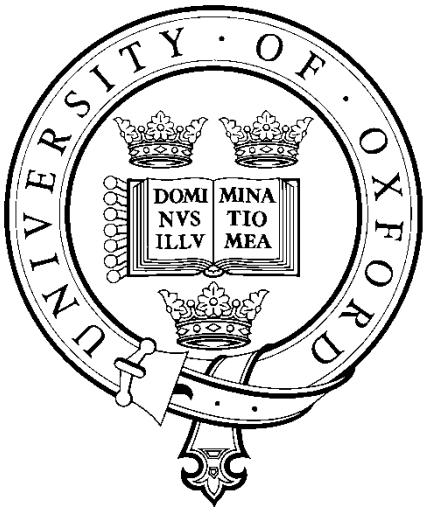
RIPARIAN RESERVES IN OIL PALM PLANTATIONS: BIODIVERSITY, ECOLOGICAL PROCESSES AND ECOSYSTEM SERVICES

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Thesis submitted for the degree of Doctor of Philosophy

Hilary Term 2014

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ABSTRACT

- As the human population expands, agricultural expansion and intensification will exert an increasing pressure on remaining habitats, especially in the tropics. Oil palm is one of the most rapidly expanding crops in these regions, and identifying management strategies that conserve biodiversity and ecosystem services in these landscapes is therefore a priority.
- I assess whether riparian forest fragments (riparian reserves) conserve species and the functions they support within oil palm landscapes. Riparian forests are legally required for their beneficial impact on hydrological dynamics and their potential to contribute to the conservation of terrestrial species is poorly documented.
- I focussed on two ecologically important indicator groups (ants and dung beetles) and the ecosystem processes that they support.
- Whilst protecting primary forest will remain the most important strategy for biodiversity conservation, I found that riparian reserves do support species of ants and dung beetles that would not otherwise persist in oil palm landscapes. However, the extent to which riparian reserves maintained key ecological functions differed between these two taxa. The amount of nutrient distribution carried out by ants in riparian reserves was similar to logged forest areas, and higher than in oil palm. In contrast, dung removal functions did not vary between these land uses.
- I also investigated how the vegetation structure and landscape context of riparian reserves affects the dung beetle communities they support. Increasing reserve width and proximity to other forest fragments had a positive impact on the species richness and diversity of dung beetles in riparian reserves.
- There was little evidence that riparian reserves enhance the provision of dung removal or pest control services in adjacent areas of oil palm.
- The results provide evidence to support the introduction and/or enforcement of legislation to protect riparian forest reserves in order to conserve biodiversity and ecological processes in oil palm landscapes.

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STATEMENT OF CONTRIBUTIONS

Owen Lewis contributed to the experimental design, data analysis and commented on drafts for all chapters.

Eleanor Slade contributed to the experimental design, data analysis and commented on drafts of Chapters 3 and 4.

Darren Mann assisted with dung beetle species identifications and the experimental design of Chapters 3 and 4, as well as commenting on drafts of these chapters.

Tom Fayle contributed to the experimental design, data analysis and commented on the draft of Chapter 5.

Arthur Chung commented on drafts of Chapters 4 and 5.

Max Gray assisted with data collection for Chapters 2, 3, and 5.

Joana Ferreira assisted with data collection for Chapters 5 and 6.

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CHAPTER 1: GENERAL INTRODUCTION

To provide a context to the results presented in this thesis, this introduction provides a brief overview of the most relevant research and current issues in conservation science. I start with a discussion of the global impact of human activity and why ecological research in this area is important. I summarise current pressures for global agriculture and possible solutions for simultaneously achieving food security and the protection of biodiversity. I then provide a brief review of existing knowledge of oil palm systems in particular, and their environmental impact. I introduce riparian ecosystems as a focal system, and provide a synthesis of the existing literature looking at the impact of converting versus protecting riparian habitats. Lastly, I provide a brief summary of the advantages of using insects as a focal taxon for answering some of the pressing ecological questions raised.

THE NECESSITY OF RESEARCH ON BIODIVERSITY AND ECOSYSTEM PROCESSES IN OUR CHANGING ENVIRONMENT

Our impact on our planet is immense, and extends to all biomes and ecosystems. As a result of the emergence of humans as a global ecological and geophysical force, the current era has been described as the Anthropocene (Steffen et al. 2007). Our impact on our environment is both impressive and alarming. About 13 million ha of forest are converted every year, which is approximately 0.13% of total global forest cover (FAO 2010). The loss of primary forest, which is particularly significant for global biodiversity, is disproportionately high (0.4% total area lost per year, FAO 2010). Greenhouse gas emissions have increased from 200 million tonnes to 289 billion tonnes per year since 1850 (UNEP 2014); climate warming has caused major reductions in polar sea ice, radically changed arctic ecosystems (Smol et al. 2005) and continues to change

weather patterns across the world. Water use, catchment modification and river pollution continue to increase, and freshwater systems are experiencing even greater biodiversity declines than terrestrial systems (Dudgeon et al. 2006). Only 0.16% of the global land area is unaffected by any of the anthropogenic stressors that degrade waterways (Vörösmarty et al. 2010). Our oceans are also suffering. The synergistic effects of overfishing, habitat destruction, ocean acidification, introduced species and pollution have caused huge declines in many marine species, simplifying food webs and creating large anoxic dead zones with unknown ecological and evolutionary consequences (Jackson 2008). Overall, the outlook for global ecosystems is concerning: a recent review of several quantified biodiversity scenarios for the C21st shows that there is a consistent prediction of species and habitat loss across marine, freshwater and terrestrial systems (Pereira et al. 2010).

If we are to mitigate environmental degradation at the same time as increasing global human welfare, we need to document these changes and understand the links between human activity and ecological systems. The millennium ecosystem assessment (MA 2005) highlighted the large scale impact of human activity on the environment, but also the wide range of ways in which human welfare and productivity relies on ecosystem services and resilience. In the decade since the MA we have increased our knowledge of the spatial and temporal trends in environmental change, the ways in which human systems depend on ecological dynamics and which approaches simultaneously achieve benefits for human societies and nature conservation. However, we are still far from fully understanding these dynamics. Robust scientific evidence of the interactions within socio-ecological systems will continue to be a critical component of developing locally appropriate sustainable natural resource management, prioritising the most important threats and selecting the most promising solutions (Ostrom 2007).

In general, the effect of landscape change and the relative success of different conservation approaches is much better documented for species and communities than ecological functions (Lewis 2009; Bagchi et al. 2011). Therefore, identifying how ecological processes change with human activity is important area if we are going to manage and conserve natural systems successfully. In particular, the effects of land use change on the delivery mechanisms of key ecosystem services and the dynamics underlying ecosystem resilience are critical areas for ecological research (Mace et al. 2012). Improving our understanding of the links between community composition and ecological processes will be a key element of this research effort.

AGRICULTURE AND LAND USE CHANGE

Agriculture has had a huge ecological impact over thousands of years, with widespread impacts on climatic, terrestrial and marine ecosystems. Agricultural expansion and intensification continue to be major drivers of habitat conversion, biodiversity loss and alterations in ecological processes (FAO 2010; Pereira et al. 2010; Phalan et al. 2011b). Altogether, agriculture covers about 38% of the Earth's terrestrial surface; this expansion has resulted in the conversion of 70% of the grassland, 50% of the savanna, 45% of the temperate deciduous forest, and 27% of the tropical forest biome (Foley et al. 2011). Globally, agricultural systems are estimated to produce one third of carbon emissions (Gilbert 2012). Each year, agricultural production, especially the manufacture of fertilisers, converts 120 million tonnes of nitrogen into forms which can pollute waterways and coastal systems (Rockström et al. 2009). Agriculture exerts a huge influence over our environment, and is therefore a particularly important focus for efforts to minimise the negative ecological impacts of human activity.

However, agricultural production will still need to increase over the next century. The human population is expected to reach 8 - 10 billion before 2100 (Lutz & Samir 2010). This population increase, coupled with requirements for a more varied diet to combat malnutrition and demands for a higher meat content with rising affluence, places agricultural systems under increasing pressure (Godfray et al. 2010). Food production may need to double in order to meet consumption in the next few decades, and the challenge of feeding the global population is likely to be further increased by climate change and biofuel crop expansion (Foley et al. 2011). Balancing the need to increase yields against the negative ecological impacts of agriculture is likely to be one of the greatest challenges of this century.

Fortunately, there are a range of solutions that can potentially mitigate the negative impact of agriculture on global biodiversity whilst retaining productivity. A dichotomy between the approaches of land-sparing (increasing yields to create space for protected, undisturbed natural habitat) and land-sharing (lower yields and more biodiversity within a larger area of farmland) has been created in order to evaluate which of these two approaches will be more successful. Quantified evidence on the impacts of the two approaches is limited, but so far the rapid decline in the majority of species with increasing yield per hectare suggests that land sparing is more likely to retain biodiversity for a given yield output from a defined area (Phalan et al. 2011b). Of course, the success of a land-sparing approach depends on high quality habitat being successfully protected, and the extent to which this occurs will rely on local governance and will vary between countries (Laurance et al. 2014). In addition, given variation in size of habitat fragments in agricultural zones, the type of agriculture and the species being studied, it is not always straightforward to identify whether a particular management system counts as land sparing or land sharing. An alternative framework for addressing the negative biodiversity impacts of agriculture has been called “sustainable intensification”. This approach accepts that food production will need to increase in some, but not necessarily all, locations (i.e. either land sparing or land sharing may be appropriate depending on the context) but that

environmental harm needs to be limited (Garnett et al. 2013). Sustainable intensification will increase yields whilst avoiding the excessive use of agricultural chemicals, reducing inefficient use of water, minimising pollution and carbon emissions, and retaining natural habitat as much as possible. In addition, managing consumption rates, reducing food waste and improving access and food distribution are central to improving our food systems (Godfray & Garnett 2014). Solutions will be locally specific, and may vary over time as market pressures and technological advances change, but there are some key elements that will be common to all sustainable food production systems.

The pressure to find solutions that maximise production and retain biodiversity will be particularly high, and particularly challenging, in the tropics. As tropical habitats are home to about 60% of the world's species, the biodiversity loss following agricultural expansion in the tropics is particularly severe (Gardner et al. 2009). The majority of agricultural expansion in the last 30 years has occurred in tropical regions, with about 80% of new croplands in the tropics replacing forests (Gibbs et al. 2010). In the coming decades, the last strongholds of relatively undisturbed tropical habitat are likely to face unprecedented pressure from land use change (Laurance et al. 2014). There is a high level of overlap between areas that have the potential to be very productive for agriculture, and that have high biodiversity value (Phalan et al. 2013). In essence, it is particularly important to establish strategies to reconcile biodiversity conservation with agriculture in tropical landscapes.

OIL PALM LANDSCAPES

Within tropical regions, oil palm (*Elaeis guineensis)* is one of the most rapidly expanding crops (Phalan et al. 2013). Palm oil is now the most widely used vegetable oil in the world, and is found in many foodstuffs, cosmetics, detergents and increasingly as a biofuel feedstock. Global

production of palm oil increased from approximately 22 million tonnes in 1970 to over 45 million tonnes in 2010, with the majority of this expansion occurring in Malaysia and Indonesia; these two countries now produce over 80% of global palm oil (FAO 2014). Between 1990 and 2010, approximately 40% of the new oil palm plantations in Indonesia and Malaysia expanded directly onto forested areas (Gunarso et al. 2013) and the conversion of forested areas to oil palm is now increasing elsewhere in the tropics. The oil palm industry is expanding in other countries in Southeast Asia, central and west Africa, Central America and the Amazon (Butler & Laurance 2010; Foster et al. 2011).

The impact of this industry on the most biodiverse and biologically unexplored regions on the planet has become a growing interest and concern for conservation biologists. Oil palm plantations have greatly simplified vegetation structure compared to native forests (Turner & Foster 2006), and they support less than 30% of the species of several groups of insects, birds, bats and primates found in forested areas (Fitzherbert et al. 2008). Whilst evidence on the impact of oil palm expansion is still accumulating for many taxa, in general conversion of forest to oil palm results in the loss of species richness or abundance, and often both (Turner et al. 2008; Foster et al. 2011). Recent studies have also shown that conversion to oil palm reduces the functional diversity of birds (Edwards et al. 2013b) and dung beetles (Edwards et al. 2013c), suggesting that the breadth and resilience of ecological processes in the plantations is also likely to be impaired relative to forest. The impact of oil palm expansion on some ecological functions is relatively well known; for example, the carbon storage within plantations is much lower than in secondary or primary forest (Berry et al. 2010), but comparisons between oil palm and other land uses have in general been carried out for very few ecological processes.

Despite the poor environmental reputation of palm oil, efforts are being made to limit the negative impact of this valuable crop. In Malaysia, for example, there is national and state level

legislation that prohibits the expansion of oil palm onto steep or riparian areas (e.g. Waters Act 1920) and the destruction of valuable habitat within oil palm landscapes, but the extent to which this is enforced can vary (e.g. Gomi et al. 2006; Ligtermoet et al. 2009). In addition there are also large non-governmental organisations that have been set up to improve the environmental and social impacts of the oil palm industry. One of the most influential organisations in this respect is the Round Table on Sustainable Palm Oil (RSPO); an international organisation set up in 2004 which now includes 571 palm oil growers, traders, manufacturers, conservation NGOs and investors that are involved in the production of palm oil and its derivatives. The RSPO sets out a set of environmental and social criteria which companies have to meet in order to become a certified member of the organisation, through which they reduce their reputational risk and gain access to a (potentially) lucrative market of consumers that are concerned with supply chain sustainability. The RSPO guidelines are primarily based on a high conservation value (HCV) approach and include specific requirements to avoid the destruction of habitat with high biodiversity value and to establish management to conserve such areas. In addition, the RSPO requires the protection of any habitat which provides key ecosystem services, such as the riparian buffers which help to preserve water quality (criterion 4.4). The RSPO has been criticised for complications in the certification process and failing to reprimand member organisations for transgressions (Mongabay 2013; Nesadurai 2013), but an increasing number of plantations are making the improvements required to obtain certification. Oil palm landscapes will continue to have a large ecological impact, due to the growth of this industry into the most biodiverse areas of the planet, but these landscapes are also an arena in which scientific evidence can be incorporated into policy and inform management guidelines. Whilst the industry is certainly causing biodiversity declines, there is still great potential to prevent the loss of many species within these landscapes.

RIPARIAN ECOSYSTEMS

Riparian ecosystems are the habitats and communities found on the shores of rivers, lakes and streams. They are dynamic systems that link aquatic and terrestrial environments, and often support a distinct flora, fauna and set of ecological processes. The importance of riparian areas in terms of supporting biodiversity and ecosystem functions is considered disproportionately large given that they are estimated to occupy less than 10% of the earth's terrestrial surface area (Naiman et al. 1993).

The distance from the water that is considered "riparian" generally varies with the size of the water feature and geomorphology of the landscape. Riparian zones are generally wider further downstream, where flooding and river channel migration affects a much wider area (Gregory et al. 1991; Naiman & Decamps 1997). As a result, the riparian zone has been described as anywhere from 1 m to 1 km from the high water line (Whitaker & Montevecchi 1997; Chen et al. 1999; Sabo et al. 2005; Rykken et al. 2007). As a result of this heterogeneity, various methods for demarcating riparian areas are used, including data on topology, the coverage of hydrophilic plants, or the structure of vegetation (Naiman & Decamps 1997).

Riparian zones differ from upland areas in several ways. First, they generally have cooler air and soil temperatures, lower wind speeds and higher humidity (Chen et al. 1999). These are particularly influential factors in arid and temperate systems, where the higher soil moisture and fertility near water sources supports more bio-diverse communities than non-riparian areas (Olson et al. 2007; Stella et al. 2013). Second, the species composition of the riparian zones is often distinct from nearby upland areas, as the interface with the aquatic environment provides a different set of resources and microhabitats (Naiman & Decamps 1997). Third, riparian zones are more dynamic as they suffer greater disturbance from erosion and flooding. The higher rate of disturbance and deposition of fertile sediment compared to upland areas can increase riparian plant productivity and species richness (Pollock et al. 1998),

which in turn affects animal communities (e.g. Olson et al. 2007). Fourth, riparian zones are exposed to different colonisation pressures due to the connectivity and dispersal of propagules through the river network (Araujo Calçada et al. 2013), and can be more vulnerable to invasion by exotic or dispersing species (DeFerrari & Naiman 1994; Planty-Tabacchi et al. 1996).

The distinct flora and fauna within riparian zones has been documented in a wide range of biomes, and makes riparian habitat a conservation concern in its own right. Riparian bird communities have been found to differ in species composition and overall abundance compared to upland areas in tropical regions (e.g. Harvey et al. 2006), arid Mediterranean systems (e.g. Palmer & Bennett 2006), temperate woodlands (e.g. Stauffer & Best 1980), and boreal coniferous forests (Darveau et al. 1995; Whitaker & Montevecchi 1997). Insect community composition and abundance also differs between riparian and upland habitats in both temperate (Rykken et al. 2007) and tropical regions (Davis et al. 2001; Nichols et al. 2013b). Higher levels of activity and richness have been recorded for some mammal species in riparian areas in arid systems (Soykan et al. 2012) and boreal systems (Spackman & Hughes 1995; Ellen Macdonald et al. 2006). A large proportion of amphibians (e.g. 30% in North America) are restricted to riparian zones and rely solely on riparian vegetation as adults (Olson et al. 2007). Plant communities in riparian zones are generally more disturbance tolerant and may have special adaptations such as higher growth rates and increased vegetation reproduction (Naiman & Decamps 1997). A global review of riparian versus upland communities carried out by Sabo et al. (2005) found strong evidence that the species composition of a wide range of taxa (including trees, lianas, mammals, birds, invertebrates and fungi) in riparian areas differs from nearby upland areas.

Riparian ecosystems are also particularly important for maintaining important ecological processes and services. Riparian vegetation is important for maintaining hydrological

dynamics, both in terms of reducing flood risk downstream and maintaining adequate water supplies (Salemi et al. 2012). Vegetation cover near rivers also maintains water quality, through reducing the run off of sediments and agricultural chemicals into rivers (Tabacchi et al. 2000; Mayer et al. 2007). The root systems of riparian plants stabilise river banks, preventing soil erosion and sedimentation rates (Pollen & Simon 2005). The build-up of wood, leaves and other organic material in rivers is directly affected by riparian vegetation, and influences the food availability for aquatic organisms, the formation of pools and the erosion of dynamics of the river (Gregory et al. 1991; de Paula et al. 2011). Through these processes, riparian vegetation also impacts aquatic fauna; invertebrate, fish and amphibians can be negatively impacted by changes in water chemistry and sedimentation rates (Olson et al. 2007). The flow of organic material into the rivers also alters food availability for aquatic species. For example, the riparian vegetation cover affects the flow of dead arthropods into rivers, which in turn affects the size of predatory fish and aquatic trophic interactions (Chan 2008). Lastly, the importance of riverside habitat is not restricted to species that are riparian specialists. It is likely that facultative use of riparian areas in times of drought also supports species that are typically found in upland areas, and that the importance of riparian zones extends beyond supporting characteristic riparian communities (Sabo et al. 2005).

