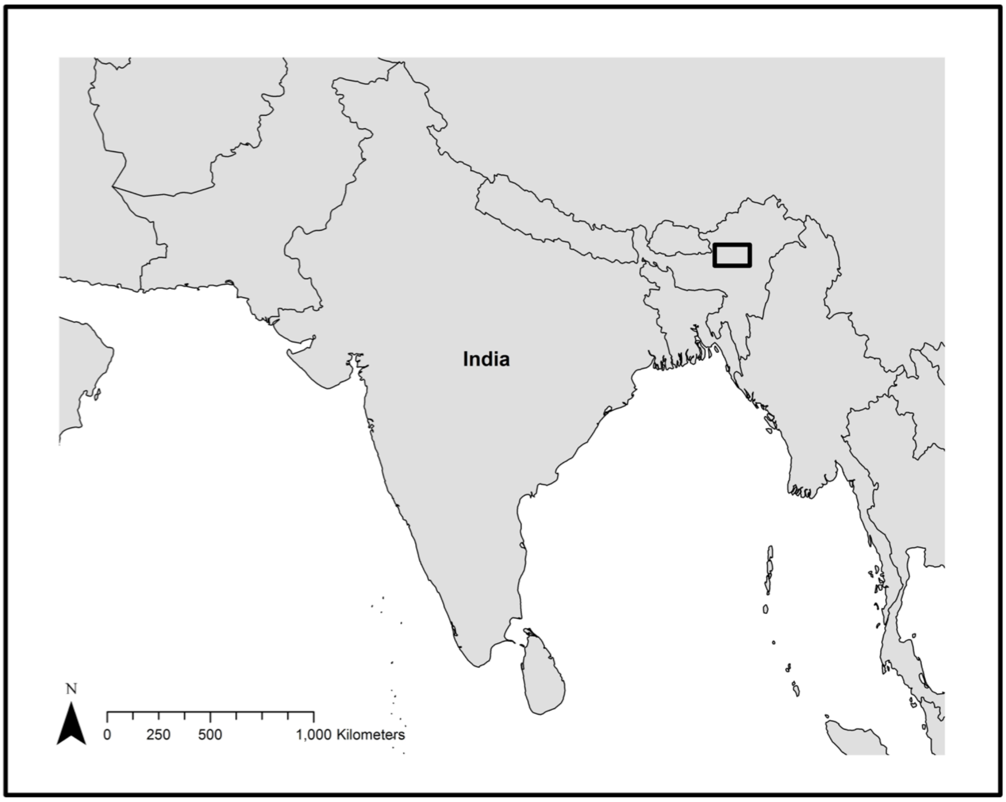


Figure 4.1: Location of the study area in Assam, India.

Humans have heavily modified the landscape across the study area, so that it now forms an agricultural mosaic with a heterogeneous assortment of small-holder rice cultivation, tea estates, and village home gardens. The region has a population density of 302 people / square kilometre (GOI, 2011). The elevation of the study area ranges between 30–100 m above sea level, and the mean annual rainfall for the region is 1,500–2,500 mm, most of which falls in the May to August monsoon (Barua & Sharma, 1999; Shrivastava & Heinen, 2007). The annual temperature range varies from an average absolute minimum of 5°C to an average absolute maximum of 35°C (Barua & Sharma, 1999).

4.4.2 *Ficus* data collection

Field data were collected between September 2009 and June 2013. We first carried out a thorough search of the area by car and foot, marking all mature *Ficus* trees with a GPSmap 62s device, typically accurate to ≤ 5 m in the open habitats the *Ficus* trees were situated in. In total, 1,857 *Ficus* trees were located, and as the landscape was quite open, we conservatively estimate that this represents $\geq 80\%$ of the *Ficus* trees in the study area (Figure 4.2). The most common *Ficus* species encountered were *F. religiosa* and *F. benghalensis*, followed by *F. rumphii*, *F. microcarpa*, *F. racemosa*, *F. benjamina* and *F. assamica*. Due to the different life history of *F. assamica,* it was excluded from the mapping exercise.

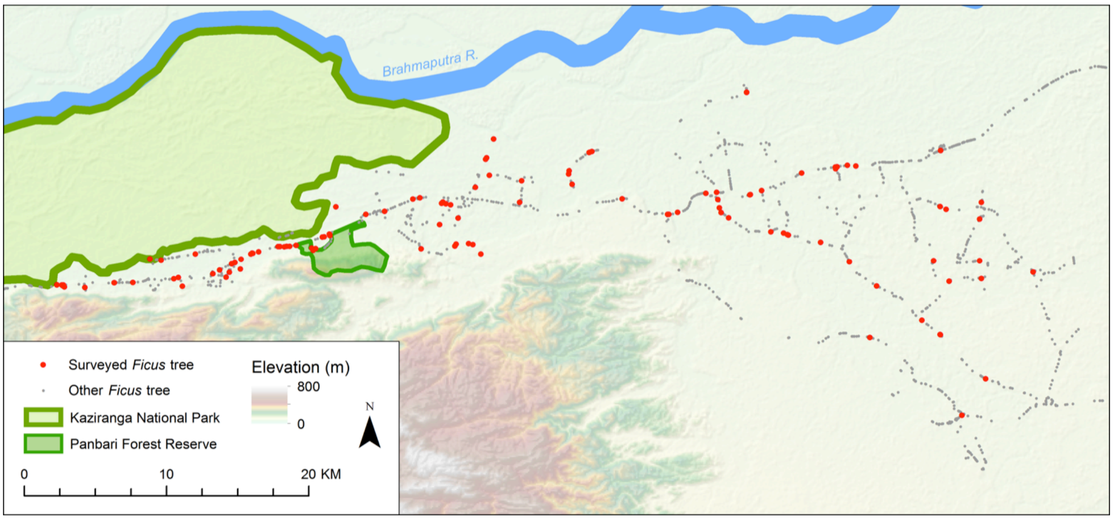


Figure 4.2: Locations of the 1,857 *Ficus* trees marked in the study area. Red circles denote surveyed trees, grey circles denote trees that were not surveyed. The linear pattern at this scale indicates the association between roads and the distribution of *Ficus* trees. Kaziranga National Park and Panbari Forest Reserve contain the only relatively intact forests in the study area.

The mapped trees were regularly checked to monitor fruit ripeness. When a tree produced a ripe crop, we measured its diameter at breast height (DBH), height, and canopy diameter along two axes. Canopy area was later calculated using the formula for an ellipse. The average height of measured *Ficus* trees was 26.58±0.72 m, (mean±SE, n=122), with a mean DBH of 1.42±0.06 m, and canopy area of 474.02±29.68 m^2. To produce a single measure for overall tree size, a Principal Components Analysis (PCA) with Kaiser stopping criterion extraction (eigenvalues >1) was conducted using DBH, height, and canopy area in IBM SPSS Statistics 22 (IBM, 2013). As the input variables were correlated with each other we used an oblique rotation method ("Direct Oblimin" in SPSS). The observed intensity of human land-use within a 100 m radius of the tree was recorded using a three-point scale (where 0 is very little human land use; 1 is some human land use, such as a village home garden or livestock grazing area; and 2 is intense human land use, in cases where a road, house, or paddy field were present). The size of fruit produced by the tree was categorised as either large (mean diameter > 150 mm) or small (< 150 mm), by measuring three recently fallen fruit. We measured the distance to the nearest protected area with intact forest by overlaying the *Ficus* GPS markers on Landsat 8 satellite images of the region in ArcGIS 10.2.1 (ESRI, 2014), and then digitised the protected area borders through an on-screen visual interpretation (Berens et al., 2008). The distance of each *Ficus* tree to the nearest protected area was then measured in kilometres using ArcGIS. In all cases, protected areas held the only high-quality forest habitat left in the study landscape. In addition to protected areas, small (≤1 ha), low-quality wooded areas were located through consultation with local landholders and marked with a GPS device. In cases where *Ficus* trees were closer to small, low-quality wooded areas than protected areas, additional measurements were made following the above procedure to estimate the distance to the nearest wooded area of any quality.

4.4.3 Frugivore data collection

Fruiting *Ficus* trees were observed to have a large ripe crop for 3–7 days. During this period we would conduct one frugivore survey per tree. Single-tree surveys are increasingly used in ecological studies (e.g. Luck & Daily, 2003; Berens et al., 2008; Breitbach et al., 2010), and can provide detailed results for the target taxa. Frugivore surveys commenced at first light (which ranged from 04:20–05:20 depending on the season) and continued for three hours. Previous studies of *Ficus* trees in the study area had demonstrated that few new species were added by repeat surveys, and that three hours was the optimum length of time to record frugivore assemblages before activity decreased as the sun rose (Cottee-Jones & Whittaker, *in review*). Surveys were only conducted in fair weather conditions. If the weather deteriorated during the survey period, the survey was abandoned and attempted again on the following day. During each survey, an observer would watch the tree from a concealed position with a good view, typically about 20 m from the trunk. Each individual bird that landed in the tree was recorded, including the time, direction, and distance of arrival. Birds that made repeated visits to and from the tree were recorded with an asterisk to avoid double counting. In situations where too many birds were arriving and leaving the tree to accurately count, the highest number of birds recorded in any one instance was used for analysis.

The same protocols were used to survey control groups of non-*Ficus* fruiting trees (“fruit trees”) and other large non-fruiting trees (“large trees”), to test if *Ficus* trees were more attractive to frugivores than other tree types. The trees selected for these control surveys were also commonly encountered species in the human-modified landscape. Fruit trees were selected depending on the ripeness of their crop, while large trees were selected as they were the largest trees in the area (judged by height). Their classifications and attributes are provided in Table 4.1.

Table 4.1: Characteristics of the isolated *Ficus* trees and the two control tree categories included in the study. DBH is diameter at breast height. Values for DBH, height, and canopy area are mean ± standard error. Different superscript letters denote significantly different means at $p<0.05$ following ANOVA and Games-Howell post hoc tests. The five most surveyed species are listed in order of decreasing number of surveys.

Characteristic	***Ficus***	**Fruit**	**Large**
Total no. of individuals surveyed	122	33	31
Total no. of species surveyed	6	12	15
DBH (m)	1.42 ± 0.06^{a}	0.45 ± 0.02^{b}	0.61 ± 0.05^{c}
Height (m)	26.58 ± 0.72^{a}	18.86 ± 1.03^{b}	20.91 ± 0.89^{b}
Canopy area (m^2)	474.02 ± 29.68^{a}	74.01 ± 7.16^{b}	130.11 ± 21.43^{c}
Five most surveyed species (in order of decreasing abundance)	*F. religiosa, F. benghalensis, F. rumphii, F. microcarpa, F. benjamina*	*Artocarpus heterophyllus, Tectona grandis, Artocarpus lakoocha, Syzgium cumini, Toona ciliata*	*Syzgium cumini* (non-fruiting), *Albizia lucidor, Albizia procera, Mangifera indica* (non-fruiting), *Neolamarckia cadamba*

4.4.4 Frugivore classifications

Immediately after the frugivore survey, the number of birds of each species recorded visiting the tree would be totalled. Nomenclature followed Grimmett et al. (2011) for the most recent detailed review of Indian bird taxonomy. Each species was classified into primary and secondary dietary guilds (frugivore, nectivore, insectivore, granivore, or carnivore) following del Hoyo et al. (1992–2002; 2003–2011). We also used these sources to classify each species' habitat preference as forest-dependent, habitat-generalist, or matrix-specialist. To cross-check the local validity of these classifications, binary logistic regression models were run for each species (excluding singletons and doubletons), with presence or absence in a *Ficus* tree as the response variable, and the distance from protected area as the predictor variable (Watson et al., 2005). The resulting predicted probabilities of occurrence were then used to plot incidence functions against distance for each species (Figure 4.3, and see Supporting information A in Section 4.10) using the R package GGplot2 (Wickham, 2009). Sharp downward curves were indicative of forest-dependent species, flat curves (no change of more than 10% over 30 km) denoted generalists, and rising curves were characteristic of matrix-specialists.

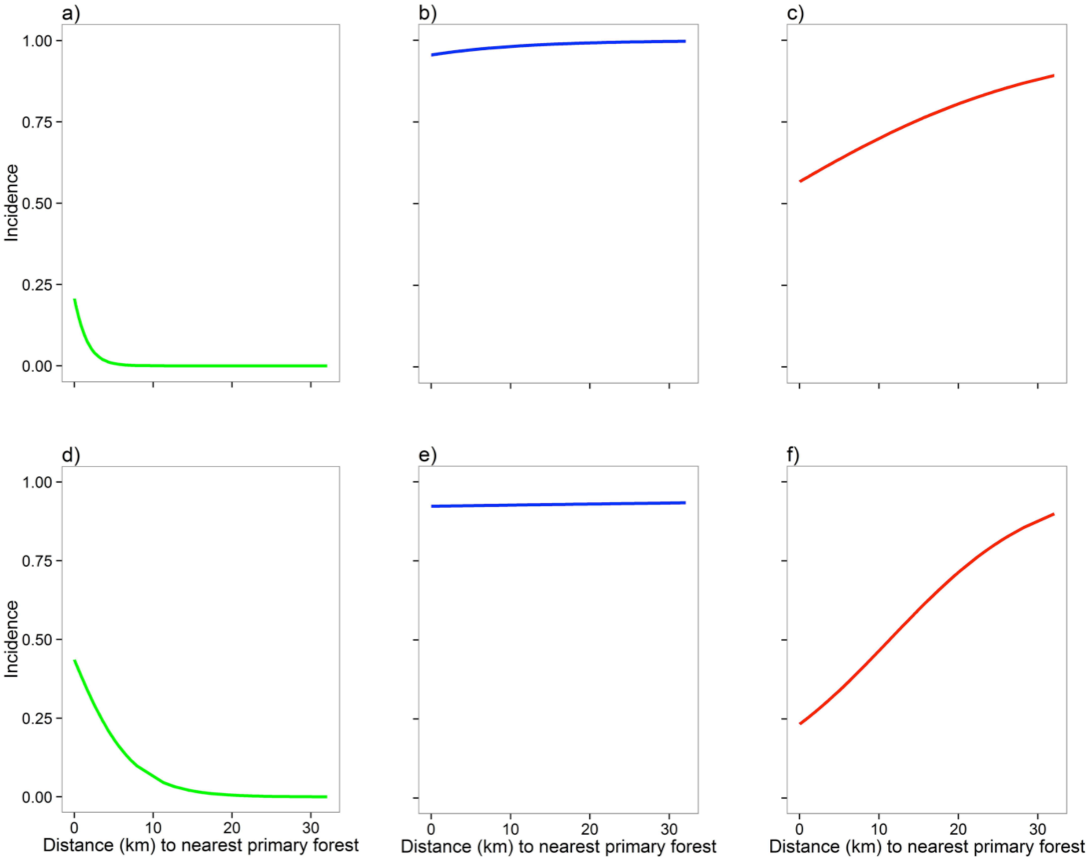


Figure 4.3: Incidence functions for six frugivore species. Species are a) Great Indian Hornbill *Buceros bicornis*; b) Red-vented Bulbul *Pycnonotus cafer*; c) Great Myna *Acridotheres grandis* d) Blue-eared Barbet *Megalaima australis*; e) Coppersmith Barbet *Megalaima haemacephala*; f) Black-hooded Oriole *Oriolus xanthornus*. Green curves represent forest-dependent species, blue represent habitat-generalists, and red represent matrix-specialists. The curves are the predicted probability of occurrence, generated through a logistic regression model with distance from the nearest primary forest as the predictor variable for each species' presence/absence data at 122 isolated *Ficus* trees. The incidence function curves of all 33 frugivore species are displayed in Supporting information A, Section 4.10. The figures were constructed using the R package GGplot2 (Wickham, 2009).

4.4.5 Ecomorphological data collection

In order to obtain ecomorphological trait data, each species recorded in the surveys was measured following Edward Grey Institute protocols at the British Natural History Museum's ornithological collections. We defined a "trait" as a measurable aspect of an organism, which determines its interaction with the environment (Flynn et al., 2009). Here we were interested in the foraging and dispersal capacity of frugivorous birds, so we measured traits associated with locomotive behaviour, dispersal ability, gape size, bill structure, and body size (Schoener, 1965; Miles & Ricklefs, 1984; Derryberry et al., 2011; Claramunt et al., 2012). Specifically, we measured four specimens of the correct local subspecies for each species recorded. In almost all cases we were able to measure specimens collected within 150 km of the study area. Two adult males and two adult females of each species were measured with 150 mm outside diameter dial callipers (accurate to 0.1 mm), wing rulers, and tail rulers (accurate to 0.5 mm) from Porzana Ltd. The measurements taken were: culmen length (from the base of the skull to the tip of the bill), bill length from nares (from the anterior of the nares to the tip of the bill), bill width (the width of the bill at the anterior of the nares), bill depth (the depth of the bill at the anterior of the nares), gape width, tarsus length (the length from the inner bend of the tibiotarsal articulation to the base of the toes, where the scalation pattern changes), wing chord (from the bend in the wing to the unflattened longest primary), Kipp's distance (the distance from the longest primary to the first secondary; Kipp, 1959), and tail length (to the tip of the longest retrix; Sutherland et al., 2004). Bill measurements excluded ornamentation, which meant the casques of *B. bicornis* and *A. albirostris* were not included in bill width or depth measurements. As weight data for birds are often variable (Clark, 1979), we preferred to measure body size through a PCA. We first conducted a PCA of tail length, wing chord, and tarsus length, using oblique rotation with Kaiser stopping criterion extraction (eigenvalues >1), which produced two components. The second of these was used as an index for locomotive ability, while the first related to body size. We then ran a PCA with bill depth, width, and length from nares using the same procedure, obtaining two components: the first related to size again, while the second was used as an index of bill shape. The first principal components of the two analyses were then used in isolation for a third PCA, which produced an index for overall body size (Trisos et al., *in press*). To create an index for dispersal ability that standardises for bird size, we calculated the hand-wing index (Claramunt et al., 2012), which is a surrogate for flight performance, migratory behaviour, and natal dispersion in birds. Only species observed eating *Ficus* fruit were retained for further analysis.

4.4.6 Functional dispersion

We calculated the functional diversity of the frugivores recorded at each *Ficus* tree to identify trends in the provision of ecological services, and to test for the existence of environmental filtering in isolated *Ficus* frugivore assemblage composition. By using trait information to define a species' ecological role within a community, a single continuous metric can be produced, which permits an assessment of functional redundancy and structured turnover in assemblages across environmental gradients (Edwards et al., 2013). We follow the definition of functional diversity as the distribution of functional traits within multidimensional niche space (Petchey & Gaston, 2006), and used Laliberté and Legendre's functional dispersion (FDis) index to measure functional diversity in our dataset (Laliberté & Legendre, 2010). This represents the spread of the species in quantitative trait space by calculating a multidimensional index of the mean distance of an individual species to the centroid of all species in the community (Laliberté & Legendre, 2010). A major advantage of FDis over other measures, such as FRic, FEve, and FDiv (Mason et al., 2005; Villéger et al., 2008; Mouchet et al., 2010; Whittaker et al., 2014) is that it can be calculated for communities composed of only two species, rather than a minimum of three. It is also independent of species richness, and can be weighted by abundance, both of which were important considerations for our study (Laliberté & Legendre, 2010; Mason et al., 2013). We calculated functional dispersion for each of our *Ficus* trees using the R package FD (Laliberté & Shipley, 2013; R Core Team, 2014).

In the absence of strong ecological reasons to weight our data, we used an unweighted trait matrix (Petchey & Gaston, 2006). As our trait data were measured on a continuous scale, rather than classified into nominal groups, a species–species uncorrected distance matrix was computed. A principal co-ordinates analysis (PCoA) was performed after the distance matrix was corrected for negative eigenvalues (Anderson, 2006; Laliberté & Shipley, 2013) to avoid introducing a bias to the functional dispersion estimates (Legendre & Anderson, 1999). These corrected PCoA axes were used to calculate the functional dispersion scores for our *Ficus* trees (Laliberté & Shipley, 2013).

4.4.7 Statistical analysis

To assess the importance of *Ficus* trees to frugivores against the two control groups (other fruit trees and large trees), we compared the estimated richness, Shannon index, observed average richness, abundance, and functional dispersion parameters across the three tree categories. Observed richness is the average number of frugivorous birds recorded across all trees in each category, while estimated richness used the "Chao 1 bias corrected" asymptotic estimator, which only includes the number of singletons and doubletons to estimate the number of undetected species (Chao, 2005).

As the sites used in this study were single trees rather than larger areas, which is unusual in an avian analysis, both observed average richness and estimated richness were retained to give the reader a better sense of the field data and their interpretation. By taking the relative abundance of species into account, the Shannon index provides a measure of the species evenness across the three tree categories. The Shannon index scores were derived from Chao and Shen's (2003) revised algorithm. Both the richness estimator and Shannon index were computed in SPADE (Chao & Shen, 2010; Chao & Shen, 2012). An analysis of variance (ANOVA) test was used to examine differences between observed species richness and abundance over the three tree categories. The data were log transformed for normality, and tested for homogeneity of variance using Levene's test. In cases where equal variances could not be assumed, Welch's F-ratio was used to identify the main effects at the p=0.05 level of significance. A Games-Howell post hoc test, which is robust to unequal sample sizes, was used to identify significant differences between groups (Field, 2009). Functional dispersion (FDis) did not conform to normality even after transformation in the fruit or large tree categories, so we used a Kruskal-Wallis test with Mann-Whitney follow-up procedures and a Bonferroni correction of p<0.0167. We also examined species richness, abundance, and FDis across the three tree types while controlling for the canopy area of each tree (see Supporting information B in Section 4.10). All ANVOAs and non-parametric equivalents were conducted in SPSS 22.0 (IBM, 2013).

We estimated Morisita's similarity index to assess the similarity between the frugivore assemblages recorded at *Ficus* trees and the two control groups in SPADE (Morisita, 1959). This index estimates the similarity of multiple communities from abundance data, taking into account unseen shared species (Chao et al., 2008). It performs better than traditional pair-wise similarity indices as it considers information shared by more than two communities, especially in cases where there are numerous rare species (Chao et al., 2005). We randomly selected 31 surveys from each tree category (all surveyed during the same season) and summed the abundance of each bird species to produce equal sample sizes.

Although we expected some structural relationships in our data, as trees that were close to the primary forest block were also close to each other, we tested the degree of spatial autocorrelation using Moran's *I* coefficient test with arbitrary distance classes and a Bonferroni correction in R (Diniz-Filho et al., 2003; Package APE: Paradis, 2014). We ran the test for frugivore abundance, richness, and functional dispersion in the 122 *Ficus* trees.

To identify the factors that influence frugivore assemblage composition in isolated *Ficus* trees, we used an information-theoretic approach to test the effect of distance from the nearest protected area, land-use intensity, tree size, fruit size, and season on frugivore richness, abundance, and functional dispersion. Distance to the nearest protected area was selected over distance to the nearest forest of any quality as it demonstrated a better fit with the response variables in initial analyses (Supporting information C in Section 4.10). Land-use intensity, fruit size, and season were categorical predictor variables. To determine "season", the months *Ficus* trees were surveyed were divided into winter (November–March), early monsoon (April–July), and late monsoon (August–October), to reflect the passage of migrants observed in the study area during field data collection. A generalised linear model (GLM) with a log-link function and Poisson error distribution was run for richness and abundance data, while the functional dispersion analyses used an identity link function with Gaussian error (Burnham & Anderson, 2002). Combinations of the five predictor variables and their second-order interaction terms were evaluated using a second-order criterion (AIC_c) to select the best model notwithstanding the small ratio between the number of input variables and observations (Anderson et al., 2001). The model with the lowest AIC_c score was taken to signify the best performing model, although all models within ΔAIC_c of the best performing model were considered to have similar support (Burnham & Anderson, 2002).

To investigate the relationship between frugivore abundance and distance from the nearest primary forest we ran a boundary analysis with a randomly distributed null model. This test can indicate whether a particular quadrant in ecological space is significantly under- or over-populated than expected by chance, taking into account both the number of data points that fall within a predetermined quadrant, and the distances of each of those points to the boundary of that quadrant. We ran 1,000 iterations of an asymmetrically distributed left triangle in the upper right quadrant in the EcoSim software package (Gotelli & Entsminger, 2000).

We also tested the significance of distance in frugivore abundance patterns by conducting a quantile regression (Koenker, 2005). This technique fits regression curves to different parts of the response variable's distribution, and is particularly useful in situations with heterogeneous variance (Cade & Noon, 2003). We plotted curves for seven quantiles (0.05, 0.1, 0.25, 0.5, 0.75, 0.9, and 0.95) using the R package quantreg (Koenker, 2013). We identified significant differences by plotting the mean slope against those for each quantile, where quantiles with 95% confidence intervals that did not overlap with the mean slope were taken to be significantly different.

To investigate the response of individual frugivore species to the four environmental predictors (distance from nearest primary forest, tree size, fruit size, and land-use intensity) we conducted a Canonical Correspondence Analysis in R using Package Vegan (Legendre & Legendre, 2012; Oksanen et al., 2013). We did not include "season" as this cannot be affected by conservation actions. By performing a weighted linear regression on the constraining predictor variables, this method is useful for testing the *a priori* hypotheses of important constraints generated through extensive field observations during data collection.

To assess whether trees supported higher or lower levels of functional diversity than would be expected by chance, we compared observed functional dispersion patterns with those of null model communities generated using the sum-of-squares reduction method ("quasi-swap", Miklós & Podani, 2004). With species richness held constant for each tree, and frugivore incidence held constant for each species, the model randomly simulated null communities from the species pool (the total number of frugivores recorded in the study; Gotelli, 2001; de Bello, 2012). We ran 10,000 simulations and tested whether the observed functional dispersion of each *Ficus* tree was significantly higher or lower than the null distribution at p=0.05, using Package Vegan in R (Oksanen et al., 2013; R Core Team, 2014). We used a paired two-tailed Wilcoxon signed-rank test to identify significant differences between the observed and expected FDis scores (Ding et al., 2013).

4.5 Results

In 122 surveys of fruiting *Ficus* trees (totalling 366 hours of observation) we recorded 98 bird species, 33 of which were frugivores that were observed eating *Ficus* fruit. Three species, the Oriental White-eye (*Zosterops palpebrosus*), Yellow-vented Flowerpecker (*Dicaeum chrysorrheum*), and Scarlet-backed Flowerpecker (*D. cruentatum*) are described as being at least partially frugivorous (del Hoyo et al., 2008), but were not observed eating figs during our surveys. In total, 30,084 (mean=246.59) individual frugivores were recorded visiting *Ficus* trees during the surveys. In addition, 33 fruit trees and 31 large trees were surveyed, which produced 460 (mean=13.94) and 224 (mean=7.23) individual frugivore records respectively.

The incidence function results demonstrated that the highest proportion of species recorded in *Ficus* trees were forest-dependent frugivores (15/33, 45.46%), followed by matrix-specialists (10/33, 30.30%), and habitat-generalists (8/33, 24.24%) (Supporting information A in Section 4.10 illustrates the incidence functions of all 33 species).

The comparison of *Ficus* trees versus other fruit trees and large trees indicated that *Ficus* trees have significantly richer frugivore assemblages, with, on average, a higher abundance of frugivores (Table 4.2). Specifically, the number of bird species differed between the groups ($F_{2,183}$=200.05, $p<0.001$, ω^2=0.47), with significant differences between *Ficus* trees and the other two categories ($p<0.001$), and no difference between fruit trees and large trees (p=0.43). The mean abundance of all birds in the three groups was significantly different (Welch's $F_{2,50}$=219.59, $p<0.001$, ω^2=0.87). The Games-Howell test revealed that *Ficus* trees had higher frugivore abundance than the other groups ($p<0.001$ in both cases), while other fruit trees and large trees were not significantly different (p=0.1). The same pattern was found for functional diversity, with *Ficus* trees having significantly higher functional dispersion than fruit or large trees (H_2=43.29, $p<0.001$; *Ficus* vs fruit: U=898, $p<0.001$, mean *Ficus* rank=87.14, mean fruit rank=44.21; *Ficus* vs large: U=724, $p<0.001$, mean *Ficus* rank=86.57, mean fruit rank=39.35), again with no statistical difference between the latter two categories (U=433, p=0.28). However, the Shannon index results suggested that the composition of avian assemblages in *Ficus* trees was less even compared to fruit trees, which in turn were less even than large trees.

Table 4.2: Differences between species richness, abundance, and functional diversity parameters across the three tree categories. Values are means ± standard error. Different superscript letters denote significantly different means. Estimated richness is the "Chao 1 bias corrected" estimator, which only uses the number of singletons and doubletons to estimate the number of undetected species (Chao, 2005). The Shannon index scores are derived from the Chao and Shen (2003) revised algorithm. Observed richness is the average number of frugivorous bird species recorded in the surveys of each tree category. Abundance is the average number of individual frugivores recorded in the surveys of each tree category. FDis is a multidimensional index of the mean distance of an individual species to the centroid of all species in the community (Laliberté & Legendre, 2010). Estimated richness and Shannon scores were considered to be significantly different where 95% confidence intervals did not overlap. For observed richness and abundance, different superscript letters denote significantly different means at $p<0.05$ for species richness and abundance using ANOVA with a Games-Howell post hoc test. For FDis, differences were tested using a Kruskal-Wallis test with Mann-Whitney follow-up procedures, using a Bonferroni correction of $p<0.0167$.

Parameter	***Ficus***	**Fruit**	**Large**
Estimated richness	26.00 ± 4.60^{a}	17.00 ± 0.30^{b}	18.20 ± 0.50^{b}
Shannon index	2.07 ± 0.02^{a}	2.22 ± 0.04^{b}	2.27 ± 0.07^{c}
Observed richness	13.02 ± 0.27^{a}	3.97 ± 0.58^{b}	2.97 ± 0.56^{b}
Abundance	246.59 ± 18.39^{a}	13.94 ± 3.27^{b}	7.23 ± 1.85^{b}
FDis	0.88 ± 0.02^{a}	0.64 ± 0.10^{b}	0.46 ± 0.10^{b}

The Morisita similarity estimates of the abundance data indicate a moderately high level of similarity between the frugivore communities recorded in fruit and large trees. However, *Ficus* trees had very low estimated similarity compared to these two groups (Table 4.3).

Table 4.3: Morisita similarity matrix of multiple communities (Chao et al., 2008), estimated from the abundance of frugivores recorded in three tree types (n=31 surveys for each group). Values are Morisita similarity estimate ± standard error, with 200 bootstrap replications. Values closer to 1.0 indicate higher community similarity. Average pairwise comparison=0.52.

	Ficus	**Fruit**	**Large**
Ficus	1.0	0.32±0.01	0.31±0.02
Fruit		1.0	0.94±0.02
Large			1.0

The Moran's *I* results indicated that there was no spatial autocorrelation at any scale for frugivore richness, with no consistent trend to the *I* coefficients, and no *p* values <0.05. Frugivore abundance and functional dispersion displayed similar patterns to each other, with significant clustering at the largest spatial scales, before a non-significant 'trend' of slight dispersion at medium and small spatial scales.

In testing the determinants of frugivore richness at isolated *Ficus* trees, the best performing GLM included distance, tree size, and season as predictor variables (Table 4.4). Specifically, frugivore richness increased as tree size increased, but decreased as the distance between the *Ficus* tree and the nearest protected area increased (Table 4.5). The season also affected species richness, with significantly more species present in *Ficus* trees in the early monsoon compared to winter. Frugivore abundance also fluctuated seasonally, with more frugivores present in the early and especially the late monsoon. Again, increasing distance caused a decrease in abundance, as did medium and high land-use intensities compared to low land-use intensity, and large fruit size compared to small. Increasing tree size also increased the number of frugivores visiting isolated *Ficus* trees. Reflecting the fluctuations in species richness and abundance with season, FDis varied seasonally, and also decreased as distance increased.

Table 4.4: Generalised Linear Model results with Akaike Information Criterion scores for finite samples for variables affecting three measures of frugivore assemblage at isolated *Ficus* trees in Assam, India. "Richness" and "Abundance" were modeled using a log-link model with Poisson error distribution. "FDis" reports the AIC_c results for frugivore functional dispersion, using an identity link function. Data are derived from 122 frugivore surveys in Golaghat District, Assam, India. Model input abbreviations are L=land-use intensity; D=distance from nearest forest; S=tree size; F=fruit size; M=season. M*S is an interaction term between season and tree size. Other denotations: K=parameters in the model; MML=Maximum Log-likelihood; AIC_c=second-order Akaike Information Criterion score for finite samples; ΔAIC_c=the difference in AIC_c scores compared to the "best" performing model; w_i=Akaike weight, the normalised model likelihoods (Burnham & Anderson, 2004). All models within 2 ΔAIC_c are presented for each response variable, or if fewer than three models had a ΔAIC_c of less than two, the three models with the most parsimonious fits are presented. In each case the "best" performing model is highlighted in bold font.