PROTECTING RIPARIAN ZONES: IMPACTS ON TERRESTRIAL BIODIVERSITY

Because riparian vegetation influences a range of ecological and hydrological processes, buffer strips next to water bodies are protected in many countries. Some countries or states specify only one buffer width for all water bodies, but many require a buffer width that is determined by some additional factors, such as the size of the water body, its structure (e.g. permanent vs seasonal, lake vs stream), the presence of fish, or the slope of the valley sides. For example, the government of New South Wales, Australia, dictates that riparian corridors of 10, 20, 30 or

40 m must be kept (on each side of the river) for 1st, 2nd, 3rd and 4th order rivers, respectively (NSW Office of Water 2012). Protection of riparian vegetation has increased throughout the USA and Canada since the 1960s, with a buffer zones of 15 – 30 m protected on average (Lee et al. 2004a). Legislation in Brazil originally stipulated riparian buffer widths based on the size of the water body, but controversially this has recently changed so that the required areas of riparian vegetation is dictated by the plot size of each individual landowner (Lees & Peres 2008; Viegas et al. 2014). In North America there has been some developments towards whole catchment management approaches, including headwater reserves or the protection of larger areas at the confluence of rivers (Rykken et al. 2007; Olson et al. 2007). The emphasis placed on protecting riparian zones may also increase in the near future; Capon et al. (2013) argue that riparian zones should be hotspots for directing adaptation efforts in the coming decades, given their combined vulnerability to human impact and importance for ecosystem services.

Whilst primarily protected for their beneficial impacts on hydrological dynamics and aquatic life, riparian buffer zones in human-modified landscapes also provide habitat for species that would not otherwise persist in a converted landscape. So far only one meta-analysis (Marczak et al. 2010) has compared riparian buffer communities to riparian areas in undisturbed habitats. The results indicate that riparian reserves can maintain species in similar or even higher abundances to undisturbed habitats, but that community composition shifts towards disturbance specialists. There are far fewer studies looking at how the terrestrial communities supported by riparian reserves compare to those in locations where no buffer is retained. However, there is evidence that for birds (Stauffer & Best 1980; Martin et al. 2006) and mammals (Brusnyk & Gilbert 1983; Cockle & Richardson 2003; Wilk et al. 2010), riparian reserves protect a higher abundance and diversity of species compared to riparian zones that are clear cut or planted with commercial crops.

Protected riparian areas can also provide corridors for species to move through converted landscapes. Though many studies mention the importance of riparian buffers for enhancing movement through human modified landscapes, there is rather little hard evidence of how important riparian corridors are for movement and dispersal as opposed to providing habitat for resident populations. Large mammals have been shown to prefer moving thorough riparian corridors than the surrounding agricultural landscape in California (Hilty & Merenlender 2004), and the use of riparian corridors by large mammals in Borneo has also been reported (Hai et al. 2001). Larger numbers of birds have been found moving through riparian buffer zones compared to adjacent cultivated areas in both temperate (Machtans et al. 1996; Shirley 2006) and tropical countries (Gillies & St. Clair 2010; Gillies et al. 2011). Similarly, mark-recapture study of bats in Nicaragua also found that more than 50% of bat movements involved riparian forest, indicating that riparian buffers may be preferred movement routes (Medina et al. 2007). More work is certainly needed to quantify the extent to which riparian fragments support permanent populations versus assisting movement and dispersal for different taxa.

It is also likely that riparian reserves support terrestrial biodiversity through a range of ecological processes over even greater spatial and temporal scales. Many bird species migrating across continents will select riparian habitat for feeding along their routes (Skagen et al. 1998). Riparian reserves can act as stepping stones for the dispersal of plants that are transmitted between river banks by the streams (Araujo Calçada et al. 2013), and also provide seed sources for regeneration of surrounding habitat (Griscom and Ashton 2011). It has been suggested that riparian zones may act as refugia for local species during climatic fluctuations (Meave et al. 1991), and that the unique characteristics of the interface between two different ecosystems can catalyse evolution and diversification (Naiman & Decamps 1997).

Overall, our understanding of the ecology of terrestrial communities in riparian buffers is limited, and the approaches taken to inform policy are inconsistent. I carried out a systematic

review of all studies on riparian reserves, riparian buffers, riparian strips and riparian forest available in ISI Web of Knowledge, Scopus and Google Scholar (and the references within these documents). From this review, it appears that the existing literature on terrestrial communities in riparian reserves is particularly biased towards temperate ecosystems and data on bird communities (see Table 1). This means that in many countries and particularly in tropical regions, there is little ecological information available to inform the legislation regarding riparian zones. Although evidence on the impacts of riparian management on aquatic organisms may be available in some cases, guidelines derived from studies on hydrological dynamics and aquatic species may not be appropriate for the terrestrial communities (Lee et al. 2004a).

To complicate matters further, a wide range of different approaches have been used to inform legal requirements and guidelines for riparian buffer width. One approach is to study undisturbed landscapes and establish the maximum distance from the river at which communities of animals or plants remain distinctly different to upland communities (e.g. Semlitsch & Bodie 2003; Olson et al. 2007). Alternatively, a number of studies have examined the movement of animals in undisturbed landscapes in order to establish the area normally used by riparian specialists, and then recommend a reserve width that covers this area (e.g. Lemckert & Brassil 2000; Medina et al. 2007; Bueno et al. 2011). Many studies use data from existing riparian reserves (see Table 2) to make a width recommendation. A common approach is to compare existing riparian buffers of various widths with undisturbed areas, in order to identify the minimum width at which the community in the buffers resembles that in the undisturbed forest. However, there is considerable variation in exactly which component of the undisturbed habitat is matched (e.g. abundance, species richness, present of focal species). An alternative method is to establish the width at which the curve of increasing abundance of focal conservation priority species reaches an asymptote, which requires no reference to undisturbed communities (e.g. Hodges & Krementz 1996). Some studies have based

recommendations for width on the presence of species generally described as woodland interior specialists, also without a direct comparison to an undisturbed reference landscape (Keller et al. 1993; Dickson et al. 1995). In the hydrological literature, width recommendations have also been based on optimising the trade-off between reductions in sedimentation and the opportunity cost of lost land for agriculture (Sparovek et al. 2002), and similar approaches would be valuable for a wider range of biodiversity and ecosystem service gains. Currently, there is a conspicuous lack of both ecological information on the communities in riparian reserves, and a consistent method for identifying the width of riparian strip that should be stipulated by policy.

Animal group	Sub-tropical & tropical regions	Temperate regions
Birds	12	34
Mammals	7	17
Amphibians/Reptiles	3	14
Insects	6	9

TABLE 1
The number of published studies that document the ecological characteristics of existing riparian reserves for 4 major animal groups in tropical and temperate regions.

Animal Group	Minimum width (m)	Water body	Location	Ecosystem type	Surrounding land use	Publication	Method used to determine width recommendation	Details
amphibians	20	1st - 3rd order rivers	Pacific Northwest, USA	Fir/hemlock forest	timber extraction	(Vesely & McComb 2002)	Compared riparian buffers to reference forest	Recommended width achieves 80% of forest species richness and abundance
amphibians	30	headwater streams	North Carolina, USA	Temperate broadleaf mixed forest	timber extraction	(Peterman & Semlitch 2009)	Compared riparian buffers to reference forest	Recommended width achieves the same salamander abundance as control sites
amphibians	46	3rd order rivers	Pacific Northwest, USA	Forests	timber extraction	(Stoddard & Hayes 2005)	Arbitrary	Recommendation based on a positive response of focal taxa to presence of riparian reserve (46m was the width of buffers in study)
amphibians and reptiles	30	rivers (size unspecified)	Texas, USA	Pine forest	timber extraction	(Rudolph & Dickson 1990)	Asymptotic threshold	Recommend width above which much smaller biodiversity gains are achieved per additional meter of forest added

Animal Group	Minimum width (m)	Water body	Location	Ecosystem type	Surrounding land use	Publication	Method used to determine width recommendation	Details
ants	50	middle order	Sydney, Australia	Eucalyptus	suburban residential	(Ives et al. 2011a)	Asymptotic threshold	Recommend the minimum width after which major compositional changes were no longer seen
birds	20	lakes and rivers 4 - 15 m width	Newfoundland, Canada	Fir forest	timber extraction	(Whitaker & Montevecchi 1999)	Compared riparian buffers to reference forest	Recommend the width that achieves similar community of forest generalist species
birds	40	1st, 2nd, 3rd order rivers	Oregon, USA	Fir forest	timber extraction	(Hagar 1999)	Compared riparian buffers to reference forest	Recommended width achieves abundance of species that matches the minimum abundance in undisturbed sites
birds	45	2nd or 3rd order river	Washington state, USA	Fir forest	timber extraction	(Pearson & Manuwal 2001)	Compared riparian buffers to reference forest	Recommended width achieves presence of all species found in undisturbed sites

Animal Group	Minimum width (m)	Water body	Location	Ecosystem type	Surrounding land use	Publication	Method used to determine width recommendation	Details
birds	50	1st and 2nd order rivers	Texas, USA	Pine forest	timber extraction	(Dickson et al. 1995)	Presence of indicator species	No reference forest. Recommendation based on presence of species generally described as woodland interior specialists
birds	60	5 - 15 m width river	Quebec, Canada	Fir forest	timber extraction	(Darveau et al. 1995)	Compared riparian buffers to reference forest	Recommended width achieves similar community composition to undisturbed sites
birds	100	~ 100 m width river	Georgia, USA	Mixed forest	timber extraction	(Hodges & Krementz 1996)	Asymptotic threshold	Recommended width based on the point above which abundance of conservation priority species no longer increases

Animal Group	Minimum width (m)	Water body	Location	Ecosystem type	Surrounding land use	Publication	Method used to determine width recommendation	Details
birds	100	rivers (size unspecified)	Maryland/Delaware USA	Wetland forest	agriculture	(Keller et al. 1993)	Arbitrary	No reference forest. Recommendation based on width at which >50% the maximum abundance of forest interior specialists are found and where neotropical migrants become abundant than local migrants
birds	100	lakes	Alberta, Canada	Boreal mixed-wood forest	timber extraction	(Lambert & Hannon 2000)	Compared riparian buffers to reference forest	Recommended width achieves local species breeding rate that matches forest
birds	150	1st, 2nd, 3rd, 4th order river	Maine, USA	Hardwood/ boreal forest	timber extraction	(Haegen & Degraaf 1996)	Compared riparian buffers to reference forest/Arbitrary	Recommendation based on requirement for buffer to be twice the area influenced by edge effect (75m)
birds	40 - 50	9 - 34 m width river	BC, Canada	Coastal montane forest	timber extraction	(Shirley & Smith 2005)	Compared riparian buffers to reference forest	Recommended width achieves the presence of a set of forest specialists

Animal Group	Minimum width (m)	Water body	Location	Ecosystem type	Surrounding land use	Publication	Method used to determine width recommendation	Details
birds and mammals	200	rivers (size unspecified)	Brazil	Tropical rainforest	agriculture	(Lees & Peres 2008)	Compared riparian buffers to reference forest	Recommended width achieves forest-like values for certain species
birds and mammals (small) and amphibians	variable widths	lakes	Alberta, Canada	Boreal mixed-wood forest	timber extraction	(Hannon et al. 2002)	Arbitrary	Recommendation based on evidence that even 200m width does not conserve old growth vertebrates, so favour variable design corridors to maximise aquatic benefits in a site specific way
mammals (arboreal)	200	rivers (size unspecified)	Australia	Tropical rainforest	agriculture and grazing	(Laurance & Laurance 1999)	Compared riparian buffers to reference forest	Recommended width achieves presence of vulnerable, completely arboreal species
mammals (small)	30	rivers (size unspecified)	BC, Canada	Fir forest	timber extraction	(Cockle & Richardson 2003)	Compared riparian buffers to reference forest	Recommended width achieves community composition similar to undisturbed sites

Animal Group	Minimum width (m)	Water body	Location	Ecosystem type	Surrounding land use	Publication	Method used to determine width recommendation	Details
mammals (small)	variable widths	5 - 15 m width river	Quebec, Canada	Boreal balsam fir forest	timber extraction	(Darveau et al. 2001)	Arbitrary	Recommendation based on evidence that different species require different widths
mammals (small) and amphibians	200	<5m width rivers	Brazil	Tropical rainforest	ranches	(de Lima & Gascon 1999)	Compared riparian buffers to reference forest	Recommended width achieves community composition similar to undisturbed sites

TABLE 2.

Width recommendations for riparian reserves and the approach used to make the recommendation, from peer reviewed research that surveyed existing riparian reserves.

INSECTS AS FOCAL TAXA FOR STUDYING BIODIVERSITY AND ECOSYSTEM PROCESSES

In order to assess the effect of oil palm expansion and different conservation strategies on biodiversity, a focus on insects has many advantages. Approximately 1 million species of insects have been described, making up more than 60% of all described animal biodiversity, and the total global species richness of insects is likely to be considerably higher than the number documented so far (Chapman 2009). If we are to successfully conserve as many animal species as possible, the insects should be a major focus of our attentions. Insects are also ecologically critically important. The diversity of feeding behaviours and life history strategies of insect species means that they support a huge range of ecological processes (Denno & Eubanks 2011). Insects are key pollinators of a vast number of plants. They are key decomposers of animal and plant tissues and are therefore central to nutrient cycling functions. Insects determine the growth and population dynamics of many species through herbivory, predation, parasitism and the transmission of disease. They are also a crucial source of food for a large number of other species. To thoroughly understand the impact of human activity and conservation strategies on ecological processes, research on insects is clearly essential.

In addition to being ecologically important, Insects are also good indicators. Given the short generation times of many insects, compared to larger groups such as vertebrates, insects can show much faster, smaller scale responses, making them more sensitive to land use change. The response of insect groups often correlates well with other groups of plants and animals, which may be harder to collect data on (Schulze et al. 2004), although in most cases no one group correlates well with all other taxa (e.g. Lawton et al. 1998; Barlow et al. 2007). In addition, surveying insects can be reasonability low cost and efficient, as inexpensive equipment can be used and large sample sizes can be obtained reasonably quickly (Kessler et al. 2011). This is especially important in tropical regions where there is a very high diversity to

be sampled and data may need to be collected quickly in order to inform management decisions in rapidly changing landscapes. However, despite their ecological importance of insects and their advantages as indicators, insects are massively under-represented in conservation prioritisation schemes and policy making (Barua et al. 2012). Collecting data on the responses of tropical insects and their ecological functions is therefore not only highly informative and cost-effective, but also filling an important information gap in conservation practice.

In this thesis, I focus on ants and dung beetles as they are reasonably good indicator taxa for tropical regions, and are also ecologically important. Two recent studies (Gardner et al. 2008; Kessler et al. 2011) that specifically evaluated the extent to which taxa show congruent responses indicate that dung beetles species richness and abundance often correlates with that of other groups. Ants are generally less strongly correlated with other taxa, in part because of the wide range of ecologically niches that they fill, but they are widely used as a biodiversity indicator group because they are present in almost every terrestrial habitat and are very sensitive to environmental change (Agosti et al. 2000). From a more practical perspective, both ants and dung beetles are relatively well described and straightforward to sample, and therefore yield large quantities of detailed data at a reasonably low cost (Kessler et al. 2011). Another key consideration is that both groups are ecologically very influential. Dung beetles provide a wide range of ecological processes, including nutrient cycling, bioturbation, seed dispersal and pest control (Nichols et al. 2008). Similarly, ants act as predators, detritivores and scavengers, and form mutualistic relationships with a wide range of other plant, insect and animal species (Lach et al. 2010). Both ants and dung beetles therefore offer an opportunity to examine biodiversity – ecosystem function relationships across natural tropical forest disturbance gradients, a topic that has received relatively little attention in comparison to studies in laboratory or temperate grassland settings (Spehn et al. 2005; Slade et al. 2011; Cardinale 2012; Bu et al. 2014). The differences in the ecology of these two groups

means that they are complementary indicator taxa to choose; ants and dung beetles may be affected very differently by human activities, and therefore surveying both provides a much broader insight into the impacts of land use change and conservation action.

STRUCTURE OF THESIS:

In this thesis, I investigate how ants and dung beetle communities and ecosystem functions change across a land use gradient from forest to oil palm. I evaluate the success of maintaining riparian reserves for the conservation of biodiversity and ecological processes in this context. I also explore the relationships between biodiversity and ecosystem function and provide insights into the delivery of a specific set of ecosystem services.

Chapter 2 provides an overview of the riparian reserves as a habitat, in comparison to areas of oil palm and much larger areas of logged forest (>10 000 ha). I present data on a range of vegetation and soil variables and examine how important biotic and abiotic characteristics vary among these land uses. I also examine soil function using bait lamina strips, a method designed to quantify the feeding activity of soil fauna and commonly applied to assess the impact of different cultivation techniques, fertilisers and soil contaminants or pollutants.

In Chapter 3, I assess the extent to which riparian reserves conserve the species and ecological processes of much larger areas of logged forest, using dung beetles as an ecological indicator. I compare the dung beetle community and dung removal function within riparian reserves to riparian areas of logged forest, and riparian areas where oil palm was planted up to the river edge. I also assess whether riparian reserves enhance dung removal services in surrounding areas of oil palm.

In Chapter 4, I provide a more thorough examination of the extent to which structural features and landscape context of the riparian reserves influence their conservation value, with the

goal of providing specific recommendations for policy and plantation managers. I also carry out a basic economic assessment of the potentially opportunity cost associated with different policy scenarios. As with chapter 1, I used dung beetles as an indicator group, exploring not only how reserve structure and landscape context affect the species richness, composition and functional diversity of the beetle communities, but investigate movement of individuals from the logged forest into, and out of, the riparian reserves.

In Chapter 5, I examine the extent to which the riparian reserves conserve the community and function of a very different group of insects: leaf litter foraging ants. The colonial structure of ant communities and the relatively low mobility of the minor (worker) caste means that they are likely to respond differently to the dung beetles. This chapter therefore provides an insight into a completely separate aspect of the ecosystem and conservation value of the riparian reserves. Using a new bait removal technique from which I could obtain species specific functional data, I quantified changes in foraging activity of ants across the forest to oil palm gradient and also explored which aspects of change in the community best explain the observed shifts in function. I used broadly the same field selection of field sites as in chapter 1, but was able to add another replicate of each land use category.

In Chapter 6, I assess the extent to which riparian reserves can provide a pest control service to the surrounding oil palm. I quantified the foraging activity of potential predators of oil palm pests using plasticine pest mimics, a method that has been used in a wide range of temperate and tropical locations to avoid the difficulty of rearing large numbers of pests and being unable to identify active predators. I also planted young oil palms to record herbivory rates in areas of oil palm near to rivers with and without riparian reserves. In this chapter I also present results on a methodological experiment to test the extent to which predation on the plasticine mimics might reflect true predation rates, but manipulating the colour and shape of the mimics.