Variable	Model	K	MML	AIC_c	ΔAIC_c	w_i
Richness	**S, M, D**	**3**	**-299.51**	**609.54**	**0**	**0.46**
	S, M	2	-301.69	611.72	2.18	0.16
	D, M	2	-301.96	612.27	2.73	0.12
Abundance	**D, S, L, F, M**	**5**	**-5233.41**	**10482.10**	**0**	**1.00**
	D, S, L, F	4	-5415.19	10843.11	361.01	0.00
	D, L, M*S	3	-5425.34	10865.66	383.56	0.00
FDis	**D, M**	**2**	**53.70**	**-96.88**	**0**	**0.24**
	M	1	52.46	-96.59	0.29	0.20
	L, M	2	54.14	-95.55	1.33	0.12
	M, F	2	52.84	-95.15	1.73	0.10

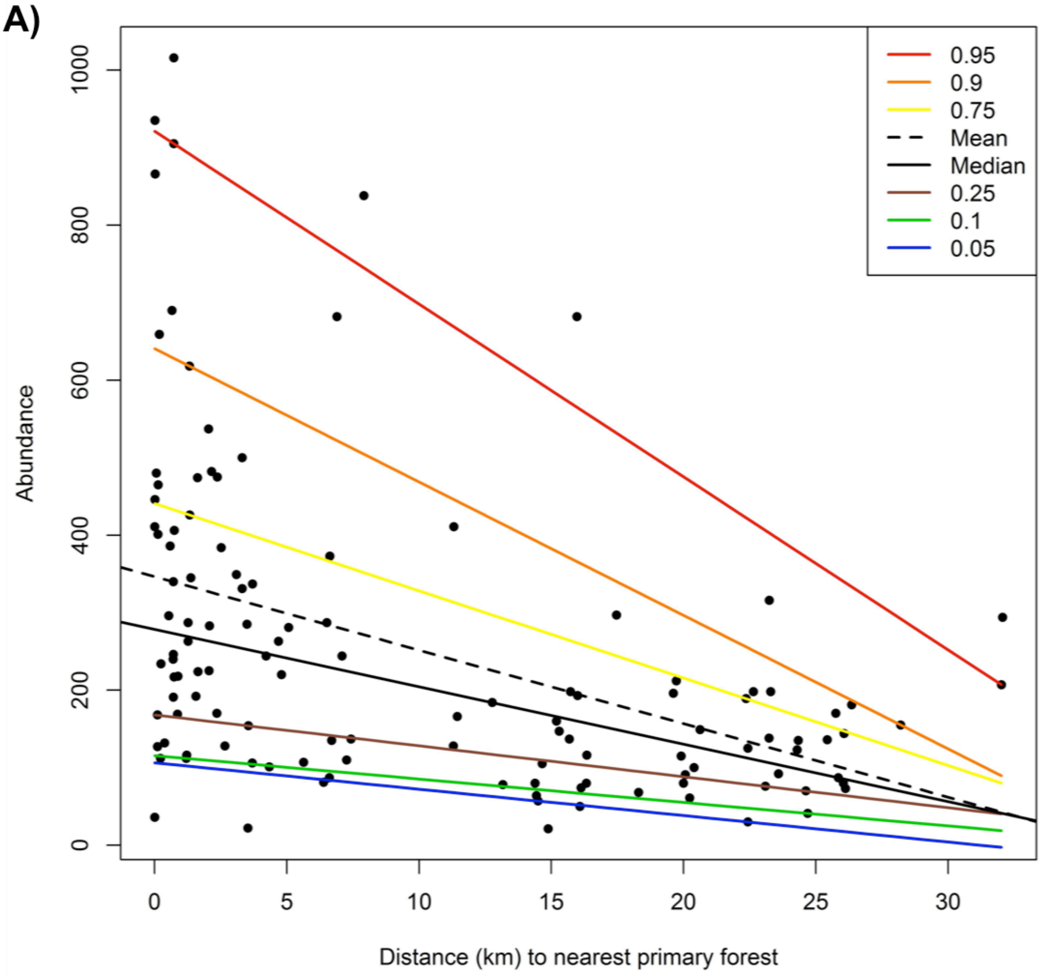
Table 4.5: Correlation coefficients for the parameters retained in the "best" performing models (see Table 4.4) for frugivores in isolated *Ficus* trees. "Richness" reports frugivore richness, "Abundance" reports frugivore abundance, and "FDis" reports frugivore functional dispersion from isolated *Ficus* trees in Assam, India. The table is continued overleaf, where the FDis section is presented.

Variable	**Parameter**	**B (estimate)±S.E.**	**Wald chi-square**	***p***
Richness	Intercept	2.52±0.05	2250.54	<0.001
	Season (late monsoon)	0.01±0.08	0.01	0.94
	Season (early monsoon)	0.22±0.06	13.63	<0.001
	Season (winter)	-	-	-
	Tree size	0.06±0.02	5.03	<0.05
	Distance	-0.01±0.003	4.34	<0.05
Abundance	Intercept	5.77±0.01	198404.11	<0.001
	Fruit size (large)	-0.22±0.01	297.02	<0.001
	Fruit size (small)	-	-	-
	Distance	-0.03±0.001	962.31	<0.001
	Land-use intensity (high)	-0.10±0.01	55.33	<0.001
	Land-use intensity (medium)	-0.69±0.02	673.07	<0.001
	Land-use intensity (low)	-	-	-
	Season (late monsoon)	0.29±0.02	353.86	<0.001
	Season (early monsoon)	0.08±0.01	31.93	<0.001
	Season (winter)	-	-	-
	Tree size	0.24±0.01	2018.32	<0.001

Variable	Parameter	B (estimate)±S.E.	Wald chi-square	*p*
FDis	Intercept	0.91±0.03	964.37	<0.001
	Season (late monsoon)	-0.11±0.04	6.76	<0.01
	Season (early monsoon)	0.04±0.03	1.65	0.20
	Season (winter)	-	-	-
	Distance	-0.003±0.002	2.50	0.11

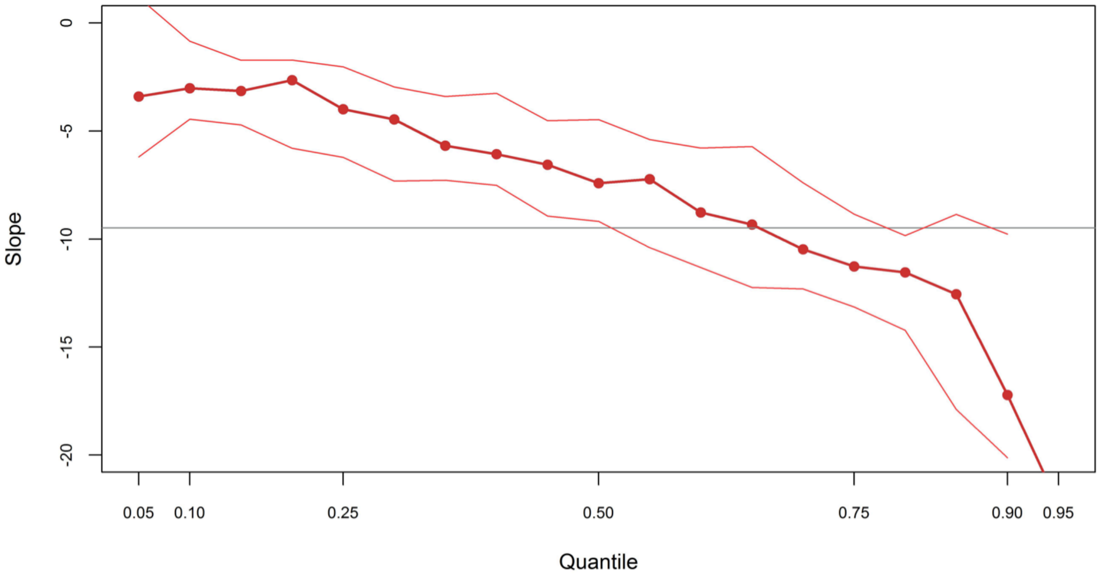
The further examination of changes in frugivore abundance with distance indicated that significantly fewer frugivores occurred in *Ficus* trees at long distances than would be expected by chance (boundary test: number of points, observed<expected, $p<0.05$; sum of squares, observed<expected, $p<0.01$). The quantile regression indicated that there was heterogeneous variance in frugivore abundance (Figure 4.4a). The lower and median quantiles (0.05, 0.1, 0.25, and 0.5) were significantly flatter than the mean slope (Figure 4.4b), indicating that some frugivores were present in similar numbers irrespective of distance. However, the higher quantiles (0.9, 0.95) were also significant, reflecting the marked decrease in occurrence of the highest frugivore abundances as distance increased. These two findings correspond with the incidence function results, where generalists were present at all trees across all distances, while forest-dependent species (which in the case of the *Treron* pigeons are large flocking species), declined sharply with distance.

A)



0.95
0.9
0.75
Mean
Median
0.25
0.1
0.05
Abundance
0
200
400
600
800
1000
0
5
10
15
20
25
30
Distance (km) to nearest primary forest

B)



Slope
0
-5
-10
-15
-20
0.05
0.10
0.25
0.50
0.75
0.90
0.95
Quantile

Figure 4.4: Quantile regression estimation of changes in frugivore abundance in isolated *Ficus* trees as a function of distance from the nearest primary forest in rural Assam, India. A) is a scatter plot of n=122 isolated *Ficus* trees with 0.05, 0.1, 0.25, 0.5 (median), 0.75, 0.9, and 0.95 quantile and the least squares mean regression estimates. B) shows the sample estimates for the slope (thick red line) with thin red lines connecting the endpoints of the 95% confidence intervals. The grey line represents the mean slope. The figures were constructed using the R package GGplot2 (Wickham, 2009).

The null model results suggested that isolated *Ficus* trees did not have higher or lower FDis than expected by chance (with species numbers held constant) ($Z=-1.12$, $p=0.27$). Only one of the 122 assemblages had values significantly different from random (0.82%), which had a lower expected mean than observed FDis score. Furthermore, observed functional dispersion declined monotonically, and did not differ from the expected functional dispersion at low or high species richness (Figure 4.5), refuting the notion that functionally unique or functionally redundant species may have been lost first through structured turnover.

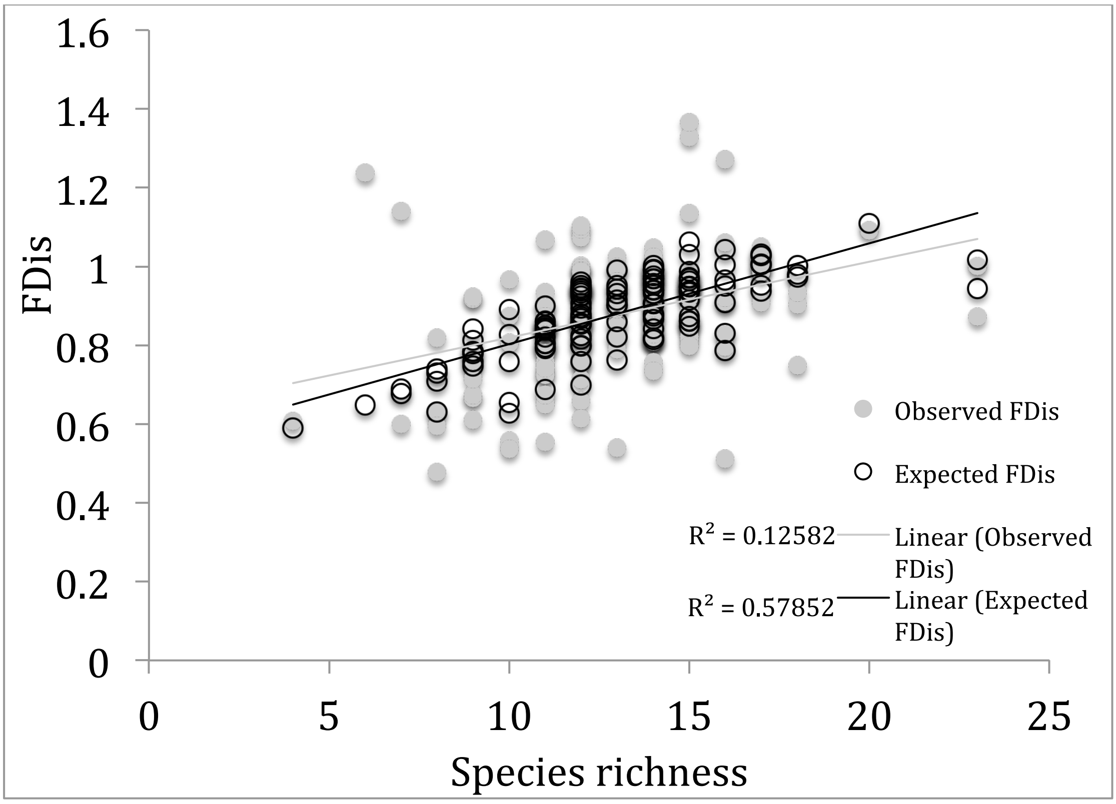


Figure 4.5: Scatter plot of observed versus expected functional dispersion for frugivorous birds in isolated *Ficus* trees. The sample size was 122 isolated *Ficus* trees in a human-modified landscape in Assam, India. Trend lines are linear regressions for both observed FDis (grey line) and expected FDis (black line). Expected FDis scores are the mean of 10,000 iterations of a quasi-swap null model, where row and column totals were held constant.

The Canonical Correspondence Analysis illustrated three important trends in species composition on isolated *Ficus* trees (Figure 4.6). First, it corroborated the incidence function analysis in highlighting the importance of distance in structuring the community. Forest-dependent species were negatively related to distance, with generalists showing no strong relationship, and matrix-specialists displaying a positive relationship. Tree size was also important, particularly for the *Treron* fruit doves, which form large flocks and so seem to prefer larger trees, which would theoretically provide a larger food resource. Interestingly, the largest species in the assemblage, the Great Indian Hornbill (*Buceros bicornis*), was not strongly associated with tree size. Few species associated with land-use intensity, although the Great Myna (*Acridotheres grandis*), which is an open-habitat, agricultural specialist, did load strongly on this axis. The third trend was for certain large-gaped species to associate with large *Ficus* fruit sizes (in particular, the Green Imperial Pigeon, *Ducula aenea*, and Red-breasted Parakeet, *Psittacula alexandri*).

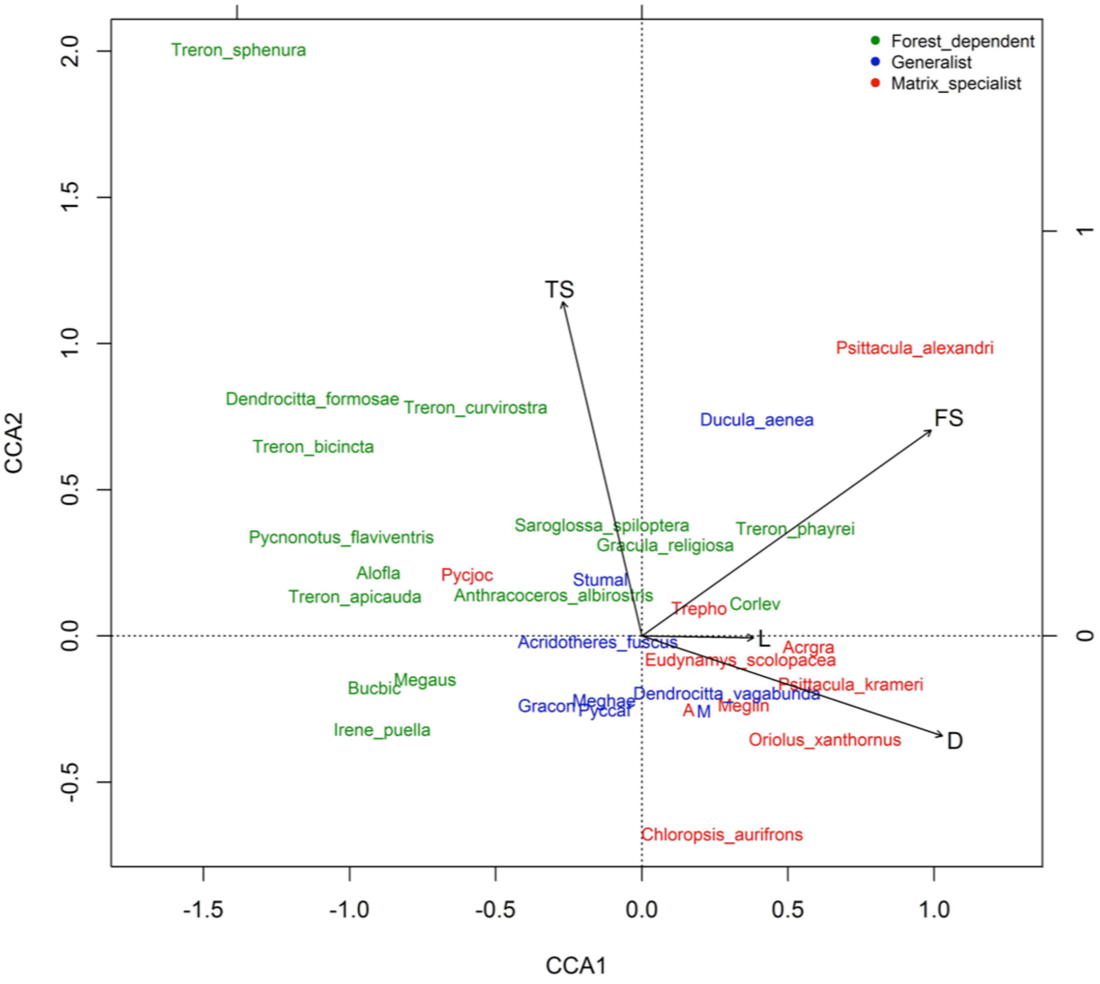


Figure 4.6: Canonical correspondence analysis showing the relationships between the abundance of individual frugivorous species and constrained environmental parameters. The direction of influence of the environmental parameters is indicated by the solid black lines, and annotations are: TS= tree size, FS= fruit size, L= land-use intensity, D= distance from nearest primary forest. Species names are colour coded according to classifications of habitat preference drawn from the literature. Common names are provided in Supporting information A, Section 4.10. Some species names are abbreviated to aid interpretation. They are: Alofla= *Alophoixus flaveolus*, Pycjoc= *Pycnonotus jocosus*, Bucbic= *Buceros bicornis*, Megaus= *Megalaima australis*, Stumal= *Sturnia malabarica*, Gracon= *Gracupica contra*, Meghae= *Megalaima haemacephala*, Pyccar= *Pycnonotus cafer*, Trepho= *Treron phoenicoptera*, Corlev= *Corvus levaillantii*, A= *Acridotheres tristis*, M= *Megalaima asiatica*, Meglin= *Megalaima lineata*, Acrgra= *Acridotheres grandis*.

4.6 Discussion

The limited scope of protected areas, combined with the extent of agricultural habitats across the world's tropics, makes it critically important to assess the capacity of human-modified landscapes for biodiversity conservation (Luck & Daily, 2003). We found that frugivorous birds interact with isolated *Ficus* trees independently of protected areas, although the scale of this interaction was highest at the forest edge. Overall, our results indicate that: 1) isolated *Ficus* trees are very important for avian frugivores in modified landscapes; 2) *Ficus* trees can conserve a large proportion of ecological function at such long distances that the avifaunas must survive independent of protected areas; 3) however, *Ficus* trees are no substitute for protected areas when it comes to conserving forest assemblages.

The importance of *Ficus* trees for forest frugivores is well established (Terborgh, 1986; Shanahan et al., 2001; Walker, 2007). However, the importance of isolated *Ficus* trees in modified habitats is little studied, and their potential role as micro-sites in matrix conservation is poorly understood (Eshiamwata et al., 2006; Caughlin et al., 2012). Here we found that they held richer frugivore assemblages, with higher abundance, than other isolated trees. The assemblages recorded in *Ficus* trees also differed in species composition from other isolated trees, indicating that they may support species that otherwise would not have adequate food resources in modified landscapes. On the other hand, the Shannon index results suggested that avian assemblages in *Ficus* trees had the lowest species evenness, while large trees had the highest. These results may reflect the close relationship between fruiting *Ficus* trees and a handful of frugivores that specialise in the fruit, such as the Asian Koel (*Eudynamys scolopacea*) and *Megalaima* barbets, which were rarely recorded in other tree types. Alternatively, the Shannon scores may be linked to the flocking behaviour of some species that were regularly recorded in *Ficus* trees, for example the Yellow-footed Green Pigeon (*Treron phoenicoptera*). The occurrence of this species in large flocks would have distorted the relative abundances of *Ficus* communities relative to the other tree types, which were usually visited by small numbers of similar subsets of species.

The importance of isolated *Ficus* trees to frugivores is also indicated by the consistency of *Ficus*–frugivore interactions: 40% of species were recorded visiting more than half of the total trees surveyed. This is a similar figure to Luck and Daily's (2003) results from isolated *Miconia* trees in Costa Rica, where 43% visited more than half of the 40 trees surveyed. The number of individual birds recorded in many of the surveys was also impressive, with a high of 1,010 frugivores recorded landing in one tree during a three-hour survey, which may be the highest published number of birds recorded feeding in a single tree. These observations provide evidence that conserving isolated trees can support bird populations in modified landscapes, offering the chance to significantly improve seed dispersal and ecological connectivity (Fischer & Lindenmayer, 2002; Sekercioglu, 2006). Furthermore, our comparisons may provide useful guidance for practitioners and policy-makers setting priorities for matrix conservation, as isolated *Ficus* trees were more attractive to frugivores in this landscape than other tree types.

Further guidance can be gleaned from our regression results, which indicated that the characteristics of isolated *Ficus* trees had a major impact on the number of frugivores they held. All sites had similar compositions and numbers of habitat-generalists (for example, *P. cafer* was recorded at 119 of the 122 surveys, *A. tristis* at 118, and *M. haemacephala* at 113, with mean abundances±standard error of 25.89±2.55, 19.57±1.70, and 11.38±1.35 respectively). However, larger trees, trees with lower surrounding land-use intensity, and trees closer to the forest, had higher frugivore abundances. Although *Ficus*-specific, the higher abundance of birds at trees with smaller fruit suggests that this fruit size may be easier to handle than larger fruit sizes. Both the boundary test and quantile regression indicated a significant relationship between the highest frugivore abundances and distance. In fact, the three trees with the highest abundance were all located within 1 km of the nearest forest, and eight of the 11 trees with more than 500 frugivores were located within 2 km. This suggests that local forests were able to support higher numbers of frugivores, which were attracted to these food resources, or that some flocking species were associated with forests, and were reluctant to visit *Ficus* trees at any considerable distance from the forest edge. Our incidence functions indicate that they were indeed reluctant to fly long distances from the forest, which supports the results of other studies on avian responses to landscape modification (Marsden et al., 2006; Thiollay, 2006; Tscharntke et al., 2008). If conserving the composition of frugivores in a landscape is a conservation priority, the near complete absence of forest-dependent species at *Ficus* trees over 1 km from the forest indicates that isolated *Ficus* trees are no substitute for protected areas (Callicott et al., 1999; Douglas et al., 2013; Hulme et al., 2013).

In a local context, the prominence of “season” in the GLM results is worth discussing. Isolated *Ficus* trees recorded higher species richness and abundance during the early and late monsoon compared to winter, with season accounting for a particularly high peak in frugivore abundances in the late monsoon. There are two possible explanations for this pattern: 1) fruit resources in protected areas may be seasonally scarce at particular times of year, and so frugivores venture further across human-modified landscapes to take advantage of isolated *Ficus* tree crops, which are available throughout the year; or 2) there is a large influx of migratory frugivores in the early and especially the late monsoon, which are absent from the study area in winter. Although no local fruit availability research has been conducted, other tropical and subtropical studies report that fruit availability generally peaks during the monsoon season (Lambert & Marshall, 1991; Kinnaird et al., 1996), which makes the former hypothesis seem unlikely. Furthermore, at least one species, the Spot-winged Starling (*Saroglossa spiloptera*), is a known longitudinal migrant, while another, the Asian Koel (*Eudynamys scolopacea*), was conspicuously absent during the winter survey, despite being recorded in 79.01% of surveys during the monsoon months. We recorded particularly high numbers of Spot-winged Starlings during the late monsoon, with flock sizes reaching 110 birds in individual *Ficus* trees, and so expect that the presence of migratory species is responsible for the identification of season as an important predictor variable.

From a functional perspective, we also found declines in functional diversity with distance. Mean functional dispersion scores were 7.13% lower in trees over 25 km from the nearest forest compared to trees within 1 km. The abundance of frugivores with the largest gape widths also decreased markedly, suggesting that, along with declines in the number of seeds removed (as implied by the drop in the highest frugivore abundances), the range of seed sizes being dispersed may also fall with distance. However, although these results are concerning, functional diversity did not crash, as demonstrated by the most distant trees recording average scores of 92.87% of those on the forest edge. In this human-modified landscape at least, the majority of functional diversity can be conserved in the absence of local protected areas, and despite the loss of most forest-dependent species in matrix habitats.

The limited "sphere of influence" of protected areas in modified landscapes is reflected in our frugivore richness results. We found only a minor distance effect, which supports Eshiamwata et al.'s findings from isolated *Ficus* trees in Kenyan farmland, albeit at different spatial scales (Eshiamwata et al., 2006). We feel the best explanation for the very small distance effect may lie in Sekercioglu et al.'s study of bird persistence in the Costa Rican agricultural landscape (Sekercioglu et al., 2007). They found that birds reside in, rather than commute to, agricultural areas, making use in particular of isolated trees. In our study, the majority of species preferred and resided in modified habitats (as demonstrated by the incidence functions), and so richness would not be expected to decline with distance.

Close to the forest edge, another trend was apparent. Although there was no significant change in richness, there was some evidence of turnover in assemblage composition. Several forest-dependent species were recorded at *Ficus* trees a few hundred metres from the forest, but were seemingly replaced by morphologically very similar species at greater distances. These include *M. australis* replaced by *M. haemacephala*, *P. flaviventris* replaced by *P. cafer*, and *D. formosae* replaced by *D. vagabunda*. The range of specific responses to distance, along with tree size, land-use intensity, and fruit size, was further illustrated in Figure 4.6. The inter-species variation provides support for Manning et al.'s continua-*Umwelt* view of variegated landscapes (Manning et al., 2004). This approach recognises the different responses of organisms to habitat disturbance, with species-specific environmental gradients and habitat preferences. In application to our dataset, it enables us to move beyond traditional forest-specialist versus matrix-generalist categorisations (Matthews et al., 2014), and identify the specific variables that individual species are responding to in modified landscapes. Furthermore, while we accept the notion of species-specific responses, grouping these species by their associations with particular variables also allows us to build conservation recommendations for targeted groups in modified landscapes.

In their recommendations for conserving seed dispersal functions in human-modified landscapes, McConkey et al. (2012) suggest that functionally unique dispersers should be the focus of conservation efforts, which should aim to maintain their ecological function rather than just their minimum viable populations. In our study system, that would mean focusing conservation efforts on the hornbills, and in particular, the Great Indian Hornbill (*B. bicornis*) (Kitamura, 2011). This would involve conserving large tracts of intact forest, as this species requires large foraging ranges (Poonswad & Tsuji, 1994; Kannan & James, 1999; Datta & Rawat, 2003; Raman & Mudappa, 2003), and only ventured further than 250 m into the matrix to feed at our isolated *Ficus* trees on one occasion. Still, in this scenario, the hornbill's minimum viable population would be conserved, but its ecological function would be limited to those forested areas, and not improve the transfer of seeds across human-modified spaces. This species is not alone in its reluctance to cross human-modified habitats, as many large-bodied frugivores, which are often classified as functionally unique, are rare matrix visitors (Sekercioglu et al., 2002; Moran et al., 2004; Vidal et al., 2013). Instead, the species recorded in isolated *Ficus* trees in our modified landscape were not clearly functionally unique, yet still supported a wide range of ecological function, even without the presence of the Great Indian Hornbill. While the loss of large-seed dispersal capacity may have undesirable ecological consequences (da Silva & Tabarelli, 2000; Moran et al., 2004), basic seed dispersal appears to continue to function well across this network of isolated *Ficus* trees (Cottee-Jones et al., *in review*).

The *Ficus* trees in this study are dependent on the role avian frugivores play in dispersing seeds away from the parent tree, reducing mortality and increasing the chance of successful germination (Laman, 1995; Cordeiro & Howe, 2003). As the protected areas in this landscape are believed to be too small to conserve low-density *Ficus* populations in the long term (Mawdsley et al., 1998), the dispersal of *Ficus* seeds into modified habitats is crucial not only for their persistence, but also for the survival of their pollinator fig wasps (Agaonidae) (Compton et al., 2000; Harrison, 2003). If frugivores failed to provide effective seed dispersal services in this system, *Ficus* trees would in all likelihood be lost from the landscape, which would also cause the local co-extinction of the fig wasps (Koh et al., 2004), with a cascade effect on numerous other *Ficus* dependent arthropods (Basset et al., 1997; Bain et al., 2013). The conservation of this relationship in disturbed landscapes should therefore be a priority in attempting to avert ecological collapse (Sodhi et al., 2010; Lindenmayer et al., 2013).

4.7 Conclusion

Although human-modified landscapes are receiving greater attention in the literature, most studies focus on the Neotropics, and shade-coffee agrosystems in particular (Komar, 2006; Tscharntke et al., 2008; Mendenhall et al., 2014). Improving our understanding of functional group change in modified landscapes still represents a critical frontier in conservation science, and few studies have considered the matrix as a conduit for seed dispersal (Tscharntke et al., 2008; McConkey et al., 2012). Here, we present the results of the largest study undertaken on isolated trees, and one of the first to study *Ficus* trees beyond the forests. We demonstrate that *Ficus* trees can be important tools in matrix conservation strategies, and may warrant preferential conservation ahead of other isolated trees. Given that *Ficus* trees are commonly found in many modified landscapes around the world's tropics, our results may be applicable on a very broad geographical scale. Isolated *Ficus* trees can conserve frugivorous ecological function at such great distances from forests that the system is likely to be independent of protected areas, and *Ficus* trees hold more frugivorous species and individuals than other isolated trees. However, the quantity of seeds removed may decline with distance as the abundance of frugivores falls, and forest-dependent species rarely venture more than a few hundred meters to feed in isolated *Ficus* trees. Therefore, while isolated *Ficus* trees may be among the best micro-sites for matrix conservation, they are still no substitute for protected areas in conserving forest-dependent bird assemblages.