Chapter 7 is a general discussion of all the results presented in the preceding chapters, in which I highlight the main conclusions of my work and place them in the context of current discussion and research on conservation strategies in agricultural areas. I also indicate topics for future study that would be particularly informative for our understanding of biodiversity within agricultural landscapes and also for the management of riparian zones.

CHAPTER 2: RIPARIAN FOREST CORRIDORS IN OIL PALM PLANTATIONS RETAIN THE VEGETATION AND SOIL STRUCTURE OF CONTINUOUS LOGGED FOREST, BUT NOT IMPORTANT SOIL PROCESSES.

ABSTRACT

The preservation of forest fragments in agricultural landscapes can increase the survival of threatened species and maintain ecosystem services. Riparian forest strips (riparian reserves) are one example of this; these buffer zones are often maintained for their beneficial impact on water quality, but can also function as corridors for species' movement and as a habitat in their own right. Whilst the ecology of riparian reserves has been relatively well documented in temperate regions, relatively little is known about their counterparts in the tropics. We assessed the vegetation structure, basic soil characteristics and soil fauna feeding activity of riparian zones in areas of continuous logged forest and areas of oil palm with and without riparian buffer strips within Sabah, Malaysian Borneo. We found that the vegetation structure, humus depth, soil density and temperature fluctuations of the riparian reserves were similar to values for continuous logged forest. However, the depth profile of soil fauna feeding activity, as measured by bait lamina strips, was more similar to areas of oil palm than continuous logged forested areas. These results indicate that although the vegetation and soil characteristics of the riparian reserves imply high conservation value for forest dependent species, key ecological processes may be altered in these linear forest fragments.

INTRODUCTION

Agricultural expansion and intensification are key drivers of the decline in native vegetation and habitat, and are likely to impact tropical regions in particular over the next 50 years (Laurance et al. 2014). However, many agricultural landscapes retain forest fragments, corridors or remnant trees which can mitigate the negative impacts of conversion to agriculture, providing valuable habitat for native species and supporting ecosystem services (e.g. Harvey et al. 2005; Sekercioglu et al. 2007; Ricketts et al. 2008). To understand the role of these habitat fragments in the conservation of biodiversity and ecosystem processes, it is important to document how their vegetation structure, species composition and ecological functions compare to alternative land uses.

Riparian forest buffers are protected in agricultural areas in many countries but their biotic and abiotic characteristics, and hence conservation value, is poorly documented for tropical regions. Also referred to as riparian strips or corridors, these reserves consist of stretches of non-crop habitat on both sides of a river. They are often protected because they reduce the run-off of agricultural chemicals and soil, thereby maintaining water quality (Lee et al. 2003; Teels et al. 2006; Mayer et al. 2007). Riparian reserves also stabilise river banks (Sweeney et al. 2004), limit the risk of floods and droughts (Salemi et al. 2012), provide recreational and aesthetic amenities (Schultz et al. 1995), and support aquatic and terrestrial wildlife (e.g. Lorion & Kennedy 2009; Marczak et al. 2010).

In general riparian reserves have higher plant species richness than adjacent monocultures, but the vegetation structure and extent to which they conserve native plant communities can vary. For example, the diversity of plant species increases with the width of riparian reserves in Brazil (Metzger et al. 1997). Lees & Peres (2008) found that understorey density, canopy cover and basal area of trees in riparian corridors is more similar to large areas of continuous forest if the corridors remain connected to the continuous forest. Similarly, Barlow et al.

(2010b) found that riparian corridors in the Amazon had a similar basal area of trees to connected areas of primary forest. However, given that the influence of forest edges can extend up to 500 m into tropical forests (Harper et al. 2005), riparian reserves in tropical regions are likely to be entirely edge habitat and vulnerable to increased tree mortality and changes in vegetation structure even compared to remaining areas of logged forest. The extent to which riparian reserve vegetation structure and community composition resembles larger areas of forest remains poorly understood, and the majority of information is from the neotropics rather than Africa or Southeast Asia.

Furthermore, very little information is available on abiotic characteristics or the rate of key ecological processes in tropical riparian reserves. Most existing research has focussed on the impact of riparian vegetation on the chemistry and biological dynamics of the water courses, rather than adjacent terrestrial habitats. Sekercioglu et al. (2007) found that riparian strips in Costa Rica tended to have lower ambient temperatures and higher humidity than surrounding coffee plantations, but were similar to nearby non-riparian forest fragments. The few studies on terrestrial processes indicate that the extent to which tropical riparian reserves resemble large areas of forest can vary for different ecological processes. Santos & Benítez-Malvido (2012) showed that leaf herbivory rates on two focal plant species are lower, and pathogen damage higher, in riparian strips compared to gaps in a large forest reserve. In contrast, Norris & Michalski (2010) found that dung removal rates in riparian reserves were similar to intact forest (> 1000 ha) in the Brazilian Amazon.

We quantified the vegetation and soil structure and measured the soil fauna feeding activity (using bait lamina strips (Kratz 1998)) within riparian reserves in oil palm plantations in Sabah, Malaysian Borneo. The ecology of riparian reserves within palm oil plantations is of particular interest as oil palm is now the dominant agricultural crop across much of South east Asia (FAO 2014), and the industry is expanding in West Africa and the South America (Butler & Laurance

2010; Foster et al. 2011). However, relatively little is known about the ecological dynamics of oil palm landscapes, and the impact of fragments of non-crop habitat within these landscapes (Savilaakso et al. 2014).

METHODS

STUDY SITES

All study sites were located within a 600 km^2 area around and including the Stability of Altered Forest Ecosystems (SAFE) project site in Sabah, Malaysian Borneo (117.50 N, 4.60 E). The area is a mixture of twice-logged lowland dipterocarp rainforest, acacia and oil palm plantations, the latter planted between 1998 and 2012. Further details are given in Ewers et al. (2011).

All sites were adjacent to a river, and at least 1.5 km apart. Over 2 field seasons (2011 and 2012) we collected data from twenty-seven sites within a riparian reserve, eight sites in areas of riparian oil palm without a riparian reserve, ten sites in logged forest (nine were in a large block of forest >10 000 ha and one was placed in a forest fragment of 550ha to ensure thorough spatial interspersion of logged forest sites with riparian reserve and oil palm sites). Widths of the riparian forest protected at the riparian reserve sites ranged between 20 m and 180 m (mean = 97 m, sd = 116), measured on one side of the river. We also set up one (reference) site in primary forest (Maliau Basin), approximately 70 km away from the SAFE project area; it was not possible to achieve adequate spatial interspersion of primary forest with the other land uses we compared. Table 1 shows the distribution of sampling points in each land use type for each year. All sampling points within each site were at least 25 m apart.

TABLE 1

Number of sites and sampling points across different land use types.

	Primary Forest		**Logged Forest**		**Riparian Reserve**		**Oil Palm (no riparian reserve)**	
Year	**2011**	**2012**	**2011**	**2012**	**2011**	**2012**	**2011**	**2012**
Sites	1	0	7	7	8	26	7	8
Sampling points	12	0	84	125	44	223	136	99
Total sampling points	**12**		**209**		**267**		**235**	

DATA COLLECTION

At each sampling point we quantified canopy density using a spherical densiometer and measured the basal area of trees using the angle or point-count method (Holgate 1967; Bitterlich 1984). We estimated the height of the tallest tree within 10 m of the sampling point, using a reference point of known height and a ruler held at arm's length. For all points with clear access to the river (n = 424), we estimated stream width. We also cut into the soil such that a clear view of the soil structure was visible and measured the depth of the humus and leaf litter layer with a ruler.

For each point sampled in 2011, we took a soil core of diameter 45 mm and depth 10 cm, from which we could measure soil density (soil from the cores was dried to constant temperature in an oven at 90 ^{o}C). For two sampling points at each site visited in 2011, we also recorded below ground temperatures over a 24-hour period. Temperature loggers (iButtons) were inserted 10 cm below the ground in sealed plastic bags, covered over gently with soil and recovered after 24 hours.

We used bait lamina sticks (manufactured by Terra Protecta GmbH, Germany) to quantify soil fauna feeding activity (Kratz 1998; Römbke et al. 2006; Hamel et al. 2007). These are plastic sticks with sixteen 2 mm diameter holes, each of which is filled with a bait consisting of 70%

cellulose powder, 27% ground bran flakes and 3% active charcoal. This method has been used to assess the impact of a wide range of human activities on the soil fauna, including forest fragmentation (Simpson et al. 2012), contamination by heavy metals or pesticides (Förster et al. 2011; Niemeyer et al. 2012), different agricultural management techniques (Birkhofer et al. 2008) and climate change (Kreyling et al. 2013). The bait lamina strips are a simple piece of plastic with a row of holes containing a cellulose bait; the strip is inserted into the ground in order to measure the feeding activity of enchytraeids, earthworms (lumbricids), and to a lesser extent collembola and mites (Helling et al. 1998; Gongalsky et al. 2008). The method therefore provides an insight into processes that contribute to the decomposition of organic material, nutrient mineralisation and the stabilisation of soil carbon.

Six strips were inserted vertically into the ground at each sampling point in a grid with 10 cm between each strip, and with the top hole just underneath the surface of the soil. All strips were removed after 5 days. The sticks were then examined in consistent lighting conditions and each hole was scored for the presence or absence of a perforation.

ANALYSIS

All analyses were carried out with the R open access software (version 3.0.2 , R Core Team 2013).

We tested for a relationship between land use and stream channel width, canopy density, basal area, soil density and humus depth separately using linear mixed models, specifying site as a random factor and applying transformations where necessary to meet assumptions (package nlme (Pinheiro et al. 2013)). Data on tree height was averaged to site level before analysis using an ANOVA in order to achieve normality and homogeneity of variance.

With only the data from sampling points within riparian reserves, we also used linear mixed models (specifying site as a random factor) to test whether there was a relationship between any soil or vegetation variables and the distance from the nearest point at which the riparian reserve system connected to logged forest.

To avoid issues of pseudoreplication within day, the data on temperature were averaged for each site and then analysed using an ANOVA. Similarly, to test for differences in temperature variation across land use types, the standard deviation of temperature values across the 24 hour period was calculated for each site and analysed using an ANOVA.

We analysed the effect of land use on the total number of holes perforated in each stick with a generalised linear mixed model (package lme4, (Bates et al. 2014)), specifying sites, transect and distance as nested random factors. To test for differences with depth, binary data on the presence or absence of a perforation in each hole within the bait laminar stick was analysed using a generalised additive mixed model (GAMM, from the package gamm4 (Wood & Scheip 2013)) with a cubic regression spline smoother. We specified land use as a fixed factor and included distance from the river, transect and site as nested random factors to account for spatial autocorrelation. Smoother selection and model reduction were based on AIC comparisons.

RESULTS

The canopy density, basal area, tree height, and humus depth of riparian reserves were not significantly different from logged forest, but they were significantly higher than in oil palm (Table 2, Fig 1 c) to e)). There were no significant differences in soil density across land use types (Table 2, Fig 1 b)). Stream widths in riparian reserve sites were significantly wider than those in forest or oil palm, but only by a couple of meters (Table 2, Fig 1 a)).

Both the mean daily temperature and the variance in temperature over a 24 hour period were higher in oil palm than in continuous logged forest and riparian reserves, but did not differ significantly between the two forested habitats (Table 2, Fig 2).

Across all land uses, there was high variation in the number of holes perforated per stick (mean ± sd in logged forest = 3.1 ± 3.5, riparian reserve = 2.8 ± 3.5, oil palm = 2.8 ± 3.8). The overall feeding activity did not differ significantly between land uses (χ^2 = 1.34, df = 2, p = 0.51). Soil fauna feeding activity decreased with soil depth across all land uses; the minimum adequate model (Table 3) retained the interaction between land use and depth, indicating a different depth profile for feeding activity in different land uses. Feeding activity in all three land uses declines over the first part of the depth profile (0 mm to 40 mm) but the initial decline in feeding activity with depth is steeper in logged forest sites. In addition, feeding activity at greater depths (40 – 80 mm) is higher in logged forest than in the other two land uses (Fig 3).

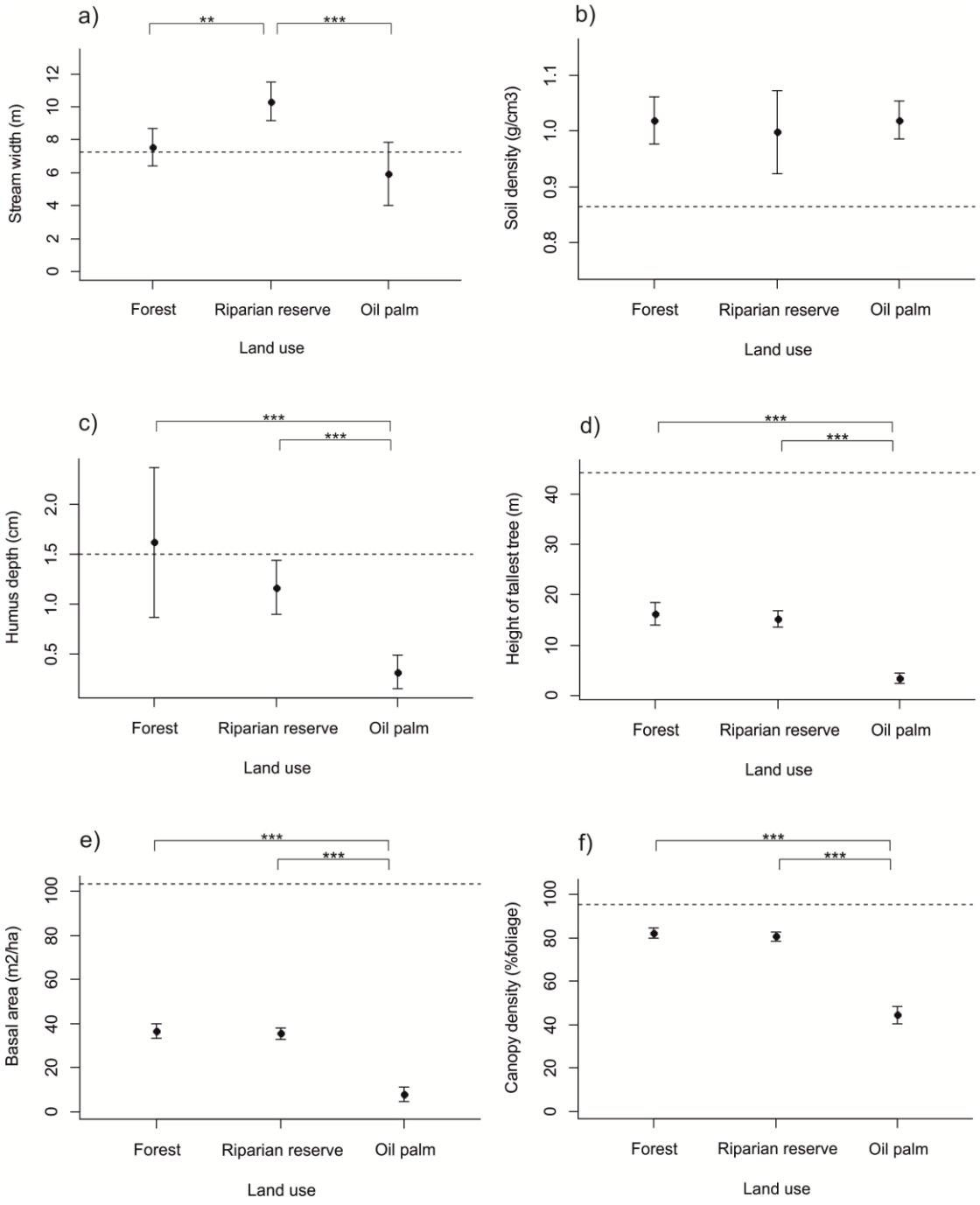


FIG 1

Comparison of land uses in terms of a) stream width, b) soil density, c) humus depth, d) height of tallest tree, e) basal area of trees f) canopy density. Plots show mean ± 95% CI, stars indicate significant differences between groups based on within model contrasts; $p \leq 0.001$ = ***, $p \leq 0.01$ = **. Dotted lines give the mean value for the one primary reference site (data not included in analyses).

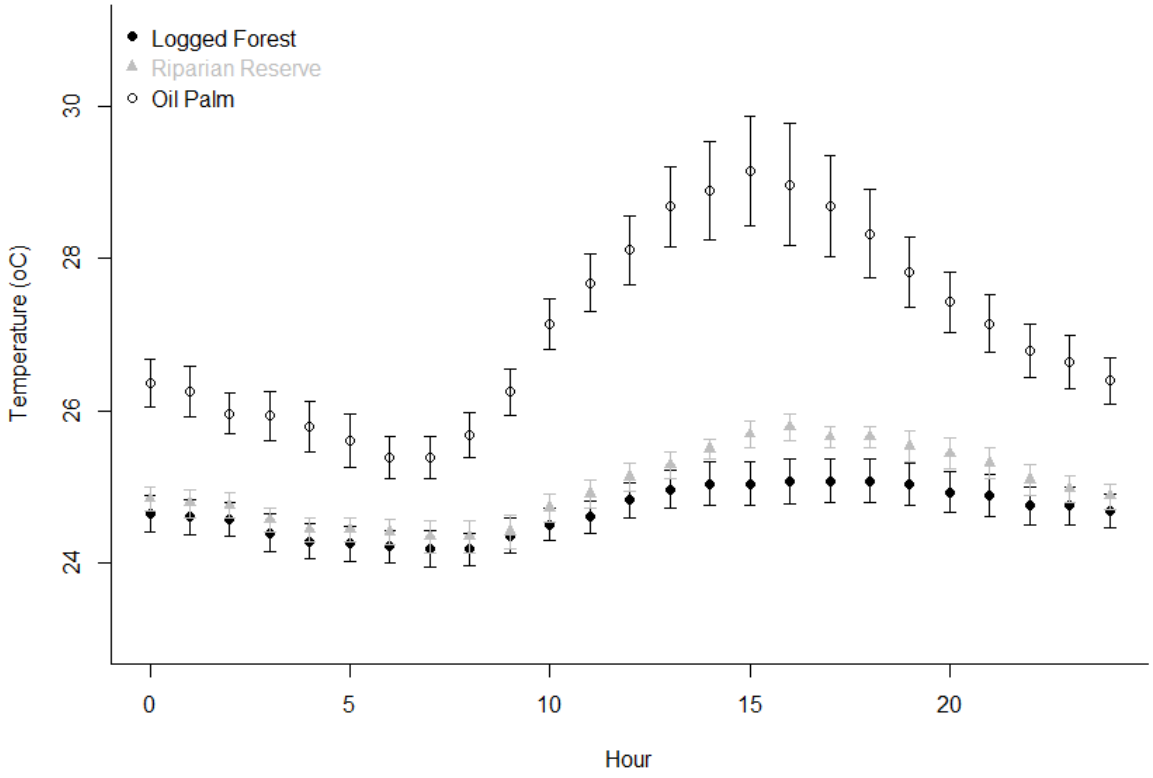


FIG 2

Temperature changes throughout the day in each land use. Plot shows mean ±95% CI for each hour (24 hour clock).