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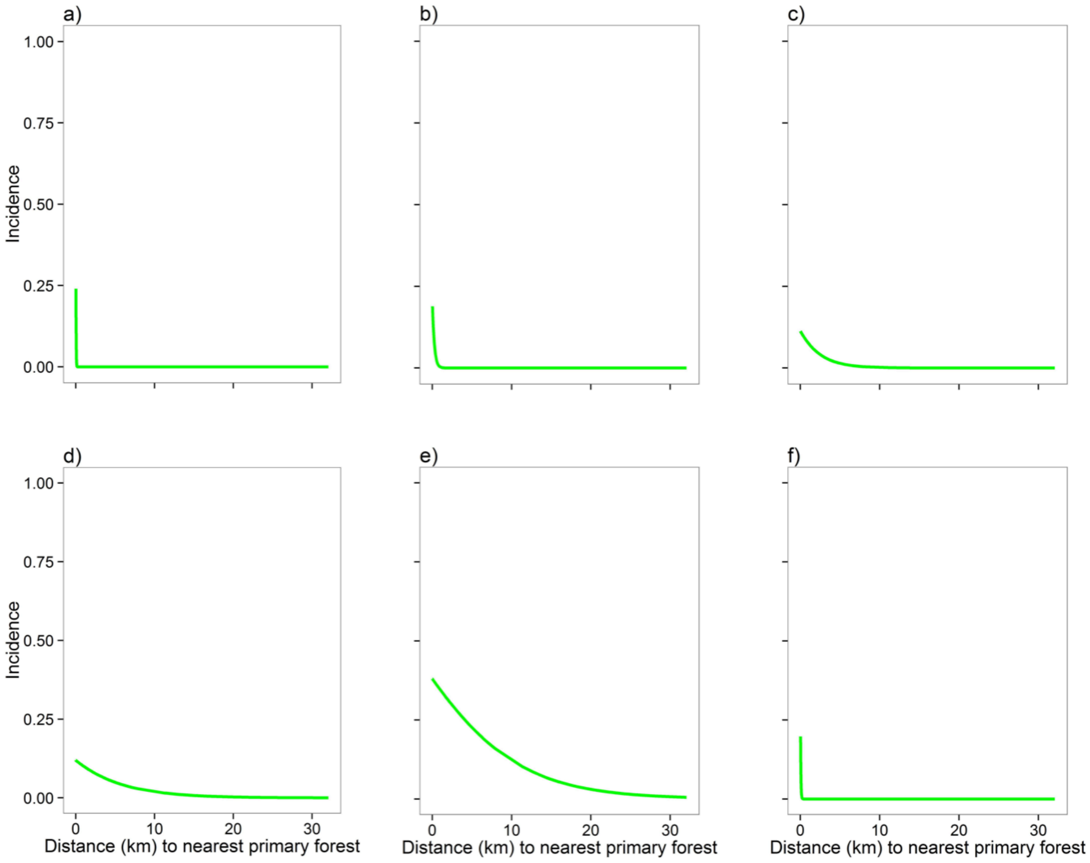
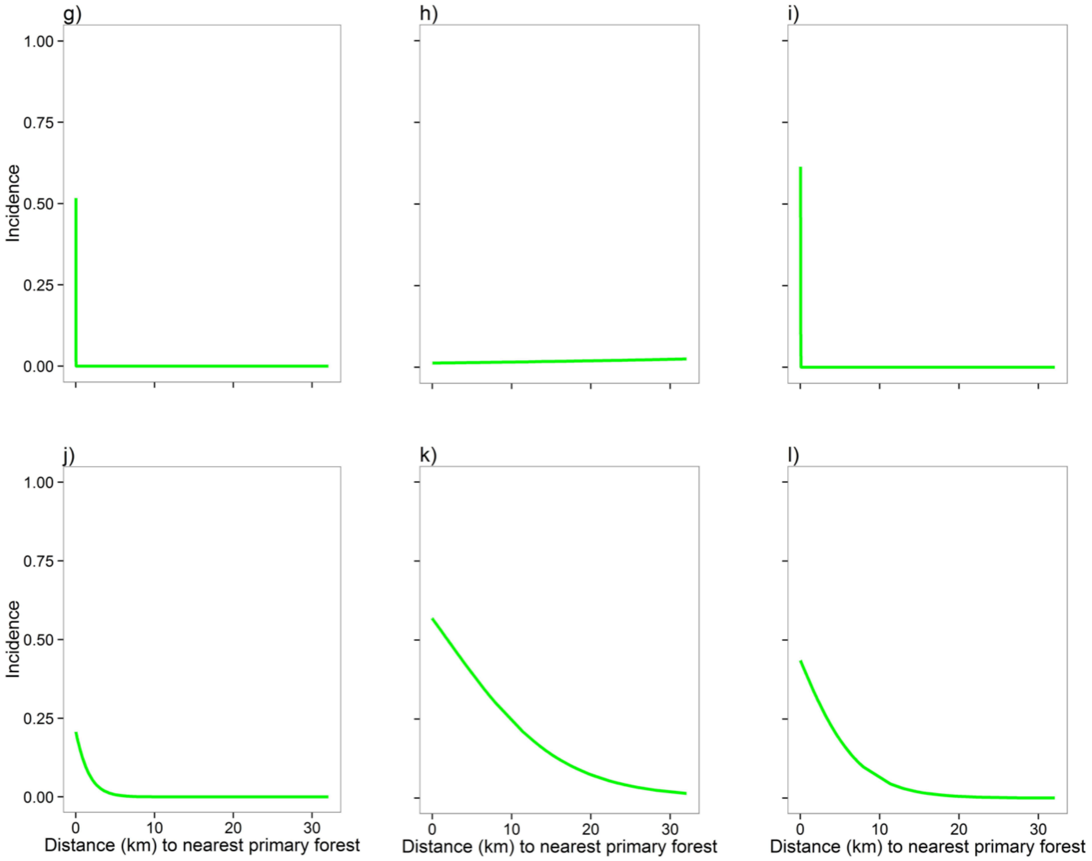
4.10 Supporting information

Supporting information A

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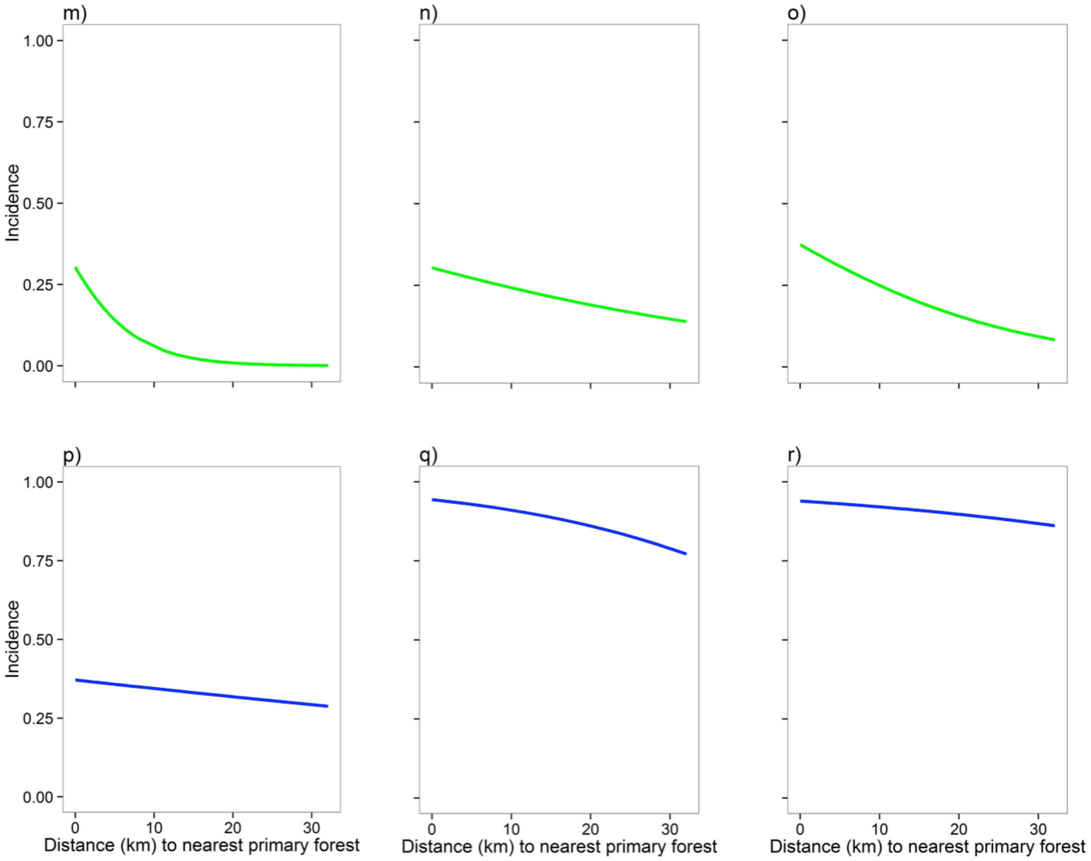
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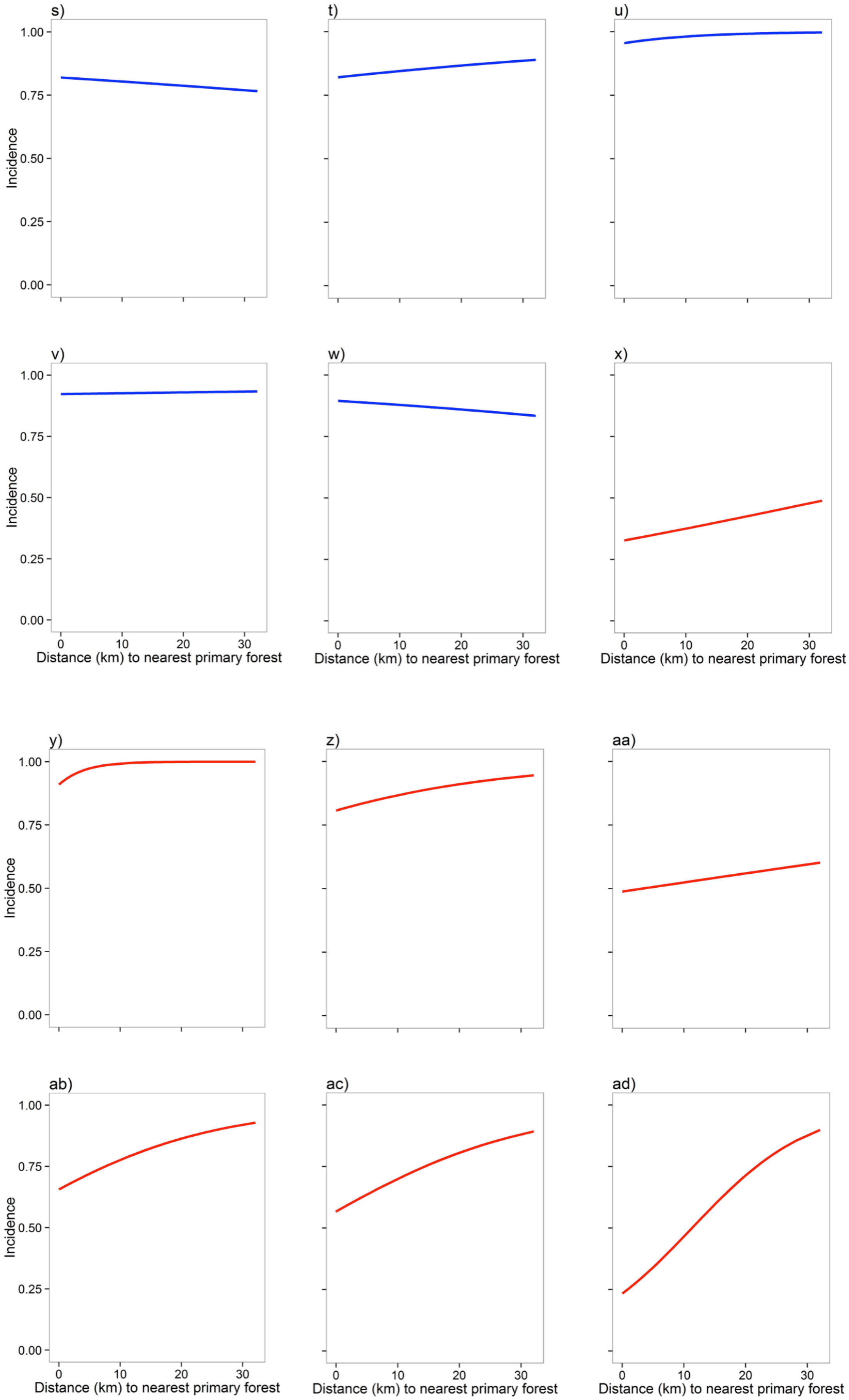
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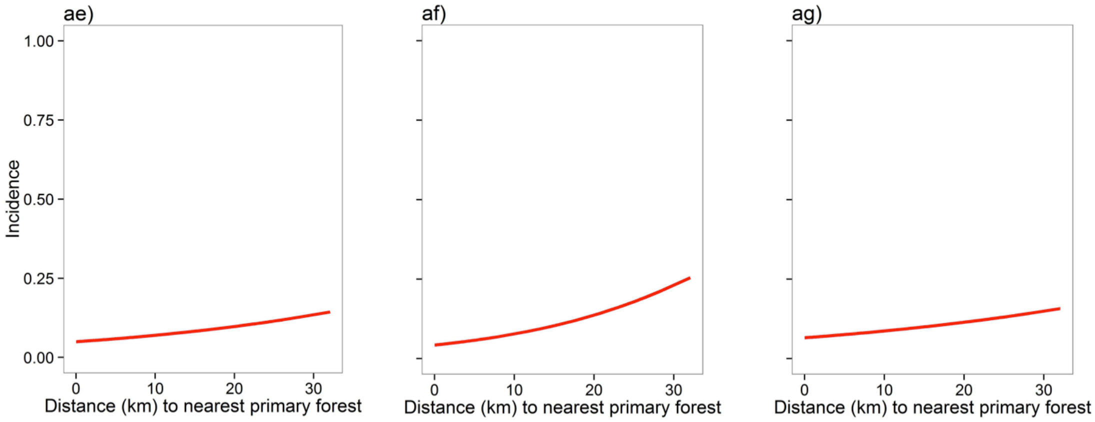

Figure 4.7: Incidence functions for all 33 frugivore species recorded in the study. Green curves represent forest-dependent species, blue represent habitat-generalists, and red represent matrix-specialists. The curves are the predicted probability of occurrence, generated through a logistic regression model with distance from the nearest primary forest as the predictor variable for each species' presence/absence data at 122 isolated *Ficus* trees. Species are a) Wedge-tailed Green Pigeon *Treron sphenura*; b) Orange-breasted Green Pigeon *Treron bicinctus*; c) Thick-billed Green Pigeon *Treron curvirostra*; d) Pin-tailed Green Pigeon *Treron apicauda*; e) Ashy-headed Green Pigeon *Treron phayrei*; f) Grey Treepie *Dendrocitta formosae*; g) Black-crested Bulbul *Pycnonotus flaviventris*; h) White-throated Bulbul *Alophoixus flaveolus*; i) Asian Fairy Bluebird *Irene puella*; j) Great Indian Hornbill *Buceros bicornis* k) Blue-eared Barbet *Megalaima australis*; l) Oriental Pied Hornbill *Anthracoceros albirostris*; m) Spot-winged Starling *Saroglossa spiloptera*; n) Hill Myna *Gracula religiosa*; o) Eastern Jungle Crow *Corvus levaillantii*; p) Green Imperial Pigeon *Ducula aenea*; q) Chestnut-tailed Starling *Sturnus malabarica*; r) Jungle Myna *Acridotheres fuscus*; s) Asian Pied Starling *Gracupica contra*; t) Rufous Treepie *Dendrocitta vagabunda*; u) Red-vented Bulbul *Pycnonotus cafer*; v) Coppersmith Barbet *Megalaima haemacephala*; w) Blue-throated Barbet *Megalaima asiatica*; x) Red-whiskered Bulbul *Pycnonotus jocosus*; y) Common Myna *Acridotheres tristis*; z) Yellow-footed Green Pigeon *Treron phoenicopterus*; aa) Asian Koel *Eudynamys scolopacea*; ab) Lineated Barbet *Megalaima lineata*; ac) Great Myna *Acridotheres grandis*; ad) Black-hooded Oriole *Oriolus xanthornus*; ae) Golden-fronted Leaf-bird *Chloropsis aurifrons*; af) Rose-ringed Parakeet *Psittacula krameri*; ag) Red-breasted Parakeet *Psittacula alexandri*. The figures were constructed using the R package GGplot2 (Wickham, 2009).

Supporting information B

To investigate the effect of area on frugivore richness, abundance, and FDis values in isolated *Ficus* trees, we conducted an additional analysis of these three scores across *Ficus*, fruit, and large trees when controlling for area. We used canopy area as the best proxy for area, and divided richness, abundance, and FDis by canopy area for each tree. After examining the assumptions of normality and heteroscedasticity, the new average values for each tree category were compared using ANOVA with Welch's F and Games-Howell post hoc tests. Means and differences at the $p<0.05$ level of significance are presented in Table 4.6.

Table 4.6: Differences between species richness, abundance, and functional diversity parameters across the three tree categories, controlled by canopy area. Values are means ± standard error. Different superscript letters denote significantly different means. Abundance is the mean number of individual frugivores recorded in each tree per m^2, and presented in tree categories. Observed richness is the mean number of frugivorous bird species recorded in the surveys of each tree per m^2, presented by category. FDis is a multidimensional index of the mean distance of an individual species to the centroid of all species in the community (Laliberté & Legendre, 2010). Different superscript letters denote significantly different means at $p<0.05$ using ANOVA with Welch's F and Games-Howell post hoc tests.

Parameter	***Ficus***	**Fruit**	**Large**
Abundance	0.64 ± 0.05^{a}	0.20 ± 0.04^{b}	0.08 ± 0.03^{c}
Observed richness	0.04 ± 0.002^{a}	0.06 ± 0.01^{b}	0.03 ± 0.01^{a}
FDis	0.003 ± 0.0001^{a}	0.01 ± 0.003^{b}	$0.006 \pm 0.001^{a,c}$

Although this test found that isolated *Ficus* trees still have higher frugivore abundances than the other two tree types when area is controlled, isolated fruit trees had higher richness and FDis/m^2 of canopy area. These results may be explained by the exceptionally large canopy areas that were used to divide *Ficus* richness and FDis scores, which cannot vary as widely as abundance records (as, in the case of richness, there was only a maximum of 33 frugivores in the study). Notwithstanding these findings, we elected to exclude area controlled results from the main analysis as we were more interested in using trees as the unit of study, as this can more directly be influenced by conservation measures. Furthermore, we felt that having a large canopy area was intrinsic to the advantage *Ficus* trees may possess over other species in terms of frugivore conservation, and so controlling for area would constrain our ability to compare the actual conservation value of each tree type.

Supporting information C

To test the adequacy of fit between either distance from isolated *Ficus* trees to the nearest protected area, or to the nearest forest of any quality and frugivore abundance, we conducted a linear regression. We ran a linear regression model for each distance measure in turn, and found that the distance from protected area had a slightly better fit (R^2=0.19) than the distance from the nearest forest of any quality (R^2=0.18). Although the difference was only marginal, we therefore decided to use distance from the nearest protected area as our distance measure throughout the analyses.

CHAPTER 5:

How to conserve insectivorous birds in human-modified tropical landscapes

5.1 Preface

While conducting avifaunal surveys of isolated *Ficus* trees for Chapter 4, it became apparent that many insectivorous birds were also visiting *Ficus* trees. Given the abundance and diversity of invertebrates both observed on *Ficus* trees in Assam, and reported in the literature from several other countries, it was surprising that no study had investigated the importance of *Ficus* trees to insectivores. This chapter seeks to address that oversight.

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The co-author contributions were as follows. Conceived and designed the study: HEWC-J, TPB. Conducted the data collection: HEWC-J. Analysed the data: HEWC-J, TJM. Wrote the paper: HEWC-J, TJM, RJW. Further details of the co-author contributions and their consent to the use of this material in this thesis are provided in Appendix 4.

This chapter has been submitted to Functional Ecology.

5.2 Abstract

The destruction of forest for agricultural expansion has created a vast estate of human-modified land in tropical regions. One group of organisms that are particularly vulnerable to the loss of forest habitat are insectivorous birds. Despite this, few conservation strategies have been identified for this group in human-modified landscapes. Here, we survey the use of 104 isolated trees by insectivorous birds in rural Assam, India. We found that isolated *Ficus* trees hold assemblages with particularly high insectivore richness and abundance when compared to other isolated fruit and large trees. They had higher functional diversity scores than expected by null simulations, although overall tree size emerged as the best predictor of functional diversity in human-modified landscapes. We argue that, where present, *Ficus* trees should be actively conserved in human-modified landscapes to maintain the composition of insectivore communities in a "*Ficus* first" strategy. More widely, we demonstrate that the conservation of large trees in human-modified landscapes may play an important role in maintaining ecological function beyond the forest edge.

Keywords Assam, conservation beyond protected areas, conservation management, ecological function, *Ficus*, functional dispersion, India, isolated trees, quasi-swap null models

5.3 Introduction

As agricultural expansion continues to fragment the world's tropical forests and occupy large areas of land (Phalan et al., 2013), it is increasingly important to devise conservation strategies for human-modified landscapes (Chazdon et al., 2009; Franklin & Lindenmayer, 2009; Gardner et al., 2009; Melo et al., 2013). Habitat fragmentation has a range of impacts on different taxa, but one group that is particularly vulnerable to habitat fragmentation is insectivorous birds, which is also the largest avian feeding guild (Lees & Peres, 2008; Tscharntke et al., 2008).

Numerous studies have demonstrated lower abundance and species richness of insectivores in human-modified landscapes compared to intact forest habitats (Canaday, 1997; Harvey et al., 2006; Marsden et al., 2006; Harvey & González Villalobos, 2007; Sekercioglu, 2012). Studies in habitat fragments have found similar results; especially when there is limited tree cover surrounding fragments (Stouffer & Bierregaard, 1995). Not only does this cause the deterioration in the conservation status of insectivorous birds (Sekercioglu et al., 2002), but it also diminishes their beneficial pest control services (Van Bael et al., 2008; Johnson et al., 2010; Karp & Daily, 2013).

In mitigating the decline of insectivorous birds in human-modified landscapes, several studied have identified the importance of isolated trees (Fischer & Lindenmayer, 2002; Manning et al., 2004). These trees can increase the abundance and richness of insectivores by providing connectivity between fragments for forest-dependent species (Harvey et al., 2006), along with feeding and nesting sites for matrix-tolerant taxa (Sekercioglu et al., 2007), thereby mediating the impact of habitat fragmentation (Sekercioglu, 2012). However, our understanding of conservation tools that are appropriate in human-modified landscapes represents a critical frontier in conservation biology (Tscharntke et al., 2008; Sekercioglu, 2012; Melo et al., 2013). For instance, in almost all cases, the presence of native trees in human-modified landscapes is preferable in comparison to non-native trees (Brockeroff et al., 2013; Douglas et al., 2013). Beyond that, however, we have very limited experimental evidence to help guide conservation practitioners working in the 2.5 billion ha of tropical land area that has been modified by humans (see Supporting information A, Section 5.10) (Petit & Petit, 2003; Fischer et al., 2006; Melo et al., 2013; FAO STAT, 2014). Even in cases where we are able to increase the abundance and richness of insectivorous birds, we do not know if that will be reflected in increases in pest control functions or other ecological services (Van Bael et al., 2008; Sodhi et al., 2010).

In their seminal study of Amazonian forest fragmentation, Stouffer and Bierregaard (1995) found that fragments surrounded by *Ceropia*, rather than *Vismia* trees, were preferentially recolonised by disturbance-sensitive insectivores. We sought to test the importance of different tree types in human-modified landscapes by comparing isolated *Ficus* (Moraceae) trees to isolated fruit trees, and isolated large non-fruiting trees.

Ficus trees have long been recognised as important food resources for frugivores (Terborgh, 1986), with almost 1,000 frugivorous bird species recorded consuming *Ficus* fruit (Shanahan et al., 2001). However, they may also be overlooked but important foraging sites for insectivores. Their co-evolved mutualism with pollinating fig wasps ((Hymenoptera, Agaonidae, Agaoninae) means that millions of fig of wasps (and non-pollinating fig wasps; Hymenoptera, Chalcidoidea) fly to and from fruiting figs (Harrison, 2003; Wang et al., 2012; Bain et al., 2013). As well as being a food resource for insectivorous birds themselves, these fig wasps are also the prey of invertebrates that inhabit *Ficus* trees (Schatz et al., 2008). Numerous other insects, including heteropterans, nematodes, coleopterans, and fruit flies, also exploit the extremely large fruit crop, which may number as many as one million syconia (Cushman et al., 1998; Bain et al., 2013). Indeed, notwithstanding chronic under-sampling, there are published records of 1,875 species of arthropod feeding on *Ficus*, including 742 species feeding on syconia, 481 feeding on sap, 369 leaf-chewers, and 283 wood borers (Basset et al., 1997). Ants (Hymenoptera: Formicidae) for example, have been found to specialise in predating non-pollinating fig wasps in some dioceous *Ficus* species, predate on fig dwelling herbivorous insects, consume partially eaten ripe syconia, and nest in figs (Schatz et al., 2008; Bain et al., 2013; Harrison, 2013). The complex bark topography of many *Ficus* species provides further habitat for arthropods (Berg & Corner, 2005), all of which suggests that *Ficus* trees may be attractive feeding sites for insectivorous birds.

We sought to test whether *Ficus* trees were particularly important foraging sites for insectivores in human-modified landscapes, relative to other tree types. Based on their importance in forest habitats, we hypothesise that scattered *Ficus* trees are more effective sites for insectivore conservation than other tree types, and that tree size and proximity to the nearest forest will be the best predictors of insectivore richness, abundance, and functional diversity.

5.4 Methods

This study involved: i) collecting field data on insectivore assemblages in isolated trees, ii) measuring trait data for the species recorded from specimen collections, iii) calculating functional diversity scores for each isolated tree assemblage, iv) evaluating the major changes in insectivore richness, abundance, and functional diversity across different isolated tree categories and other environmental parameters.

5.4.1 Study area

The study took place from April 2012 to June 2013 in the Golaghat District of Assam, North-east India. The study site is a ≈250 km^2 area bounded by the Western Range of Kaziranga National Park at N26 34.394 E93 15.433, the city of Jorhat at N26 46.198 E94 12.678, and the town of Golaghat at N26 27.819 E93 54.978. The elevation of the study area ranges between 30–100 m above sea level, and the mean annual rainfall for the region is 1,500–2,500 mm, most of which falls in the June to September monsoon (Barua & Sharma, 1999; Shrivastava & Heinen, 2007). The annual temperature range varies from an average minimum of 5°C to an average maximum of 35°C (Barua & Sharma, 1999).

The original habitat of moist subtropical deciduous forest was largely cleared following the local commercialisation of tea production in 1840 (Shrivastava & Heinen, 2007). Remnants of the original forest remain in the 7.65 km^2 Panbari Forest Reserve on the edge of the Karbi Hills, and in the 430 km^2 Kaziranga National Park (Barua & Sharma, 1999). Other small areas of forest regrowth exist, but are typically less than 1 ha. Agriculture is the dominant land-use, with a mixture of small-holder rice cultivation, village home gardens, and large commercial tea estates. Common plants grown in home gardens include bamboo (*Bambusa* spp.), bananas (*Musa* spp.), betel palm (*Areca catechu*), and jack fruit (*Artocarpus heterophyllus*). The area has a population density of 302 people per square kilometre (GOI, 2011).

5.4.2 Focal tree sampling

To compare differences in insectivore assemblages at isolated trees in this extensively human-modified landscape we identified focal trees in three categories: 1) isolated *Ficus* trees with small, brightly coloured syconia, which we surveyed when in fruit; 2) isolated fruit trees that did not belong to the *Ficus* genus, which we surveyed when in fruit; 3) large, non-fruiting trees (Table 5.1). Isolated *Ficus* tree surveys were restricted to species with small, brightly coloured syconia, as a previous study (Cottee-Jones & Whittaker, *in review*) had found significantly lower bird species richness and abundance at *Ficus* trees with large, dull coloured syconia. The selection of focal *Ficus* and other non-*Ficu*s fruit trees (herein in "fruit trees") was determined by their fruiting cycle; only trees with large crops of ripe fruit were surveyed. Large non-fruit trees (herein "large trees") were randomly selected from the largest trees in the landscape, exclusive of the two previous groups, with a minimum circumference at breast height of over 1 m.

For each tree, we measured the diameter at breast height (DBH), estimated the maximum tree height with a clinometer, and estimated the canopy area by measuring the canopy diameter at ground level along two axes, and then calculating the area using the formula for an ellipse. To obtain a single estimate for tree size, a Principal Components Analysis with Kaiser stopping criterion extraction (eigenvalues >1) was conducted using DBH, maximum height, and canopy area in IBM SPSS Statistics 22 (IBM, 2013). As the input variables were correlated with each other we used an oblique rotation method ("Direct Oblimin" in SPSS). The intensity of human land-use within a 100 m radius of each focal tree was recorded using a three-point scale (where 0 is very little human land use; 1 is some human land use, such as cultivation; and 2 is intense human land use, in cases where a road, house, or paddy field were present).

Table 5.1: Characteristics of the three isolated tree groups surveyed in Assam, India. DBH is diameter at breast height. Values for DBH, height, and canopy area are mean ± standard error. Different superscript letters denote significantly different means at $p<0.05$ following ANOVA and Games-Howell post hoc tests. The five most surveyed species are listed in order of decreasing number of surveys.

Characteristic	***Ficus***	**Fruit**	**Large**
Total no. of individuals surveyed	40	33	31
Total no. of species surveyed	6	12	15
DBH (m)	1.51±0.13 ^{a}	0.45±0.02 ^{b}	0.61±0.05 ^{c}
Height (m)	27.29±1.40 ^{a}	18.86±1.03 ^{b}	20.91±0.89 ^{b}
Canopy area (m^2)	489.32±67.29 ^{a}	74.01±7.16 ^{b}	130.11±21.43 ^{c}
Five most surveyed species (in order of decreasing abundance)	*F. religiosa, F. benghalensis, F. rumphii, F. microcarpa, F. benjamina*	*Artocarpus heterophyllus, Tectona grandis, Artocarpus lakoocha, Syzgium cumini, Toona ciliata*	*Syzgium cumini* (non-fruiting), *Albizia lucidor, Albizia procera, Mangifera indica* (non-fruiting), *Neolamarckia cadamba*

We measured the distance to the nearest protected area with intact forest by marking the focal trees with a GPSmap 62s device, and then overlaying the GPS markers on Landsat 8 satellite images of the region in ArcGIS 10.2.1 (ESRI, 2014). We digitised the protected area borders through an on-screen visual interpretation (Berens et al., 2008), and then measured the distance (in km) of each focal tree to the nearest protected area using functionality available in ArcGIS. In all cases, protected areas held the only high-quality forest habitat left in the study landscape. In addition to protected areas, small (≤1 ha), low-quality wooded areas were located through consultation with local landholders and marked with a GPS device. In cases where focal trees were closer to small, low-quality wooded areas than protected areas, additional measurements were made following the above procedure to produce a variable for the distance to the nearest wooded area of any quality. Before conducting any analyses, the suitability of these two distance measurements was compared using linear regression (Supporting information B, Section 5.10).

5.4.3 Insectivore surveys

Each focal tree was surveyed once, for three hours, from first light. Single tree surveys are increasingly used in ecological studies (for example, see Luck & Daily, 2003; Berens et al., 2008; Breitbach et al., 2010) and give a good indication of the bird assemblage interacting with an individual tree. Surveys were only conducted in fair weather conditions. If the weather deteriorated during the survey period, the survey was abandoned and attempted again on the following day. During the survey, an observer would watch the tree from a concealed position with a good view, typically about 20 m from the trunk. Each individual bird that landed in the tree was recorded, and birds that made repeated visits to and from the tree were denoted with an asterisk to avoid double counting. Trees in the *Ficus* and fruit categories were only surveyed when the crop was large (for the species) and ripe. Surveys were conducted by HEWCJ and six local field assistants, who were professional bird guides from Kaziranga National Park, with training and experience in scientific data collection. As our focal trees were isolated in open habitats, single tree surveys helped minimise the problems associated with observer bias and the detectability of target taxa. Deforestation in the study area occurred over 150 years ago, and was largely uniform in timing, so differential rates of matrix assemblage relaxation were not considered to have an effect on bird communities in the study area (Komar, 2006). As all trees were surveyed in the same season, the presence or absence of migratory species was consistent across the three tree groups.

Each species was classified into primary dietary guilds (frugivore, nectivore, insectivore, granivore, or carnivore; omnivores were classified according to their main food type, and were not included in any further analyses on insectivorous birds as they may have been attracted to *Ficus* and fruit trees by the fruit present) and forest-dependency (forest-dependent, habitat-generalist, matrix-specialist) following del Hoyo et al. (1992–2002; 2003–2011). Nomenclature also followed del Hoyo et al. (1992–2002; 2003–2011). To cross-check the local validity of the forest-dependence classifications, we also plotted incidence functions for species that were recorded more than twice (the model fit for singletons and doubletons was too poor for reliable incidence estimation). Only presence or absence data from the *Ficus* surveys were used as the three categories were not comparable, and the *Ficus* data set was the largest. First binary logistic regression models were run, with the distance from the nearest protected area as the predictor variable (Watson et al., 2005). The resulting predicted probabilities of occurrence were then used to plot incidence functions against distance for each species (Supporting information C, Section 5.10). Species with sharp downward curves could then be confirmed as forest-dependent, species with a flat curve (no overall change greater than 10% over 30 km) were confirmed as habitat-generalists, while species with curves that rose as distance increased were confirmed as matrix-specialists (Ruiz-Gutiérrez et al., 2010; Neuschulz et al., 2012).

5.4.4 Ecomorphological data collection

To calculate functional diversity scores, we preferred to use ecomorphological trait data from the insectivores recorded in the surveys rather than guild classifications extracted from the literature or assessed using our field experience. We defined a “trait” as a measurable aspect of an organism, which determines its interaction with the environment (Flynn et al., 2009). Here we were interested in the foraging and dispersal capacity of insectivorous birds, so we measured traits associated with locomotive behaviour, dispersal ability, gape size, bill structure, and body size (Schoener, 1965; Miles & Ricklefs, 1984; Derryberry et al., 2011; Claramunt et al., 2012). In order to obtain ecomorphological trait data, each species recorded in the surveys was measured following Edward Grey Institute protocols at the British Natural History Museum’s ornithological collections. Specifically, we measured four specimens of the local subspecies for each species recorded. In almost all cases we were able to measure specimens collected within 150 km of the study area. Two adult males and two adult females of each species were measured with 150 mm outside diameter dial callipers (accurate to 0.1 mm), wing rulers, and tail rulers (accurate to 0.5 mm) from Porzana Ltd. The measurements taken were: culmen length (from the base of the skull to the tip of the bill), bill length from nares (from the anterior edge of the nares to the tip of the bill), bill width (the width of the bill at the anterior of the nares), bill depth (the depth of the bill at the anterior of the nares), gape width, tarsus length (the length from the inner bend of the tibiotarsal articulation to the base of the toes, where the scalation pattern changes), wing chord (from the bend in the wing to the unflattened longest primary), Kipp’s Distance (the distance from the longest primary to the first secondary; Kipp, 1959), and tail length (to the tip of the longest retrix; Sutherland et al., 2004).

As weight data for birds are often variable (Clark, 1979), we preferred to measure body size through a PCA. We initially conducted a pair of PCA analyses, one for locomotive ability (with input measurements of tail length, wing chord, and tarsus length) and one for bill shape (with bill depth, width, and length from nares) using oblique rotation with Kaiser stopping criterion extraction (eigenvalues >1). Each of these PCAs produced two components. In both cases, the first related to size, while the second components were taken as indices for locomotive ability and bill shape, respectively. To produce one index for body size, we ran an additional PCA using the first components from the original analyses (Trisos et al., *in press*). To create an index for dispersal ability that standardises for bird size, we calculated the hand-wing index (Claramunt et al., 2012), which is a surrogate for flight performance, migratory behaviour, and natal dispersion in birds.