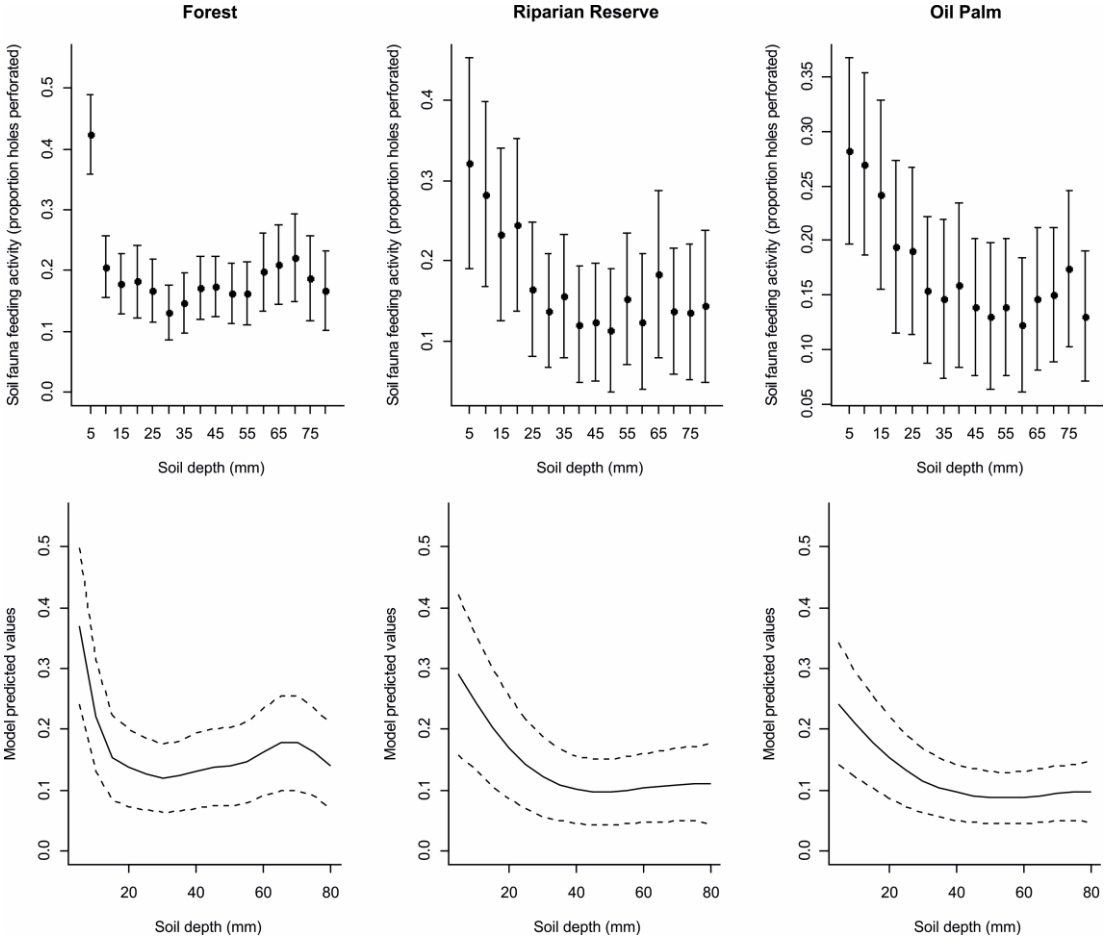


FIG 3

Top panels show the proportion of holes perforated at different depths (mean ± 95%); proportions were calculated for data pooled across all six bait laminas placed at each sampling point. Lower panels show the GAMM predicted values (mean ± 95% CI) from the analysis on binary data for each hole in each bait lamina strip.

Model	df	F	p
Stream width ~ land use	2, 381	10.9	0.0002 ***
Stream width ~ distance along RR	1, 233	1.68	0.205
Soil density ~ land use	2, 240	0.26	0.77
Soil density ~ distance along RR	1, 29	0.005	0.95
Humus depth ~ land use	2, 663	46.6	<0.001 ***
Humus depth ~ distance along RR	1, 209	0.097	0.76
Tree height ~ land use	2, 43	66.8	<0.001 ***
Tree height ~ distance along RR	1, 209	0.64	0.43
Basal area ~ land use	2, 663	271.5	<0.001 ***
Basal area ~ distance along RR	1, 209	0.496	0.49
Canopy density ~ land use	2, 663	177.1	<0.001 ***
Canopy density ~ distance along RR	1, 209	0.13	0.73
Mean daily temperature ~ land use	2, 19	26.7	<0.001 ***
Variance daily temperature ~ land use	2, 19	19.9	<0.001 ***

TABLE 2

Results of linear mixed models testing for an effect of land use or distance from forest on vegetation, soil and temperature variables; “distance along RR” refers to the distance measured along the riparian network to the nearest point at which the riparian corridor connected with the remaining large block of logged forest.

	df	Chi.sq	p
landuse	2	1.01	0.603
s(depth) : Forest	5.98	89.4	<0.001 ***
s(depth) : Riparian Reserve	2.98	49.8	<0.001 ***
s(depth) : Oil Palm	2.97	74.4	<0.001 ***

TABLE 3

Output of GAMM: feeding activity ~ landuse*s (depth), where s () = use of cubic regression spline smoother. Note that df, Chi.sq and p values are estimated for smoothers

DISCUSSION

As agriculture continues to expand across tropical regions, identifying opportunities for the conservation of biodiversity within these agricultural landscapes is becoming increasingly important. We found that riparian reserves in oil palm plantations maintain the coarse vegetation and soil structure found in larger areas of continuous secondary forest and therefore increase the habitat heterogeneity of oil palm landscapes. However, we also found that the feeding activity of soil fauna was not conserved, indicating that important ecological processes are altered in the riparian reserves relative to forest.

SIGNIFICANCE OF VEGETATION AND SOIL STRUCTURE FOR BIODIVERSITY CONSERVATION

Overall, the biotic and abiotic characteristics of riparian reserves indicate that they provide habitat that is not otherwise available within oil palm landscapes. The canopy density, basal area, humus depth and tree height of riparian reserves are very similar to continuous areas of logged forest and higher than in areas planted with oil palm. Also, both the mean temperature and daily variance in temperature within riparian reserves is similar to logged forest areas and lower than in sites planted with oil palm. As logged forest retains more species than oil palm areas (Berry et al. 2010; Edwards et al. 2011), our results suggest that riparian reserves can provide habitat for forest dependent species that would not otherwise move through or persist in oil palm plantations.

The data we collected gives some insight into the components of biodiversity that are likely to benefit from the protection of riparian reserves. The lower temperatures in riparian reserves relative to oil palm will benefit species vulnerable to desiccation, such as invertebrates (e.g. woodlice) and amphibians. The preservation of the humus layer is also likely to benefit groups that feed on soil, fungi or decaying leaves and woody matter, such as the species rich *Termes*

termites (Termitinae), which feed on highly decayed plant material (Eggleton et al. 1999) and are normally found in lower numbers in oil palm than in forest (Luke 2010). Of course, the small area within the reserves means that they are unlikely to support many large vertebrates; a viable population of clouded leopard, for example, is thought to need at least 350 km^2 of forest (Wilting et al. 2006). However, the riparian reserves may provide movement corridors for species such as the orang-utan, which nest in forest fragments when moving through agricultural areas (Russon et al. 2001) or leopard cats, which use forest fragments as refuges when foraging in oil palm areas (Rajaratnam et al. 2007). The similarities in vegetation and soil structure between riparian reserves and forest indicate that riparian reserves may support a range of forest dependent communities and further research in this area is likely to be very useful for biodiversity conservation.

ECOLOGICAL PROCESSES AND THE BAIT LAMINA METHOD

Our data indicate that riparian reserves do not conserve all aspects of soil processes within logged forest areas even though the vegetation and soil structure are broadly very similar. The lack of consistency between above and below ground characteristics has also been found in riparian buffers in California which had higher plant species diversity than surrounding cropland but similar levels of soil carbon and microbial and nematode diversity (Young-Mathews et al. 2010). This suggests that soil processes within riparian buffers can be heavily affected by adjacent agricultural conversion, and other important ecological processes may also be altered or impaired within riparian reserves. Further research on a wider range of ecological processes would be beneficial to establish the extent to which this the case and if there are associated consequences for biodiversity conservation.

Differences on the depth profile of soil fauna activity across land uses may be explained by differences in the community of soil fauna present and the soil structure. Feeding activity

within the first 3 cm of soil was higher in riparian reserves and oil palm than in logged forest. This may be because large quantities of fertiliser are applied to oil palm plantations (Corley & Tinker 2003) and these chemicals also run into the riparian reserves. Higher nitrate and phosphate residues could support higher densities of microbes and soil fauna in the top layers of these soils (Zhu et al. 2013). However, Lee-Cruz et al. (2013) found that the abundance of bacteria within the top 5 cm of soil did not differ significantly between logged forest and oil palm, although the community composition did. The differences in feeding activity may therefore be due to differences in the composition of bacterial and soil fauna communities. In addition, at greater depths (6 cm to 8 cm), feeding activity was higher in logged forest than in oil palm and riparian reserves. Even though we did not find any differences in soil density, it is still possible that the soil structure in the riparian reserves and oil palm have been damaged by the process of conversion to plantation, which could affect the activity of soil fauna at greater depths. Studies of bait lamina strips in Russia indicate that soil texture (compaction, stone density) determines the vertical stratification of soil fauna feeding activity as measured by bait lamina strips (Gongalsky et al. 2004).

Very few studies have used the bait lamina method in tropical regions and our data show that bait lamina strips can detect differences in soil fauna feeding activity across land uses in the tropics. In particular, we found that an advantage of the bait lamina method is that it can detect very small scale differences in the depth profile of soil fauna feeding activity. Many studies of tropical soil processes use litter bags or other methods that do not investigate changes with depth (McGlynn & Poirson 2012). As we did not find any overall difference in soil fauna feeding activity, but did find subtle differences in the depth profile of feeding activity, it is possible that much finer spatial scales need to be investigated to thoroughly document the effects of land use change on ecological processes. The feeding rates in our logged sites were similar to those in secondary forest in the Amazon (Römbke et al. 2006), and also suggest that appropriate exposure times for in the tropics (5 – 6 days) are much lower than the two to

three weeks normally used in temperate regions (e.g. Geissen & Brümmer 1999; Simpson et al. 2012). We found high levels of variation in soil fauna feeding activity even between strips very close to each other, and would recommend using higher numbers of sticks at each site if possible, to overcome this noise.

For more information to be obtained from bait lamina strips used in tropical regions, we need further research on the variation in soil fauna with depth and experiments establishing which fauna remove the bait in the strips. Studies investigating which groups feed on bait lamina strips have used enchytraeids, collembola and other native soil fauna from temperate soils (Helling et al. 1998; Gongalsky et al. 2008), but Römbke et al. (2006) suggest that other groups, such as oribatid mites may be more important in soils in the Amazon. Very little information is available on which groups are responsible for feeding on bait lamina strips in tropical regions and how these fauna vary with soil depth, which hinders a detailed interpretation of the patterns of feeding activity we observed.

RIPARIAN RESERVES IN A WIDER CONSERVATION CONTEXT

Discussion of the value of riparian habitat often focuses on much larger rivers than those we surveyed, but our results indicate that legislation regarding smaller waterways could also have an important impact on biodiversity conservation. Certainly in Sabah, discussion of the protection of riparian vegetation focusses on much larger rivers, such as the Kinabatangan (e.g. Hai et al. 2001; WWF 2014), which is wider than 100 m for much of its length. The streams we surveyed were all less than 15 m in width, and there are many more waterways of this size across the oil palm landscapes of Southeast Asia. If the vegetation along all these waterways was similar to that in logged forest, as it was at our sites, riparian reserves could provide a large area of non-crop habitat and increase habitat diversity dramatically across oil palm landscapes.

However, it is possible that without strict protection the habitat value of riparian reserves could decay quite swiftly. They are not only entirely edge habitat in most cases, but also easily accessible to human communities who may require and extract timber or other resources. As Lees & Peres (2008) found in Brazil, riparian reserves that are no longer connected to large areas of forest have lower basal areas and canopy cover, suggesting that as the boundary of remaining forest retreats, riparian reserves are likely to deteriorate in terms of habitat value and similarity to logged forest. Our field sites are in an area of relatively recently converted land (Ewers et al. 2011) and may therefore be at risk of degradation. Although we found that the vegetation structure was similar to logged forest, effective protection of the reserves could be essential to ensure this continues to be the case.

Nevertheless, our results also indicate that protecting undisturbed habitat will remain a much more important conservation priority than protecting riparian vegetation. The riparian zones in both logged forest and riparian reserves had lower canopy density, basal area, tree heights and higher soil density than primary forest; these are standard effects of logging and the soil compaction that it causes (Hattori et al. 2013). The irreplaceable value of primary forests is well recognised (e.g. Gibson et al. 2011), and whilst our results indicate that riparian reserves have the potential to provide valuable habitat for forest dependent species, we do not suggest that this be used as a justification to convert large areas of forest.

CONCLUSIONS

Overall, the structural vegetation and soil characteristics of riparian reserves are very similar to that of twice logged forest and dramatically different from the structure of oil palm areas. This indicates that that they can provide valuable habitat that may not otherwise be available in oil palm plantations and could make a significant contribution to terrestrial species conservation. However, despite the similarity of riparian reserve vegetation to logged forest areas, the soil

fauna activity within the reserves appears to be influenced by the surrounding oil palm planation. It is likely that there are also other ecological functions that are also impaired within the riparian reserves relative to large areas of logged forest, and this highlights the unparalleled importance of protection large tracts of forest for the successful conservation of biodiversity and ecosystem processes. Nevertheless, based on the data presented here, the extent to which riparian reserves improve the persistence of biodiversity ecological functions within tropical agricultural landscapes deserves further attention.

CHAPTER 3: DO RIPARIAN RESERVES SUPPORT DUNG BEETLE BIODIVERSITY AND ECOSYSTEM SERVICES IN OIL PALM DOMINATED TROPICAL LANDSCAPES?

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ABSTRACT

Agricultural expansion and intensification are major threats to global biodiversity, ecological functions and ecosystem services. The rapid expansion of oil palm in forested tropical landscapes is of particular concern given their high biodiversity. Identifying management approaches that maintain native species and associated ecological processes within oil palm plantations is therefore a priority. Riparian reserves are strips of forest retained alongside rivers in cultivated areas, primarily for their positive hydrological impact. However, they can also support a range of forest-dependent species or ecosystem services. We surveyed communities of dung beetles and measured dung removal activity in an oil palm-dominated landscape in Sabah, Malaysian Borneo. The species richness, diversity, and functional group richness of dung beetles in riparian reserves was significantly higher than in oil palm, but lower than in adjacent logged forests. The community composition of the riparian reserves was more similar to logged forest than oil palm. Despite pronounced differences in biodiversity we did not find significant differences in dung removal rates among land uses. We also found no evidence that riparian reserves enhance dung removal rates within surrounding oil palm. These results contrast previous studies showing positive relationships between dung beetle species richness and dung removal in tropical forests. We found weak but significant positive relationships between riparian reserve width and dung beetle diversity, and between reserve vegetation complexity and dung beetle abundance, suggesting that these features may increase the conservation value of riparian reserves. The similarity between riparian reserves and logged forest demonstrates that retaining riparian reserves increases biodiversity within

oil palm landscapes. However, the lack of correlation between dung beetle community characteristics and dung removal highlights the need for further research into spatial variation in biodiversity ecosystem function relationships and how the results of such studies are affected by methodological choices.

INTRODUCTION

Agricultural expansion and intensification are currently amongst the main causes of decline in global biodiversity and ecosystem services (Phalan et al. 2013). However, large areas of agriculture will continue to be a key feature of our landscapes as the human population expands (Godfray et al. 2010). These cultivated landscapes can contribute to the persistence of biodiversity and delivery of ecosystem services, but appropriate, active management is required to achieve this (Garnett et al. 2013; Melo et al. 2013).

Successful management of biodiversity and ecological processes in tropical agricultural landscapes is important. Tropical landscapes are often particularly bio-diverse, highly productive for cultivation, and influence ecological functions and services on a global scale (Balmford & Whitten 2003). Whilst primary forests are critically important for conserving tropical biodiversity and ecosystem functions (Gibson et al. 2011) and once-logged forests in Southeast Asia also have high conservation value (Slade et al. 2011; Edwards et al. 2011), focussing on these habitats alone is not sufficient. The area of land dedicated to crops or livestock is much greater than that in reserves or un-modified by humans (Ellis & Ramankutty 2008), and the landscapes surrounding protected areas may strongly influence their success (Laurance et al. 2012). Moreover, modified agricultural landscapes can also be an important habitat in their own right (Mendenhall et al. 2012).

Retaining areas of native vegetation along rivers can help maintain biodiversity and ecological functions within agricultural areas. These linear forest fragments are called riparian strips,

buffer zones, stream management zones, or riparian reserves (the latter is used in Malaysia). They are primarily retained because riparian forest reduces run-off into streams, improving water quality and benefitting aquatic fauna (Sweeney et al. 2004; Mayer et al. 2007). Riparian reserves are also able to support forest dependent communities of many terrestrial taxa, including birds, small mammals and amphibians (Marczak et al. 2010). They are generally well protected legally and are a common feature of many agricultural landscapes (Lee et al. 2004b; Barlow et al. 2010b), so offer a feasible, realistic option to improve biodiversity within cultivated areas.

Nevertheless, the ecological roles of riparian reserves remain poorly understood, particularly in Southeast Asia. The majority of existing studies on riparian reserves focus on temperate regions, and particularly on bird species (see Marczak et al. (2010) for a review). To our knowledge, there are only 15 studies in tropical regions that evaluate the ecological characteristics of existing riparian reserves, all of which focus on the neotropics or north-western Australia (Hill 1995; de Lima & Gascon 1999; Laurance & Laurance 1999; Graham & Blake 2001; Galindo-González & Sosa 2003; Harvey et al. 2006; Medina et al. 2007; Lees & Peres 2008; Gillies & St. Clair 2008, 2010; Norris & Michalski 2010; Rodríguez-Mendoza & Pineda 2010; Barlow et al. 2010b; Gillies et al. 2011; Viegas et al. 2014).

Here, we investigate the ecological impact of riparian reserves in the oil palm plantations of Sabah, Malaysian Borneo. Palm oil is now the world's primary vegetable oil, a major biofuel feedstock, and a component in many household products (Fitzherbert et al. 2008). Global annual production of palm oil more than doubled between 1970 and 2010, with more than 80% of the total now produced by Malaysia and Indonesia (FAO 2014). Production in South East Asia is still increasing and oil palm plantations are also likely to expand in west Africa and Amazonia (Butler & Laurance 2010; Foster et al. 2011). Establishing successful conservation strategies in oil palm areas therefore has implications for landscapes across the world.