5.4.5 Functional diversity calculation

We follow the definition of functional diversity as the distribution of functional traits within multidimensional niche space (Petchey & Gaston, 2006), and used Laliberté and Legendre's functional dispersion (FDis) index to measure functional diversity in our dataset (Laliberté & Legendre, 2010). This represents the spread of the species in quantitative trait space by calculating a multidimensional index of the mean distance of an individual species to the centroid of all species in the community (Laliberté & Legendre, 2010). A major advantage of FDis over other measures, such as FRic, FEve, and FDiv (Mason et al., 2005; Villéger et al., 2008; Mouchet et al., 2010; Whittaker et al., 2014) is that it can be calculated for communities composed of only two species, rather than a minimum of three, which was important for the species-poor insectivore assemblages in the isolated trees. It is also independent of species richness, and can be weighted by abundance, both of which were important considerations for our study (Laliberté & Legendre, 2010; Mason et al., 2013). We calculated functional dispersion for each of our focal trees using Package FD in Programme R (Laliberté & Shipley, 2013; R Core Team, 2014).

In the absence of strong ecological reasons to weight our data, we used an unweighted trait matrix (Petchey & Gaston, 2006). As our trait data were measured on a continuous scale, rather than classified into nominal groups, a species–species uncorrected distance matrix was computed. A Principal Co-ordinates Analysis (PCoA) was performed after the distance matrix was corrected for negative Eigenvalues (Anderson, 2006; Laliberté & Shipley, 2013). Negative Eigenvalues cannot be represented in Euclidean space, and so were corrected following Anderson (2006) to avoid introducing a bias to the functional dispersion estimates (Legendre & Anderson, 1999). These corrected PCoA axes were used to calculate the functional dispersion scores for our focal trees (Laliberté & Shipley, 2013). Functional dispersion could not be computed for trees with no insectivore records, but these trees were included in further analyses with index scores of 0. Similarly, trees with only one species of insectivore were given a score of 0 following Laliberté and Shipley (2013).

To assess whether trees supported higher or lower levels of functional diversity than would be expected by chance, we compared observed functional dispersion patterns with those of null model communities generated using the sum-of-squares reduction method ("quasi-swap", Miklós & Podani, 2004). With species richness held constant for each tree, the model randomly simulated null communities from the species pool (the total number of insectivores recorded in the study; Gotelli, 2001; de Bello, 2012). To avoid computational problems, only focal trees with more than two insectivore species records were included in the null model. We ran 10,000 simulations and tested whether the observed functional dispersion of each tree was significantly higher or lower than the null distribution at $p=0.05$, using Package Vegan in R (Oksanen et al., 2013; R Core Team, 2014). This allowed us to determine whether changes in functional diversity reflected changes in species richness over the different tree categories, or whether there were any structural responses to assemblage composition (Flynn et al., 2009; Edwards et al., 2013). We also produced Z scores for each null community to enable standardised comparisons across tree categories.

5.4.6 Statistical analysis

In addition to reporting the average richness of trees in each category, we estimated the richness of the three tree categories using the Chao 1 bias corrected estimator, for situations where species detectability is relatively equal (Chao et al., 2005). As we conducted single tree surveys, we believed the detectability of species in surveyed trees was uniformly very high. As there were many singletons and doubletons in the insectivore communities, along with a small number of very abundant species, we preferred this estimator to other methods as it performs better with heterogeneous data (Chao et al., 2005). We also estimated the Shannon diversity index using the Chao and Shen (2003) algorithm as a relatively large fraction of species were missing in the fruit and large tree categories. We identified significant differences between tree categories in these indices if their 95% confidence intervals did not overlap.

We estimated Morisita's (1959) similarity index to assess the similarity between insectivore assemblages recorded in the three isolated tree categories. This index estimates the similarity of multiple communities from abundance data, taking into account unseen shared species (Chao et al., 2008). We randomly selected 31 surveys from each tree category and summed the abundance of each bird species to produce equal sample sizes. The richness estimates and indices were computed in SPADE (Chao & Shen, 2010; Chao & Shen, 2012) with 200 bootstrap replications.

We expected some spatial autocorrelation in our data, as trees close to the forest were also close to each other, given that we could only survey and therefore measure distances from the nearest protected area in one direction. However, our survey strategy, where we alternated the timing of our surveys to ensure we were not surveying trees in close proximity at similar times, should help reduce the chance of an inflated Type I error. To test for spatial autocorrelation in the dataset, we estimated Moran's *I* coefficient for insectivore richness, abundance, and functional dispersion in all tree categories, using arbitrary distance classes and a Bonferroni correction (Diniz-Filho et al., 2003; Package APE: Paradis, 2014).

Differences in insectivore richness across the tree categories were tested using one-way analysis of variance (ANOVA). The data were square-root transformed for normality, and tested for homogeneity of variance using Levene's test. A Games-Howell post hoc test, which is robust to unequal sample sizes, was used to identify significant differences between the pair-wise categories (Field, 2009). Differences between the abundance of insectivores across the tree categories did not meet the assumptions of non-parametric tests, even after log or square root transformations. Instead, we compared the categories using a Kruskal-Wallis test with Mann-Whitney U post hoc tests, using a Bonferroni correction of $p=0.0167$ to avoid a Type I error (Field, 2009). In addition, we examined the difference in abundance, richness, and FDis across the three tree types when controlling for the canopy area of the tree (Supporting information D, Section 5.10).

To analyse the composition of assemblages in the isolated trees compared to the "primary" forest at Panbari Forest Reserve, we compiled an inventory of the resident insectivore species, and those migrants that were present during April–June, from Barua and Sharma (1999). We followed the literature in classifying each of these species as forest-dependent, generalist, or matrix-specialist. We then compared the proportion of forest-dependent species listed for Panbari to the proportions recorded in our isolated tree surveys, using a Friedman test with post hoc Wilcoxon signed rank test to identify any significant differences between the proportion of forest-dependent species in Panbari compared to each of our isolated tree categories.

Many fruit and large focal trees returned functional dispersion index scores of zero, as fewer than two insectivore species were recorded in them, producing an overdispersed distribution. We therefore also used a Kruskal-Wallis test for differences between mean FDis scores for the three tree categories, followed by Mann-Whitney U tests with a Bonferroni correction.

Using the null model simulation output, we used a paired two-tailed Wilcoxon signed-rank test to identify significant differences between the observed and expected FDis scores in each tree category (Ding et al., 2013). Z score data met the assumptions of normality, and so an ANOVA was conducted with Games-Howell post hoc tests to compare different tree categories.

The effect of tree size, land-use intensity, distance from the nearest protected area, and tree type on insectivore richness, abundance, and functional diversity were examined using an information-theoretic approach (Burnham & Anderson, 2002; 2004). A generalised linear model with a linear link function was run for the square-root transformed insectivore richness data with combinations of four predictor variables (tree type, tree size, land-use intensity, and distance from protected area) and one second-order interaction term based on *a priori* hypotheses (land-use intensity*distance from the nearest protected area). A second-order criterion, AIC_c, was used to select the best model due to the small ratio between the number of input variables and observations (Anderson et al., 2001). The same predictor variables were used to analyse the insectivore abundance data, but in this case the model had a log-link function with Poisson error distribution model, as the count data did not meet parametric assumptions. To account for the overdispersed functional diversity data, we used a quasi-AIC (QIC) approach as a metric for model parsimony (Anderson et al., 1994; Richards, 2008). Model selection was based on quasi-likelihood AIC_c values, correcting for the small input:observation ratio (Burnham & Anderson, 2002). A linear link function and the same predictor variables were used to model functional dispersion as were used to model species richness and abundance.

5.5 Results

We surveyed a total of 40 *Ficus* trees, 33 fruit trees, and 31 large trees in the study area. Over the 104 surveys, 34 species of insectivorous bird were recorded. The most frequently recorded species were the Oriental White-eye (*Zosterops palpebrosus*) with 55 records, Common Tailorbird (*Orthotomus sutorius*) with 54, and the Oriental Magpie Robin (*Copsychus saularis*) with 53. The Oriental White-eye was also the most abundant species, with 146 individual records, followed by the Great Tit (*Parus major*) with 86, and the Oriental Magpie Robin with 84.

For the species recorded more than twice in the *Ficus* surveys, the incidence function plots indicated that more species were matrix specialists (11 out of 18; 61.11%) than any other category (Figure 5.1). Five species had flat curves (27.78%), indicating they were generalists, while the predicted probability of two species deceased as the distance from protected area increased (11.11%), indicating that they were dependent on forests.

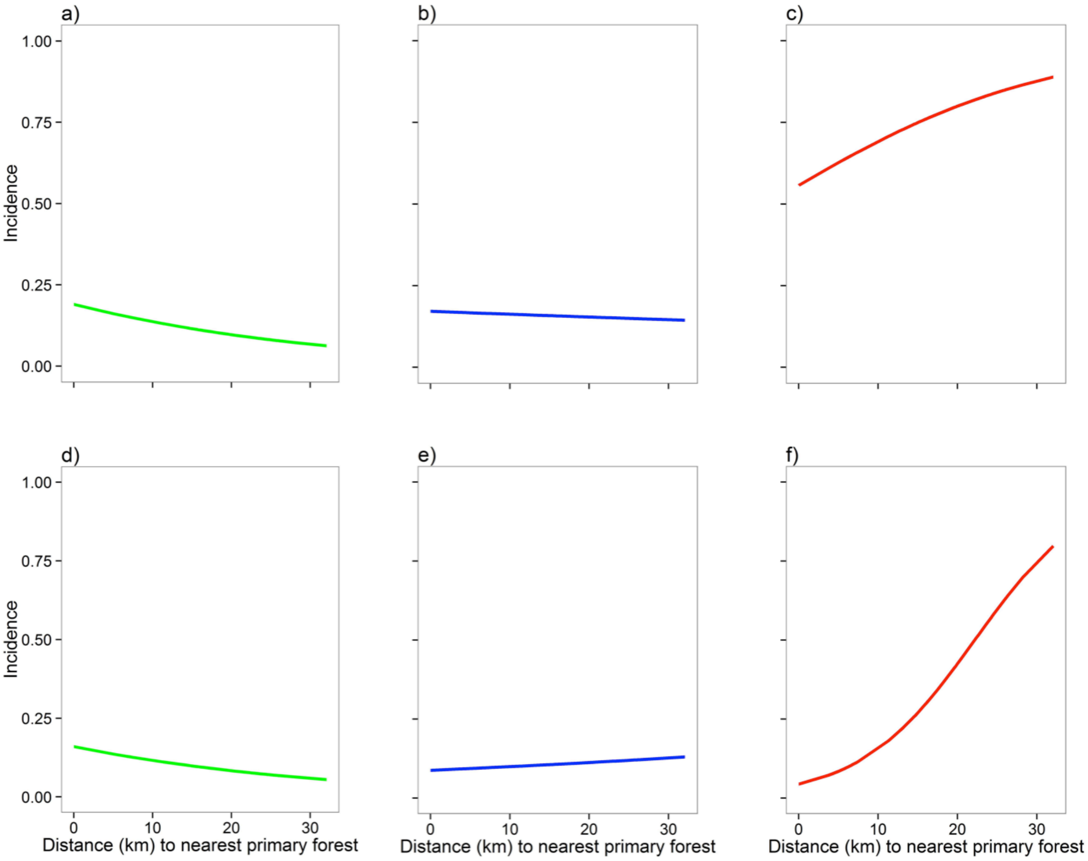

Figure 5.1: Incidence functions for six insectivore species recorded during the study in Assam, India. Green curves represent forest-dependent species, blue represent habitat-generalists, and red represent matrix-specialists. Species are a) Hair-crested Drongo *Dicrurus hottentottus*; b) Black-rumped Flameback *Dinopium benghalense*; c) Great Tit *Parus major*; d) Large Cuckoo-shrike *Coracina macei*; e) White-breasted Kingfisher *Halcyon smyrnensis*; f) Crimson Sunbird *Aethopyga siparaja*. The curves are the predicted probability of occurrence, generated through a logistic regression model with distance from the nearest protected area as the predictor variable for each species' presence/absence data at 40 isolated *Ficus* trees. The figures were constructed using the R package GGplot2 (Wickham, 2009).

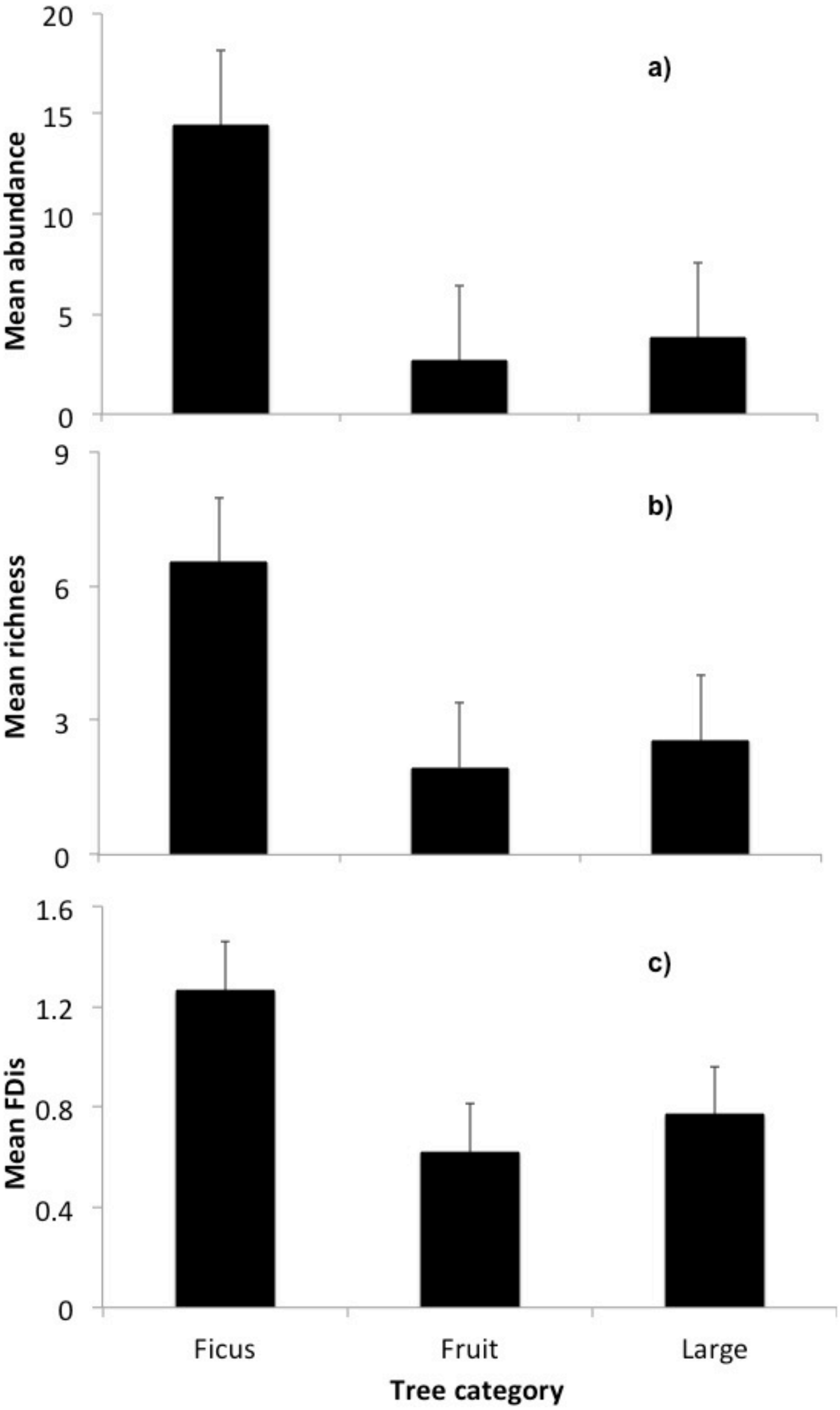

Figure 5.2: Mean insectivore abundance, richness, and FDis (functional dispersion) recorded in isolated tree assemblages in Golaghat District, Assam, India. For *Ficus* trees: n=40; fruit: n=33; and large: n=31. Error bars are standard error.

The richness estimates predicted that *Ficus* trees were visited by considerably more species than were the other tree categories, followed by large trees and then fruit trees (Figure 5.2). The diversity indices produced similar scores after 200 bootstrap replications, and the Morisita comparisons also indicated a high degree of similarity between tree categories (Tables 5.2 & 5.3).

Table 5.2: Morisita pair-wise similarity matrix of multiple communities, for insectivorous birds in three categories of isolated tree (Chao et al., 2008) in Assam, India. Values are Morisita similarity estimate ± standard error, with 200 bootstrap replications. Values closer to 1.0 indicate higher community similarity. Average pairwise comparison=0.88.

	Ficus	**Fruit**	**Large**
Ficus	1.0	0.82±0.06	0.93±0.04
Fruit		1.0	0.88±0.07
Large			1.0

The examination of mean richness across the three tree categories indicated the existence of statistically significant differences, with a very large effect size ($F_{(2,103)}=61.74$, $p<0.001$, $r=0.74$). Games-Howell post hoc tests indicated that the difference in richness between *Ficus* trees and fruit trees, along with *Ficus* trees and large trees, were significant ($p<0.001$ in both cases). However, no significant difference was identified between fruit trees and large trees ($p=0.52$).

Table 5.3: Differences between insectivorous bird species richness, abundance, and function diversity parameters across the three tree categories in Assam, India. Values are means ± standard error. Different superscript letters denote significantly different means at $p<0.05$ for species richness, Z scores, and functional dispersion using ANOVA, and $p<0.0167$ for insectivore abundance using the Kruskal-Wallis test with Mann-Whitney post hoc procedures. Estimated richness is the "Chao 1 bias corrected" estimator, which only uses the number of singletons and doubletons to estimate the number of undetected species (Chao, 2005). The Shannon index scores are derived from the Chao & Shen (2003) revised algorithm. Estimated richness and Shannon scores were considered to be significantly different where 95% confidence intervals did not overlap. Species richness is the average number of insectivorous bird species recorded in the surveys of each tree category. Abundance is the average number of individual insectivores recorded in the surveys of each tree category. FDis is a multidimensional index of the mean distance of an individual species to the centroid of all species in the community (Laliberté & Legendre, 2010). Z scores were obtained from FDis null model simulations (excluding focal trees with fewer than two insectivore species records), and represent the standard deviation from the mean.

Parameter	***Ficus***	**Fruit**	**Large**
Estimated richness	38.20 ± 6.40^{a}	14.00 ± 1.80^{b}	$23.00 \pm 6.00^{a\,b}$
Shannon index	2.64 ± 0.06^{a}	2.24 ± 0.11^{b}	$2.53 \pm 0.11^{a\,b}$
Species richness	6.95 ± 0.38^{a}	1.91 ± 0.23^{b}	2.55 ± 0.45^{b}
Abundance	11.95 ± 0.96^{a}	2.67 ± 0.37^{b}	3.68 ± 0.74^{b}
FDis	1.26 ± 0.07^{a}	0.73 ± 0.11^{b}	0.85 ± 0.15^{b}
Z score	-0.32^{a}	-0.06^{a}	0.31^{a}

Insectivore abundance also differed significantly according to tree type ($H_{(2)}=55.17$, $p<0.001$), with a mean rank of 80.10 for *Ficus* trees, 33.33 for fruit trees, and 37.29 for large trees. The follow-up Mann-Whitney tests found that significant differences existed between the mean insectivore abundance in *Ficus* trees and fruit trees (U=48,

$p<0.001$), and *Ficus* trees and large trees (U=128, $p<0.001$). Again, there was no significant difference between fruit trees and large trees (U=491, $p=0.78$).

We recorded a significantly lower proportion of forest-dependent species in our isolated tree surveys compared to Barua and Sharma's (1999) inventory of the insectivore avifauna at a local intact forest ($\chi^2_{(3)}=242.31$, $p<0.001$; Panbari forest compared to *Ficus*: Z=-9.06, $p<0.001$; fruit: Z=-9.90, $p<0.001$; large: Z=-9.59, $p<0.001$) (Figure 5.3).

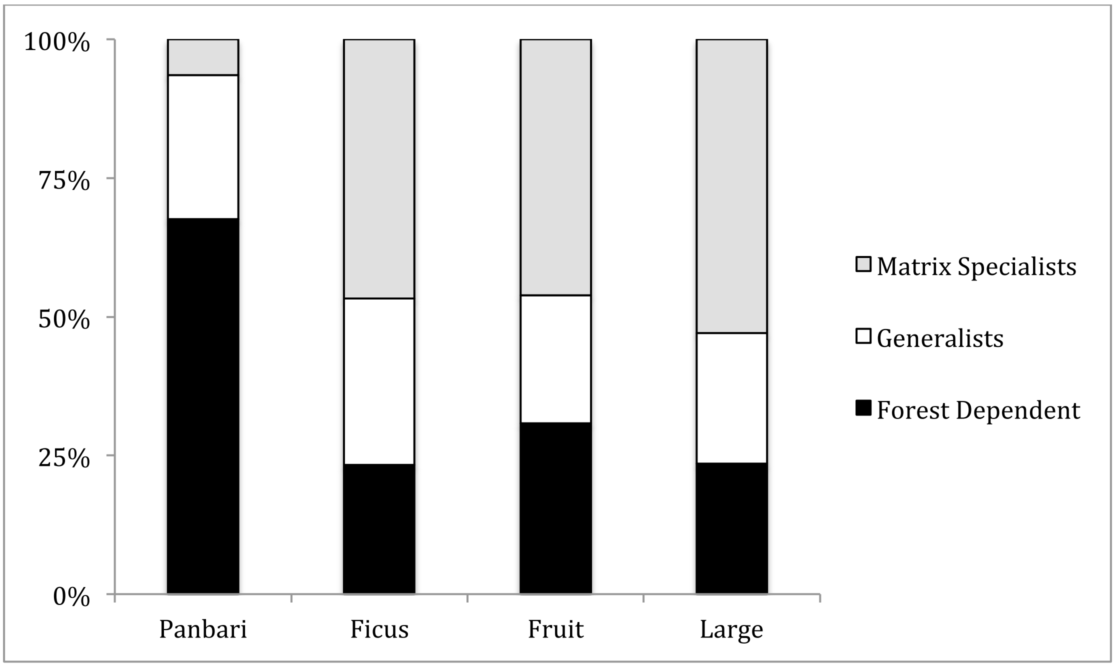

Figure 5.3: The proportion of forest-dependent, matrix-specialist, and generalist insectivore bird species recorded at a local intact forest (Panbari Forest Reserve), and three isolated tree categories. The inventory of insectivores present at Panbari was taken from Barua and Sharma, 1999. Differences in the proportion of forest-dependent species were significant when compared to the three tree categories ($\chi^2_{(3)}=242.31$, $p<0.001$; Panbari compared to *Ficus*: Z=-9.06, $p<0.001$; fruit: Z=-9.90, $p<0.001$; large: Z=-9.59, $p<0.001$).

The functional dispersion test found a significant relationship across the three tree types ($H_{(2)}=18.17$, $p<0.001$). *Ficus* trees had the highest mean rank (68.13), followed by large trees (45.34), and finally fruit trees (40.29). In common with the pattern described above for species richness and abundance, significant differences were found between the FDis scores of *Ficus* trees and fruit trees ($U=296$, $p<0.001$), and *Ficus* trees and large trees ($U=359$, $p<0.015$), while no significant difference was identified between fruit and large trees ($U=472.5$, $p=0.59$) (Table 5.3).

The observed functional dispersion of insectivore assemblages across the three tree types was lower in exactly 50% of cases, and higher in 50% of cases, than expected by chance (Table 5.4). *Ficus* trees had higher functional dispersion than the null simulations predicted, given the number of species recorded in each tree, although this difference was not significant in any of the 40 *Ficus* trees surveyed (Figure 5.4 and 5.5a). The difference between observed FDis and expected FDis was significant in *Ficus* trees ($Z=-2.25$, $p<0.05$), but not in fruit ($Z=-0.68$, $p=0.49$) or large trees ($Z=-0.72$, $p=0.47$). *Ficus* trees also had, on average, negative and lower Z scores in comparison to the other tree groups (Table 5.3; Figure 5.4), although no significant differences were reported from the Z scores obtained from the null model simulations ($F_{(2,75)}=2.69$, $p=0.07$, $r=0.26$).

Table 5.4: Comparison of observed FDis to mean expected FDis, as simulated by 10,000 iterations of the quasi-swap null model for insectivorous bird FDis across three tree categories in Assam, India. Values are percentages with *n* in parentheses. FDis scores could not be included for nine fruit trees and nine large trees where only one species was recorded. These trees were excluded from the null modelling, along with a further five fruit trees and three large trees that had no insectivore records during the survey. The final number of trees included in each category was: 40 *Ficus*, 19 fruit, and 19 large. Only 2/78 (2.56%) of simulated trees had observed scores that differed significantly from scores expected by chance (at $p<0.05$). Both of these trees were large trees, and both had lower expected mean FDis scores than observed.

Tree category	FDis lower than null expectation	FDis higher than null expectation
Ficus	40% (16)	60% (24)
Fruit	57.89% (11)	42.11% (8)
Large	63.16% (12)	36.84% (7)

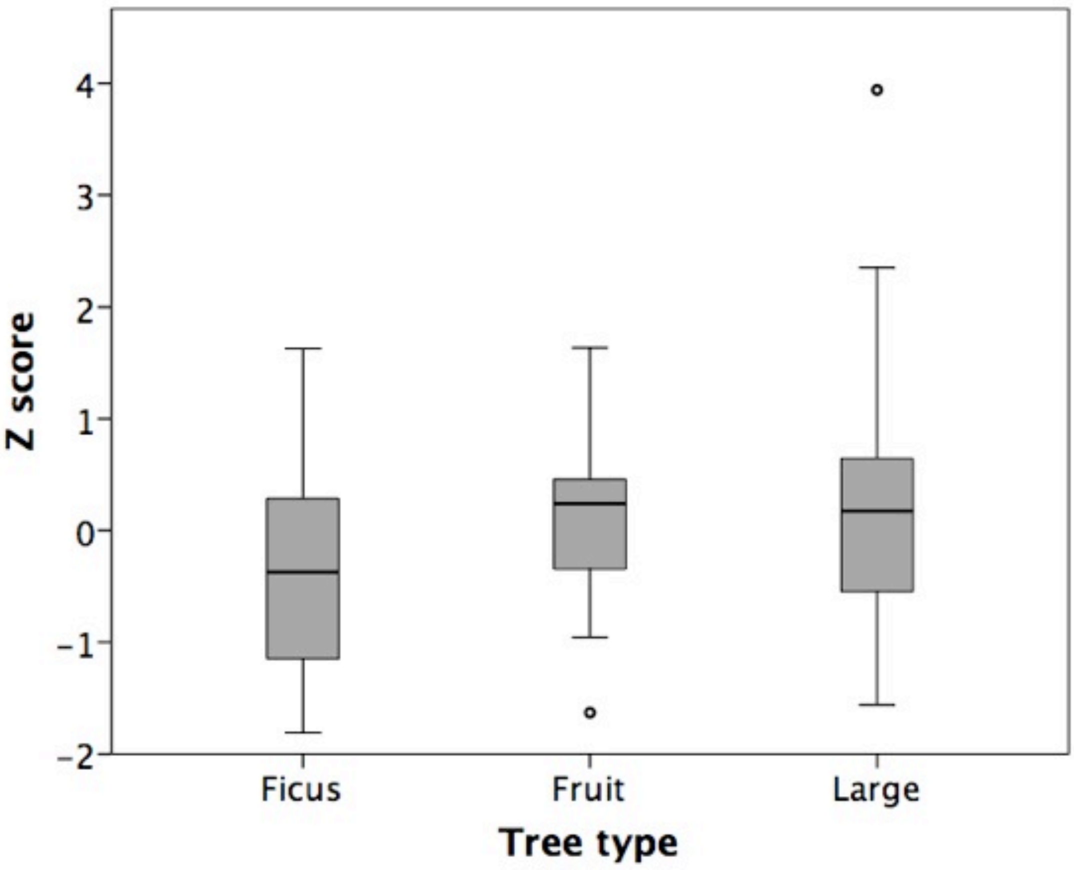

Figure 5.4: The mean Z score of functional dispersion in each tree type for insectivorous birds visiting isolated trees in a human-modified landscape in Assam, India. The Z score is the number of standard deviations a value is above the mean. Z scores were calculated from 10,000 null model simulations where species richness was held constant for each tree. Z scores above zero indicate that the species assemblage in a tree type is more functionally diverse than would be expect by chance from the pool of species recorded.

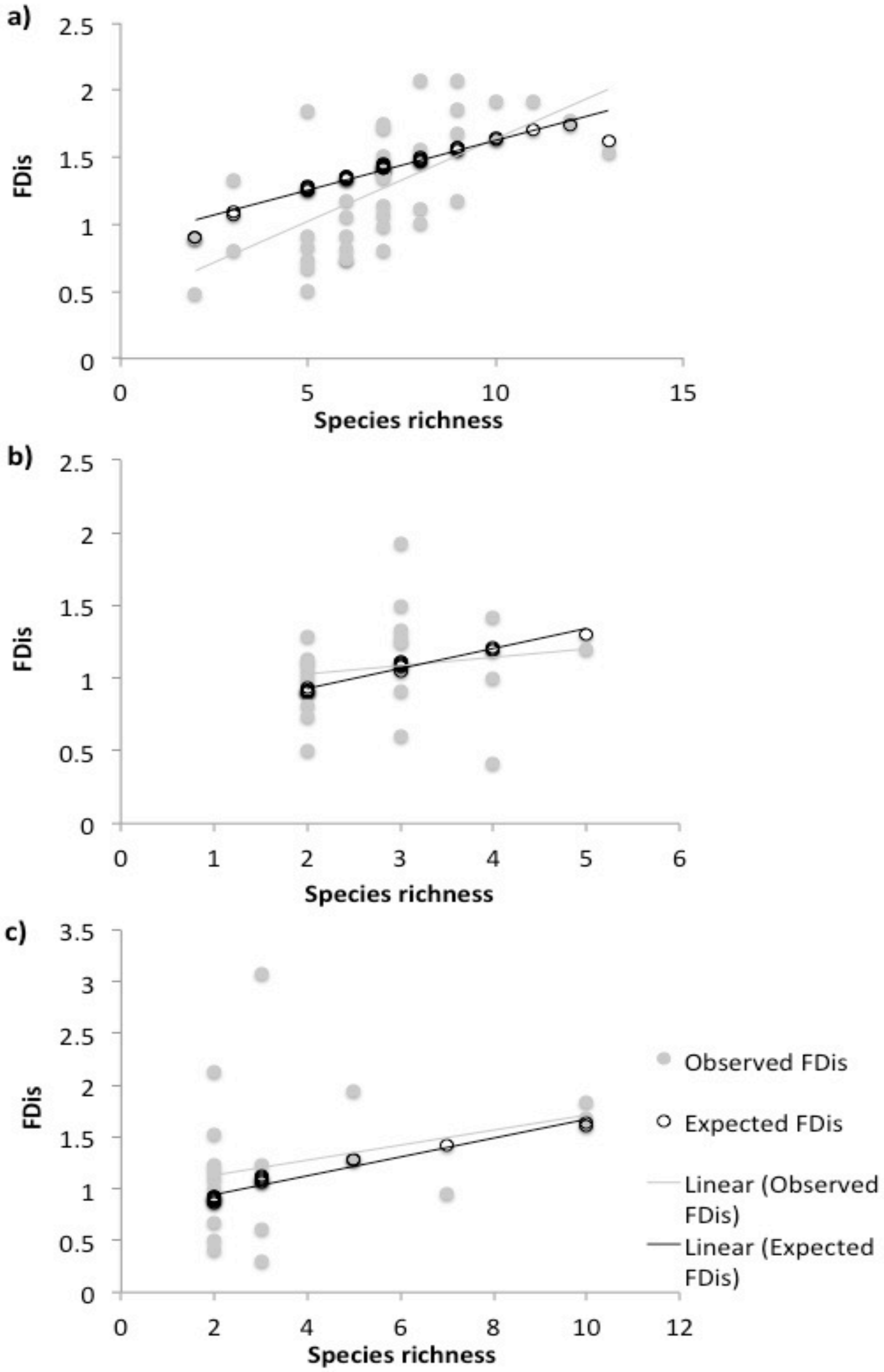

Figure 5.5: Comparison of expected and observed functional dispersion in insectivorous birds (FDis) in a) *Ficus* trees; b) fruit trees; c) large trees in Assam, India. Lines are linear regressions, species richness is the insectivore species richness. Note the different axis scales. Expected FDis scores were simulated using the quasi-swap method with 10,000 iterations. The mean scores of those simulations for each tree are presented here as the "null mean". Observed FDis scores are calculated from

insectivore abundance records from the isolated tree surveys (40 *Ficus*, 19 fruit tree, and 19 large tree surveys were included in the analysis). R^2 values for the regressions are: a) null mean=0.95, observed FDis=0.43; b) null mean=0.96, observed FDis=0.02; c) null mean=0.95, observed FDis=0.08.

The Moran's *I* test for spatial autocorrelation in our data indicated that there was significant spatial autocorrelation in some distance classes for insectivore richness, abundance, and functional dispersion. However, there was no consistent trend in either the direction of *I* coefficients or their significance. Almost all *I* coefficients were ±0.1 of 0, and all were <0.25, suggesting that although there was some spatial structure in the data, it was not uniformly or strongly more or less spatially related than would be expected by chance (Diniz-Filho et al., 2003).