We chose dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) as a focal group to assess the conservation value of the riparian reserves. Dung beetles are described as a "high performance indicator" for tropical regions: their community metrics vary with habitat disturbance or fragmentation, they show congruency with several other taxa, and are low-cost to survey (Gardner et al. 2008; Nichols & Gardner 2011). Dung beetles also provide important ecological functions such as dung removal and bioturbation (Nichols et al. 2008), which are of wider significance to entire ecosystems.

Here, we assess whether riparian reserves support dung beetle communities and dung removal rates characteristic of larger areas of forest. We examine how the structure of riparian reserves could be managed to improve the extent to which they retain communities similar to those in logged forest. We also ask whether riparian reserves enhance the provision of dung removal services to the surrounding oil palm areas.

METHODS

STUDY SITES

All study sites were located within a 600 km^2 area around and including the Stability of Altered Forest Ecosystems (SAFE) project site in Sabah, Malaysian Borneo (117.5^o N, 4.6^o E). The area is a mixture of twice-logged lowland dipterocarp rainforest, acacia and oil palm plantations, in which palms were planted between 1998 and 2011. Further details are given in Ewers et al. (2011).

We selected 23 focal sites along river banks. Seven were located in logged forest (areas of continuous forest at least 500 ha in size), seven in areas of continuous oil palm with no riparian reserve adjacent to the river, and eight in areas of oil palm with a riparian reserve adjacent to the river (Fig S1 shows these sites). One site was located in Maliau Basin primary forest reserve

(70 km from the SAFE project) as a reference point, but there were no other primary forest sites near enough to allow spatial interspersion of replicate primary forest sites. Since all the remaining primary forest in Sabah is already protected (Reynolds et al. 2011), evaluating the ecological characteristics of large areas of logged forest versus a network of smaller forest strips is more informative for future conservation action. All our sites were separated by at least 1.5 km and the riparian reserve sites were at least 900 m (mean distance 3.3 km, s.d. = 2.5 km) from the logged forest boundary. Given that dung beetle movement within a 48 hr period is thought to be less than 500 m (Roslin 2000; Larsen & Forsyth 2005), it is therefore unlikely that dung beetles were drawn to the riparian reserve traps from the logged forest areas.

At each site we set up a sampling grid of 12 points, consisting of four transects perpendicular to the river (Fig S2). Transects were 100 m apart, with sampling points at 0 m, 50 m and 100 m from the high water line. The spacing of the grid conforms to standard methods of dung beetle sampling (Larsen & Forsyth 2005). Due to variation in width of the riparian reserves (mean 49 m, s.d. = 30 m, referring to forest width on one side of the river), where the riparian reserve was narrow, some points in these grids fell in the surrounding oil palm area.

Data Collection and Analysis

All data were collected between the end of February and the beginning of July 2011. Seasonal changes in the lowland dipterocarp forests of Borneo are very limited (Walsh & Newbery 1999a; Kumagai et al. 2005) and these months all fall in the slightly drier half of the year (Hamer et al. 2005).

All analyses were carried out in R (R Core Team 2013) using the packages vegan (Oksanen et al. 2013), lme4 (Bates et al. 2014) and nlme (Pinheiro et al. 2013).

DUNG BEETLE COMMUNITY AND LAND USE

Dung beetles were collected using pitfall traps baited with 25g of human dung. Human dung attracts a wide variety of species (Davis et al. 2001; Larsen et al. 2006) and is recommended as a standardised bait in tropical forests (Marsh et al. 2013). Each trap consisted of a plastic cup (8 cm top diameter, 5.5 cm bottom diameter, 12.5 cm depth) half-filled with a solution of water, detergent and salt. The traps were protected from the rain with a cover and collected after 48 hours. The order of sites was randomised and traps were set at no more than 2 sites in each 48 hour period.

We could not obtain sufficient human dung to supply both the traps and the dung piles, so we used cattle dung for the dung removal experiment (see below). Preliminary work in similar forest sites in Sabah shows that large cattle dung baits attract a similar species composition to smaller human dung baits, with the exception of some carrion feeding species found in higher abundances in human dung (Slade et al. (2011), E. Slade and D. Mann, unpublished data). To compare species and dung removal results, we removed data on these carrion feeding species (n = 13, highlighted in Table S1) from all analyses apart from those testing for the effect of riparian reserve structural features on the entire dung beetle community.

For each sampling point (trap) we calculated dung beetle abundance, the number of functional groups present (using classifications based on diurnal versus nocturnal activity, body length and method of dung removal after Slade et al. (2007)), alpha diversity (Shannon index) and total biomass. We weighed beetles from 24 species taken from across the whole range of body sizes (between 7 – 51 individuals per species, average = 27, s.d. = 8) and used a polynomial

regression to estimate biomass for the remaining species ($Log_{10}(mass) = -1.64 + 5.61*Log_{10}(length) – 4.39*Log_{10}(length)^2 + 1.99*Log_{10}(length)^3$, $R^2 = 0.982$).

For each site we calculated beta diversity (mean Sørensen's similarity index) and species richness (using coverage-based rarefaction methods (Chao & Jost 2012) through the iNEXT online software (Hsieh et al. 2013). Coverage based methods of rarefaction provide a more informative comparison of richness among multiple samples than individual or sample based methods of rarefaction as the ratio of species richness is not compressed (Chao & Jost 2012). Rarefied species richness could not be calculated at the trap level due to four traps having only one or two beetles.

Wherever possible we retained data at the highest spatial resolution (trap level) for analyses. For response variables where this was the case (abundance, functional group richness, diversity, and biomass), we analysed the effect of land use (logged forest, riparian reserve or oil palm) with generalised linear mixed models, using transect nested within site as a random factor. Where response variables could only be calculated at the site level (beta diversity and rarefied species richness), we analysed the effect of land cover with a generalised least squares model. For all models, appropriate error distributions were specified and transformations or weight structures (varIdent function as described by (Zuur et al. 2009))) applied where necessary. For all analyses testing for an effect of land use, we excluded data from points that fell outside of the forest strip at the narrowest riparian reserve sites so that we were carrying out a true test for differences between the three land uses. Some traps were lost due to flooding or other disturbances, so data were only obtained from 201 traps in total (82 from logged forest sites, 43 from inside riparian reserves and 76 from oil palm sites).

Differences in community composition across land uses were explored using De-trended Correspondence Analysis (DCA, vegan function 'decorana'), which performs well as an ordination method for displaying similarity of tropical insect communities along an

environmental gradient (Brehm & Fiedler 2004). We tested for significant differences in community composition using a permutational analysis of variance (vegan function 'adonis') with 999 permutations and site as a grouping variable.

To determine whether the relative abundance of the functional groups differed between logged forest and riparian reserves we ran a mixed model with abundance as a response variable and functional group, land-use and their interaction term as predictors.

DUNG REMOVAL AND LAND USE

To record dung removal activity, uniform pats of 700g of cow dung were set out at each sampling point (n = 12 at each site) and collected after 24 hours. Large herbivores, such as the tembadau or wild cow (*Bos javanicus* d'Alton), Asian elephant (*Elephus maximus* L.) and bearded pig (*Sus barbatus* Müller) occur within the study area so the experimental dung pats resemble those occurring naturally. Dung removal experiments were carried out at least 1 month after pitfalls traps were collected, in order to avoid interference but also remain close enough for dung beetles assemblages to be similar (Slade et al. 2011). The order in which sites were visited was randomised. The dung was frozen for a minimum of 24 hours before the experiment to kill any invertebrates already present. Data on mass loss were corrected for evaporation using estimates from three evaporation controls set at each site. For the controls, the cow dung was placed in a flat-bottomed sieve with mosquito netting sealed around the top (both 1mm mesh), to prevent entry of any dung beetles.

The effect of land use on the mass of dung removed was analysed with a general linear mixed model, with transect nested in site as random factors and a log transformation for the response variable. As with the data for beetle communities, for the riparian reserve sites we

only used data from within the forest strips (total n = 212: 84 from logged forest sites, 44 from within riparian reserve vegetation, 84 from oil palm sites).

We assessed whether the relationship between dung beetle community characteristics and dung removal was consistent across all land use types with a GLM including land-use, rarefied species richness (correlated with diversity R^2 = 0.6, P = 0.004), biomass (correlated with abundance, R^2 = 0.7, P = 0.0002), functional group richness and all two-way interactions. As this analysis included coverage-based rarefied species richness all other data were averaged to the site level.

DUNG BEETLE COMMUNITY STRUCTURE AND RIPARIAN RESERVE CHARACTERISTICS

To analyse the effect of riparian reserve width and vegetation complexity on the dung beetle community we included data on all dung beetle species (both carrion and dung feeders). In order to test whether increasing the proportion of area in the riparian zone left as native vegetation impacts the dung beetle community, we included all the points in the sampling grid at each riparian reserve site (n = 95). Data were combined for each transect as this was the resolution at which riparian forest width could be measured (using GIS software (ArcMap version 10.1)). A similar approach was used by Viegas et al. (2014) to test whether reserve width affects dung beetle communities in the Amazon.

To assess the vegetation structure at each sampling point, we measured humus depth, canopy density (using a spherical densitometer) and basal area (using the angle point method (Bitterlich 1984)). We estimated the height of the tallest tree to the nearest 5m using a ruler held at arm's length and a known reference height at the base of the tree. We scored the under-storey vegetation density (below 2m) and midstorey vegetation density (between 2m and 5m) on an ordinal scale of sparse (fewer than 20 stems or branches) medium (20 – 60 stems or branches) and dense (few patches of light and 60 – 100+ stems or branches). To obtain one numerical index summarising the greatest variation in these data, we ran a metric scaling analysis on all these measurements. The first axis was positively correlated with canopy density, tree height, humus depth, basal area and midstorey density. Since this output is therefore capturing variation in the 3-dimensional structure of the habitats, we refer to it as a vegetation complexity index.

We analysed the effect of vegetation complexity on dung beetle abundance, biomass, diversity, functional group richness, and species richness using only data from sampling points falling within the riparian reserve forest. To test for any effects of reserve width or vegetation

complexity we used generalised linear mixed models, with site as a random factor and specified error families where appropriate.

PROVISIONING OF DUNG REMOVAL SERVICES BY RIPARIAN RESERVES

We analysed the effect of riparian reserves on dung removal rates in the surrounding oil palm area in two ways. First, we compared the dung removed in oil palm adjacent to a riparian reserve (i.e. from sampling points at riparian reserve sites that fell outside the riparian forest, n = 52) and in oil palm without an adjacent riparian reserve (and also at least 50 m from the river bank, n = 56). Second, using only the data from sampling points in oil palm adjacent to a riparian reserve, we analysed the effect of distance from the riparian reserve boundary on the mass of dung removed. We used a generalised linear mixed model with presence/absence of riparian reserve or distance from the reserve boundary as a fixed factor for the two analyses respectively. In both cases we specified transect nested within site as a random factor and applied log transformations to meet model assumptions.

RESULTS

DUNG BEETLE COMMUNITY STRUCTURE AND LAND USE

In total we identified 73 species from 9135 dung beetles (Table S1). The iNEXT software estimate for species coverage of the raw data was greater than 0.91 (>91% of species present were recorded) at all sites, and all species richness curves were approaching the asymphote (Fig S4), indicating that we had sampled the community thoroughly.

We found a significant effect of land use on dung beetle biomass and a weakly significant effect of land use on abundance (Table 1). The biomass in riparian reserves was intermediate between oil palm and logged forest, but not significantly different from either (Fig. 1b).

Species richness (Table 2), diversity and functional group richness (Table 1) also varied significantly with land use. Riparian reserve species richness (Fig 1c), diversity (Fig 1d) and functional group richness (Fig 1e) were significantly lower than in logged forest and higher than in oil palm. We found no difference in within-site beta diversity (mean Sørensen's similarity index) among the different land use types (Table 2).

Three of the seven functional groups were missing completely from oil palm sites: small nocturnal tunellers, small diurnal rollers, and large nocturnal rollers. In contrast, all functional groups were found in at least one of the riparian reserves sites. However, we found a significant interaction between land cover and functional group on dung beetle abundance ($\chi^2 = 59.8$, df = 6, $p < 0.0001$). This indicates that functional groups vary in the extent to which they are negatively impacted by the conversion from logged forest to riparian reserve (Table 3). The most negatively impacted functional groups were the large diurnal tunellers and large diurnal rollers.

The community composition of the riparian reserves was more similar to logged forest than oil palm, although a distinct difference in the communities of the reserves and larger forested areas remains ($F_{1,193}$= 21.4, p = 0.001, Fig 2).

The single primary forest reference site (not included in the analyses above) had much higher mean dung beetle abundance (145% of logged forest), biomass (319% of logged forest), diversity (115% logged forest), and functional group richness (114% logged forest) than all other land use types (Fig 1). However, the species richness of the reference primary forest site fell within the range of the logged forest sites (Fig 1c).

DUNG REMOVAL AND LAND USE

The proportion of dung removed across all sites was low (mean = 0.1, sd = 0.14). There was no significant relationship between dung removal and land cover, species richness, diversity, functional group richness or any of the two-way interactions (Table 2).

DUNG BEETLE COMMUNITY AND RIPARIAN RESERVE CHARACTERISTICS

There was no significant relationship between riparian reserve width and vegetation complexity (Table 1).

We found no evidence of a relationship between reserve width and dung beetle abundance, biomass, or functional group richness (Table 1). However, there was a significant positive relationship between width and diversity and a weakly significant positive relationship between riparian reserve width and dung beetle rarefied species richness (Shannon index, Table 1, Fig 3).

We found a positive relationship between the vegetation complexity of the riparian reserve forest and beetle abundance (Table 1). However, we found no significant effects of vegetation complexity on biomass, species richness, diversity or functional group richness (Table 1).

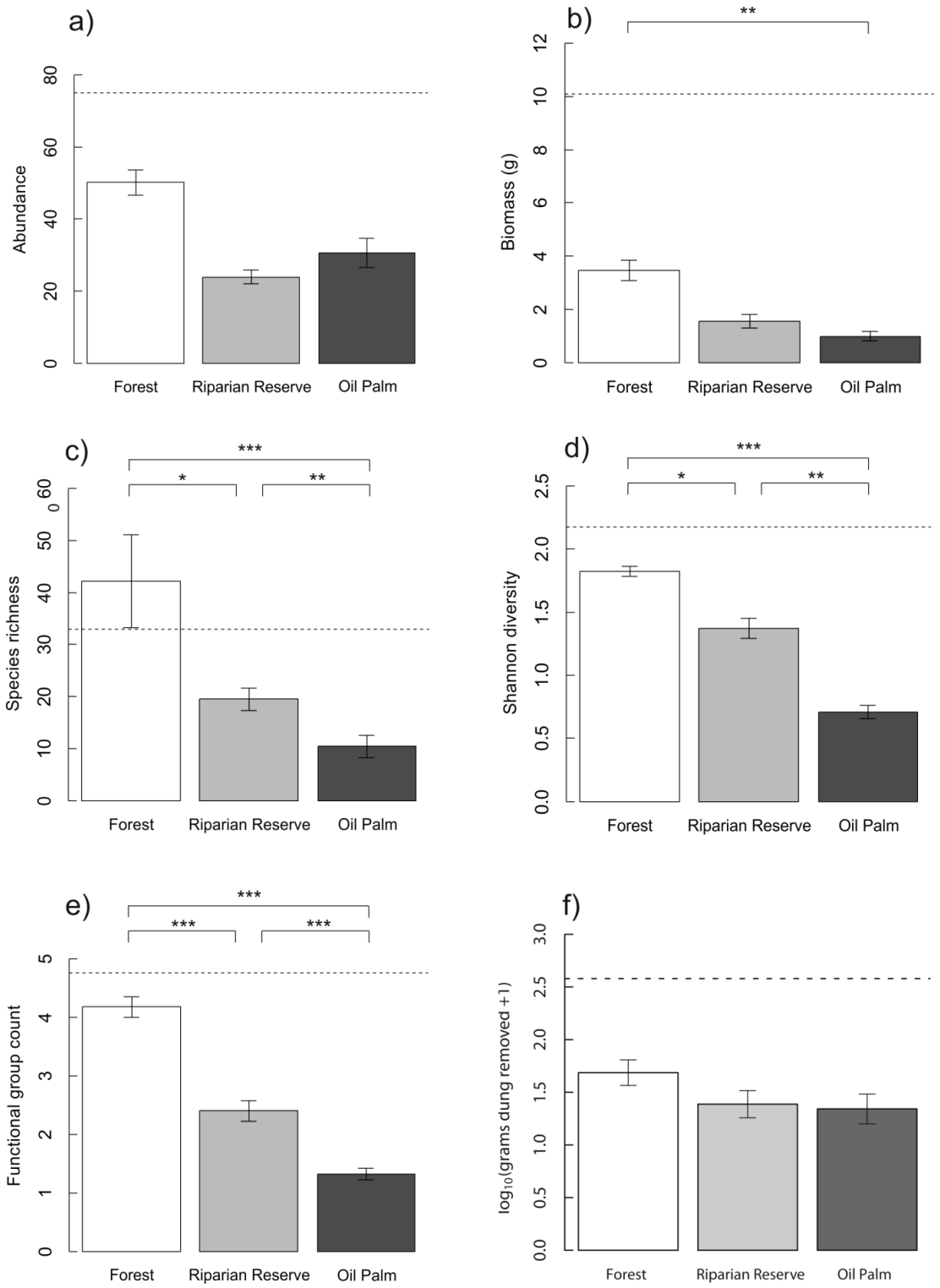


FIG 1

Effect of land cover on (a) dung beetle abundance, (b) biomass, (c) coverage-based rarefied species richness, (d) diversity (Shannon index) (e) functional group richness and (f) dung removal. All panels show means and standard errors. The dotted lines indicate values for the one primary forest reference site (for visual comparison only; the data were not included in the analysis). Stars denote significant differences between groups based on model contrasts (* = $p<0.05$, ** = $p < 0.01$, *** = $p<0.001$).

PROVISIONING OF DUNG REMOVAL SERVICES BY RIPARIAN RESERVES

Dung removal did not differ significantly between oil palm with and without riparian reserves, and we found no significant effect of distance from the riparian reserve boundary on the mass of dung removed (Table 1).