The information-theoretic assessment of insectivore richness predictors found the most support for models containing tree type. The model with the lowest AIC_c score contained tree type and tree size, although models with tree type, size, and surrounding land-use intensity, or just tree type and land-use intensity were also within two AIC_c of the "best" performing model (Tables 5.5 & 5.6). In the model with the most support, *Ficus* trees had the largest effect on richness, which was significant at $p<0.001$.

Table 5.5: Generalised Linear Model results with Akaike Information Criterion scores for variables affecting three measures of insectivore assemblage at isolated focal trees in Assam, India. "Richness" reports the square-root transformed insectivore richness using a normal link function. "Abundance" reports insectivore abundance using a log-link model with Poisson error distribution. "FDis" reports the quasi-AIC$_c$ results for insectivore functional dispersion, using an identity link function. Data are derived from 104 insectivore surveys in Golaghat District, Assam, India. Model input abbreviations are T=tree type; L=land-use; D=distance from nearest protected area; S=tree size. Other denotations: K=parameters in the model; MML=Maximum Log-likelihood; AIC$_c$=second-order Akaike Information Criterion score for finite samples; ΔAIC$_c$=the difference in AIC$_c$ scores compared to the "best" performing model; w_i=Akaike weight, the normalised model likelihoods (Burnham & Anderson, 2004); and QIC$_c$ and ΔQIC$_c$= the quasi-AIC$_c$ equivalents of AIC$_c$ and ΔAIC$_c$ for overdispersed data (Richards, 2008). The "best" performing model in each case is highlighted in bold font.

Variable	Model	K	MML	AIC$_c$	ΔAIC$_c$	w_i	QIC$_c$	ΔQIC$_c$
Richness	**T, S**	**2**	**-65.05**	**140.70**	**0**	**0.26**		
	T, S, L	3	-63.04	141.25	0.55	0.20		
	T, L	2	-64.23	141.32	0.61	0.19		
	T, S, L, D	4	-62.03	141.58	0.87	0.17		
	T, D, S	3	-64.49	141.85	1.15	0.15		
Abundance	**T, S, L**	**3**	**-290.00**	**592.88**	**0**	**0.36**		
	T, S	2	-292.51	593.91	1.03	0.21		
	T, L	2	-291.85	594.31	1.43	0.17		
	T, S, L, D	4	-289.64	594.44	1.57	0.16		
FDis	**S**	**1**				**0.41**	**42.88**	**0.00**
	T, S	2				0.12	45.35	2.47
	T	1				0.10	45.71	2.83

For insectivore abundance, tree type was again consistently identified as an important predictor in all the models with good support. The best performing model contained tree type, tree size, and surrounding land-use intensity. Again, *Ficus* trees had the highest beta coefficients, which were significant at $p<0.001$.

The best model fit for functional dispersion was one that contained only tree size. The beta coefficients of the best performing model indicated a significant increase in functional dispersion as tree size increased. No other models were within a selection threshold of two QIC from the best performing model, although a model which included tree type with tree size scored 2.47.

Table 5.6: Correlation coefficients for the parameters retained in the "best" performing models for insectivorous birds in isolated trees in Assam, India (see Table 5.5). "Richness" reports insectivore richness, "Abundance" reports insectivore abundance, and "FDis" reports insectivore functional dispersion from three types of isolated tree.

Variable	Parameter	B (estimate)	S.E.	Wald chi-square	*p*
Richness	Intercept	1.87	0.09	475.86	<0.001
	Tree type (*Ficus*)	0.80	0.13	38.86	<0.001
	Tree type (Fruit)	-0.10	0.11	0.73	0.39
	Tree type (Large)	-	-	-	-
	Tree size	0.16	0.06	7.81	<0.01
Abundance	Tree type (*Ficus*)	2.32	0.07	1138.22	<0.001
	Tree type (Fruit)	0.94	0.15	39.28	<0.001
	Tree type (Large)	1.26	0.15	75.62	<0.001
	Land-use intensity (Low)	0.36	0.16	5.23	<0.05
	Land-use intensity (Medium)	0.07	0.10	0.45	0.50
	Land-use intensity (High)	-	-	-	-
	Tree size	0.92	0.05	3.71	0.054
FDis	Intercept	0.94	0.01	6323.21	<0.001
	Tree size	0.30	0.05	34.47	<0.001

5.6 Discussion

The conversion of tropical forest to agricultural production causes changes in insectivorous species composition, and decreases in functional diversity (Tscharntke et al., 2008; Lewis, 2009; Azhar et al., 2013; Edwards et al., 2013). However, we found that isolated *Ficus* trees provide important micro-site level habitat for insectivores in the human-modified Assamese landscape. Compared to the other tree categories, *Ficus* trees had consistently higher insectivore richness and abundance, suggesting that *Ficus* trees may be more effective conservation tools in modified landscapes than other isolated trees. However, the majority of the species recorded in the isolated trees were matrix-specialists, and are therefore of low conservation concern. If conserving functional diversity and ecological services such as pest control was a priority (and assuming that the birds recorded in isolated trees are also foraging on agricultural crops), the conservation of large trees *per se* may be the most effective strategy. In this case, isolated *Ficus* trees would again be a conservation priority, as they were the largest trees in the study area.

In analysing the incidence functions of insectivores recorded at *Ficus* trees, three patterns emerged. The group with the most members were the matrix-specialists, which were species such as the Great Tit (*Parus major*), Common Iora (*Aegithina tiphia*), and Crimson Sunbird (*Aethopyga siparaja*). These birds showed a distinct preference for non-forest habitats, with increasing predicted probabilities of occurrence as the distance from the forest increased. Given that there were a further five species with flat curves (habitat-generalists), 89% of the 18 species that were recorded sufficiently frequently for inclusion in this analysis, showed no dependency on proximity to forests over a 32 km scale.

The final group showed downward predicted probabilities with distance from protected area, indicating some degree of forest-dependency (k-selected, Diamond, 1974). The incidence functions of this group indicated that very few forest-dependent species visited isolated trees in modified habitats. However, several species found in the isolated trees, which were reported to be forest-dependent in the literature, were excluded from the incidence function analyses because they were only recorded once or twice. Whether forest-dependent species travelled out to isolated trees in modified landscapes before returning to the forest, or whether these species were resident only in modified habitat close to forests through a spill-over mechanism is hard to determine without tracking individuals. Interactions with isolated trees are likely to vary by species within this group, and evidence from a tracking study in Costa Rica suggests that insectivores that feed over an extensive home range can reside in production landscapes (Sekercioglu et al., 2007).

One species that did not fit into any group well was the Large Cuckoo-shrike (*Coracina macei*). This species is widely regarded as a habitat-generalist, or even a matrix-specialist (Taylor, 2005). However, our incidence function curve indicates it declines with distance from the protected area. This species was only recorded in four out of the 40 *Ficus* trees, and so perhaps that is too few for accurate incidence function modelling. Alternatively, our threshold of a 10% decline over 30 km may be too strict, and perhaps a 20% decline would have been a more appropriate partition between forest-dependent and generalist species. If it were reclassified, there would only be one forest-dependent species left that was recorded more than twice (the Hair-crested Drongo *Dicrurus hottentottus*).

Although our results consistently find *Ficus* trees to have the highest richness and abundance scores, tree type was not included in the best fitting model for functional dispersion. The identification of tree size as the best predictor of functional dispersion suggests that the best methods for retaining species richness in a modified landscape may not be the best method for preserving ecological function. This does not dismiss *Ficus* trees as unimportant, however, as despite making a considerable effort to survey the largest non-*Ficus* trees in the landscape, the results presented in Table 5.1 demonstrate that *Ficus* trees, on average, were larger than the largest non-*Ficus* trees. This is perhaps unsurprising as hemi-epiphytic *Ficus* species, such as those included in this study, use the largest non-*Ficus* trees as hosts during the early stages of their life cycle (Laman, 1996) before strangling them, which inevitably makes them larger than the original tree.

We found that isolated *Ficus* trees have higher functional dispersion than expected by chance (Figure 5.4 & 5.5), and that functional dispersion falls at a faster rate than would be expected as species richness declines, indicating the influence of some form of environmental filtering. However, this pattern was not identified in the two other tree categories, suggesting that the filter effect only applied to *Ficus* trees. This may be because *Ficus* trees have higher maximum species richness, which includes some functionally unique species in richer assemblages, or that the functionally unique insectivores in *Ficus* trees are particularly vulnerable to environmental changes in human-modified landscapes.

Given the results of a number of studies that have analysed invertebrate communities on *Ficus* trees, it is surprising that no previous research has studied the importance of *Ficus* trees for insectivorous bird richness or abundance. In comparison to two other tree types, our results suggest that researchers may have overlooked the importance of *Ficus* trees for insectivores. This may be a consequence of the focus on seed dispersal and frugivory in *Ficus* trees, which may be a more important ecological service

(Sekercioglu, 2006), and is certainly a more obvious interaction (Walker, 2007). Indeed, in his study of the dietary specialisations of frugivorous birds in lowland Sulawesi, Walker (2007:347) commented that insectivory is "harder to observe", especially as discrete prey consumption incidents can be difficult to discern. One illustration of this may be the Oriental White-eye (*Zosterops palpebrosus*), which has been reported consuming *Ficus* fruit in Pakistan and Thailand (Poonswad et al., 1998 and Roberts, 1992 in Shanahan et al., 2001). While we do not question the veracity of these records, especially in light of Compton et al.'s (1996) observations of *Ficus* consumption in captive Cape White-eyes (*Z. pallidus*), we did not see a single incidence of frugivory from the 107 Oriental White-eyes recorded over 120 hours of observation. Instead, we regularly saw Oriental White-eyes gleaning near the base of, or on the surface of, *Ficus* syconia, which we interpreted as incidences of insectivory. These observations were supported by reports in the invertebrate *Ficus* literature of ant, homopteran, and fig wasp behaviour, which identified the base and surface of *Ficus* syconia as important feeding and egg laying locations.

Several studies have argued for the need to conserve isolated trees in human-modified habitat (Harvey & Haber, 1999; Luck & Daily, 2003; Manning et al., 2004; 2006; Sekercioglu et al., 2007; Fischer et al., 2010). Our results build upon these arguments, adding that isolated trees can be important resources for insectivores as well as frugivores (Luck & Daily, 2003), and tree-hole nesters (Manning et al., 2004). We consider this a valuable finding, as we have few conservation strategies focused on this vulnerable group in modified landscapes. We also add that *Ficus* trees may be particularly important for insectivorous birds in human-modified landscapes. In our study area at least, this implies that conserving *Ficus* trees ahead of other tree types may be a more effective conservation strategy than conserving isolated trees at random. If *Ficus* trees are found to be similarly important to insectivorous birds in modified landscapes on a wider spatial scale, a "*Ficus* first" approach to isolated tree conservation may be effective across the tropics. Although additional studies on *Ficus* trees and insectivores are lacking, *Ficus* have been found to support rich and abundant insect communities wherever they have been studied (Thomas, 1988; Compton & Hawkins, 1992; Basset & Novotny, 1999; Pereira et al., 2000; Bain et al., 2013).

The richness estimators predicted that *Ficus* trees were visited by a higher number of insectivore species than the other two categories, a finding that was supported by the richness analysis of variance tests. Although higher richness implies that *Ficus* trees may be more valuable sites for conservation, there is a risk that they hold more species because they are attracting a particular and different assemblage to the other tree types, so that conserving *Ficus* trees may drive community divergence and eventually result in a non-analogue scenario where birds more representative of the wider habitat are lost (Vegas-Vilarrúbia et al., 2011). However, the Shannon diversity index and Morisita scores are similar across all three groups, allaying these concerns, and indicting that *Ficus* trees are in fact simply attracting more species from the same species pool.

In addition to testing the importance of isolated *Ficus* trees for insectivores in other parts of the tropics, it may also be worth investigating the importance of isolated *Ficus* trees to migratory insectivores. The decline in migratory insectivores has been well documented in both the Nearctic (Robbins et al., 1989; Komar, 2006) and Palearctic (Sanderson et al., 2006; Vickery et al., 2014), as migratory insectivores face challenges at all stages of their movement cycle (Reif, 2013). As part of a wider study, we surveyed 24 isolated *Ficus* trees, using the same methodology, in November and December 2012. The seasonal differences in insectivore richness and abundance meant we could not compare these trees to the surveys presented here, as 66 individuals of an additional 11 migratory insectivores were recorded. They included four *Phylloscopus* warblers and the Grey-headed Canary Flycatcher (*Culicicapa ceylonensis*), which in several cases appeared to centre their wintering territories on isolated *Ficus* trees. It would be interesting to see if future studies, that set out to rigorously compare the use of different isolated tree types, find similar results for overwintering insectivores. If so, it would suggest that there is more scope to conserve migratory insectivores in intensely modified landscapes than previously acknowledged (Petit & Petit, 2003; Perfecto et al., 2004; Perfecto & Vandermeer, 2008).

Although the results suggest *Ficus* trees may be more valuable in insectivore conservation than other fruiting or large trees, the generalised linear models indicate that tree size and land-use intensity may also be important in determining their use by insectivores in modified landscapes. The models suggest we should prioritise the conservation of large trees, and reduce the intensity of land-use in their immediate vicinity. This reflects the arguments of Lindenmayer et al. (Lindenmayer et al., 2012; 2013), who advocate that large, old trees have especially high conservation value. The functional diversity results also carry more general implications for modified landscapes that lack *Ficus* trees. The finding that large trees are linked to higher functional dispersion suggests that landscapes with large isolated trees will conserve more functional diversity than equivalent landscapes without large trees. As such, this is a useful empirical test of Lindenmayer et al.'s assertion that large old trees are more ecologically important than younger trees, especially in agricultural landscapes (Lindenmayer et al., 2012).

The conservation of large trees in modified landscapes presents significant challenges, however. It requires a long-term vision with extensive commitment from landowners (Manning et al., 2004), and can incur substantial costs if natural regeneration is insufficient (Fischer et al., 2010). The regeneration of *Ficus* trees may be particularly challenging, as many species are epiphytic in their early life stages, and so depend upon the presence of large host trees (Leighton & Leighton, 1983). Fortunately, evidence from the study area indicates that, in this region at least, *Ficus* trees are regenerating faster in modified habitats than are isolated trees in other parts of the world (Gibbons et al., 2008; Cottee-Jones et al., *in review*). If the conservation of isolated *Ficus* trees was adopted in legislation, there is scope for future work to focus on thresholds for the tree size required to qualify for protection, and the size of buffer zones around isolated trees where land-use practices may be restricted.

5.7 Conclusion

The conversion of forest to agriculture has a particularly negative impact on insectivorous birds, which are believed to provide important ecological pest control services. In human-modified landscapes, the conservation of isolated trees has been identified as a means of preserving ecological function. Here we build on these observations and find that *Ficus* trees are particularly important in conserving insectivore richness and abundance, demonstrating for the first time the overlooked importance of *Ficus* trees for insectivorous birds. However, the size of the isolated tree appears to be the most important determinant of high functional diversity. Therefore, we argue that successful conservation strategies in human-modified landscapes need to incorporate measures to safeguard the future of both isolated *Ficus* trees and large trees *per se* to achieve dual compositional and functional goals.

5.8 Acknowledgements

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5.10 Supporting information

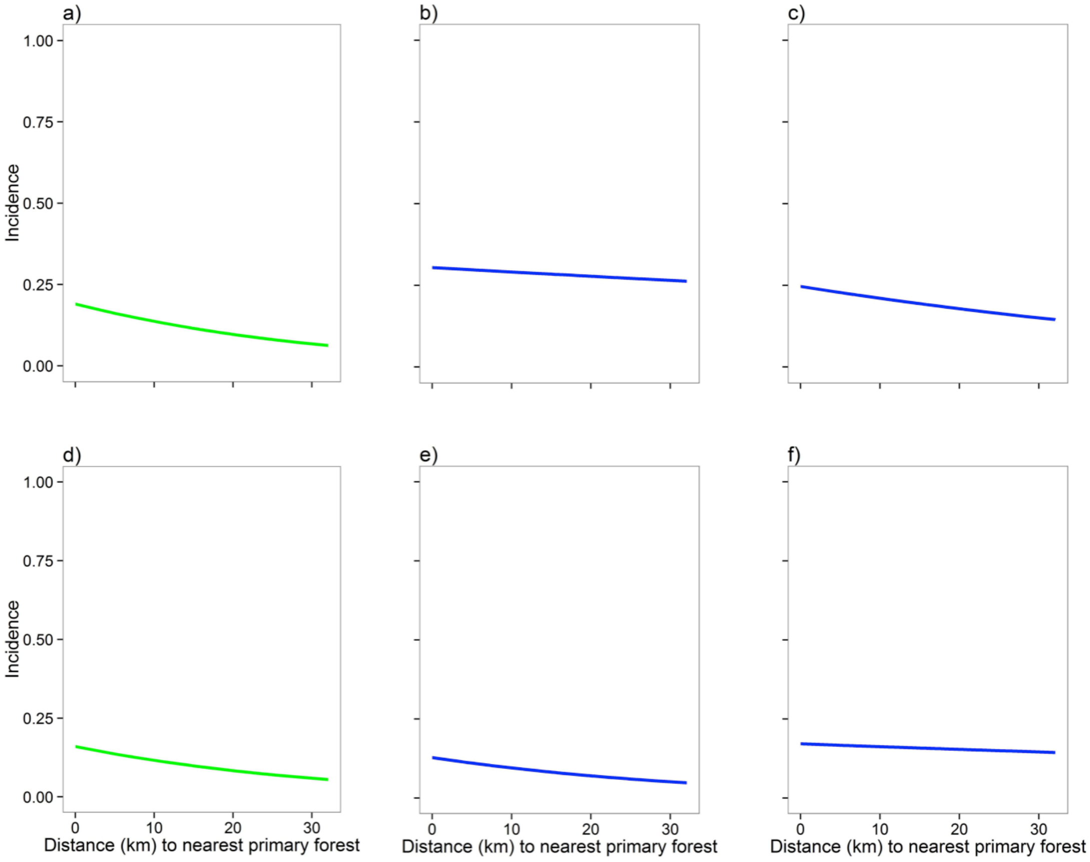
Supporting information A

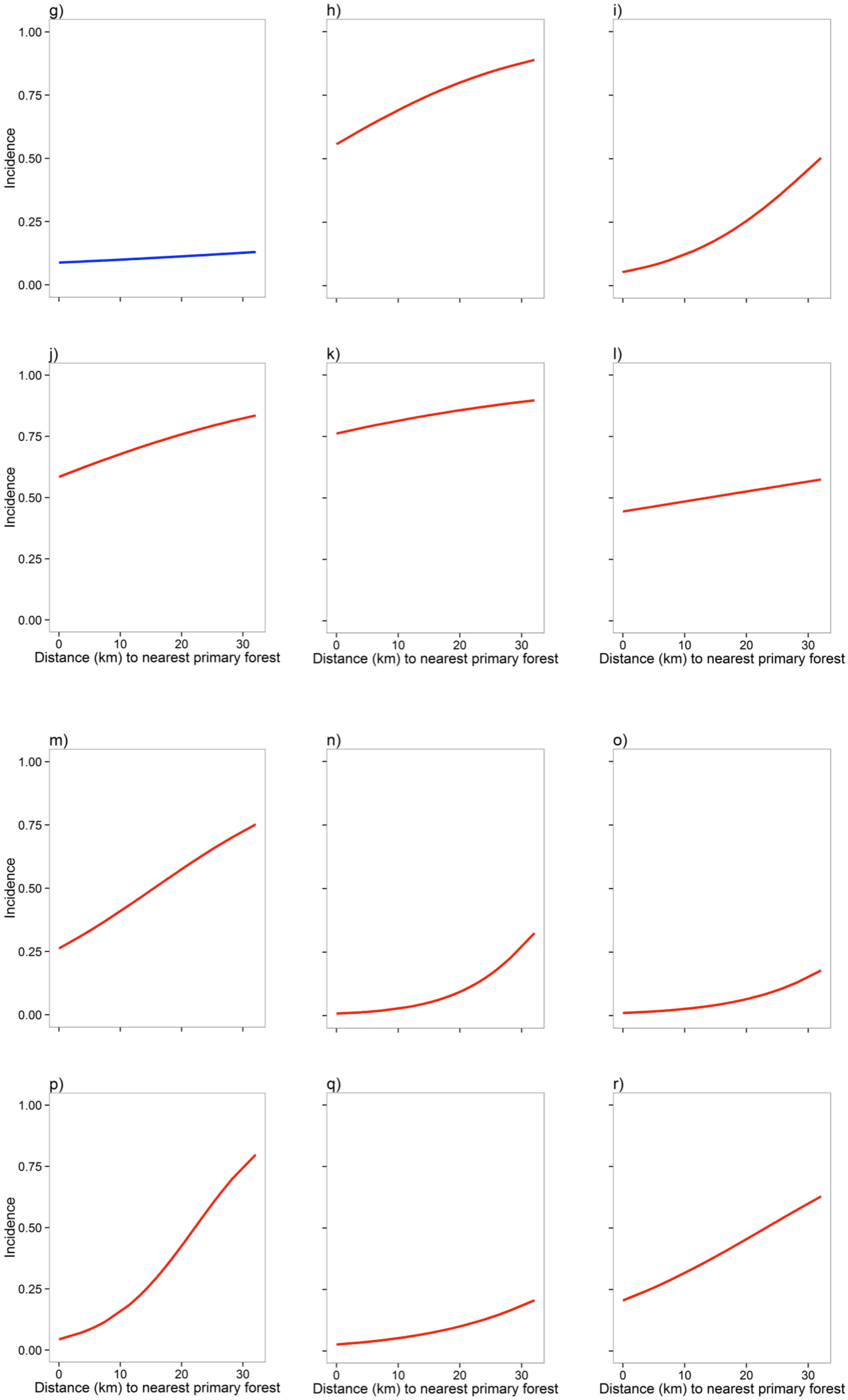
To calculate the area of land under agricultural production in the world's tropics, we followed the methodology of Phalan et al., 2013. We defined tropical countries as those that have at least one-third of their land area between the Tropics of Cancer and Capricorn, producing a list of 129 countries. We downloaded data on the extent of total agricultural area in each of these countries for the most recent year (2011) from FAO STAT (2014). We summed these figures to produce an estimate of the total land area under agricultural production in tropical countries (2,455,649,900 ha, rounded to 2.5 billion ha).

Supporting information B

To determine which distance measure to use in our analyses (isolated tree to nearest protected area, or isolated tree to nearest forest of any quality), we ran two linear regression models to find the best fitted line for distance and insectivore abundance. First we Log10 transformed our insectivore abundance data, as initial tests found a leptokurtic distribution in the standardised residuals P-P plot. We then ran a linear regression model for each distance measure in turn. We found that the distance from protected area had a better fit (R^2=0.35) than the distance from the nearest forest of any quality (R^2=0.26), and so used the distance from the nearest protected area as our distance measure throughout the analyses.

Supporting information C

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Incidence
1.00
0.75
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0.25
0.00
0
10
20
30
Distance (km) to nearest primary forest

Figure 5.6: Incidence functions for 18 insectivore species recorded in the study. Green curves represent forest-dependent species, blue represent habitat-generalists, and red represent matrix-specialists. The curves are the predicted probability of occurrence, generated through a logistic regression model with distance from the nearest protected area as the predictor variable for each species' presence/absence data at 40 isolated *Ficus* trees. Species are a) Hair-crested Drongo *Dicrurus hottentottus*; b) Black Drongo *Dicrurus macroercus*; c) Red-throated Flycatcher *Ficedula albicilla*; d) Large Cuckoo-shrike *Coracina macei*; e) Indian Roller *Coracias benghalensis*; f) Black-rumped Flameback *Dinopium benghalense*; g) White-breasted Kingfisher *Halcyon smyrnensis*; h) Great Tit *Parus major*; i) Common Iora *Aegithina tiphia*; j) Oriental Magpie Robin *Copsychus saularis*; k) Oriental White-eye *Zosterops palpebrosus*; l) Common Tailorbird *Orthotomus sutorius*; m) Scarlet-backed Flowerpecker *Dicaeum cruentatum*; n) Indian Cuckoo *Cuculus micropterus*; o) Greater Flameback *Chrysocolaptes lucidus*; p) Crimson Sunbird *Aethopyga siparaja*; q) Asian Barred Owlet *Glaucidium cuculoides*; r) Fulvous-breasted Woodpecker *Dendrocopos macei*. The figures were constructed using the R package GGplot2 (Wickham, 2009).

Supporting information D

To investigate the effect of area on insectivore richness, abundance, and FDis values in isolated *Ficus* trees, we conducted an additional analysis of these three scores across *Ficus*, fruit, and large trees when controlling for area. We used canopy area as the best proxy for area, and divided richness, abundance, and FDis by canopy area for each tree. After examining the assumptions of normality and heteroscedasticity, the new average values for each tree category were compared using ANOVA with Welch's F and Games-Howell post hoc tests, and a Kruskal-Wallis test in the case of FDis (Table 5.7).

Table 5.7: Differences between insectivore species richness, abundance, and functional diversity parameters across the three tree categories, controlled by canopy area. Values are means ± standard error. Abundance is the mean number of individual insectivores recorded in each tree per m^2, and presented in tree categories. Observed richness is the mean number of insectivorous bird species recorded in the surveys of each tree per m^2, presented by category. FDis is a multidimensional index of the mean distance of an individual species to the centroid of all species in the community (Laliberté & Legendre, 2010). No significant differences were found at $p<0.05$ using ANOVA with Welch's F (following significant Levene's test results for all three measures: Abundance $_{(2,101)}=3.21$, $p<0.05$; Observed richness $_{(2,101)}=4.41$, $p<0.05$), or a Kruskal-Wallis test for FDis.

Parameter	***Ficus***	**Fruit**	**Large**
Abundance	0.04±0.004	0.04±0.01	0.04±0.01
Observed richness	0.02±0.002	0.03±0.01	0.03±0.01
FDis	0.004±0.001	0.01±0.002	0.01±0.004

This test found that there were no significant differences in abundance, richness, or FDis between isolated *Ficus*, fruit, or large trees per m^2 of canopy area. This result verifies the importance of tree size for insectivore abundance, species richness, and FDis. We elected to exclude area controlled results from the main analysis as we were more interested in using trees as the unit of study, as this can more directly be influenced by conservation measures. Furthermore, we felt that having a large canopy area was intrinsic to the advantage *Ficus* trees may possess over other species in terms of insectivore conservation, and so controlling for area would constrain our ability to compare the actual conservation value of each tree type.

CHAPTER 6:

Differences in relative seed dispersal effectiveness in sympatric *Megalaima* barbets in a human-modified landscape

6.1 Preface

Along with the abundance and diversity of insectivorous birds visiting *Ficus* trees, another aspect of relationship between birds and isolated *Ficus* trees that was striking during the surveys was the bird interactions while feeding in the tree. In this chapter, interactions of congeneric barbets, which are major fig consumers, and the consequences for seed dispersal were analysed as a case study.

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The co-author contributions were as follows. Conceived and designed the study: HEWC-J. Conducted the data collection: HEWC-J. Analysed the data: HEWC-J. Wrote the paper: HEWC-J, TJM, RJW. Further details of the co-author contributions and their consent to the use of this material in this thesis are provided in Appendix 4.

This chapter has been submitted to Oecologia.

6.2 Abstract

Seed dispersal is a critical ecological function, which in tropical forests is heavily reliant on mutualistic interactions between frugivorous birds and plants. Beyond the forest edge, in human-modified landscapes, the breakdown of this relationship can have negative consequences for both plants and frugivores, threatening the long-term persistence of both groups. Here we study the strength of the relationship between an important group of frugivores (*Megalaima* barbets) and a critically important food source (*Ficus* trees) in a human-modified landscape in Assam, India. We surveyed the barbets feeding at 62 isolated *Ficus* trees, logging 186 hours of observation, and recording four species of congeneric barbet. We found that smaller barbets are less abundant on larger-fruited *Ficus* trees, while large barbets have the same abundance across fruit sizes. This result supports observational records from studies of different *Megalaima* barbet assemblages around Asia, suggesting a common driver of sympatric barbet community composition that is consistent across both space and taxa. Inter-species resource partitioning patterns also indicate that, despite the high diversity of closely related taxa, their ecological roles are complimentary rather than redundant. Finally, despite the most abundant species, *M. haemacephala*, disrupting seed dispersal by preferring to bite unripe fruit, we found that *Ficus* seeds are still effectively dispersed in the study landscape by the larger *M. lineata*.

Keywords Assam, conservation, *Ficus*, functional redundancy, human-modified landscape, India, plant–frugivore mutualism, seed dispersal biogeography

6.3 Introduction

Vertebrate seed dispersal is a critical process in sustaining plant population dynamics (Howe & Smallwood, 1982; Loayza & Rios, 2013). In intact tropical forests, seeds dispersed further away from their parent plant face a lower risk of density-dependent mortality, and so have a higher chance of survival (Janzen, 1970; Connell, 1971; Howe & Miriti, 2004). To achieve this, an estimated 90% of tropical forest plants disperse their seeds through mutualistic interactions with frugivores (Howe & Smallwood, 1982; Jordano, 2000), a mechanism which is widely recognised for determining the structure of plant communities in tropical forests (Tiffney & Mazer, 1995; Terborgh et al., 2002; Schupp et al., 2010).

Beyond intact tropical forests, the mutualistic relationship between frugivorous seed dispersers and plants may suffer from reduced functionality. For example, Cordeiro and Howe (2003) report that in fragmented forests, birds that dispersed the large *Leptonychia usambarensis* seeds were rarer in small fragments, and that where fewer seeds were removed from fruiting trees, more seedlings aggregated under the crown of parent trees, compared to continuous forest. Beyond the forest edge, in human-modified landscapes, the state of the mutualistic relationship between plants and seed dispersers may be of even greater concern (Sekercioglu, 2006; McConkey et al., 2012). High human population densities and intense land-use may deter dispersers from foraging in isolated fruit trees. Where this occurs, negative consequences for the frugivores may include population collapses, range contractions, or even extinction (Farwig & Berens, 2012; Caves et al., 2013) while the plant mutualists may suffer from reduced dispersal and therefore lower recruitment (da Silva & Tabarelli, 2000).

The effectiveness of seed dispersal depends on the attributes of the frugivores involved (Bas et al., 2006). A frugivore's foraging behaviour can influence both the quantity (the number of seeds consumed) and quality (where they are dispersed, their probability of germination) of seed dispersal (Poulsen et al., 2002; Schupp et al., 2010). In this respect a frugivore's fruit handling behaviour, the way a frugivore manipulates and consumes fruit, is crucial (Fleming, 1986). For birds, frugivores may be divided between biters, mashers, and swallowers (Foster, 1987; Levey, 1987). Each of these fruit handling techniques has different consequences for the effectiveness of seed dispersal, with bitten and mashed fruit more likely to result in seeds being deposited under the parent plant, while swallowed fruit is more likely to be dispersed away from the parent, and therefore germinate and grow successfully (Terborgh et al., 2002).

To examine the effectiveness of seed dispersal in human-modified landscapes, we studied the mutualistic interaction between four species of an important genus of frugivorous birds, the *Megalaima* (Capitonidae) barbets, and scattered *Ficus* L. (Moraceae) trees. Their extremely large crop sizes, intra-crown fruit ripening synchrony, inter-tree asynchrony, relatively short intervals between fruiting, unusual nutritional composition, and aseasonal fruiting pattern mean *Ficus* trees are a critical fruit resource in intact tropical forests (Leighton & Leighton, 1983; Terborgh, 1986; Lambert & Marshall, 1991; O'Brien et al., 1998; Kinnaird et al., 1999; Shanahan et al., 2001). There is also increasing evidence that they are important conservation structures in human-modified landscapes, at least partially supporting numerous frugivorous and insectivorous bird species (Eshiamwata et al., 2006; Cottee-Jones & Whittaker, *in review*; Cottee-Jones et al., *in review*), and fostering rainforest regeneration (Slocum, 2001; Guevara et al., 2004; Cottee-Jones et al., *in review*).

Megalaima barbets are widespread and specialised Asian frugivores. They exhibit a high degree of dietary specialisation towards *Ficus* fruit, and search out fruiting figs over large distances (Shanahan et al., 2001; Short & Horne, 2001). One radio-tracking study of *M. henricii* in intact forest recorded individuals travelling up to 700 m from roosting to feeding sites, and spending 71–85% of diurnal time in a fruiting *Ficus* (Lambert, 1989a). Other studies of *Megalaima* barbets in India have suggested that the occurrence of several similar species indicates complementary seed dispersal patterns, rather than ecological redundancy, with observations of co-existing barbets preferentially feeding on *Ficus* fruit of different sizes, depending on their beak dimensions (Yahya, 2013). This supports Lambert's work, which revealed a degree of resource partitioning in the *Megalaima* barbets of lowland Malaysia (Lambert, 1989b). In his study, the smallest species, *M. australis*, was commonly observed in the canopies of small fruited *Ficus* trees, but absent from *Ficus* with a fruit width greater than 20 mm. Meanwhile the largest species, *M. chrysopogon*, was more abundant on larger fruited *Ficus*, and two barbets of intermediate weight occurred in lower numbers at *Ficus* trees of all fruit sizes. Although no studies have focused on their fruit handling behaviour, Shananhan has observed a *Calorhamphus* barbet (*C. fuliginosus*) swallowing small (7 mm diameter) *F. obscura* figs whole, mashing 11 mm *F. subgelderi* figs, but only pecking at 30 mm *F. subcordata* figs (Shanahan et al., 2001).

In light of these gaps in the literature, we sought to determine 1) whether barbets exhibit seasonal flocking patterns, which would effect the biogeography of dispersed seeds; 2) whether barbets exhibit a degree of species-specific resource partitioning depending on *Ficus* fruit size, an absence of which would indicate some ecological redundancy; and 3) whether barbet fruit handling techniques, and therefore dispersal effectiveness, vary according to fruit ripeness.

6.4 Methods

6.4.1 Study area

We conducted this study from October 2012 to June 2013 in a mixed agricultural landscape in Golaghat District, Assam, India (N26 27.819 E93 54.978). The study area receives an average of 1,500–2,500 mm of rain per year, and is characterised by strong monsoon seasonality, with heavy precipitation between May and August (Shrivastava & Heinen, 2007). The area lies between 30–100 m above sea level with temperatures ranging from a mean annual minimum of 5°C to a mean annual maximum of 35°C (Barua & Sharma, 1999). The original habitat of moist subtropical deciduous forest was cleared following the local commercialisation of tea production in 1840 (Shrivastava & Heinen, 2007), producing a heterogeneous mix of small-holder rice cultivation, tea estates, and village home gardens today.

6.4.2 *Ficus* trees

Across this heavily modified landscape, large scattered trees of the *Ficus* genus are fairly common (mean density=3.17±0.26 mature trees/km^2; Cottee-Jones et al., *in review*). The approximately 750 species of *Ficus* found worldwide exhibit a great range of growth forms and fruit presentation patterns (Chaudhary et al., 2012). The species included in this study were all hemi-epiphytic species that grew to be large (mean±standard error=25.45±0.99 m in height, range=12.74–51.70 m) semi-deciduous or evergreen trees. Three of these species (*F. religiosa*, *F. rumphii*, and *F. microcarpa*) have small fruit (mean diameter when ripe=131±4 mm), while one (*F. benghalensis*) has larger fruit (182±5 mm). All species, when mature, produce very large fruit crops (with tens of thousands of fruits) asynchronously throughout the year, with each fruit containing a mean of 104±18 small seeds (*unpublished data*).

6.4.3 Barbet surveys

We surveyed the barbets foraging at fruiting *Ficus* trees scattered in the human-modified landscape from October–December (“winter”) and then from March–June “monsoon”). For each barbet survey, we identified a *Ficus* tree with a large ripe crop and surveyed it for three hours, starting at first light (which ranged from 04:20–05:20 depending on the season). Surveys were only conducted in fair weather conditions. The fruit widths for each survey tree were estimated by collecting eight freshly fallen fruit, which were then dissected with a sharp knife and measured using a finely marked ruler.

During the survey period, an observer stood in a concealed position with a good view of the tree, typically about 20 m from the trunk. The observer used a pair of 10 × 50 binoculars to record the number of barbets of each species visiting the tree during the survey period. For instances where the total number of barbets was unclear due to numerous repeat visits, the maximum number of barbets in the tree at any one time was used. The four barbet species encountered in this study were very inconspicuous once in a *Ficus* trees, aside from their distinctive vocalisations. Therefore, while their presence was easy to detect, recording their abundance demanded assiduous observation of all birds landing in and leaving the tree.

During periods when barbets were feeding during a survey, a second observer would opportunistically watch an individual bird until it moved out of sight. The high numbers of birds, frequency of movement, density of foliage, and height the birds typically foraged at meant it was difficult to follow an individual for more than one minute. The observer recorded the number of fruits each barbet consumed according to the fruit handling method and fruit ripeness. Fruit handling was classified as one of biting, mashing, or swallowing, while fruit ripeness was judged by the size and colour of the fruit. Unripe fruits were smaller than 110±2 mm in diameter for *F. religiosa*, *F. rumphii*, and *F. microcarpa*, and 150±4 mm in *F. benghalensis*, and were light green in colouration in all species (ripe fruits were dark red, black, white, or orange, depending on the species). The fruit was then categorised as being either unripe (small and green), having intermediate ripeness (for cases where ripeness was hard to determine), or ripe (large and maturely coloured). For consistency, the same observer (HEWC-J) made all records of fruit ripeness. These data were entered into a table for each barbet species, recording the number of fruits consumed per tree in each category: unripe, bitten; unripe, mashed; unripe, swallowed; intermediate bitten; etc.

We also kept a record of the distances barbets flew when leaving a *Ficus* tree. These departure distances were hard to measure empirically due to the frequency of barbet departures, the long distances and numerous physical obstacles involved. Instead, we classified departure distances into one of three categories: short, medium, and long. "short" was for birds flying to perches within 50 m of the tree, "long" for birds flying away over the horizon, and "medium" for any distance in between. We only recorded the distance of departure in cases where we could confirm the barbet had stopped its journey in that category (except for the "long" group), and so not every barbet recorded in the surveys had a departure distance record.

6.4.4 Ecomorphological data collection

Our observations in the field suggested that the four barbets recorded exhibited considerable morphological variation, from the small Coppersmith (*M. haemacephala*) and Blue-eared Barbets (*M. australis*), to the intermediate Blue-eared Barbet (*M. asiatica*), and finally the large Lineated Barbet (*M. lineata*). To quantify this variation, we measured the ecomorphological traits of these species from specimens held in the ornithological collections of the British Natural History

Museum. We followed Edward Grey Institute protocols in measuring four specimens of each species, taking care to select specimens of the correct subspecies, and which were collected close to the study area (which was possible for all species). Two adult males and two adult females of each species were measured with 150 mm outside diameter dial callipers (accurate to 0.1 mm) and wing rulers (accurate to 0.5 mm) from Porzana Ltd. The measurements taken were: bill length from nares (from the anterior of the nares to the tip of the bill), gape width, tarsus length (the length from the inner bend of the tibiotarsal articulation to the base of the toes, where the scalation pattern changes), wing chord (from the bend in the wing to the unflattened longest primary), and Kipp's Distance (the distance from the longest primary to the first secondary) (Kipp, 1959; Sutherland et al., 2004). To create an index for dispersal ability that standardises for bird size, we calculated the hand-wing index (Claramunt et al., 2012) from the two wing measurements; this index is a surrogate for flight performance, migratory behaviour, and natal dispersion in birds. The measured characteristics of the four barbets were tested for significant differences using ANOVA, with a Bonferroni post hoc test.

6.4.5 Statistical analysis

To identify any distance effects we plotted incidence functions for the four barbet species. First we marked the locations of each *Ficus* tree with a GPSmap 62s device, and then overlayed the GPS markers on Landsat 8 satellite images of the region in ArcGIS 10.2 (ESRI, 2014). We digitised the protected area borders through an on-screen visual interpretation (Berens et al., 2008), and then measured the distance (in km) of each focal tree to the nearest protected area using ArcGIS. In all cases, protected areas held the only high-quality forest habitat left in the study landscape. Using a larger data set of isolated *Ficus* surveys collected with the same field methods from 2009–2013 (n=122), we ran binary logistic regression models with species presence or absence as the response variable, and distance from the nearest forest as the predictor variable (Watson et al., 2005). The resulting predicted probabilities of occurrence were then used to plot incidence functions against distance for each species. Although the Blue-eared Barbet is reported to occur in human-modified habitats (Short & Horne, 2002), we only recorded five individuals in our surveys, despite it being common in a neighbouring forest (Panbari Forest Reserve, N26 36.727 E93 29.722). This, combined with the sharp downward incidence function curve, meant we excluded it from further analysis.

To determine whether barbets altered their flocking behaviour depending on the season, we compared the mean number of barbets recorded per survey during winter and the monsoon, which was tested for significance using a Mann-Whitney U test as the data did not meet parametric assumptions. We then compared mean flock sizes per species for all surveys with a Kruskal-Wallis test and Mann-Whitney U post hoc tests with a Bonferroni correction of p=0.0167 to identify significant differences between pairs of species (Field, 2009).

To identify any resource partitioning between species, we tested the abundance of the three barbet species recorded in the surveys against the survey tree fruit size. We performed a Multivariate Analysis of Covariance (MANCOVA), with fruit size as a fixed effect, season as a covariate, and log-transformed barbet abundances as the dependent variable (we used a log10+1 transformation to achieve normality). Fruit size was classified by grouping survey trees into two categories: trees with small (<16 mm) or large (>16 mm) mean fruit widths. 16 mm was selected as the cut-off between groups as this was the median fruit width across all samples. We used Box's M test to examine the assumption of equality of covariance matrices, Levene's test to examine the assumption of multivariate normality, and Pillai's Trace to manage the unequal sample sizes in our fixed effect. We followed-up the MANCOVA with univariate ANOVA post hoc tests (with Levene's test for the assumption of homogeneity of variance and a Bonferroni correction of $p=0.0167$), and a discriminant functions analysis to identify specific differences between species (Field, 2009).

To determine fruit handling patterns, we calculated the proportion of consumed fruits that were handled with each method for each species, split into groups according to fruit ripeness. We conducted a Friedman test to examine whether fruit handling behaviours differed statistically depending on ripeness within each species. We followed this with post hoc Wilcoxon signed rank tests to assess specific differences between the two most indicative handling groups: biting unripe fruit, and swallowing ripe fruit.

We then examined differences in the flight distances of barbets when leaving a *Ficus* tree, to provide an indication of the effectiveness of different species as seed dispersers across the landscape. We followed this by cross-tabulating barbet departure distances by barbet species, and testing the difference in observed value against the difference in expected values with a Pearson Chi-square test, saving the adjusted standardised residuals. All analyses were conducted in IBM SPSS Statistics 22 (IBM, 2013).

6.5 Results

We conducted a total of 62 barbet surveys at fruiting *Ficus* trees, logging 186 hours of observation. Of these surveys, 24 were completed in the winter, and 38 were completed in the monsoon, while 20 *Ficus* trees were categorised as having large fruit, and 42 as small. Barbets were recorded during all 62 surveys, with a modal richness of three species. The most frequently recorded species was the Coppersmith Barbet, which was recorded at 92% of surveys (57/62). The Coppersmith was followed by the Blue-throated and Lineated Barbets, which were both recorded at 85% of surveys (53/62), and finally the Blue-eared Barbet, which was only recorded at 5% of surveys (3/62). The most abundant species was also the Coppersmith Barbet, with 421 individuals, followed by the Blue-throated (296), Lineated (199), and Blue-eared (5) Barbets.

The Lineated Barbet has a significantly larger than gape width than the other barbets ($F_{(3,12)}=50.89$, $p<0.001$, $r=0.96$) (Table 6.1). The Blue-throated Barbet's bill length and gape width was significantly smaller than the Lineated Barbet, but significantly larger than both the Blue-eared and Coppersmith Barbets (ANOVA for bill length: $F_{(3,12)}=180.11$, $p<0.001$, $r=0.99$). The two smaller barbets were very similar in all characteristics except for the hand-wing index of dispersal ability, where the Coppersmith Barbet had a significantly higher score than the Blue-eared Barbet (Figure 6.1).

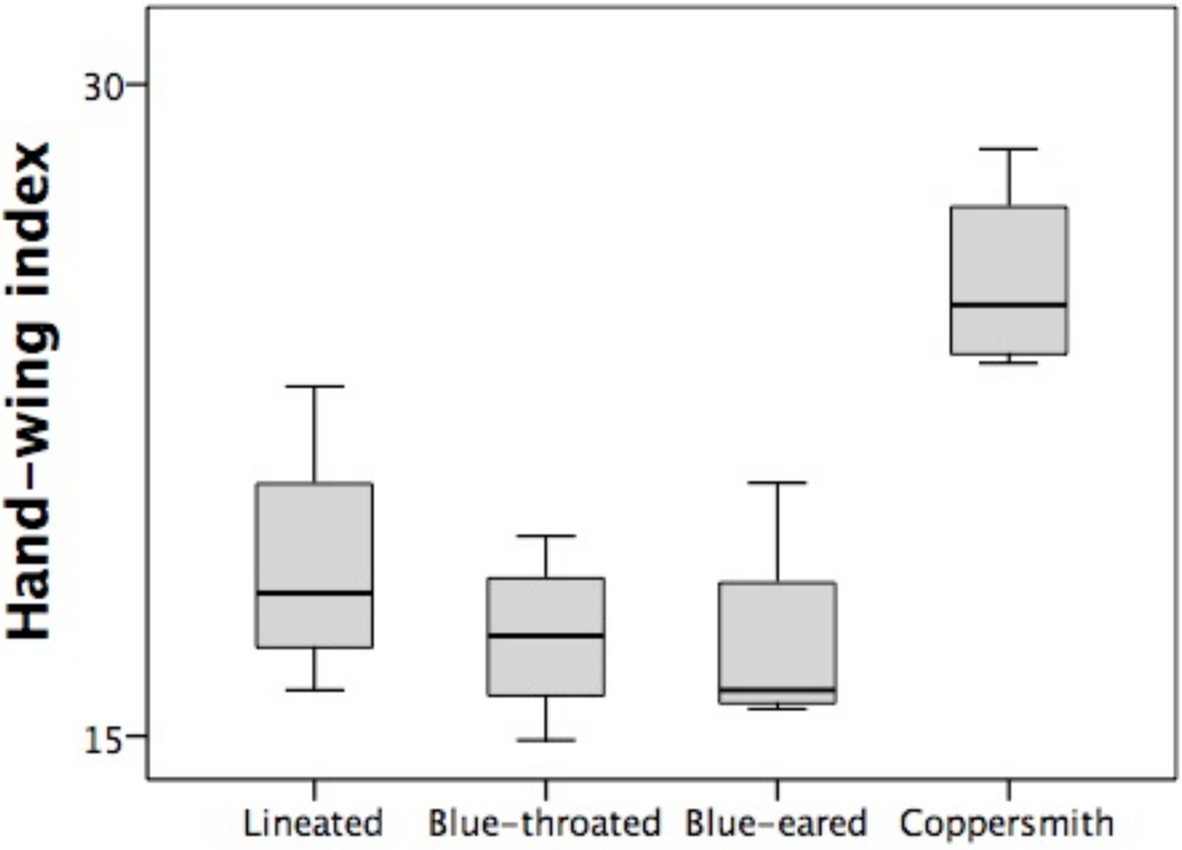

Figure 6.1: Box-and-whisker plot of hand-wing index scores for four *Megalaima* barbet species. Measurements were taken from two adult male and two adult female specimens of each species. Solid lines are the mean, boxes are one standard deviation, and whiskers are the range for each species. Details of significant differences are provided in Table 6.1.

The barbet incidence function plots also emphasised the difference between the two smaller barbets (Figure 6.2). While the Coppersmith Barbet had a very high and consistent incidence across all distances, the Blue-eared Barbet displayed a downward curve as distance from the nearest forest increased, indicative of forest dependent species. The Blue-eared Barbet showed a slight decrease as distance increased, while the Lineated Barbet showed a clear increase, indicating its tolerance of human-modified landscapes.

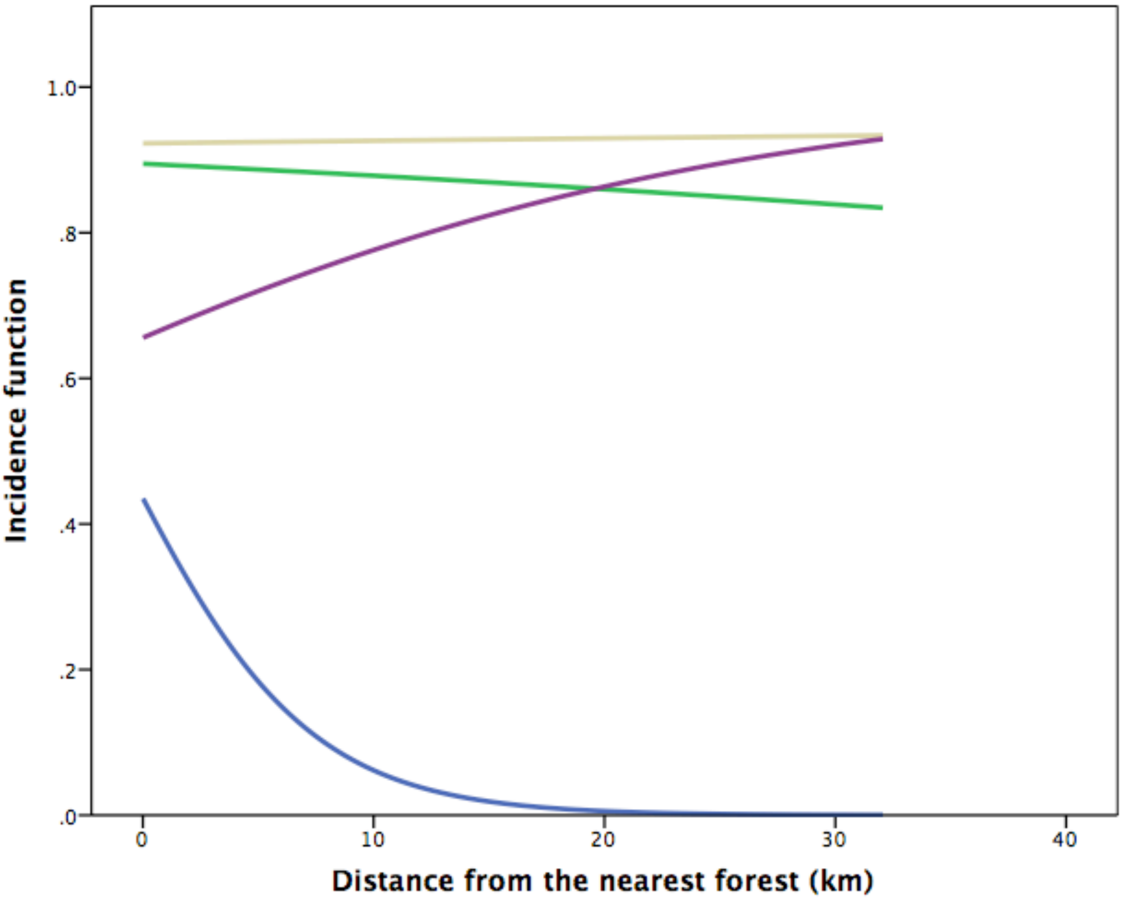

Figure 6.2: Incidence functions of four barbet species, plotted as the predicted probability of each species' occurrence with increasing distance from the nearest intact forest, in Assam, India. The curves are derived from a logistic regression model with distance from the nearest intact forest as the predictor variable, and each species' presence/absence as the response variable. The dataset used to plot these curves was garnered from a larger study of isolated *Ficus* trees in the same landscape (n=122), using the same survey methods. Species are: beige=Coppersmith Barbet *M. haemacephala*; blue=Blue-eared Barbet *M. australis*; green=Blue-throated Barbet *M. asiatica*; purple=Lineated Barbet *M. lineata*.

Our analysis of barbet flocking behaviour revealed seasonal differences between winter and the monsoon. In winter, a mean of 28.21±3.78 (±standard error) barbets were recorded per tree, while during the monsoon this figure decreased to 6.42±0.63. This change in flock sizes between seasons was statistically significant (U=107, p<0.001, r=0.64). Mean flock sizes varied between species (mean±standard error:

Coppersmith Barbet 6.79±1.21; Blue-throated Barbet 4.77±0.69; Lineated Barbet 3.21±0.51), although the Kruskal-Wallis test did not indicate that these differences were significant ($H_{(2)}=5.46$, $p>0.05$).

The Box's M and Levene's tests indicated that the assumptions for the MANCOVA were tenable, while Pillai's Trace suggested that fruit size (0.18, $F_{(3,57)}=4.16$. $p<0.05$) and season (0.43, $F_{(3,57)}=14.37$, $p<0.001$) had a significant effect on barbet abundances. The follow-up univariate ANOVAs indicated that fruit size had a significant effect on the abundance of Coppersmith Barbets ($F_{(1,59)}=11.43$, $p<0.01$), but not on Blue-throated ($F_{(1,59)}=0.03$, $p>0.0165$) or Lineated Barbets ($F_{(1,59)}=0.01$, $p>0.0165$). We also identified a discriminant function which significantly differentiated between groups (Wilks' lambda $\Lambda=0.85$, $\chi^2_{(3)}=9.73$, $p<0.05$). The correlations between outcomes and the discriminant function revealed that Coppersmith Barbet abundance loaded very highly ($r=0.88$), while Blue-throated Barbet ($r=0.01$) and Lineated Barbet ($r=0.01$) were very poor group predictors. The group centroids output indicated that this function discriminates between small (0.29) and large (-0.61) fruit sizes. Reclassification of cases based on the new canonical variables was fairly successful: 71% of the cases were correctly reclassified into their original categories.

For all three species, there was a significant difference between the fruit handling method and fruit ripeness Coppersmith Barbet: $\chi^2_{(8)}=58.82$, $p<0.001$; Blue-throated Barbet: $\chi^2_{(8)}=25.48$, $p<0.01$; Lineated Barbet: $\chi^2_{(8)}=24.19$, $p<0.01$) (Figure 6.3). The post hoc tests indicated that Coppersmith Barbets bit significantly more unripe fruits compared to the number of ripe fruits swallowed ($Z=-3.11$, $p<0.01$), while Blue-throated Barbets showed no significant difference between these two behaviours (Z=-

0.98, $p>0.05$), and Lineated Barbets swallowed significantly more ripe fruits compared to the number of unripe fruits they bit ($Z=-2.37$, $p<0.05$).

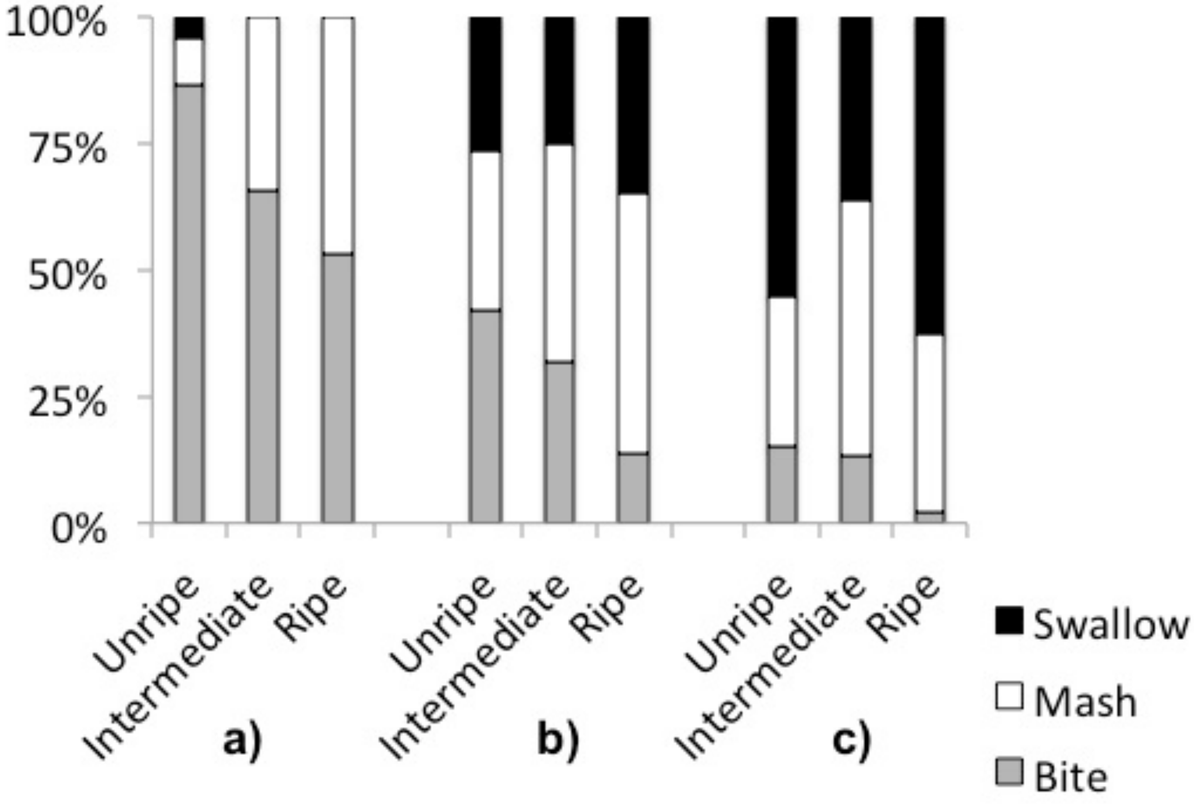

Figure 6.3: The percentage of fruits in each ripeness category swallowed, mashed, or bitten by three *Megalaima* barbet species over 186 hours of observation in 22 isolated *Ficus* trees in Assam, India. Fruit ripeness was judged by size and colour. The same observer (HEWC-J) made all fruit ripeness assessments. Species are: a) Coppersmith Barbet *M. haemacephala*; b) Blue-throated Barbet *M. asiatica*; c) Lineated Barbet *M. lineata*.

The results of the Pearson Chi-square test indicated that barbet departure distances were significantly different ($\chi^2_{(4)}=59.18$, $p<0.001$) (Figure 6.4). The adjusted standardised residuals indicated that far fewer Coppersmith Barbets were undertaking medium length departure flights than expected (adjusted residual=-3.1), and far more were taking long departure flights than expected (4.9). In contrast, Blue-throated Barbets were making far fewer long flights than expected (-4.1), while Lineated

Barbets were making slightly fewer short flights (-1.4), and more medium fights (2.2) than expected.

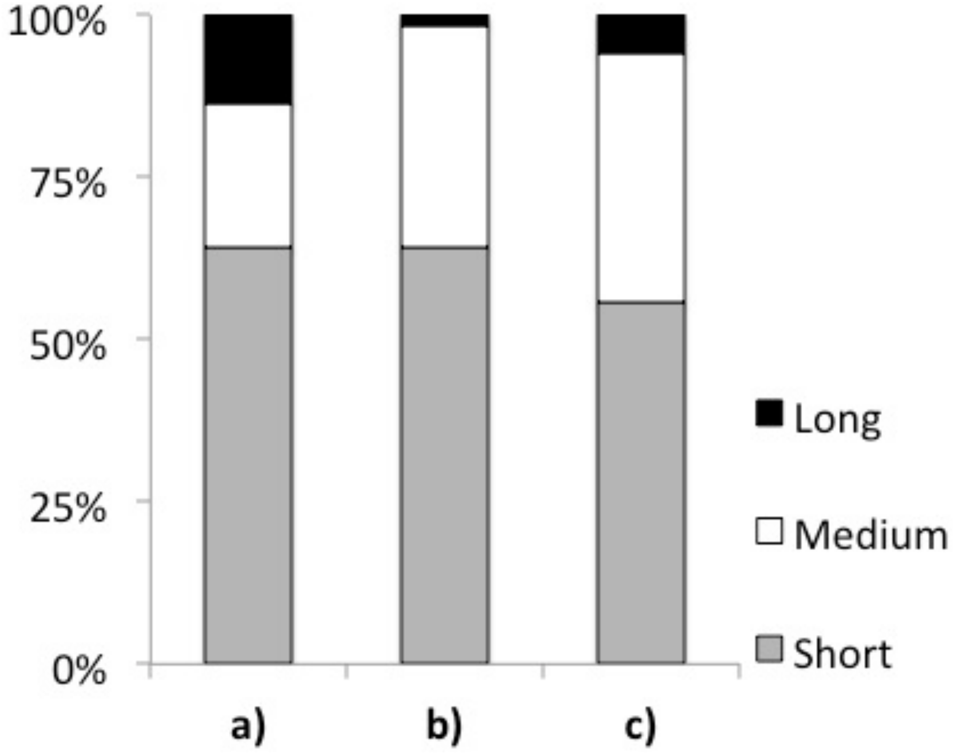

Figure 6.4: Proportion of departure flight distances in short, medium, or long categories for three species of barbet after feeding in isolated *Ficus* trees in Assam, India. Species are: a) Coppersmith Barbet *M. haemacephala*; b) Blue-throated Barbet *M. asiatica*; c) Lineated Barbet *M. lineata*. Departure distances were classified as "short" for birds flying to perches within 50 m of the *Ficus* tree, "long" for birds flying over the horizon, and "medium" for any distance in between. Data derived from observations of 384 Coppersmith Barbet, 420 Blue-throated Barbet, and 286 Lineated Barbet departure flights.

Table 6.1: Ecomorphological measurements of four barbet species recorded in isolated *Ficus* trees in Assam, North-east India. Nomenclature follows Short & Horne, 2002. For weight measurements, the range of males (M) and females (F) is given, followed by the mean in parentheses, where reported (Short & Horne, 2002). All other measurements are averaged over two adult male and two adult female specimens, and are given as the mean of these measurements ± SE. Bill lengths were measured from the anterior of the nares to the tip of the bill. Gape widths were measured from the widest point at the base of the gape The wing:tarsus ratio gives a standardised score for locomotive ability. The hand-wing index is a standardised measure of dispersal ability (Claramunt et al., 2012). For each species, the unflattened wing cord and the distance from the longest primary to the first secondary (Kipp's distance) were measured, before standardisation following Claramunt et al.'s formula. Higher hand-wing index scores indicate greater dispersal ability. Where ANOVAs were significant, different superscript letters in each column indicate significantly different post hoc test scores ($p<0.05$). No significant differences were recorded across the wing:tarsus ratio.

Name	**Weight (g)**	**Bill length from nares (mm)**	**Gape width**	**Wing:tarsus ratio**	**Hand-wing index**
Coppersmith Barbet, *M. haemacephala*	M 30–49.6 (41.5) F 39.4–52.2 (45.8)	13.33 ± 0.23^{a}	14.70 ± 0.48^{a}	4.17±0.19	25.49 ± 1.12^{a}
Blue-eared Barbet, *M. australis*	26–39	14.30 ± 0.40^{a}	13.35 ± 0.32^{a}	4.53±0.22	17.14 ± 1.23^{b}
Blue-throated Barbet, *M. asiatica*	61–103	18.90 ± 0.42^{b}	18.50 ± 0.83^{b}	4.26±0.36	17.28 ± 0.97^{b}
Lineated Barbet, *M. lineata*	M 117–205 (145.6) F 134–170 (151.8)	23.93 ± 0.36^{c}	24.33 ± 0.94^{c}	4.55±0.13	18.92 ± 1.48^{b}

6.6 Discussion

Our results demonstrate that barbets are able to survive in a human-modified landscape, in some cases in high numbers. Indeed, every tree in the study was visited by at least one species of barbet, indicating that they were also fairly widespread. The incidence functions add further support, as the Coppersmith showed no dependency on nearby forests, while the Blue-throated Barbet and Lineated Barbet both increased in likely incidence further into the human-modified landscape (Figure 6.2). The abundance of barbets feeding at fruiting *Ficus* in this landscape offers some promise that the mutualistic plant-frugivore relationship and seed dispersal mechanisms may still be functional.

Although three species were commonly observed (Coppersmith, Blue-throated, and Lineated), the Blue-eared Barbet was only observed in fruiting *Ficus* trees on five occasions. In other parts of its extensive range, the Blue-eared Barbet is reported to venture into patches of tall trees and old plantations on a seasonal basis (Short & Horne, 2001), with some post-breeding dispersal into these habitats suspected (Short & Horne, 2002). These reports agree with our observations, where three of the five Blue-eared Barbets recorded lacked the distinctive black and red facial markings of adult birds, indicating that they were probably dispersing juvenile birds (Grimmett et al., 2011). These field observations, combined with the downward incidence function curve, may partly be explained by the hand-wing index measurements. Although the Coppersmith Barbet, which was widespread across all distances in the human-modified landscape, had measurements that were very similar to the Blue-eared Barbet, the two species differed significantly in their hand-wing index scores. This suggests that the Coppersmith Barbet is morphologically more suited to travelling longer distances in human-modified habitats, while the Blue-eared Barbet is less well adapted to travelling beyond the forest edge. To the best of our knowledge, this is the first documented case of dispersal ability explaining differing responses to habitat modification congeneric species.

For the three commonly observed species, our analysis of their group sizes indicated the existence of different social structures depending on the season. During *Ficus* tree surveys from October to December, the average number of barbets visiting a *Ficus* tree was more than three times higher than group sizes recorded from March to June. In this second survey period, several barbet nests were discovered in the surrounding landscape, while none were detected from October to December (Figure 6.5). Therefore we suggest that the seasonal differences in flocking behaviour were related to breeding cycles, with larger non-breeding flocks forming in the winter survey period. This flocking behaviour may have important consequences for seed dispersal, as these flocks may have been less territorial than breeding barbets, and therefore more likely to travel longer distances in search of fruit (which appeared to be scarce across the study area at the time). Follow-up studies tracking the movements of barbets inhabiting non-forest ecosystems in different seasons would help clarify the significance of this initial finding.

Figure 6.5: Photographs of nesting Lineated (left) and Coppersmith (right) Barbets, taken in Assam, India, during April 2013 by HEWC-J.