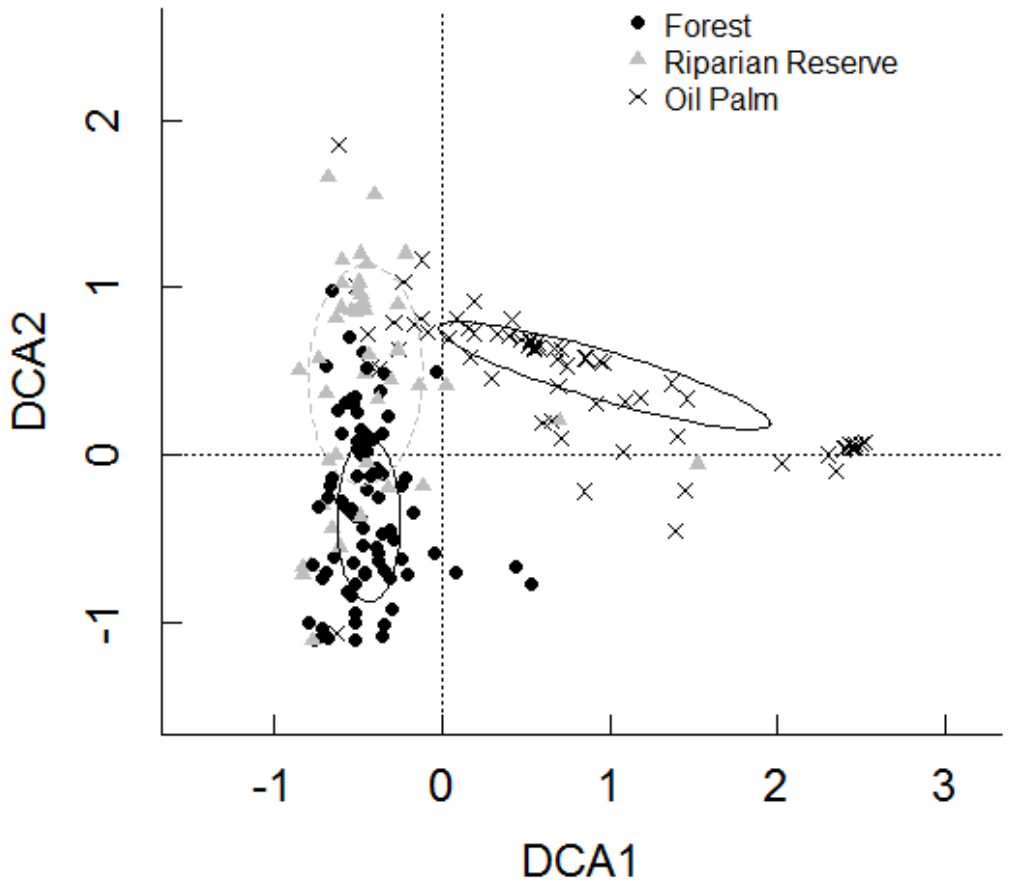


FIG 2
Detrended Correspondence Analysis (DCA) plot indicating that riparian reserve community composition is more similar to forest than oil palm. Ellipses show standard deviation around the mean for each land use.

Model	χ^2	df	*P*
abundance ~ land cover	5.9	2	0.051
biomass ~ land cover	7.9	2	0.019 *
shannon diversity ~ land cover	22.7	2	< 0.0001***
functional group count ~ land cover	28.8	2	< 0.0001***
abundance ~ riparian reserve width	0.62	1	0.43
biomass ~ riparian reserve width	0.05	1	0.82
species richness ~ riparian reserve width	3.69	1	0.055
shannon diversity ~ riparian reserve width	5.45	1	< 0.02 *
functional group richness ~ riparian reserve width	1.15	1	0.28
abundance ~ vegetation complexity	5.95	1	0.015 *
biomass ~ vegetation complexity	0.54	1	0.46
species richness ~ vegetation complexity	0.3	1	0.58
shannon diversity ~ vegetation complexity	0.0004	1	0.98
functional group richness ~ vegetation complexity	0.0005	1	0.98
dung removed ~ land cover	4.6	2	0.10
dung removed in oil palm ~ presence/absence of riparian reserve	0.58	1	0.45
dung removed in oil palm ~ distance to riparian reserve boundary	2.11	1	0.15
vegetation complexity ~ riparian reserve width	1.8	1	0.18

TABLE 1

Effects of land cover and habitat characteristics on dung beetle community metrics and dung removal using data at the trap level (or pooled to transect level for analyses with width as a fixed factor). Test statistics given for comparison of model specified against the null model (response ~ 1).

Model	F	df	*P*
species richness ~ land cover	16.9	2, 19	< 0.0001***
beta diversity ~ land cover	1.9	2, 19	0.18
dung removed ~ sp.rich*land.cov + biomass*land.cov + f.rich*land.cov	0.8	11, 10	0.67
dung removed ~ sp.rich + biomass + f.rich	1.7	3, 18	0.2

TABLE 2

Effects of land cover and habitat characteristics on dung beetle community metrics and dung removal on response variables that could only be calculated at site level. Abbreviations as follows: sp.rich = species richness, land.cov = land cover, f.rich = functional.group.richness

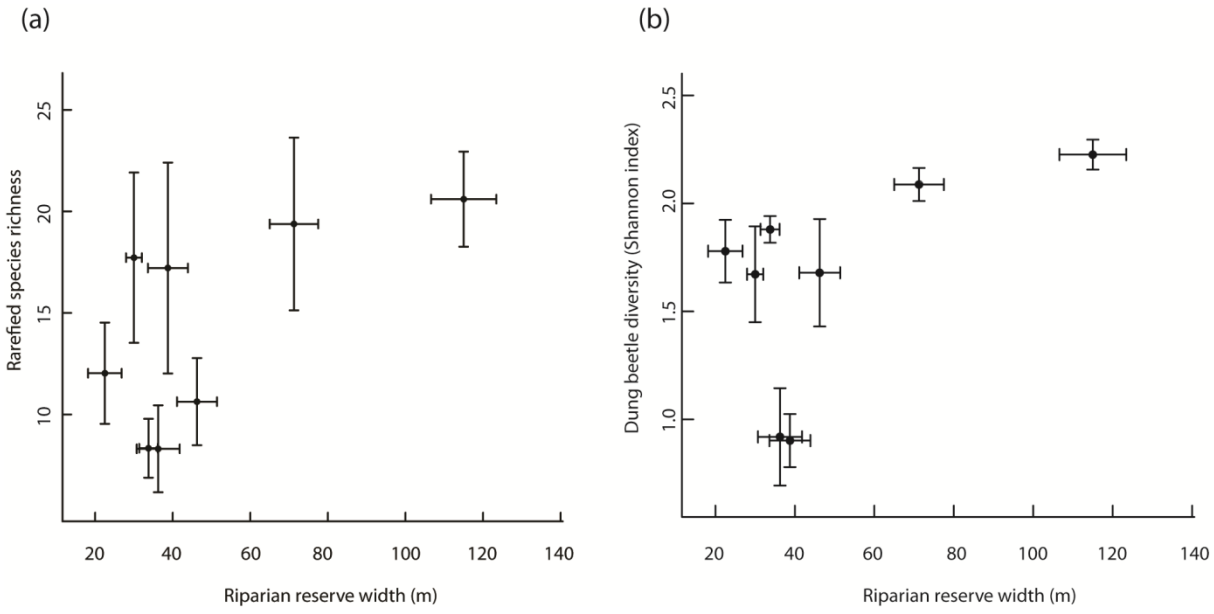


FIG 3

Relationship between riparian reserve width and (a) rarefied species richness and (b) diversity (Shannon index). Plots show mean ± s.e. for each replicate site.

TABLE 3
Model output of GLMM (dung beetle abundance ~ land cover * functional group), showing parameter estimates and standard error for the percentage decline in abundance of each functional group in riparian reserve sites relative to logged forest sites.

Functional Group	No. species in group	Estimate % decline	S.E. % decline	*P*
Large Diurnal Tunellers	1	89.48	17.70	0.0002 ***
Large Diurnal Rollers	2	80.19	15.78	0.0002 ***
Small Diurnal Rollers	1	71.92	12.74	0.0001 ***
Small Diurnal Tunellers	21	18.65	5.60	0.0054 **
Large Nocturnal Tunellers	4	32.96	18.64	0.3
Small Nocturnal Tunellers	3	95.32	71.8	0.2
Large Nocturnal Rollers	1	86.48	207.1	0.7

DISCUSSION

The rapid expansion of oil palm plantations throughout the tropics threatens many forest species. Whilst large protected areas will undoubtedly remain the priority for conservation in these areas, riparian reserves are a potential opportunity to increase the biodiversity retained within agricultural areas. Our data show that, compared to areas of oil palm, riparian reserves of at least 30 m width (on each side of the river) support dung beetle communities more similar to those in adjacent areas of logged forest. We found some effects of reserve width and vegetation complexity on the diversity and abundance of the dung beetles, suggesting that these structural features may also make a limited contribution the biodiversity benefits of the riparian reserves.

Previous studies on dung beetle communities and dung removal function in Bornean rainforests have shown a positive relationship between dung beetle species or functional

group richness and dung removal function (Slade et al. 2007, 2011). Our data suggest that this relationship may not hold in riparian zones, and that the presence of a riparian reserve does not increase dung removal in surrounding areas of oil palm.

DUNG BEETLE COMMUNITY STRUCTURE AND LAND USE

We found that dung beetle communities in oil palm plantations had lower biomass, species richness, diversity, and functional group richness than larger areas of forest. Similar studies in Borneo have also found that dung beetle species richness and diversity declines with logging and conversion to plantations (Davis et al. 2001; Edwards et al. 2013c). In contrast to these studies, we did not find a decline in dung beetle abundance across the land use gradient, but this may be because we did not make a comparison with primary forest sites.

The species richness, functional group richness, diversity and overall community composition of dung beetle communities within riparian reserves were more similar to forest than oil palm. These results provide strong evidence that protecting riparian reserves retains biodiversity within oil palm landscapes, when compared to plantations where oil palm is planted up to the river bank. Riparian reserves are not, however, an adequate substitute for large areas of logged or primary forest. In addition, further work is needed to establish whether dung beetles are able to maintain viable, self-supporting populations within riparian reserves, rather than comprising transient visitors or sink populations (Barlow et al. 2010a).

The functional diversity of the oil palm was lower than both the logged forest and riparian reserves. Rollers and nocturnal species were particularly negatively affected by conversion to oil palm. The greater sensitivity of these groups after conversion to oil palm was also reported by Edwards et al. (2013c) and may be connected to limited temperature tolerance. The riparian reserve network retained all functional groups, but each site tended to support fewer

functional groups than logged forest sites. The drop in average functional group richness between forest and riparian reserves was due to the loss of diurnal species (both small and large, rollers and tunellers), which may be due to a decline in diurnal mammal species (Andresen & Laurance 2007). These results suggest that the isolation of forest strips results in different trait-dependent responses compared to conversion to oil palm. Our findings contrast the global study carried out by Nichols et al. (2013a), who found that for the afro-eurasian tropics nocturnal species are more affected by forest modification, and diurnal species are more negatively affected by conversion to plantation. However, Nichols et al. (2013a) were comparing all forest modification to a primary forest baseline, whereas we are comparing oil palm and riparian reserves to a logged forest baseline, which may explain this discrepancy.

As well as supporting dung beetle species that would not survive if oil palm were planted along river banks, riparian reserves are likely to benefit a range of other taxa. In Borneo, riverine forest corridors are recognised as important habitat for some mammalian species, including the orang-utan, proboscis monkey and pygmy elephant (Venkataraman et al. 2009), but little research has been carried out on the importance of riparian reserves for many other groups in this region. Riparian reserves in the neotropics support communities of birds, amphibians and small mammals found in undisturbed forest (de Lima & Gascon 1999; Lees & Peres 2008) and also facilitate movement of forest specialists through agricultural land (Gillies & St. Clair 2008). Alongside the hydrological benefit of riparian reserves, their role in conserving terrestrial species should be more widely recognised by sustainable management guidelines. This is especially the case in Sabah where all the remaining primary forest is already protected and increasing conservation in cultivated landscapes is arguably the highest priority (Reynolds et al. 2011).

DUNG REMOVAL AND LAND USE

Despite the significant differences among beetle communities in different land uses, we did not detect a significant effect of land cover on dung removal rates over 24 hours, nor any significant relationship between dung removal and species richness, biomass or functional group richness. This contrasts a number of studies which show strong positive correlations between dung beetle species richness or functional group richness and dung removal rates (Slade et al. 2011; Gollan et al. 2013; Braga et al. 2013), and also with evidence that dung removal rates in Amazonian riparian reserves are higher than in surrounding pasture (Norris & Michalski 2010).

There are several possible explanations for these results. First, dung removal rates were low (e.g. compared to those in primary forest nearby; Fig. 1 (f)), and it is possible that a difference in removal would be seen if dung pats were left out for longer and a greater proportion of mass was removed. Secondly, it is possible that differences in the communities attending the two bait types diminish our ability to detect correlations between biodiversity and function; Nichols et al. (2013b) discuss how dissimilarities between the response of dung beetles communities and dung burial rates to human impact in the Amazon may be an artefact of surveying the community and function at separate times with different baits. However, correlations have previously been detected using different baits within similar forests in Borneo (Slade et al. 2011). Thirdly, it is possible that there is spatial variation in the relationship between dung beetle community composition and dung removal. Since the mortality of dung beetle larvae may increase with soil moisture content (Sowig 1995) dung beetles may not build nests (bury dung) near rivers even though they come to baits to feed. The positive relationship between species richness and dung removal may therefore break down in riparian zones, but additional data on how dung removal and soil moisture vary is needed to confirm this. Therefore, while there may be local and regional variation in

biodiversity-ecosystem function relationships within tropical forests, the extent to which these relationships are affected by sampling methodology needs to be further resolved.

The lower functional group richness in riparian reserves compared to forest may affect important ecological processes inside the reserves. In particular, roller species are less abundant in the reserves. As these species roll dung balls, often containing seeds, horizontally away from the dung pat they can potentially reduce the negative effects of seed clumping and seedling competition (Lawson et al. 2012). It is therefore possible that germination and dispersal dynamics of plant species in the reserves is impaired relative to logged forest. Other processes such as soil bioturbation, soil fertilisation and parasite suppression that are mediated by dung beetles (Nichols et al. 2008) may also be reduced in the riparian reserves as a result of the decline in some functional groups.

DUNG BEETLE COMMUNITY STRUCTURE AND RIPARIAN RESERVE CHARACTERISTICS

Our results suggest that the width and vegetation complexity of riparian reserve may have a positive impact on dung beetle diversity and abundance, respectively. Although these relationships are weak, these findings are of direct relevance to management and policy specifications. Legal requirements for the protection of riparian forest exist in a number of countries (Marczak et al. 2010; Barlow et al. 2010b, Sabah Water Resources Enactment, 1998), and riparian reserves are also included in the criteria for certification of sustainable palm oil production (e.g. by the Round Table on Sustainable Palm Oil (Criterion 4.4 (RSPO 2013)). However, very little ecological information has influenced the details of these guidelines (Barlow et al. 2010b; Ewers et al. 2011). Our findings highlight the need for further research to clarify the importance of the structural features of riparian reserves.

PROVISIONING OF DUNG REMOVAL SERVICES BY RIPARIAN RESERVES

Grazing of cattle underneath oil palms is expanding in Malaysia (Latif & Mamat 2002), and the requirement for dung removal services within these landscapes is likely to increase. However, our results suggest that retaining riparian reserves within oil palm plantations may not contribute to an increase in dung removal services within surrounding oil palm.

CONCLUSIONS

Overall, it is evident that riparian reserves can contribute towards the conservation of dung beetle communities that are threatened by the expansion of oil palm, but that the extent to which they support dung removal activity and other terrestrial ecosystem services requires further study over greater spatial and temporal scales. Nevertheless, the results presented here indicate that riparian reserves should be more widely recognised as a conservation strategy for terrestrial biodiversity. We must emphasise that we do not recommend riparian reserves within oil palm plantations as an alternative to protecting large areas of primary or secondary forest. On the contrary, we feel that as an addition to such protection, riparian reserves should be more widely recognised as a promising opportunity for conservation in tropical agricultural landscapes.

SUPPLEMENTARY MATERIAL

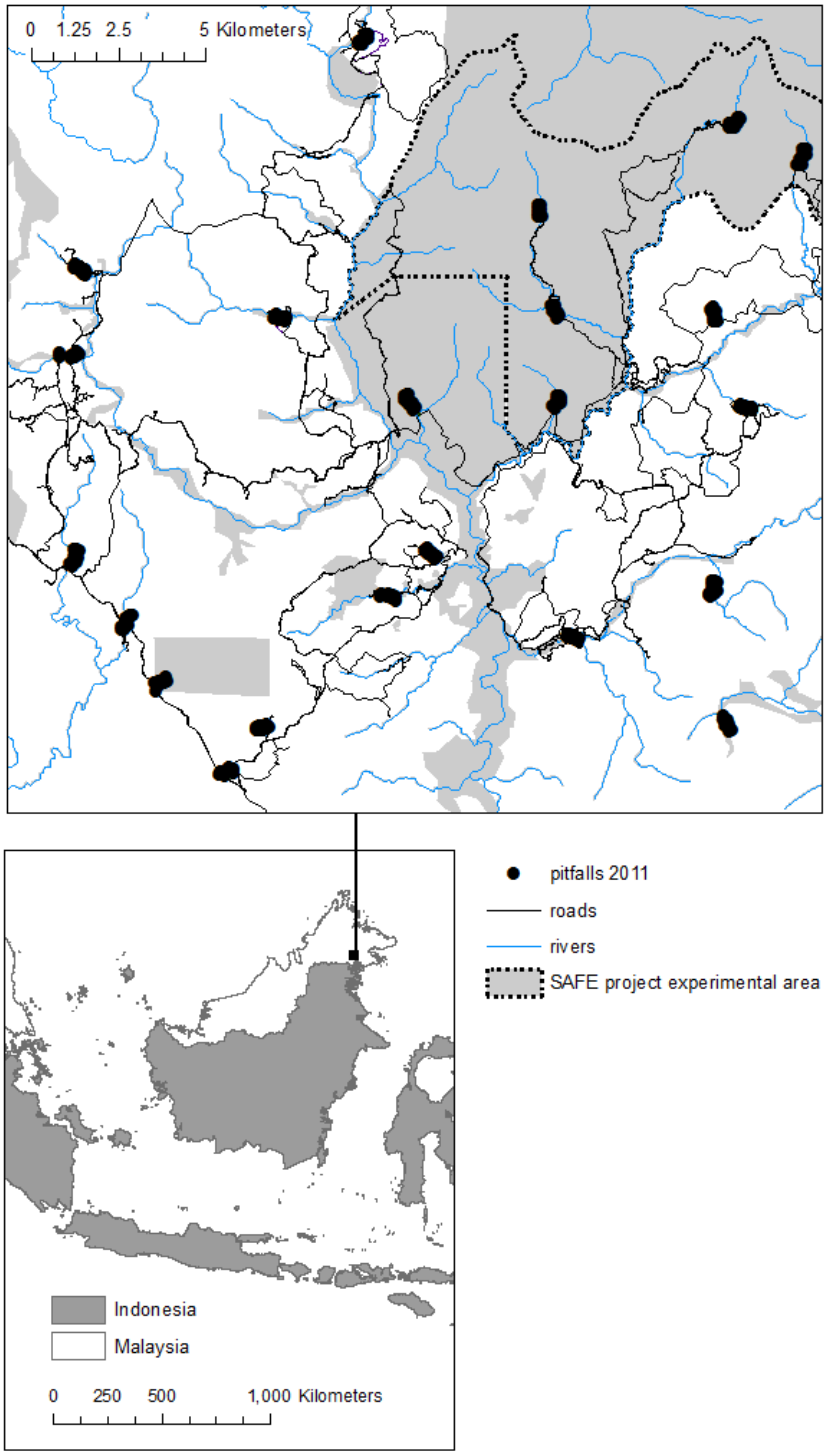


FIG S1

A map of the field sites used in this study. The dotted black line gives the boundary of the SAFE experimental area. The solid grey shaded area is the remaining logged forest, and the white area is the matrix of plantations. The sampling points are shown by black circles. The lower panel gives the location of the study area within Sabah, Northern Borneo.