The inter-species comparison of barbet abundances on *Ficus* trees with different fruit sizes indicated that Coppersmith Barbets are more responsive to different fruit sizes than the other two species. The occurrence of Blue-throated and Lineated Barbets at very similar abundances on all *Ficus* trees, irrespective of fruit size, indicates that fruit size is not a limiting factor in their foraging behaviour. Other authors have found similar results, and argued that beak size drives *Megalaima* barbet resource partitioning according to fruit width (Lambert, 1989b; Yahya, 2013). For example, in a study of barbets in South-west India, Yahya (2013) found that *M. viridis*, a barbet of similar proportions to the Blue-throated Barbet, fed almost equally on *Ficus* fruit smaller than 8 mm, 8–16 mm, and larger than 16 mm. However *M. rubricapilla* (which has now been split to *M. malabarica*), a barbet of similar proportions to the Coppersmith Barbet, showed a marked preference for smaller *Ficus* fruit, with 70% of feeding records derived from trees with fruit smaller than 8 mm, and only 10% from trees with fruit larger than 16 mm (Yahya, 2013). This, combined with other records from Lambert (1989b), and observations of *M. zeylanica* and the Coppersmith Barbet at Borivili National Park (Yahya, 2013), suggest that *Megalaima* barbet assemblages may follow a compositional pattern that is consistent across space and taxa. While gape width appears to be an important driver in this pattern (Lambert, 1989b; Yahya, 2013), competitive exclusion through aggressive behaviour from the larger species may also be a factor. Larger barbets have been reported to destroy the nests of smaller barbets (Yahya, 2013), and during this study, barbets were observed chasing other *Megalaima* species away from branches laden with ripe *Ficus* fruit on several occasions. In each instance, the aggression was structured by size, with Lineated Barbets chasing both other species, and Blue-throated Barbets chasing Coppersmith Barbets, while Coppersmith Barbets were never observed chasing the larger species. Whatever the driver, this consistent resource-partitioning pattern indicates that these barbets are not ecological equivalents, but rather complement the fruit consumption patterns of their relatives.

Although these results show that *Megalaima* barbets have different fruit size preferences, they do not provide an indication of seed dispersal effectiveness across species. Even in closely related species, important differences in seed dispersal effectiveness may exist, revealing functional complementarity rather than redundancy (Sekercioglu, 2006). For example, in the turacos (Musophagidae), three sympatric species in Rwanda exhibited different seed dispersal patterns (Sun et al., 1997): the smallest species dispersed the highest percentage of seeds away from the parent tree, the intermediate-sized species deposited the seeds most evenly, and the largest species dispersed seeds the farthest (Sun et al., 1997). In our study, the three barbet species exhibited different *Ficus* fruit handling behaviours depending on the ripeness of the fruit. The Coppersmith Barbet showed a preference for biting unripe fruit, the Blue-throated Barbet preferred mashing fairly ripe and ripe fruit, and the Lineated Barbet preferred swallowing ripe fruit. This indicates that Coppersmith Barbets, despite being abundant and widespread frugivores in the study landscape, with the greatest likelihood of making long-distance flights after feeding in a *Ficus* tree, may not be very effective seed dispersers. By favouring fruit that is unripe, they are consuming seeds that are unlikely to germinate. Furthermore, by biting the fruit, they are mainly consuming pulp, while the majority of the seeds fall to the ground beneath the parent tree. This contrasts with the larger Lineated Barbet, which by swallowing ripe fruit, is more likely to consume seeds that will germinate, and to disperse the seeds away from the parent plant. Many other authors have highlighted the special role that larger frugivores play in seed dispersal, being particularly important for large-seeded, late-successional plants (Whittaker et al., 1997; Moran et al., 2004; Sekercioglu, 2006). However, their vulnerability to hunting and land-use change means that large frugivores are usually rare in human-modified landscapes (Jensch & Ellenberg, 1999).

In our study area, the abundant supply of *Ficus* fruit, coupled with the inconspicuous nature of *Megalaima* barbets (Short & Horne, 2001; Yayha, 2013), may help conserve valuable seed dispersal services across this degraded landscape.

6.7 Conclusion

In degraded habitats such as this study system, the plant–frugivore relationship is believed to be under threat, with few frugivores and limited seed dispersal. However, this study found *Megalaima* barbets to be common and widespread at isolated *Ficus* trees in a human-modified landscape. This included the 205 g Lineated Barbet, which as a rare example of a large frugivore persisting in a degraded landscape, may be a particularly important seed disperser in this context. We found seasonal differences in barbet flocking behaviours, which are likely to produce temporal fluctuations in seed dispersal patterns, and which certainly warrant further study. On analysing the abundances of three barbet species recorded in *Ficus* trees with varying fruit sizes, we discovered a pattern of resource partitioning that closely mirrors that found in other studies of *Megalaima* barbets in South-west India and Malaysia. This suggests the drivers of *Megalaima* barbet assemblage composition are likely to be consistent across space and taxa. Finally, we found that the smallest and most abundant species, the Coppersmith Barbet, may actually be a very ineffective seed disperser, especially compared to the larger Lineated Barbet. Even in these closely related barbet species, their seed dispersal functions are complimentary, rather than redundant, and have differing degrees of effectiveness.

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CHAPTER 7:

Tropical forest restoration: *Ficus* trees are the key

7.1 Preface

Forest restoration is an increasingly important and contested topic. Tropical deforestation has created a vast estate of human-modified land, while several competing approaches have been suggested to help accelerate forest restoration. One strategy is to use isolated trees as the foci of restoration nuclei. Therefore, in this chapter, the potential of *Ficus* trees to serve as restoration nuclei is compared to other common isolated trees in Assam.

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The co-author contributions were as follows. Conceived and designed the study: HEWC-J. Conducted the data collection: HEWC-J. Analysed the data: HEWC-J, OB. Wrote the paper: HEWC-J, LBC, RJW. Further details of the co-author contributions and their consent to the use of this material in this thesis are provided in Appendix 4.

This chapter is under review at Biotropica.

7.2 Abstract

Forest restoration is an increasingly important tool to slow and indeed reverse global deforestation rates. One low cost strategy to accelerate forest restoration is the use of scattered native trees that persist across disturbed landscapes and which may act as foci, attracting increased seed dispersal and recruitment around them. *Ficus* trees, which are considered to be critically important components of tropical ecosystems, may be particularly attractive to seed dispersers in that they produce large and nutritionally rewarding fruit crops. Here we evaluate the effectiveness of *Ficus* trees in inducing restoration compared to other common scattered trees. We studied the sapling communities growing under 207 scattered trees, and collected data on seed rain at 55 trees in a modified landscape in Assam, India. We found *Ficus* trees have more sapling species around them than non-*Ficus* trees, with higher average stem heights and significantly more saplings of large tree species. Sapling densities were twice as high under *Ficus* trees compared to non-*Ficus*, and seed rain densities of non-parent trees were significantly higher under *Ficus* trees than other fruit or non-fruit trees. These results suggest that *Ficus* trees may be more effective forest restoration agents than non-*Ficus* trees, and therefore the conservation of scattered *Ficus* trees in disturbed landscapes should be prioritised.

Keywords *Ficus*, focal trees, forest restoration, India, sapling recruitment, scattered trees, seed dispersal

7.3 Introduction

While showing some signs of slowing, global deforestation rates remain very high, accounting for an estimated 13 m ha of forest annually (FAO, 2010). This results in the loss of biodiversity, reduced carbon sequestration, and the loss of local ecosystem services, which are of critical importance to some of the world's most vulnerable people (MEA, 2005; TEEB, 2010). In many regions, however, the loss of forest cover is being offset by increasing afforestation (FAO, 2010). In ameliorating the problems described above, the benefits of restoring degraded lands are clear. Several options for forest restoration exist: large-scale sapling replanting, commercial plantations, tree islands, focal trees, and passive succession (Holl, 2012; Singh et al., 2012; Zahawi et al., 2013). Given the often slow pace of passive succession, due to limited seed dispersal and low recruitment rates (Holl et al., 2000), artificial techniques that accelerate this process provide increasingly attractive conservation strategies.

Utilising surviving ecological structures, such as remnant trees, can present a cost-effective restoration approach (Guevara & Laborde, 1993; McIntyre, 2002; Holl et al., 2013). Remnant trees attract frugivores across disturbed landscapes, thereby facilitating seed dispersal (Guevara et al., 1992; Galindo-González et al., 2000; Holl et al., 2000). They also stabilise local microclimatic conditions and provide nutrients under their canopies, both of which improve seed recruitment rates (Guevara et al., 1992; Zahawi & Augspruger, 1999; Holl et al., 2000; Loik & Holl, 2001; Zahawi & Augspruger, 2006). Therefore, by improving dispersal and recruitment in disturbed habitats, remnant trees may act as regeneration foci, helping to develop a nucleated pattern of succession (Guevara et al., 1986; Elmqvist et al., 2002; Lindenmayer & Franklin, 2002; Manning et al., 2006; Schlawin & Zahawi, 2008).

The effectiveness of remnant trees has been demonstrated in Neotropical pasture (Guevara et al., 1992; Guevara & Laborde, 1993; Slocum, 2001), Australian savannahs (Dorrough & Moxham, 2005), and temperate field landscapes (McDonnell & Stiles, 1983). However, the characteristics of remnant trees which best serve restoration remain poorly understood. For example, how do isolation and tree size influence seed immigration and survival in the immediate vicinity of a remnant tree (cf. MacArthur & Wilson, 1967; Whittaker & Ferández-Palacios, 2007)? A handful of studies have found remnant tree height to increase seed deposition (Slocum & Horvitz, 2000; Slocum, 2001), while no consistent relationship has been found between the distance to forest edge and either seed rain or sapling density (Slocum, 2001; Zahawi & Augspurger, 2006; but see Robinson & Handel, 1993 and Schlawin & Zahawi, 2008). Another important concept of remnant tree-led restoration is the ability of woody vegetation to expand beyond the perimeter of the tree's canopy, yet little evidence for this process has been documented (Zahawi & Augspurger, 2006; Cole et al., 2010). And finally, the effectiveness of different remnant tree species in encouraging faster restoration, or directing restoration towards a particular community composition, remains poorly known (Slocum, 2001).

Seed dispersal has often been cited as a limiting factor in forest restoration studies (Cole et al., 2010; Holl et al., 2013; Zahawi et al., 2013). Fleshy-fruited trees are believed to be the most effective species at attracting frugivores over disturbed habitats and thus prove to be more effective restoration nuclei than other species (Slocum, 2001). *Ficus* in particular is believed to be a very important genus of fleshy-fruited tree for a wide range of frugivores (Leighton & Leighton 1983; Terborgh, 1986; Janzen, 1988; Lambert & Marshall, 1991; Shanahan et al., 2001; Kinnaird & O'Brien, 2005). Within intact forests, the unusual asynchronous fruiting cycle, large crop sizes, and pantropical availability of *Ficus* means that over 1,200 tropical birds and mammals have been recorded consuming *Ficus* fruit (Shanahan et al., 2001). Beyond the forest edge in Neotropical pastures, Guevara and Laborde (1993) recorded 47 species of frugivorous bird feeding in four isolated *Ficus* trees over 247 hours of observation, and Slocum (2001) found *Ficus* trees to have higher seed rain, greater density of saplings, and higher sapling diversity than three other tree genera. If sufficient evidence of the importance of *Ficus* trees as regeneration nuclei can be gathered, policy makers may be encouraged to more actively conserve remnant *Ficus* trees, as well as devising strategies to include *Ficus* trees in new plantings.

We sought to test hypotheses on the importance of remnant *Ficus* trees as restoration nuclei in an agricultural mosaic landscape beyond the Neotropics. In particular, we aimed to test the following hypotheses: 1) that isolated *Ficus* trees harbour a greater diversity and density of saplings than other common remnant trees (Slocum, 2001); 2) that density of seed rain decreases with isolation and landscape disturbance (Schlawin & Zahawi, 2008); 3) that height, isolation, and local grazing intensity influence the density of saplings growing under them (Guevara et al., 2004); and 4) that sapling densities differ between the area under the crown and in a 5 m radius beyond the immediate vicinity of the crown (Guevara et al., 1992).

7.4 Methods

7.4.1 Study area

The study was conducted between October 2012 and June 2013 in the Golaghat District of Assam, North-east India. The study site is a ≈250 km^2 area bounded by the Western Range of Kaziranga National Park at N26 34.394 E93 15.433, the city of Jorhat at N26 46.198 E94 12.678, and the town of Golaghat at N26 27.819 E93

54.978. The elevation of the study area ranges between 30–100 m above sea level, and the mean annual rainfall for the region is 1,500–2,500 mm, most of which falls in the May to August monsoon (Barua & Sharma, 1999; Shrivastava & Heinen, 2007). The annual temperature range varies from an average minimum of 5°C to an average maximum of 35°C (Barua & Sharma, 1999).

The original habitat of moist subtropical deciduous forest was largely cleared following the local commercialisation of tea production in 1840 (Shrivastava & Heinen, 2007). Remnants of the original forest remain in the 7.65 km^2 Panbari Forest Reserve on the edge of the Karbi Hills, and in the 430 km^2 Kaziranga National Park (Barua & Sharma, 1999). The landscape is an agricultural mosaic, with a heterogeneous assortment of small-holder rice cultivation, tea estates, and village home gardens. The area has a population density of 302 people per square kilometre (GOI, 2011).

7.4.2 Sapling sampling

We randomly selected 103 mature isolated *Ficus* trees, and another 104 mature non-*Ficus* trees that were commonly found in the anthropogenic landscape. The *Ficus* focal trees were large, hemi-epiphytic species, comprising of 26 *F. benghalensis*, which has large fruit (mean diameter=182 mm, n=62), with the rest small-fruited species (mean diameter=131 mm, n=47), comprising 57 *F. religiosa*, 13 *F. rumphii*, 5 *F. microcarpa*, and 3 *F. benjamina*. Non-*Ficus* trees comprised of 28 species, the most common of which were *Mangifera indica* (12 individuals) and *Albizia saman* (11 individuals). A species list of non-*Ficus* trees, and the number of each used in this study, is provided in the Supporting information.

We recorded the species of each of these 207 focal trees and measured the diameter at breast height, height, and canopy diameter along two axes. Canopy area was later calculated using the formula for an ellipse. We also recorded the grazing intensity of the area under the canopy using a three point rank scale (where 0 is very little evidence of grazing; 1 is some livestock occasionally graze the site; and 2 is large numbers of livestock frequently graze the site). The human land use of the area under the canopy was also recorded using a similar three-point scale (where 0 is very little human land use; 1 is some human land use, such as cultivation; and 2 is intense human land use, in cases where a road, house, or paddy field are present under the canopy).

At each focal tree, we identified and measured the height of all saplings growing under the canopy, and then all the saplings growing in a 5 m radius around the edge of the canopy. A sapling was defined as a woody-stemmed plant 20–200 cm tall. Several sources were used to establish the saplings' taxonomy (Kanjilal et al., 1934–1940; Bora & Kumar, 2003; Sarma et al., 2010).

7.4.3 Seed rain sampling

Seed rain was measured under 35 fruiting *Ficus* trees, 10 fruiting non-*Ficus* trees, and 10 non-fruit trees. Seed traps were constructed out of a fine (0.5×0.5 mm) mesh net, with square sides measuring 50 cm (making the total area of a trap 0.25 cm^2). They were erected one metre above the ground to avoid seed predation, and a small stone was placed in the centre to prevent wind inverting the net. Seed traps were placed 4 m away from the trunk of each tree. In the case of large *Ficus* trees, a second seed trap was placed at 8 m from the trunk. In eight cases, seed traps were also placed 4 m beyond the edge of the crown to quantify the amount of seed rain falling just beyond the crown perimeter. For fruiting *Ficus* trees, the material caught in seed traps was collected once every 2–3 days, for other trees it was collected once a week. Leaf litter and twigs that fell into the traps were carefully brushed to collect seeds before being discarded. The material was dried in plastic bottles over several days, and then sorted by species and counted using a hand-held 10× magnifying lens. Seeds were classed as being either zoochorous or anemochorous by morphology. Traps that were damaged by humans, livestock, or, in one case, wild elephants (*Elephas maximus* L.), were excluded from analysis.

7.4.4 Statistical analysis

To control for area, and facilitate the use of frequentist methods, we calculated the density of saplings growing under and around *Ficus* and non-*Ficus* focal trees before further analysis. We used a Mann-Whitney U test to determine significant differences in observed sapling richness and sapling density between *Ficus* and non-*Ficus* focal trees. We used t-tests to identify significant differences between the two focal tree types in mean sapling heights and differences in sapling densities in a 5 m radius beyond the canopy. A factorial ANOVA was used to identify any interaction effects between tree type and the change in sapling density between the area under the canopy, and the 5 m radius beyond the canopy.

Sapling species were classified into groups depending on their dispersal syndrome (animal, wind, or gravity) and life history (large tree, small tree, or shrub). These data were square root transformed, before differences in the densities of these groups under *Ficus* and non-*Ficus* focal trees were analysed with MANOVA using Pillai's trace as the test statistic and follow-up ANOVAs.

We calculated diversity, dominance, and similarity measures for the sapling communities recorded under and within 5 m of *Ficus* and non-*Ficus* focal trees. For diversity, we used the Shannon diversity index with bias-corrected maximum likelihood ratio. We used a Simpson dominance index with maximum likelihood estimator for dominance, and to compare community similarity we used Sørensen's abundance index with 200 simulations. All formulae followed Chao and Shen (2012) and the analyses were computed in the SPADE software package (Chao & Shen, 2010).

To test the significance of *Ficus* focal tree characteristics for sapling densities, we used an ANCOVA with grazing intensity as the fixed factor, and with distance to the nearest primary forest and focal tree height as covariates. Tree height was used as a proxy for tree size, with diameter at breast height data excluded to avoid multicollinearity. The dependent variable, dispersed sapling density, was square root transformed for normality. Sidak post hoc tests were used to identify differences within grazing intensity categories.

To analyse total seed rain densities and dispersed seed rain densities, we compared the density of seed rain falling per metre squared per week across the five net positions: (i) under non-fruit trees, (ii) under fruiting non-*Ficus* trees, (iii) 4 m from the trunk of *Ficus* trees, (iv) 8 m from the trunk of *Ficus* trees, and (v) 4 m beyond the canopy of *Ficus* trees. We performed a Kruskal-Wallis test, with a Jonckheere-Terpstra test to determine any trends in the data, followed by four Mann-Whitney U tests with a new critical value of 0.0125 to identify specific differences between dependent variables.

We looked at the impact of landscape factors on both seed rain and sapling density. To analyse the influence of land-use intensity and distance from a forest seed source, we divided the sapling density and seed rain data from type (iii) nets (*Ficus* 4 m nets) into four categories following Luck and Daily (2003): focal tree near a forest, with low land-use intensity; near, high intensity; far, low intensity; and far, high intensity. The trees were split into near and high categories according to the median measured distance to the nearest “intact” forest. The differences in seed rain and sapling densities were tested for significance using a one-way ANOVA with Gabriel post hoc tests. Other than where specified, all analyses were conducted using IBM SPSS Statistics 21 (IBM, 2012).

7.5 Results

A total of 7,078 saplings, comprising 117 species, were recorded under or in a 5 m vicinity of the 207 focal trees. 114 of these species were found under *Ficus* trees, while 59 species were found at non-*Ficus* focal trees. 53 species were unique to *Ficus* trees, while three were unique to non-*Ficus* trees. Of the total saplings, 5,791 were recorded under or around the 103 *Ficus* trees, and 1,287 were recorded under or around the 104 non-*Ficus* trees. 4,420 saplings were recorded under the canopies of *Ficus* trees, with an additional 1,371 recorded in a 5 m radius of the canopy edge. 791 saplings were recorded under the canopies of non-*Ficus* trees, with an additional 496 recorded in a 5 m radius.

While *Ficus* canopies (mean±standard error=424.11±35.31 m^2) typically had a larger area than non-*Ficus* trees (130.79±16.98 m^2), sapling densities under *Ficus* tree canopies (median=0.06/m^2) were still significantly higher than under non-*Ficus* trees (median=0.03/m^2), U=4446, z=-2.124, p<0.05, although the effect size was small (r=-0.15).

The heights of saplings also differed depending on focal tree type. On average, saplings growing under the canopies of *Ficus* trees had higher heights (mean±standard error =43±2.23 cm) than under non-*Ficus* trees (32.3±2.43 cm). This difference was significant $t_{(205)}=-3.243$, $p<0.05$; although once again the effect size was small ($r=0.22$).

Excluding the area under the canopy, the density of saplings growing in a 5 m radius of *Ficus* tree canopies ($0.036\pm0.01/m^2$) was significantly higher than the density of saplings growing in a 5 m radius of the canopies of non-*Ficus* trees ($0.016\pm0.004/m^2$) ($t_{(180)}=-2.863$, $p<0.05$, $r=0.21$). However, there was no significant interaction effect between the type of tree and the area under the canopy versus the 5 m radius; $F_{(1,410)}=0.57$, $p>0.05$, $r=0.04$. This suggests that while sapling densities differed significantly, the drop in densities from beneath the canopy to immediately beyond the canopy perimeter was not significantly different according to the type of tree (for means and standard errors, see Table 7.1).

Table 7.1: Differences in sapling characteristics at non-*Ficus* and *Ficus* focal trees in Assam, India. Sapling densities are m^2, values are means±SE with range beneath. The column reporting "sapling density in a 5 m radius" encompasses a 5 m radius from the edge of the canopy, and excludes the area under the canopy. Different letters in each column denote significantly different means (see text for test types).

Focal tree type	**n**	**Sapling density under the canopy**	**Sapling density in a 5m radius**	**Sapling height**	**Animal dispersed sapling density**
Non-*Ficus* tree	104	0.07 ± 0.01^{a}	0.016 ± 0.004^{a}	32.3 ± 2.43^{a}	0.02 ± 0.0002^{a}
		0–1.06	0–0.33	0–100.11	0–0.11
Ficus tree	103	0.11 ± 0.02^{b}	0.036 ± 0.006^{b}	43 ± 2.23^{b}	0.04 ± 0.0008^{b}
		0–1.32	0–0.44	0–135.50	00.72

Focal tree type had a significant effect on the densities of saplings when classified into groups according to their dispersal ecology ($V=0.09$, $F_{(3,203)}=6.6$, $p<0.05$). Separate univariate analyses on the outcome variables revealed significant differences between animal dispersed ($F_{(1,205)}=14.43$, $p<0.05$) and wind dispersed saplings

($F_{(1,205)}$=7.68, p<0.05) according to focal tree, but not for gravity dispersed saplings ($F_{(1,205)}$=3.31, p>0.05). The type of focal tree also had a significant effect on the densities of saplings according to their life histories (V=0.08, $F_{(3,203)}$=5.97, p<0.05). Follow-up univariate contrasts found significant differences between the density of large trees ($F_{(1,205)}$=15.64, p<0.05) and shrubs ($F_{(1,205)}$=8.05, p<0.05), but not for the density of small trees ($F_{(1,205)}$=3.01, p>0.05).

The observed sapling species richness indicated sapling communities were richer under and around *Ficus* trees compared to non-*Ficus* trees (U=2843, z=-5.87, p<0.001; Table 7.2). However, the Shannon diversity index and Simpson dominance index were similar for both focal tree types, and the Sørensen's index score suggested very high homogeneity in community composition.

Table 7.2: Richness, diversity, dominance, and community similarity indices for different focal tree types in Assam, India. Aside from observed "Sapling richness", scores are Maximum Likelihood Estimators ± standard error. Different superscript letters for "Sapling richness" indicate significant differences between focal tree types according to a Mann-Whitney U test (p<0.001). H' and DI were not significantly different between focal tree types (p>0.05).

Focal tree type	**n**	**Sapling richness**	**Shannon index (H')**	**Simpson index (DI)**	**Sørensen 's index**
Non-*Ficus* tree	104	59 ^{a}	3.07±0.13	0.08±0.01	0.97±0.01
Ficus tree	103	114 ^{b}	3.02±0.24	0.11±0.03	

The effect of grazing intensity on sapling densities was significant ($F_{(2,98)}$=7, p<0.05, r=0.35), while neither the distance to the nearest forest (F=0.17, p>0.05, r=0.04) nor focal tree height had a significant effect (F=0.38, p>0.05, r=0.06). The Sidak-corrected post hoc comparisons revealed that focal trees with low grazing intensity had significantly higher sapling densities than trees with medium (p<0.05) or high grazing intensities ($p<0.05$), while there was no significant difference in the density of saplings between focal trees with medium and high grazing intensities ($p>0.05$).

Overall seed rain results were significantly different across the 5 experiment types ($H_{(4)}=10.317$, $p<0.05$) (Table 7.3). The group of particular interest, the dispersed seeds, also returned a significant result ($H_{(4)}=18.76$, $p<0.05$). An upward trend in dispersed seed rain densities was detected from non-fruit, to fruit, and then to *Ficus* trees with nets at 4m from the trunk ($z=2.969$, $p<0.05$, $r=0.31$). The Mann Whitney U tests found no significant difference between fruit and non-fruit trees ($U=187$, $z=-0.434$, $p>0.0125$), or between *Ficus* tree nets at 4m and *Ficus* tree nets at 8m ($U=683$, $z=-0.741$, $p>0.0125$). However, the tests did find a significant difference between non-fruit trees and *Ficus* trees at 4m ($U=339$, $z=-2.575$, $p<0.0125$), and fruit trees and *Ficus* trees with nets at 4m ($U=326.5$, $z=-2.764$, $p<0.0125$).

Table 7.3: Seed rain densities at different net types placed under or close to different Assamese focal trees. Seed rain densities are m^2/week, values are means±SE. Different letters on each line denote significantly different means according to Mann-Whitney tests with a critical value of 0.0125. No tests were performed on *Ficus* 4 m beyond as no seeds were recorded in this category.

Net type	n	Overall seed rain	Dispersed seed rain
Non-fruit tree	20	$4.42±2.16^a$	$2.19±0.97^a$
Fruit tree	20	$155.65±71.10^a$	$3.5±1.87^a$
Ficus tree (4 m)	54	$18,492.14±2,768.66^b$	$12.73±3.00^b$
Ficus tree (8 m)	28	$12,297.75±2,184.67^b$	$18.82±10.93^b$
Ficus tree (4 m beyond the canopy)	8	$98.41±34.79^a$	-

At the landscape scale, seed rain densities showed no significant variation across the four distance and land-use intensity categories ($F_{(3,48)}=0.515$, $p>0.05$, $\omega=0.17$) (Table 7.4). While the model found a significant difference for the sapling density data

($F_{(3,99)}$=3.2, $p<0.05$, ω=0.25), no specific categories were significantly different in the post hoc tests.

Table 7.4: Seed rain densities at *Ficus* trees in four landscape categories: near intact forest in low land-use intensity; near intact forest with high land-use intensity; far from intact forest with low land-use intensity; far from intact forest with high land-use intensity. Seed rain densities are dispersed seeds per m^2 per week, values are means±SE. There was no significant difference between categories for seed rain density: $F_{(3,48)}$=0.515, $p>0.05$, ω=0.17. Sapling densities are true means±SE per m^2 before transformation. The model identified a significant difference across categories for sapling density: $F_{(3,99)}$=3.2, $p<0.05$, ω=0.25; but no specific differences between groups were detected by the post hoc tests.

	Near, low	**Near, high**	**Far, low**	**Far, high**
Seed rain density	11.33±5.79 (n=11)	14.73±6.41 (n=15)	5.83±2.92 (n=10)	16.13±6.45 (n=16)
Sapling density	0.15±0.05 (n=26)	0.06±0.01 (n=26)	0.19±0.08 (n=16)	0.08±0.02 (n=35)

7.6 Discussion

Our results demonstrate the important role isolated *Ficus* trees can play in ecological restoration. The density of saplings growing under *Ficus* trees in the study was twice as high as the density of saplings growing under other non-*Ficus* trees, while the species richness and height of these saplings was also significantly higher under *Ficus* trees. This indicates that *Ficus* trees are more effective restoration nuclei than other remnant tree types. With regards to the communities developing around *Ficus* trees, the diversity and dominance index scores were comparable to non-*Ficus* trees, while the Sørensen's index found *Ficus* and non-*Ficus* trees to support very similar communities. This suggests that *Ficus* trees are supporting the regeneration of plant communities that are representative of the general landscape, and not simply favouring frugivore-dispersed species, which would still restore forests, but which would likely produce assemblages of novel compositional structure (Corbin & Holl, 2012).

This pattern of higher densities but equivalent diversity concurs with Slocum's (2001) Neotropical results, where he found high community similarity in sapling assemblages around remnant trees in open and closed pasture types, but twice as many sapling recruits in the enclosed system. While the driver in Slocum's case was grazing pressure, in this system it appears that propagule dispersal may have been the limiting factor for non-*Ficus* communities. Indeed the seed rain results suggest that increased dispersal may be an important factor in increasing sapling densities under *Ficus* trees. Dispersal limitation has been cited as a major constraint on ecological restoration in a range of environments (Holl et al., 2000; Slocum, 2001; Albornoz et al., 2013). However, in this study, *Ficus* trees had significantly higher rates of non-parent seed rain than random trees or other fruiting trees, and significantly higher densities of zoochorous plant species growing under and around them. This suggests that frugivores are either preferentially visiting *Ficus* trees, or for some other reason are dispersing seeds under *Ficus* trees more effectively than other tree types, which corresponds with the findings of several studies that found a high abundance and richness of frugivorous birds and bats at isolated *Ficus* trees (Guevara & Laborde, 1993; Galindo-González et al., 2000; Eshiamwata et al., 2006).

Other reasons for higher sapling densities under *Ficu*s trees may include the abiotic environment. The large size and dense canopies of *Ficus* species analysed in this study provided a high amount of shade (Slocum, 2001; Guevara et al., 2004; Dhanya et al., 2013a), which may enhance soil moisture levels, and facilitate seed germination and growth, especially in forest-specialist tree species (Loik & Holl, 2001). Soil nutrients under *Ficus* trees may also differ from non-*Ficus* trees, with a higher biomass of leaf fall and high levels of minerals such as calcium and potassium from decomposing *Ficus* fruit (O'Brien et al., 1998; Wendeln et al., 2000; Dhanya et al., 2013b). Therefore the microclimate and soil nutrient balance under *Ficus* trees may also be more conducive to seed germination and sapling growth than other tree types. In practice, an interaction between these factors is likely to be at play (Vieira et al., 1994). Indeed, in Slocum's study of four focal tree species in Neotropical pastures, the high amount of shade under *Ficus* trees, along with good incoming seed dispersal (*Ficus* trees received the highest rate and richness of seed rain; Slocum & Horvitz, 2000), resulted in *Ficus* trees having the most diverse and dense sapling assemblages (Slocum, 2001).

The higher sapling densities may also help explain the higher heights found in saplings under *Ficus* trees compared to non-*Ficus* trees. Contrary to our findings, Slocum (2001) found slower sapling growth rates under *Ficus* trees compared to open canopy, low shade focal tree species, prompting him to suggest that the Neotropical *Ficus* trees involved may not be very effective recruitment foci in early successional stages. However, in another Neotropical study, Guevara et al. (2004) found sapling communities 4–5 m tall growing under isolated *Ficus* trees. The sapling densities reported by Guevara et al. and recorded in our study are both higher than those reported by Slocum. Further work will be required to determine if the patterns reported here are specific to the taxa or the region, or are more generally representative of Old World *Ficus*.

For restoration nuclei to be successful, saplings must establish and mature beyond the perimeter of the nucleus itself. Our results indicate that *Ficus* trees have denser sapling communities in a 5 m perimeter of the canopy edge than non-*Ficus* trees, but that the rate of decline in sapling densities away from the canopy is comparable in both tree types. This is consistent with findings for isolated Mexican *Ficus* trees, where sapling densities decreased around the perimeter of focal trees (Guevara et al., 1992), along with findings around remnant trees in Costa Rica (Sclawin & Zahawi, 2008), and tree islands in Honduras (Zahawi & Augspruger, 2006).

There was also no decline in seed rain with distance to the nearest forest, or land-use intensity. This has previously been explained by the small range and absolute distances between the seed trap and the nearest forest (usually of 20–50 m; Holl, 1999; Cubiña & Aide, 2001; Zahawi & Augspruger, 2006; Pejchar et al., 2008; Cole et al., 2010), which would provide only a minor barrier to dispersal. However, the present study was carried out at a much larger scale, with a range of 0.011–32.06 km, and an average of 16.81 km from the seed trap to the nearest forest. This suggests that the frugivores acting as dispersal vectors were not sensitive to isolation or disturbance, and therefore may have been matrix generalists rather than forest specialists (Devictor et al., 2008). This is supported by studies of remnant trees and tree islands in Neotropical pastures, where most of the frugivores recorded were open habitat species (Guevara & Laborde, 1993; Zahawi & Augspruger, 2006).

If *Ficus* trees are to be conserved with a view to facilitating restoration, our results suggest that they should play an important role regardless of height of tree or distance from the nearest forest. This corresponds with other studies of remnant trees, where woody plant recruitment was not correlated with height, diameter at breast height, or distance separating the remnant trees from source areas (Guevara et al., 1992; Slocum, 2001). However, our results do indicate that if reforestation is desired, livestock should be restricted from grazing under or around *Ficus* trees, as we found the density of saplings to be significantly higher under trees with low grazing pressure compared to trees of moderate or high pressure. This supports the work of Guevara et al. (2004), who found a dense canopy 4–5 m tall under five Neotropical *Ficus* trees where livestock had been excluded for three years. In the present and other studies, the dominance of grazing pressure over tree size and isolation suggests that local human impacts are more important constraints to restoration than landscape level biogeographical factors. Fortunately, solutions to over-grazing are cheap and can quickly be implemented, with simple bamboo fences generally effective at excluding goats and other livestock (*personal observation*).