Species name	Taxonomic reference
Caccobius (Caccobius) bawangensis	Ochi, Kon & Kikuta, 1997
Caccobius (Caccobius) binodulus	Harold, 1877
Catharsius dayacus	Lansberge, 1886
Catharsius renaudpauliani	Ochi & Kon, 1996
Copris (Copris) agnus	Lansberge, 1875
Copris (Paracopris) ramosiceps	Gillet, 1921
Copris (Copris) sinicus	Hope, 1842
Microcopris doriae	Harold, 1877
Microcopris hidakai	Ochi & Kon, 1996
Ocicanthon masumotoi	**Ochi & Arayi, 1996**
Ocicanthon dytiscoides	**Boucomont, 1914**
Ocicanthon danum	**Krikken & Huijbregts, 2007**
Ocicanthon woroae	**Ochi, Ueda & Kon, 2006**
Oniticellus tessellatus	Harold, 1879
Onthophagus (Micronthophagus) aff. arayai	Ochi & Kon, 2007
Onthophagus (Sinonophagus) aff. angustatus sp. 1	Boucomont, 1914
Onthophagus (Sinonophagus) aff. angustatus sp. 2	Boucomont, 1914
Onthophagus (Onthophagus) aphodioides	Lansberge, 1883
Onthophagus (Parascatonomus) aurifex	**Harold, 1877**
Onthophagus (Onthophagus) batillifer	Harold, 1875
Onthophagus (Onthophagus) borneensis	Harold, 1877
Onthophagus (Parascatonomus) brendeli	**Ochi, Kon & Barclay, 2009**
Onthophagus (Gibbonthophagus) cervicapra	Boucomont, 1914
Onthophagus (Pseudophanaeomorphus) chandrai	Ochi, 2007
Onthophagus (Onthophagus) deflexicolis	Harold, 1877
Onthophagus (Onthophagiellus) aff. deliensis	Lansberge, 1885
Onthophagus (Parascatonomus) dux	**Sharp, 1875**
Onthophagus (Onthophagiellus) aff. falculatus	Boucomont, 1914
Onthophagus (Gibbonthophagus) fujii	Ochi & Kon, 1995
Onthophagus (Onthophagiellus) aff. hidakai	Ochi & Kon, 1995
Onthophagus (Onthophagus) incisus	Harold, 1877
Onthophagus (Indachorius) aff. cheyi	Ochi & Kon, 2006
Onthophagus (Indachorius) danumensis	Ochi, Kon & Barclay, 2009
Onthophagus (Indachorius) woroae	Ochi & Kon, 2006
Onthophagus (Pseudophanaeomorphus) johkii	Ochi & Kon, 1994
Onthophagus (Onthophagiellus) aff. kawaharai	Ochi & Kon, 2007
Onthophagus (Serrophorus) laevis	Harold, 1880
Onthophagus (Serrophorus) muelleri	Lansberge, 1883
Onthophagus (Onthophagus) aff. borneensis	Harold, 1877
Onthophagus (Gibbonthophagus) nigriobscurior	Ochi, Kon & Tsubaki, 2009
Onthophagus (Onthophagus) obscurior	Boucomont, 1914
Onthophagus (Onthophagus) ochromerus	Harold, 1877
Onthophagus (Pseudophanaeomorphus) aff. phanaeides	Frey, 1956
Onthophagus (Onthophagiellus) aff. tridentitibialus	Ochi & Kon, 2008
Onthophagus (Onthophagus) pacificus agg.	Lansberge, 1895
Onthophagus (Onthophagus) pastillatus	Boucomont, 1919
Onthophagus (Onthophagus) pavidus	Harold, 1977
Onthophagus (Onthophagus) simboroni	Ochi & Kon, 2006
Onthophagus (Pseudophanaeomorphus) quasijohkii	Ochi & Kon, 2005
Onthophagus (Sinonthophagus) rorarius	Harold, 1877
Onthophagus (Parascatonomus) rudis	**Sharp, 1875**
Onthophagus (Onthophagus) rugicollis	Harold, 1880
Onthophagus (Onthophagus) aff. rutilans	Sharp, 1875
Onthophagus (Parascatonomus) sarawacus	**Harold, 1887**
Onthophagus (Parascatonomus) semiaurreus	**Lansberge, 1883**
Onthophagus (Parascatonomus) semicupreus	**Harold, 1877**

Onthophagus (Indachorius) aff. semidanumensis	Ochi, Kon & Barclay, 2009
Onthophagus (Gibbonthophagus) taeniatus	Boucomont, 1914
Onthophagus (Paraphaenaemorphus) trituber	Wiedemann, 1823
Onthophagus vethi	Krikken, 1977
Onthophagus (Onthophagus) vulpes	Harold, 1877
Onthophagus (Onthophagus) waterstradti	Boucomont, 1914
Onthophagus (Onthophagus) sp. A	
Onthophagus (Onthophagus) sp. LGD	
Onthophagus (Indachorius) sp. 5	
Panelus sp. 1	
Panelus sp. 2	
Paragymnopleurus maurus	Sharp, 1875
Paragymnopleurus sparsus	Sharp, 1875
Paragymnopleurus striatus	Sharp, 1875
Proagoderus watanebei	Ochi & Kon, 2002
Synapsis ritsemae	Lansberge, 1874
Sysyphus thoracicus	Sharp, 1875
Yvescambefortius sarawakus	Gillet, 1926

TABLE S1

Full species names and taxonomic reference for the dung beetles caught and identified. Those in bold are primarily fruit or carrion feeders and were removed from all analyses on the effect of land cover so comparisons could be made to dung removal data.

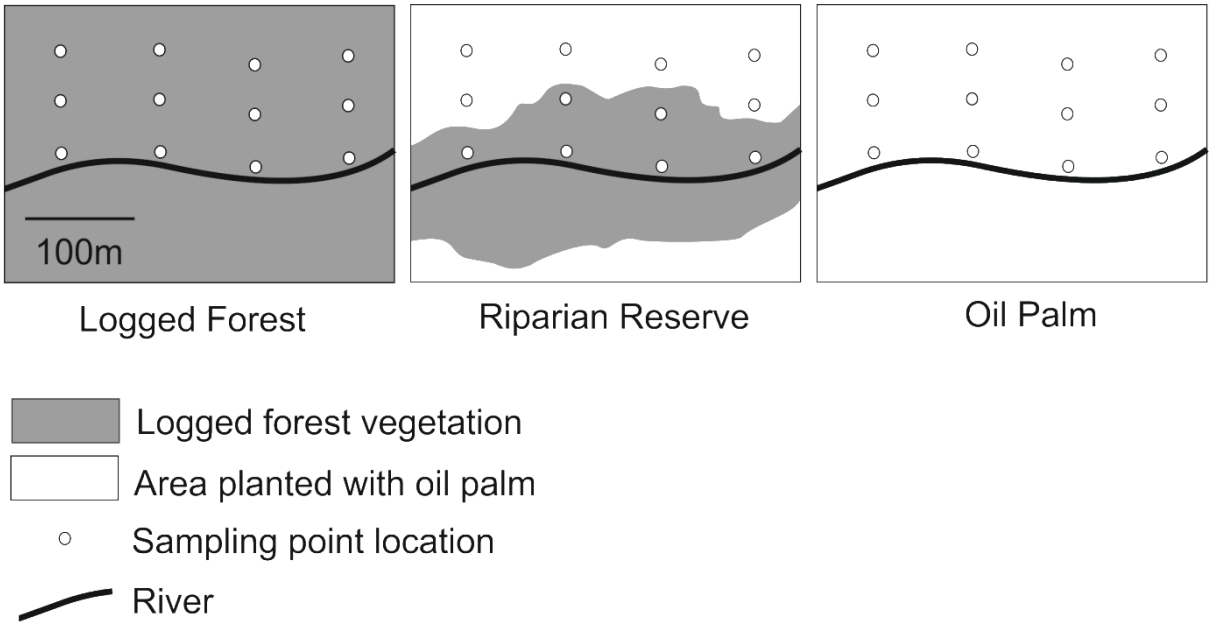


FIG S2

Arrangement of sampling points in riparian zones within each land use. Distribution of points follows the standard approach for dung beetle sampling, and was kept constant across all land uses as the density of baited traps might affect trap attractiveness. Data from all the forest points, all the oil palm points, and the points within the riparian forest were used to assess differences in dung beetle community and dung removal function across land uses. Data from within the riparian reserves only was used to test for effects of riparian reserve vegetation complexity on community metrics. The data from all points at the riparian reserve sites was used to assess the effects of increasing the area of non-crop vegetation (i.e. increasing riparian reserve width) within the riparian zone of the plantations.

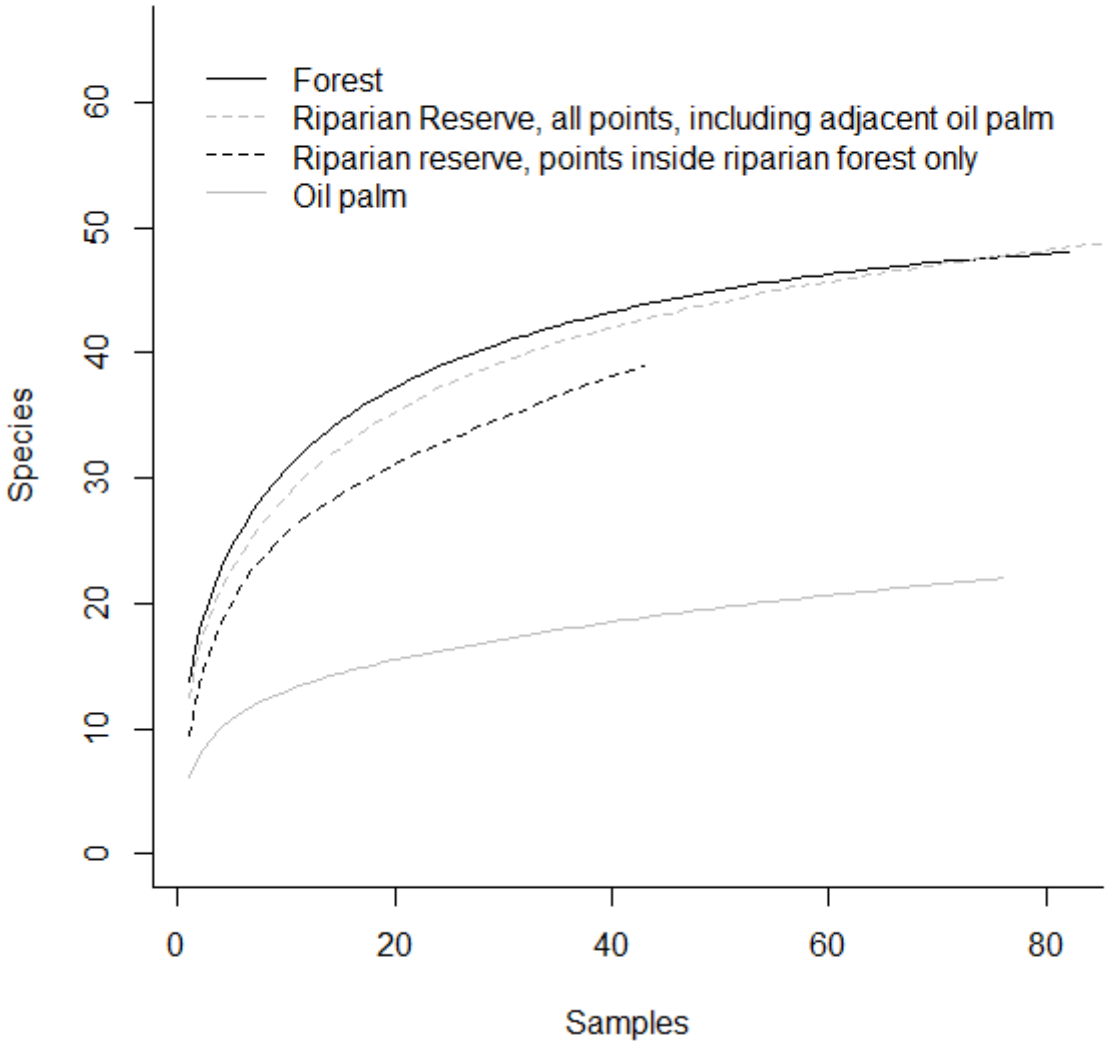


FIG S3

Species accumulation curves for data from baited pitfall traps.

CHAPTER 4: DESIGNING OIL PALM LANDSCAPES TO RETAIN BIODIVERSITY: INSIGHTS FROM A KEY ECOLOGICAL INDICATOR GROUP

ABSTRACT

Tropical landscapes and species across the world are being affected negatively by agricultural expansion and intensification. Oil palm cultivation is among the most rapidly expanding land uses in the tropics. Palm oil is an important product for markets worldwide and a highly profitable industry for developing tropical countries, so it is important that approaches for mitigating the impact of oil palm expansion on biodiversity are identified. We surveyed dung beetles, a key indicator taxon, across 23 riparian reserves (forest buffer strips retained along the margins of streams) and five logged forest reference sites in Sabah, Malaysian Borneo. We assessed how the structural features and landscape context of the riparian reserves affected the species richness, community composition and functional trait diversity of forest dependent species. We found a positive relationship between reserve width and both species richness and diversity but no relationship between reserve width and dung beetle abundance or functional diversity. Overall, dung beetle abundance in riparian reserves was 54% less than in logged forest areas, but all species observed in the logged forest were found in at least one riparian reserve site. Species richness of dung beetle communities did not diminish with distance from forest, although changes in community composition did occur at greater distances. The amount of forest cover in the surrounding landscape improved the retention of species within riparian reserves and increases in vegetation complexity also corresponded with higher functional richness (FRic) and functional dispersion (FDis). Whilst the species richness of 30 m reserves was only 10% lower than in logged forest, our data indicate that riparian reserves of at least 50 – 80 m are needed for species richness and diversity to equal that in nearby logged forest. These observations, particularly if they apply more widely to forest-dependent taxa, should be taken into account when setting policy and sustainability guidelines

for oil palm plantations, both in areas undergoing conversion from forest and in existing oil palm plantations where forest restoration is required.

INTRODUCTION

Tropical landscapes hold the majority of the planet's biodiversity and are a priority for conservation action (Gardner et al. 2009). Currently, agricultural expansion and intensification are amongst the major drivers of change in tropical regions (Laurance et al. 2014), and so the management of tropical agricultural areas is crucial for determining the survival of many forest-dependent species. In recent decades, oil palm cultivation has been one of the most rapidly expanding land uses in the tropics, causing widespread loss of biodiversity. The area planted with oil palm has nearly doubled in the last 20 years and the majority of this expansion has occurred in Malaysia and Indonesia, which now produce over 80% of global palm oil (FAO 2014). In these two countries, approximately 40% of oil palm expansion has been onto forested land (Gunarso et al. 2013). As oil palm generally supports less than 30% of the vertebrate, insect, amphibian and plant species found in native forest (Fitzherbert et al. 2008), the growth of the industry has become an increasing concern to the conservation community. Oil palm cultivation is also rapidly increasing in west Africa and the Neotropics (Butler & Laurance 2010), making the industry an influential factor for tropical landscapes worldwide.

Nevertheless, the production of palm oil is important for the economy of many countries, and oil palm plantations are set to remain a dominant feature of tropical landscapes for the foreseeable future. Palm oil is the world's most widely used vegetable oil; it is a common ingredient in many food products, cosmetics and detergents, and it is increasingly widely used as a biofuel feedstock. The global demand for palm oil is still growing (FAOSTAT 2013), and so

mitigating the environmental impact of oil palm plantations and setting appropriate sustainability standards is of great importance.

Despite the global influence of this crop, relatively little research has documented the biodiversity impacts of oil palm or evaluated strategies which could maintain forest-dependent species within these landscapes (Savilaakso et al. 2014). However, a number of legal requirements already protect non-crop habitat within oil palm plantations, including requirements to retain forest on steep slopes and along riverbanks (e.g. Malaysian National Forestry Act 1993 and Sabah Water Resources Enactment 1998). These specifications are primarily made to limit soil erosion, landslides and flood risk, as well as preserving water quality (Mayer et al. 2007; Zhang et al. 2013). In other agricultural systems the retention of this non-crop habitat supports species that would otherwise be lost (Marczak et al. 2010), but the extent to which this occurs in oil palm plantations is poorly understood. A better understanding of the conservation value of forest fragments can inform both national policy and guidelines for voluntary sustainability certification, such as those required by the Roundtable on Sustainable Palm Oil (RSPO).

Currently, the precise requirements for these landscape features (e.g. the width of riparian reserves) is based on very little ecological data (Ewers et al. 2011). For riparian reserves, it is also probable that recommendations based on hydrological processes are not adequate for terrestrial fauna (Lee et al. 2004a; Viegas et al. 2014). As well as providing habitat in their own right, remnants of native habitat are also important for providing connectivity, as they facilitate dispersal of bird and mobile invertebrates across agricultural landscapes (Haddad et al. 2003; Gillies et al. 2011; Slade et al. 2013). There is some evidence that birds (Koh 2008a) and orchid bees (Livingston et al. 2013) may disperse several kilometres into adjacent oil palm from forested areas, and that other species such as butterflies or ants may only move a few hundred meters from a forest boundary into oil palm plantations (Lucey & Hill 2012; Lucey et

al. 2014). However, data on the role of forest remnants in increasing the permeability of oil palm landscapes remains limited.

With improved understanding of how they contribute to the dynamics of terrestrial communities, there is considerable opportunity to improve the conservation value of these forest fragments. Here, we focus on the role of riparian reserves (also referred to as strips, buffers or corridors) in maintaining biodiversity in oil palm landscapes. The results presented in Chapter 3 and similar research from the Amazon (Barlow et al. 2010b; Viegas et al. 2014), demonstrate the role of riparian reserves in increasing species richness and diversity within agricultural landscapes. In this paper, we quantify the impact of several structural features of riparian reserves that could be specified in policy or management guidelines, as well as assessing the influence of wider contextual landscape features on riparian reserve communities.

We used dung beetles as an indicator group, as they are sensitive to habitat disturbance (Slade et al. 2011), their responses are congruent to those of other animal groups (Gardner et al. 2008) and they provide important ecological functions (Nichols et al. 2008). In this paper, we quantify the impact of reserve structure and landscape context on the traditional biodiversity metrics of species richness and alpha and beta diversity, as well as quantifying the response of a range of functional metrics using species-specific trait data. Functional traits provide an insight into how species' responses to land use change may be dependent on their life-history and ecological niches, and can reveal shifts in community composition that are not necessarily picked up by traditional metrics (Mouillot et al. 2013). Recent studies in Borneo have shown that the response to conversion to oil palm in both vertebrate and invertebrate species differs with body size and trophic level (Senior et al. 2013), and that the functional diversity of dung beetles in particular is lower in oil palm than in logged forest (Edwards et al. 2013c).