7.7 Conclusion

We found isolated *Ficus* trees in human landscapes to support richer, denser, and taller sapling communities than non-*Ficus* trees. While the abiotic conditions under *Ficus* trees may play a role, our findings suggest that seed dispersal, which is often a major limiting factor in ecological restoration, is higher under *Ficus* trees than other tree types. Promisingly, seed rain rates under *Ficus* trees did not deteriorate with either distance from the nearest forest or land-use intensity, suggesting it is robust to isolation and disturbance. Further good news is the similarity of communities developing under and around *Ficus* trees and non-*Ficus* trees. We found no evidence to suggest *Ficus* trees are generating non-analogue forest assemblages, dominated by a small suite of species ecologically compatible with *Ficus* life-histories. This suggests that, at least in the study region, if not elsewhere, conservation strategies that preferentially conserve isolated *Ficus* trees over other tree species may offer a faster route towards forest restoration, especially if livestock grazing intensity was controlled under and in the immediate vicinity of *Ficus* trees.

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7.10 Supporting information

Table 7.5: A list of the non-*Ficus* focal trees analysed in this study, with the number of individual trees analysed recorded in the second column.

Species	**Number studied**
Adenanthera pavonina L.	1
Albizia lucidior (Steud.) I.C.Nielsen	1
Albizia procera (Roxb.) Benth.	4
Albizia saman (Jacq.) Merr.	11
Alstonia scholaris (L.) R. Br.	6
Artocarpus heterophyllus Lam.	6
Artocarpus lakoocha Roxb.	7
Bombax ceiba L.	2
Carallia brachiata (Lour.) Merr.	1
Cassia fistula L.	7
Dillenia indica L.	3
Dysoxylum binectariferum Hook f. ex. Bedd.	2
Gmelina arborea Roxb.	6
Heliotropium indicum L.	1
Lagerstroemia speciosa (L.) Pers.	4
Litsea monopetala (Roxb.) Pers.	1
Magnolia mannii (King) Figlar	2
Mangifera indica L.	12
Mesua ferrea L.	1
Murraya koenigii (L.) Spreng.	1
Neolamarckia cadamba (Roxb.) Bosser	3
Pongamia pinnata (L.) Pierre	5
Premna bengalensis C.B.Clarke	3
Spondias mombin L.	1
Spondias pinnata (L. f.) Kurz	2

Syzygium cumini (L.) Skeels	5
Tetrameles nudiflora R. Br.	3
Toona ciliata M.Roem.	3

CHAPTER 8:

Achieving dual conservation and development outcomes through isolated *Ficus* trees

8.1 Preface

While collecting field data on the plants growing under isolated *Ficus* trees, it soon became apparent that several of them had important medicinal or subsistence properties that benefitted the local community. By identifying the human-uses of plants recorded under isolated trees, this chapter evaluates the ecological goods *Ficus* trees can deliver to rural subsistence communities in comparison to other common trees in Assam.

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The co-author contributions were as follows. Conceived and designed the study: HEWC-J. Conducted the data collection: HEWC-J. Analysed the data: HEWC-J, OB. Wrote the paper: HEWC-J, LBC, RJW. Further details of the co-author contributions and their consent to the use of this material in this thesis are provided in Appendix 4.

This chapter has been accepted by Ambio.

8.2 Abstract

Many of the world's rural populations are dependent on the local provision of economically and medicinally important plant resources. However, increasing land-use intensity is depleting these resources, reducing human welfare, and thereby constraining development. Here we investigate a low cost strategy to manage the availability of valuable plant resources, facilitated by the use of isolated *Ficus* trees as restoration nuclei. We surveyed the plants growing under 207 isolated trees in Assam, India, and categorised them according to their local human-uses. We found that *Ficus* trees were associated with double the density of important high-grade timber, firewood, human food, livestock fodder, and medicinal plants compared to non-*Ficus* trees. Management practices were also important in determining the density of valuable plants, with grazing pressure and land-use intensity significantly affecting densities in most categories. Community management practices that conserve isolated *Ficus* trees, and restrict livestock grazing and high-intensity land-use in their vicinity, can promote plant growth and the provision of important local resources.

Keywords Assam, community management, conservation, development, *Ficus*, human-uses, India, regeneration

8.3 Introduction

Dependence on ecosystem goods and services is common in rural areas across the globe (MEA, 2005). In rural India, households are dependent on forest and private resources for timber, firewood, and medicinal products (Natarajan, 1995; Heltberg et al., 2000; Phondani et al., 2013). However, increasing environmental degradation is causing a decline in the provision of ecosystem goods and services, exacerbating poverty and reducing human welfare (Maginnis & Jackson, 2002; MEA, 2005; TEEB, 2010). In Meghalaya, India, for example, forest degradation has not only reduced the availability of firewood, but has also reduced the richness of medicinally important flora (Laloo et al., 2006). The decline in natural capital is particularly problematic as modern substitutes are beyond the means of the poorest households (Gadgil, 1993; TEEB, 2010), while it also increases the marginalisation of stigmatised social groups (Heltberg et al., 2000).

It is therefore important to increase the availability of subsistence and economically important ecological goods and services in rural areas (MEA, 2005; Chokkalingam et al., 2006; Rey Benayas et al., 2009). Various authors have suggested forest plantations, direct seeding, and natural succession as strategies to increase tree cover and eco-service provision (Lamb et al., 2005; Chazdon, 2008; Rey Benayas et al., 2009; Hall et al., 2011). However, government sponsored schemes have achieved limited or mixed success (Dewees, 1995; Nibbering, 1999; Dudley et al., 2005; van 't Veld et al., 2006; Wuethrich, 2008; Le et al., 2012), while private tree planting initiatives are constrained by insufficient access to resources such as labour, land, and finance (Arnold et al., 2006; Gebreegziabher & van Kooten, 2013). One novel solution may be the use of isolated trees as the foci of vegetation restoration, taking advantage of the natural process of seed dispersal (Toh et al., 2002; Manning et al., 2006). As fruit-bearing tree species are likely to be more attractive to frugivorous seed dispersers, *Ficus* trees, which have extremely large crop sizes, may provide particularly useful nuclei in the regeneration of economically important flora (Shanahan et al., 2001; Howe & Miriti, 2004; Caughlin et al., 2012).

Furthermore, in some regions, *Ficus* trees have enhanced cultural status through their associations with major religions, local faiths, or traditional belief systems (Gaultier, 1996; Huabin, 2003; Wilson & Wilson, 2013). *Ficus* trees are used as sites of worship in many faiths, and taboos on cutting down large *Ficus* trees have been reported from several sites across Asia (Horowitz, 1998; Long & Zhou, 2001; Wilson & Wilson, 2013). The cultural standing of *Ficus* trees may be instrumental in conserving their populations in rural landscapes by lowering mortality from direct felling, potentially increasing their importance as food sources for frugivores and restoration sites for plants.

Cultural considerations centered on religious, spiritual, and aesthetic values also mean that *Ficus* trees are commonly found on public land: along roads, in markets, in town squares, and at temple sites (Barua et al., *in prep*; Cottee-Jones et al., *in review*). Land tenure may affect livestock grazing pressure and the likelihood of human clearance, and so the growing locations of isolated *Ficus* trees may also have an influence on their suitability as sites for the provision of useful plant resources.

In this study, we sought to discover whether isolated trees increase the local availability of natural goods and services. Specifically, we aimed to test: 1) whether economically or medicinally valuable plant species grew under isolated trees; 2) whether isolated *Ficus* trees supported more valuable plants than other common isolated trees; and 3) which land management practices affected the density of valuable plants growing under isolated trees.

8.4 Methods

8.4.1 Study area

The study was conducted from October 2012 to June 2013 in the Golaghat District of Assam, North-east India. The study area was a ≈250 km^2 region bounded by Kaziranga National Park at N26 34.394 E93 15.433, the city of Jorhat at N26 46.198 E94 12.678, and the town of Golaghat at N26 27.819 E93 54.978. The altitudinal range of the study area is 30–100 m above sea level, and the mean annual rainfall in the region is 1,500–2,500 mm, most of which falls in the May to August monsoon (Shrivastava & Heinen, 2007). The annual temperature range varies from a mean minimum of 5°C to a mean maximum of 35°C (Barua & Sharma, 1999). The original habitat of moist subtropical deciduous forest was largely cleared for commercial tea production in 1840 (Shrivastava & Heinen, 2007). The landscape is an agricultural mosaic, with a heterogeneous assortment of small-holder rice cultivation, tea estates, and village home gardens, with a population density of 302 people per square kilometre (GOI, 2011).

8.4.2 Focal tree sampling

We surveyed 207 mature isolated trees, of which 103 were *Ficus* trees, and 104 were non-*Ficus* trees. To select trees, we would stop after driving or walking for 500 m, measure any *Ficus* trees present, and select the three largest non-*Ficus* trees in the area for measurement. In all cases, focal trees had to be a minimum of 30 m from the nearest *Ficus* tree or non-*Ficu*s focal tree. We repeated this sampling process until we had over 100 focal trees of each type.

We recorded the species of each of these 207 focal trees and measured the diameter at breast height (DBH) with a tape measure, estimated the maximum tree height with a clinometer, and estimated the canopy area by measuring the canopy diameter at ground level along two axes, and then calculating the area using the formula for an ellipse (Table 8.1). We also recorded the grazing intensity of the area under the canopy by consulting local landowners and observing grazing damage. Although wild Asian Elephant (*Elephas maximus*) and several species of deer (Cervidae) inhabited the area, the overwhelming majority of grazing pressure came from domestic animals, and in particular, goats and cattle. We ranked grazing intensity using a three point scale where 0 is very little evidence of grazing; 1 is some livestock occasionally graze the site; and 2 is large numbers of livestock frequently graze the site. The human land-use of the area under the canopy was also recorded from observations using a similar three point scale (where 0 is very little human land-use; 1 is some human land-use, such as a village home garden or livestock grazing area; and 2 is intense human land-use, in cases where a road, house, or paddy field are present under the canopy). Finally, the land tenure at each focal tree's growing location was recorded as being under either private or public ownership, which was determined through consultation with nearby households.

Table 8.1: Characteristics of isolated *Ficus* and non-*Ficus* focal trees surveyed in Assam, India. DBH is diameter at breast height. Values for DBH, height, and canopy area are mean±standard error. Different superscript letters denote significantly different means at $p<0.05$ following ANOVA. Codes for land tenure are PU=public land ownership, PR=private land ownership. Codes for land-use intensity and grazing intensity are H=high, M=medium, L=low. The percentages indicate the proportion of *Ficus* and non-*Ficus* focal trees that were recorded in each land tenure, land-use intensity, and grazing intensity category.

Characteristic	***Ficus***	**Non-*Ficus***
Total no. of individuals surveyed	103	104
Total no. of species surveyed	5	28
Land tenure	PU=71%; PR=29%	PU=44%; PR=56%
Land-use intensity	H=59%; M=36%; L=5%	H=44%; M=54%; L=2%
Grazing intensity	H=50%; M=46%; L=5%	H=39%; M=56%; L=5%
DBH (m)	1.38±0.07 ^{a}	0.54±0.03 ^{b}
Height (m)	24.38±0.74 ^{a}	18.43±0.59 ^{b}
Canopy area (m^2)	424.11±35.31 ^{a}	130.79±16.86 ^{b}

8.4.3 Vegetation surveys

At each focal tree, we identified and measured the height of plants growing under the canopy. We restricted our measurements to trees, shrubs, and vines 20–200 cm in height, and identified the species found following several sources (Kanjilal et al., 1934–1940; Bora & Kumar, 2003; Sarma et al., 2010). To classify the plant species into human-use groups, we identified important local uses of natural resources through consultation with local households and regional plant use publications (Dutta, 2006; Laloo et al., 2006), which produced six groups: high-grade timber, low-grade timber, firewood, human food, livestock fodder, and medicinal resources. Plants with multiple uses (60 of 91, 66%) were placed in several different groups.

8.4.4 Statistical analysis

We calculated the density of plants growing under each focal tree for each human-use group. To compare the difference in mean plant densities between *Ficus* and non-*Ficus* trees, we carried out a MANOVA with Pillai's Trace and follow-up univariate contrasts, using the human-use groups as independent variables. To identify the land management practices that affected plant densities, we used a MANOVA with Pillai's Trace and Bonferroni post hoc tests, as two of the independent variables had three groups. The independent variables were grazing intensity, land-use intensity, and land ownership. All analyses were conducted in IBM SPSS Statistics 21 (IBM, 2012).

8.5 Results

The *Ficus* focal trees were large, hemi-epiphytic species, comprising 26 *F. benghalensis*, which has large fruit (mean diameter=182 mm, n=62), with the rest small-fruited species (mean diameter=131 mm, n=47), comprising 57 *F. religiosa*, 13 *F. rumphii*, 5 *F. microcarpa*, and 3 *F. benjamina*. Non-*Ficus* trees comprised 28 species, the most common of which were *Mangifera indica* (12 individuals) and *Albizia saman* (11 individuals). A species list of non-*Ficus* trees and the number of each used in this study is provided in Supporting information A, Section 8.10.

We recorded 7,078 plants and 117 species growing under the 207 focal trees. Of these, 73 were identified to species level, and 26 had no locally identified human-use. Twenty-six species were identified as being a good resource for high-grade timber, 16 for low-grade timber, 34 for firewood, 39 for human food, 32 for livestock fodder, and 59 for medicinal products (see Supporting information B, Section 8.10, for a list of all species and their classifications).

Ficus trees were associated with higher plant densities in each human-use category than were non-*Ficus* trees (Table 8.2). Indeed, the type of focal tree had a significant effect on the density of valuable plants growing under the tree canopy (V=0.6, $F_{(6,200)}=50.92$, $p<0.001$). Follow-up univariate contrasts confirmed that significant differences existed between the densities of plants growing under *Ficus* versus non-*Ficus* trees in all usage categories (Table 8.3).

Table 8.2: Densities of plants in each human-use category under isolated *Ficus* and non-*Ficus* focal trees in Assam, India. Values are mean±standard error, with the range in parentheses. Significance levels are annotated by asterisks: *=$p<0.05$; **= $p<0.01$; ***= $p<0.001$.

Focal tree type (n)	High-grade timber	Low-grade wood	Firewood	Human food	Livestock fodder	Medicinal resource
Ficus tree (103)	0.018±0.004*** (0–0.26)	0.009±0.002** (0–0.09)	0.03±0.01*** (0–0.37)	0.02±0.004** (0–0.28)	0.01±0.001* (0–0.09)	0.04±0.01** (0–0.33)
Non-*Ficus* tree (104)	0.01±0.001 (0–0.08)	0.01±0.001 (0–0.04)	0.01±0.002 (0–0.010)	0.01±0.001 (0–0.08)	0.002±0.001 (0–0.03)	0.02±0.01 (0–0.44)

Land-use practices also had an effect on the densities of valuable plants. Grazing intensity and human land-use intensity both had a significant effect, as did interactions between grazing and land-use, and land-use and ownership (Table 8.4). Ownership alone, and grazing and ownership did not have an effect at the $p>0.05$ confidence level.

Table 8.3: Follow-up ANOVA contrasts of differences between the densities of plants growing under *Ficus* versus non-*Ficus* trees in all human-usage categories, Assam, India. All differences were significant at the $p<0.05$ level.

Human-use category	**F**	**d.f.**	***p***
High-grade timber	12.53	1, 205	<0.001
Low-grade timber	5.90	1, 205	<0.05
Firewood	16.93	1, 205	<0.001
Human food	11.81	1, 205	<0.01
Livestock fodder	5.64	1, 205	<0.05
Medicinal resource	11.23	1, 205	<0.01

Bonferroni post hoc tests indicated that grazing had an effect on the densities of high-grade timber, low-grade timber, firewood, and human food plants (all $p<0.05$). However, there was no difference in livestock fodder ($p>0.3$ for all) or medicinal ($p>0.1$ for all) plant densities between areas subject to low, medium, and high grazing pressure. The tests also indicated that land-use intensity was significant at all levels for high-grade timber, low-grade timber, and firewood plants (all $p<0.05$). Land-use intensity did not have an effect for human food between medium and high land-use intensities ($p<0.05$), and for medicinal plants between low and medium land-use intensities ($p<0.1$). For livestock fodder, the post hoc tests were only significant between low and high land-use intensities ($p<0.02$).

Table 8.4: MANOVA results with Pillai's Trace (V), on the affect of land management practices on the density of valuable plants growing under all 207 focal trees, Assam, India.

Management practice	**V**	**F**	**d.f.**	***p***
Grazing intensity	0.13	2.25	12, 376	<0.001
Land-use intensity	0.18	3.02	12, 376	<0.001
Ownership	0.04	1.22	6, 187	0.30
Grazing*Land-use	0.29	3.34	18, 567	<0.001
Grazing*Ownership	0.09	1.55	12, 376	0.09
Land-use*Ownership	0.14	2.31	12, 376	<0.01

8.6 Discussion

Our results demonstrate the important role of isolated *Ficus* trees in the regeneration of locally important plant species. The densities of plants growing under *Ficus* trees were significantly higher than under non-*Ficus* trees in all economic and medicinal human-use categories. In some case, the average densities of plants were two (firewood, human food, livestock fodder, medicinal resources) or almost three (high-grade timber) times higher under *Ficus* trees than under non-*Ficus* trees.

It appears likely that the higher densities of valuable plants growing under *Ficus* trees is a consequence of *Ficus* trees supporting higher plant densities *per se*, as has been demonstrated in studies from the Neotropics (Slocum, 2001; Guevara et al., 2004). However, the exact reasons for a higher density of useful plants growing under *Ficus* trees compared to non-*Ficus* trees are hard to disentangle. Mature hemi-epiphytic *Ficus* trees have larger fruit crops than most other plant species (Kinnaird et al., 1996), and so may attract a wider range and higher abundance of frugivores, which in turn would generate a greater density of seed rain (Guevara et al., 2004; Cole et al., 2010). However, *Ficus* trees also ameliorate environmental conditions under their canopies, with humidity, light, temperature, substrate texture, and soil nutrient levels more closely representing closed forest than the conditions commonly found under many non-*Ficus* trees in disturbed landscapes (Dhanya et al., 2013). In the absence of further evidence, it seems reasonable to assume that some combination of greater seed rain and ameliorated growing conditions may explain the higher densities of plants growing under *Ficus* trees compared to non-*Ficus* trees, most of which are also valued by the local community for subsistence and the provision of commercial goods.

Land management practices were important in determining plant densities. The significantly lower plant densities in higher land-use intensities for three categories suggest that land-use planning decisions have a high impact on the local provision of economically important plants. The cultivation of human food plants in residential areas may have increased the supply of their seeds in high land-use areas, which may help explain the absence of a difference between human food plants densities at medium and high land-use sites (Shrivastava & Heinen, 2007). The sacredness of *Ficus* trees in Assam may have also had an influence on land-use around them. 15% of *Ficus* trees in the study area are reported to have shrines or to grow at temple sites (Barua et al., *in prep*), which customarily have cleared compounds that are devoid of vegetation. Although this means that some *Ficus* trees may be unsuitable restoration nuclei, the conservation of these trees for religious reasons should help augment the overall *Ficus* population size in the landscape (Caughlin et al., 2012).

Grazing by domestic animals is recognised as a major constraint to vegetation restoration in many areas of the tropics, including Assam (Harvey et al., 2011; Holl &

Aide, 2011; Murgueitio et al., 2011; Bhatta, 2011; Barnes et al., 2014). Here, the existence of differences in plant densities between low, medium, and high grazing pressures in four human-use categories suggests that managing grazing pressure would produce higher densities of economically important plants. While excluding livestock entirely from the area under isolated *Ficus* trees would be the most effective strategy, these results indicate that other management plans, which recognise the trade-off between the need for grazing space and the local provision of valuable plants, would also work (Chakravarty-Kaul, 2013). Suitable alternatives might be to selectively exclude certain domestic animals, such as goats, or to only allow grazing for short periods in a monthly cycle (Fischer et al., 2009). One challenge to implementing such a system may involve land-ownership issues. Interestingly, the results indicate that land tenure was not a statistical predictor of plant density, suggesting that similar densities are found on public and private land. However, the lack of interaction with grazing suggests that livestock graze the area under focal trees at a similar intensity regardless of ownership, presenting a potential problem in regulating grazing under focal trees on public land (Francis et al., 2013).

With 59 species, the richness of medicinally important plants found under isolated trees in the study was comparable to the richness reported in sacred groves in other states of North-east India (Laloo et al., 2006). As the focal trees in this study provide a much smaller area for plants to grow, yet are of comparable richness to the larger sacred groves, a micro-site strategy may be effective in conserving the resources needed to treat a broad range of illnesses, and helps explain how the use of traditional medicines has persisted following deforestation. The local presence of these medicinal resources is likely to be very useful to local households, who have a detailed understanding of how to use them, and who do not have access to modern health care facilities (Phondani et al., 2013).

The recognition of the role isolated *Ficus* trees play in regenerating economically and medicinally important plants in rural areas is important from both a conservation and development perspective. If land planning and grazing management initiatives are implemented around these trees, biodiversity metrics and indicators are likely to improve at a local scale, while landscape connectivity is likely to improve at a regional scale. Furthermore, if the areas under isolated *Ficus* trees are well managed, they are likely to provide important resources for local households over long timescales, aligning conservation and development objectives through community resource management (Hutton & Leader-Williams, 2003; Adams et al., 2004; Martin et al., 2009). As the cost of reducing grazing and vegetation clearance under *Ficus* trees is low (Barnes et al., 2014), and as *Ficus* trees occur in rural landscapes across the tropics (Slocum, 2001; Guevara et al., 2004; Eshiamwata et al., 2006; Caughlin et al., 2012), the conservation of *Ficus* trees and the communities associated with them could yield low-cost improvements to human welfare on a global scale.

8.7 Conclusion

The importance of isolated trees for conserving biodiversity has only recently been recognised (Manning et al., 2006; Fischer et al., 2010). Here we demonstrate that the conservation of isolated trees may also help to improve the livelihoods of rural households through the provision of a wide range of economic and medicinal resources. If “bottom-up” community-led initiatives could successfully encourage the conservation of isolated *Ficus* trees, restricting land-use and controlling livestock grazing in their vicinity, they are likely to achieve both conservation and development benefits.

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8.10 Supporting information

Supporting information A

Table 8.5: A list of the non-*Ficus* focal trees included in this study, from Assam, India. The number of individual trees analysed per species is recorded in the second column.

Species	Number studied
Adenanthera pavonina L.	1
Albizia lucidior (Steud.) I.C.Nielsen	1
Albizia procera (Roxb.) Benth.	4
Albizia saman (Jacq.) Merr.	11
Alstonia scholaris (L.) R. Br.	6
Artocarpus heterophyllus Lam.	6
Artocarpus lakoocha Roxb.	7
Bombax ceiba L.	2
Carallia brachiata (Lour.) Merr.	1
Cassia fistula L.	7
Dillenia indica L.	3
Dysoxylum binectariferum Hook f. ex. Bedd.	2
Gmelina arborea Roxb.	6
Heliotropium indicum L.	1
Lagerstroemia speciosa (L.) Pers.	4
Litsea monopetala (Roxb.) Pers.	1
Magnolia mannii (King) Figlar	2
Mangifera indica L.	12
Mesua ferrea L.	1
Murraya koenigii (L.) Spreng.	1
Neolamarckia cadamba (Roxb.) Bosser	3
Pongamia pinnata (L.) Pierre	5
Premna bengalensis C.B.Clarke	3
Spondias mombin L.	1

Spondias pinnata (L. f.) Kurz	2
Syzygium cumini (L.) Skeels	5
Tetrameles nudiflora R. Br.	3
Toona ciliata M.Roem.	3

Supporting information B

Table 8.6: Taxonomic list of plants recorded under the focal trees in Assam, India, and their published human-uses. All species for which a human-use could be identified in the field are listed here. A tick denotes an important human-use. Abbreviations for mature growth form are: BT=big tree; ST=small tree; S=shrub; V=vine. A threshold of 20 m height at maturity was used to differentiate big trees from small trees. In 18 cases the scientific name of the plant could not be determined, but its local human-use was still recorded.

Scientific name	Family	Growth form	Timber	Low-quality wood	Firewood	Human food	Animal fodder	Medicinal
Spondias mombin L.	Anacardiaceae	BT	✔	✖	✔	✔	✖	✖
Spondias pinnata (L. f.) Kurz	Anacardiaceae	BT	✖	✖	✖	✖	✖	✔
Mangifera indica L.	Anacardiaceae	BT	✖	✔	✔	✔	✔	✔
Annona squamosa L.	Annonaceae	ST	✖	✖	✖	✔	✔	✖
Artabotrys hexapetalus (L.f.) Bhandari	Annonaceae	S	✖	✖	✖	✖	✖	✖
Alstonia scholaris (L.) R. Br.	Apocynaceae	BT	✖	✔	✔	✖	✖	✔
Unknown	Apocynaceae	S	✖	✖	✖	✖	✖	✔
Oroxylum indicum (L.) Kurz	Bignoniaceae	ST	✖	✖	✖	✖	✖	✔
Cordia fragrantissima Kurz	Boraginaceae	ST	✔	✖	✔	✖	✖	✖
Canarium bengalense	Burseraceae	ST	✖	✖	✖	✖	✖	✖

Roxb.								
Cassia fistula L.	Caesalpiniaceae	ST	✔	✖	✔	✔	✔	✔
Caesalpinia cucullata Roxb.	Caesalpiniaceae	V	✖	✖	✖	✖	✖	✔
Unknown	Caesalpiniaceae	S	✖	✖	✖	✖	✖	✔
Unknown	Caesalpiniaceae	S	✖	✖	✖	✖	✖	✖
Unknown	Caesalpiniaceae	ST	✖	✖	✖	✖	✖	✔
Carica papaya L.	Caricaceae	ST	✖	✖	✔	✔	✔	✖
Terminalia catappa L.	Combretaceae	BT	✔	✖	✔	✖	✔	✔
Dillenia indica L.	Dilleniaceae	ST	✔	✔	✔	✔	✔	✔
Shorea robusta Gaertn.	Dipterocarpaceae	BT	✔	✖	✔	✖	✖	✔
Unknown	Dipterocarpaceae	ST	✔	✔	✖	✖	✖	✖
Macaranga indica Wight	Elaeocarpaceae	ST	✖	✖	✖	✖	✖	✔
Elaeocarpus floribundus Blume	Elaeocarpaceae	ST	✖	✖	✖	✔	✔	✖
Mallotus albus (Roxb. ex Jack) Müll. Arg.	Euphorbiaceae	ST	✖	✖	✖	✖	✖	✔
Jatropha curcas L.	Euphorbiaceae	S	✖	✖	✖	✖	✖	✔
Unknown	Gentianaceae	ST	✖	✖	✖	✖	✖	✔
Premna bengalensis C.B.Clarke	Lamiaceae	BT	✖	✖	✖	✔	✖	✔
Gmelina arborea Roxb.	Lamiaceae	BT	✔	✖	✔	✔	✔	✔
Callicarpa arborea Roxb.	Lamiaceae	ST	✖	✖	✖	✔	✔	✔
Clerodendrum infortunatum L.	Lamiaceae	S	✖	✖	✖	✖	✖	✔
Vitex negundo L.	Lamiaceae	S	✖	✖	✖	✖	✖	✔
Unknown	Lamiaceae	ST	✖	✖	✖	✔	✔	✔
Litsea monopetala (Roxb.) Pers.	Lauraceae	ST	✖	✔	✔	✖	✔	✔
Phoebe goalparensis	Lauraceae	ST	✔	✖	✖	✖	✖	✖

Hutch.								
Lagerstroemia speciosa (L.) Pers.	Lythraceae	BT	✔	✖	✖	✖	✖	✔
Magnolia mannii (King) Figlar	Magnoliaceae	ST	✔	✖	✔	✔	✖	✖
Magnolia griffithii Hook.f. & Thomson	Magnoliaceae	ST	✔	✖	✔	✖	✖	✖
Magnolia champaca (L.) Baill. ex Pierre	Magnoliaceae	BT	✔	✖	✔	✖	✖	✔
Hibiscus rosa-sinensis L.	Malvaceae	S	✖	✖	✖	✖	✖	✔
Bombax ceiba L.	Malvaceae	BT	✖	✔	✔	✖	✖	✔
Urena lobata L.	Malvaceae	S	✖	✖	✖	✖	✖	✔
Unknown	Malvaceae	S	✖	✖	✖	✖	✖	✔
Melastoma malabathricum L.	Melastomaceae	S	✖	✖	✖	✖	✖	✖
Dysoxylum binectariferum Hook f. ex. Bedd.	Meliaceae	BT	✔	✔	✔	✖	✖	✖
Toona ciliata M.Roem.	Meliaceae	BT	✔	✖	✖	✖	✖	✖
Albizia procera (Roxb.) Benth.	Mimosaceae	BT	✔	✖	✔	✖	✖	✖
Albizia lucidior (Steud.) I.C.Nielsen	Mimosaceae	ST	✔	✖	✔	✖	✖	✖
Albizia saman (Jacq.) Merr.	Mimosaceae	BT	✖	✔	✔	✖	✖	✖
Parkia timoriana (DC.) Merr.	Mimosaceae	BT	✖	✔	✔	✖	✖	✖
Artocarpus lakoocha Roxb.	Moraceae	BT	✔	✔	✔	✔	✔	✖
Artocarpus heterophyllus Lam.	Moraceae	ST	✔	✔	✔	✔	✔	✔
Ficus racemosa L.	Moraceae	BT	✖	✖	✖	✔	✔	✔
Ficus religiosa L.	Moraceae	BT	✖	✔	✔	✖	✔	✔

Ficus microcarpa L.	Moraceae	BT	✖	✖	✖	✖	✔	✔
Ficus benghalensis L.	Moraceae	BT	✖	✖	✖	✖	✔	✔
Morus alba L.	Moraceae	ST	✖	✖	✔	✔	✔	✔
Syzygium cumini (L.) Skeels	Myrtaceae	BT	✔	✖	✔	✔	✖	✔
Psidium guajava L.	Myrtaceae	ST	✖	✖	✔	✔	✔	✔
Nyctanthes arbor-tristis L.	Oleaceae	S	✖	✖	✖	✔	✔	✔
Pongamia pinnata (L.) Pierre	Papilionaceae	ST	✖	✖	✔	✖	✖	✔
Unknown	Papilionaceae	S	✖	✖	✖	✔	✖	✔
Passiflora foetida L.	Passifloraceae	V	✖	✖	✖	✔	✔	✖
Baccaurea ramiflora Lour.	Phyllanthaceae	BT	✖	✖	✖	✔	✔	✖
Carallia brachiata (Lour.) Merr.	Rhizophoraceae	ST	✔	✖	✔	✔	✔	✔
Prunus armeniaca L.	Rosaceae	ST	✖	✖	✖	✔	✔	✖
Prunus domestica L.	Rosaceae	ST	✖	✖	✖	✔	✔	✖
Psilanthus bengalensis (Roxb. ex Schult.) J.-F.Leroy	Rubiaceae	S	✖	✖	✖	✔	✖	✔
Coffea arabica L.	Rubiaceae	S	✖	✖	✖	✔	✖	✔
Neolamarckia cadamba (Roxb.) Bosser	Rubiaceae	BT	✔	✔	✖	✖	✖	✖
Catunaregam spinosa (Thunb.) Tirveng.	Rubiaceae	S	✖	✖	✖	✖	✖	✖
Murraya koenigii (L.) Spreng.	Rutaccae	ST	✖	✔	✔	✔	✖	✔
Citrus medica L.	Rutaccae	ST	✖	✖	✖	✔	✖	✔
Citrus reticulata Blanco	Rutaccae	ST	✖	✖	✖	✔	✔	✖
Citrus maxima (Burm.) Osbeck	Rutaceae	ST	✖	✖	✔	✔	✔	✔
Flacourtia jangomas	Salicaceae	ST	✔	✖	✔	✔	✔	✔

(Lour.) Raeusch.								
Salix tetrasperma Roxb.	Salicaceae	ST	✔	✖	✔	✖	✖	✖
Santalum album L.	Santalaceae	ST	✔	✖	✖	✖	✖	✔
Tetrameles nudiflora R. Br.	Tetramelaceae	BT	✖	✔	✔	✖	✖	✖
Camellia sinensis (L.) Kuntze	Theaceae	S	✖	✖	✖	✔	✖	✖
Pyrenaria barringtoniaefolia Seem.	Theaceae	S	✖	✖	✔	✔	✔	✖
Aquilaria malaccensis Lam.	Tymelaeaceae	BT	✔	✖	✖	✖	✖	✔
Unknown	Unknown	-	✖	✖	✖	✔	✖	✖
Unknown	Unknown	-	✖	✖	✖	✔	✖	✔
Unknown	Unknown	-	✖	✖	✖	✔	✔	✔
Unknown	Unknown	-	✖	✖	✖	✖	✖	✔
Unknown	Unknown	-	✖	✖	✖	✔	✖	✔
Unknown	Unknown	S	✖	✖	✖	✖	✖	✔
Unknown	Unknown	S	✖	✖	✖	✖	✖	✔
Unknown	Unknown	S	✖	✖	✖	✖	✖	✖
Lantana camara L.	Verbenaceae	V	✖	✖	✖	✖	✖	✔
Unknown	Verbenaceae	-	✖	✖	✖	✖	✖	✖
Leea indica (Burm. f.) Merr.	Vitaceae	S	✖	✖	✖	✖	✖	✔