We test the hypotheses that riparian reserves of greater width and vegetation complexity increase the extent to which riparian reserve fauna resemble communities in logged forest. We also assess how the amount of forest remaining in the area around the reserves, and the distance to the nearest point at which the reserve joins a large (>2000 ha) area of logged forest affect dung beetle communities. We specifically examine the role of riparian corridors in facilitating dispersal through oil palm landscapes using data collected from flight intercept traps. In conclusion, we present policy recommendations for riparian reserve width in oil palm landscapes, and calculate the possible impacts of these policy options for oil palm yield.

METHODS

STUDY SITES

All study sites were located within a 600 km^2 area around and including the Stability of Altered Forest Ecosystems (SAFE) project site in Sabah, Malaysian Borneo (117.50 N, 4.60 E). The area is a mixture of twice-logged lowland dipterocarp rainforest, acacia and oil palm plantations, in which palms were planted between 2006 and 2012. Further details of the project area are given in Ewers et al. (2011). All data collection was carried out between September and November 2012.

EFFECTS OF RIPARIAN RESERVE STRUCTURE AND LANDSCAPE CONTEXT ON DUNG BEETLES

Dung-baited pitfall traps were set at 23 riparian reserve sites and five logged forest reference sites (a map of sampling locations is given in Fig S1). We selected riparian reserve sites that maximised the number of sites, range of reserve widths and distances from the forest, whilst also ensuring that all sites were surrounded by oil palm plantations on both sides and at least 1 km apart; this spatial distribution allows the dung beetle assemblages at each site to be

treated as independent samples (Larsen & Forsyth 2005). Forest river sites were selected to achieve spatial interspersion with riparian reserve sites as far as possible. At each site we set five traps, each baited with 25g human dung and collected these after 48 hours, following standard methods for surveying dung beetle communities (see Chapter 3 for further details on trap construction). One trap was placed at each corner of a 50 m x 25 m rectangle, such that two traps were approximately 1 m above the high water line and 50 m part, two traps were placed 25 m from the high water line and 50 m apart, and one trap in the centre of the rectangle. This design ensured that all traps were within the riparian reserve vegetation at all sites and also that sampled the community of dung beetles at that point along the riparian reserve thoroughly (traps within 50 m of each other are likely to be sampling the same dung beetle community (Larsen & Forsyth 2005)). Traps were set at a maximum of two sites during each 48 hour period.

We surveyed the dung beetle community at the five logged forest sites to obtain a reference for what we might expect a desirable riparian reserve community to resemble. The conditions under which riparian reserve communities do not differ from riparian communities in large areas of forest can then be used for management specifications. This approach has been used by a number of studies making recommendations for riparian zone width in other countries (e.g. de Lima & Gascon 1999; Hagar 1999; Pearson & Manuwal 2001). We used logged forest comparison sites to set this reference as there was no primary forest within 50 km of our field sites. In addition, it is unrealistic to expect that that the degraded riparian reserve forest should be managed with the goal of resembling undisturbed primary forest.

Dung beetles (Scarabaeidae, Scarabaeinae) were identified to species using literature from Mann (2008) and reference collections held at the OUMNH. We combined data from all five traps at each site to calculate the following community metrics for a) the total complement of dung beetles and b) the subset of species endemic to Borneo (highlighted in Table S1): dung

beetle abundance, biomass, rarefied species richness, alpha diversity (Shannon index) and beta diversity (species turnover between traps within a site; mean Sørensen's similarity index). To calculate biomass, we weighed beetles from 24 species taken from across the whole range of body sizes (between 7 – 51 individuals per species, average = 27, s.d. = 8) and used a polynomial regression to estimate biomass from body length measurements for the remaining species (Log_{10} (biomass) = -1.64 + 5.61*Log_{10}(length) – 4.39*$Log_{10}(length)^2$ + 1.99*$Log_{10}(length)^3$, R^2 = 0.982).

For the total complement of dung beetles at each site we also calculate three indices of functional diversity (Villéger et al. 2008; Laliberté & Legendre 2010): a) functional richness (FRic), the total volume of the centroid in trait-space that is occupied by the species at each sampling point, b) functional dispersion (FDis), the average distance of species from the centroid, weighted by their relative abundances, and c) functional evenness (FEve), the evenness of the distribution and relative abundances of the species.

For each site we calculated the average width of the reserve from measurements at both ends and the centre of the trap rectangle (widths are given for one side of the river, to match current policy terminology), the distance to the point at which the riparian reserve joined the nearest large (> 2000 ha) block of logged forest (both along the corridor and linear distance) and the proportion of forest cover within a buffer zone of radius 1 km around each trapping site. All landscape level variables were calculated in a GIS (ArcMap version 10.1) using GPS points of the trap locations, tracks of the riparian reserve boundaries and a land cover map. The land cover map was derived from a maximum likelihood supervised classification of SPOT satellite images combined with digitised maps of the plantations. Distances to the nearest large block of forest measured in a straight line versus along the corridor were very highly correlated ($r = 0.90$, $df = 21$, $p < 0.0001$), so for all analyses we used only distance along the corridor as this is more ecologically relevant for species that use the riparian forest. The area

of forest in the 1 km radius buffer and width of riparian reserves were also correlated ($r = 0.69$, $df = 21$, $p = 0.0002$). Therefore, to measure how the forest in the 1km buffer zone varied from what we would expect based only on the measurement of width at the point of trapping, we regressed the area of forest in the buffer against the width of the reserve and used the residuals for subsequent analyses. Area was square-root transformed to have the same dimensions as buffer width, and width was log transformed to meet linear model assumptions.

To calculate a measure of vegetation complexity at each site, we measured humus depth, canopy density (using a spherical densiometer) and basal area (using the angle point method (Bitterlich 1984)). We estimated the height of the tallest tree to the nearest 5m using a ruler held at arm's length and a known reference height at the base of the tree, and scored the under-storey vegetation density (below 2m) and mid-storey vegetation density (between 2m and 5m) on an ordinal scale of sparse (fewer than 20 stems or branches) medium (20 – 60 stems or branches) and dense (few patches of light and 60 – 100+ stems or branches). To obtain one numerical index summarising the greatest variation in the vegetation data that we could use in subsequent analyses, we carried out a metric scaling analysis on all the vegetation and soil measurements. The first axis of this analysis was positively correlated with canopy density, tree height, humus depth, basal area and mid-storey density and explained 54% of the total variation in the data. Since this output is therefore capturing variation in the 3-dimensional structure of the vegetation, we refer to it as a vegetation complexity index.

Using only data from the riparian reserve sites, we ran linear models to test for a relationship between each of the dung beetle community metrics listed above and riparian reserve width, distance to the nearest logged forest, area of forest within a 1 km radius (relative to what would be expected for reserve width), vegetation complexity and all two way interactions apart from the interaction between width and distance to nearest logged forest (we did not have sufficient data to test for this interaction as we had no sites where the riparian reserve

was wide and also far from the forest). Riparian reserve width was log transformed to meet model assumptions. Variables were removed from the model in order of least significance until the minimal adequate model was obtained.

For all cases in which there was a significant relationship between a particular dung beetle community metric and riparian reserve width, we used the model-predicted values to explore the sensitivity of the dung beetle community to changes in reserve width that could be implemented in legislation or management guidelines. We took the mean and lower bound of the 95% confidence interval (CI) for each metric in logged forest sites and found the width at which species richness in riparian reserves matched the forest values. For all response variables where there was no effect of riparian reserve width, distance to the nearest logged forest, proportion of forest in the surrounding area or vegetation complexity, we carried out a subsequent analysis to test whether the communities across all riparian reserve sites differed from the logged forest reference sites.

We then tested whether riparian reserve width, distance to the nearest logged forest, proportion of forest in the surrounding area, and vegetation complexity explained differences in riparian reserve community composition of a) the total dung beetle dataset and b) the subset of Borneo endemics using a PERMANOVA (permutational multivariate analysis of variance) with 1000 permutations. We plotted differences in species community composition with a non-metric multidimensional scaling ordination. To clarify the changes in community composition in riparian reserves furthest from the logged forest along the riparian reserves, we also summarised data for the five forest sites and five riparian reserve sites furthest from the forest.

RIPARIAN RESERVES AS CORRIDORS

Movement from the continuous logged forest into and along the corridors was investigated using flight intercept traps (FITs) at four spatially independent locations (all > 6 km apart) where a riparian reserve corridor joined the large area of logged forest. At each of these corridor junctions, FITs were set at 0 m, 200 m, 500 m, and 1 km from the point where the riparian reserve met the logged forest, following the design of previous research assessing dispersal of invertebrates into forest corridors (Hill 1995). For each trapping location we calculated riparian reserve width, and proportion of forest cover in a 1 m radius and vegetation complexity, as for the pitfall trap sites (see above).

Each FIT was made from fine black nylon mesh (mesh size = 0.5 cm, dimensions = 1.5 m x 2 m), stretched taught between two small trees and pegged down so that the bottom was flush with the soil. Ten collection trays (30 cm long, 20 cm wide, 10 cm depth) were placed on the ground on each side of the net and filled with a solution of water, detergent and salt. All FITs were protected by a rain cover. Tray contents were collected separately for each side of the FIT every 48 hours for 6 days.

All FITs were placed so that they were perpendicular to the river, so that the trays on one side collected the insects intercepted by the net as they flew along the corridor in a direction away from the forest, and the other side collected insects intercepted as they flew along the corridor back towards the forest. Wherever possible, traps were placed across ‘natural paths’ in the forest, i.e. existing clearer sections through which insects were likely to be flying. No vegetation was cut or cleared.

Dung beetles (Scarabaeidae, Scarabaeinae) were separated from the samples and identified to species. For each FIT we calculated the abundance, biomass, species richness and alpha diversity (Shannon index) of dung beetles. We tested whether each of these was predicted by

distance along the corridor, side of the trap (facing towards versus away from the forest) and the distance by side interaction using a linear mixed effects model with FIT location specified as a random factor.

COSTING DIFFERENT POLICY SCENARIOS

To estimate the yield impact of increasing buffer widths in a representative oil palm landscape (managed as several plantations but owned by the same company), we used the river map for our study area (325 km^2) and calculated the total area that would be covered by riparian reserve with policy recommendations for buffer widths of 30 m (the target width in our study area (Ewers et al. 2011)), 50 m, 80 m and 150 m (as measured on one side of the river, to match existing policy phrasing). We combined this with recent estimates of yield (tonne fresh fruit bunches ha^{-1} $month^{-1}$) obtained from Benta Wawasan plantation managers. This data covered 28 representative oil palm blocks (total area 15.1 km^2) in 2011, 2012 and 2013. We also adjusted the total yield to account for the percentage of un-plantable land in this landscape, using statistics obtained from local plantation offices across the entire study area.

All the above analyses were carried out in the R statistical software (version 3.0.2 (R Core Team 2013)) using the packages lme4 (Bates et al. 2014 p. 4), vegan (Oksanen et al. 2013) and FD (Laliberté & Shipley 2011).

RESULTS

From the pitfall traps we identified 5775 individual beetles of 59 species (including 27 Borneo endemics), and from the FITs we identified 3306 individuals of 68 species (including 33 Borneo endemics). Species lists and abundance for pitfall traps are given in Table S1 and for FITs in Table S2.

EFFECTS OF RIPARIAN RESERVE STRUCTURE AND LANDSCAPE CONTEXT ON DUNG BEETLES

All dung beetle species found in the logged forest were also recorded in at least one riparian reserve site. There was no significant effect of riparian reserve width, distance from forest, forest cover in a 1 km radius, buffer habitat complexity or any two way interactions on either the abundance or biomass of dung beetles (both overall and for the Borneo endemics subset, $p > 0.06$ in all cases). There was also no significant difference between dung beetle biomass in riparian reserves and logged forest for all species combined ($F_{1,26} = 0.93$, $p = 0.34$) or Borneo endemics ($F_{1,26} = 3.58$, $p = 0.07$), although the trend in the data for the endemics was that biomass in the riparian reserves was lower. However, dung beetle abundance in the riparian reserves was 54% lower than logged forest for all species combined ($F_{1,26} = 10.48$, $p = 0.0033$, mean ± sd for forest = 68 ± 22 and riparian reserves = 37 ± 20) and 50% lower for Borneo endemics ($F_{1,26} = 13.35$, $p = 0.001$, mean ± sd for forest = 30 ± 10 and riparian reserves = 15 ± 8).

There was a significant positive effect of riparian reserve width on the rarefied species richness of the whole dung beetle community ($F_{1,21} = 9.01$, $p = 0.007$, Fig 1 a)) and the subset of Borneo endemics ($F_{1,21} = 5.49$, $p = 0.029$, Fig 1 b)). There was also a significant effect of both width and proportion forest cover in the surrounding landscape on the diversity of dung beetles overall ($F_{2,20} = 8.64$, $p = 0.002$, Fig 1 c) and Fig S3), but no significant effect of any explanatory variables

on the diversity of endemic beetles ($p > 0.11$ in all cases). There was also no significant difference between the diversity of endemic species in logged forest and riparian reserves ($F_{1,26} = 1.25$, $p = 0.27$). Table 1 gives the widths at which the mean and lower 95% CI for species richness and diversity in the riparian reserves match the mean and lower 95% CI for the logged forest sites (corresponding to arrows in Fig 1).

	Width (m) where riparian reserve mean = logged forest mean	Width (m) where riparian reserve lower 95% CI = logged forest lower 95% CI
All species richness	80	53
Endemic species richness	48	31
All species diversity	150	84
Endemic species diversity	No relationship with width	No relationship with width

TABLE 1

Widths at which community metrics of dung beetles in riparian reserves are equal to the mean and lower 95% CI for logged forest sites.

There was no significant effect of any of the predictor variables on total or endemic beta diversity (species turnover between traps at the same site; $p > 0.15$ in all cases). There was also no significant difference in beta diversity between forest and riparian reserves for all dung beetles ($F_{1,26} = 1.28$, $p = 0.27$) or endemics ($F_{1,26} = 0.89$, $p = 0.35$).

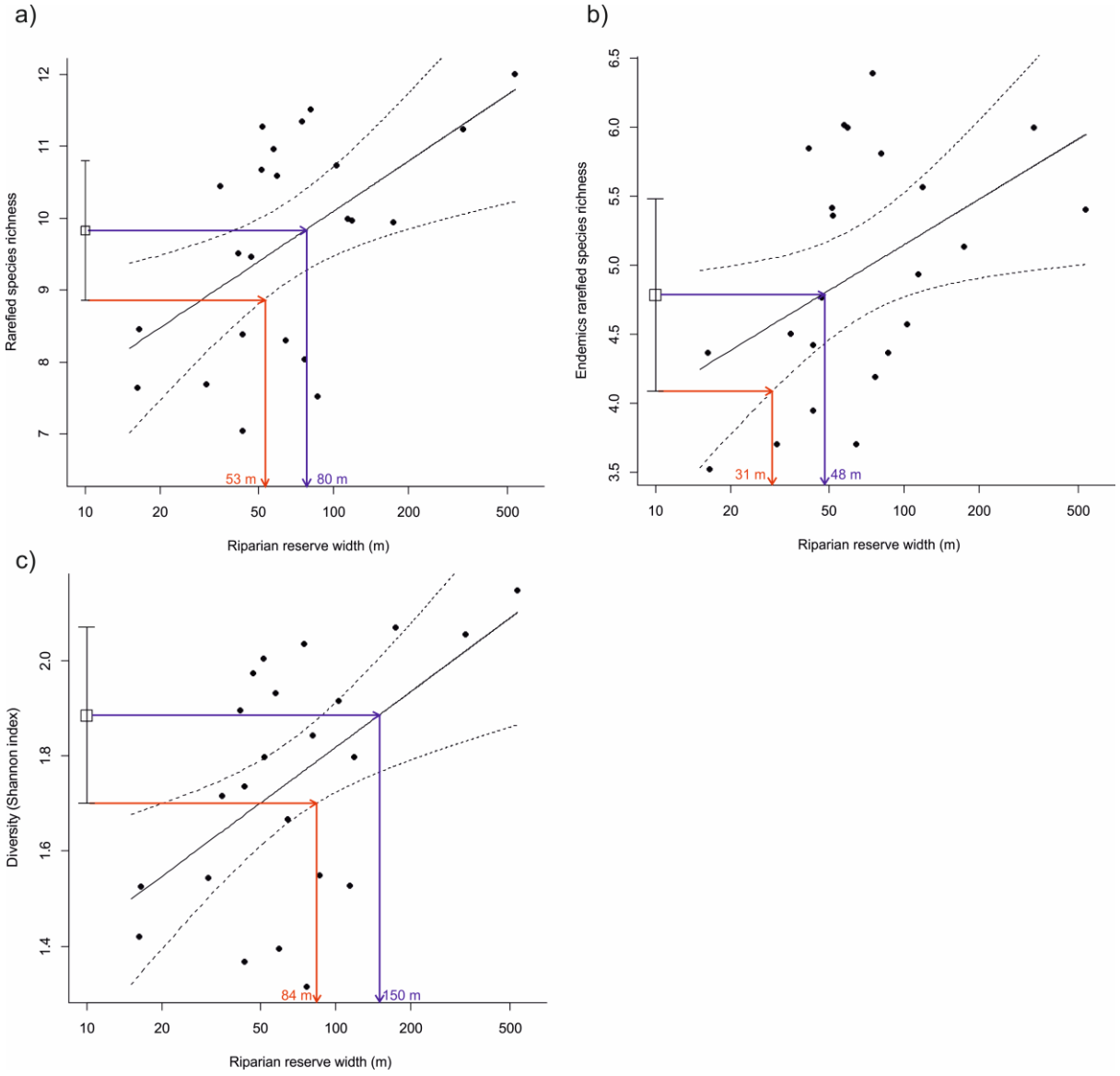


FIG 1

The species richness of all dung beetles (a), the species endemic to Borneo (b) and the diversity of all dung beetles (c) increase with riparian reserve width. Full circles show values for the riparian reserve sites. The solid and dotted lines show the model predicted values and 95% confidence intervals; unlogged width values are shown for ease of interpretation although the analysis was conducted on logged riparian reserve widths. Square and bars give the mean and 95% CI for the logged forest sites. As there was also a significant relationship between diversity and area of forest in the surrounding area, model predications in panel c) were obtained by specifying the average value for forest in the surrounding area.

There was a significant positive relationship between the vegetation complexity of the reserves and both functional richness (FRic, $F_{1,21} = 5.0$, $p = 0.036$, Fig 2 a)) and functional dispersion (FDis, $F_{1,21} = 7.85$, $p = 0.011$, Fig 2 b)). However, functional evenness (FEve) was unrelated to the width of the riparian reserves, vegetation structure, distance from the nearest logged forest, amount of forest in the surrounding area or any two way interactions ($p > 0.06$ in all cases). FEve also did not differ between logged forest and riparian reserves ($F_{1,26} = 3.0779$, $p = 0.09$).

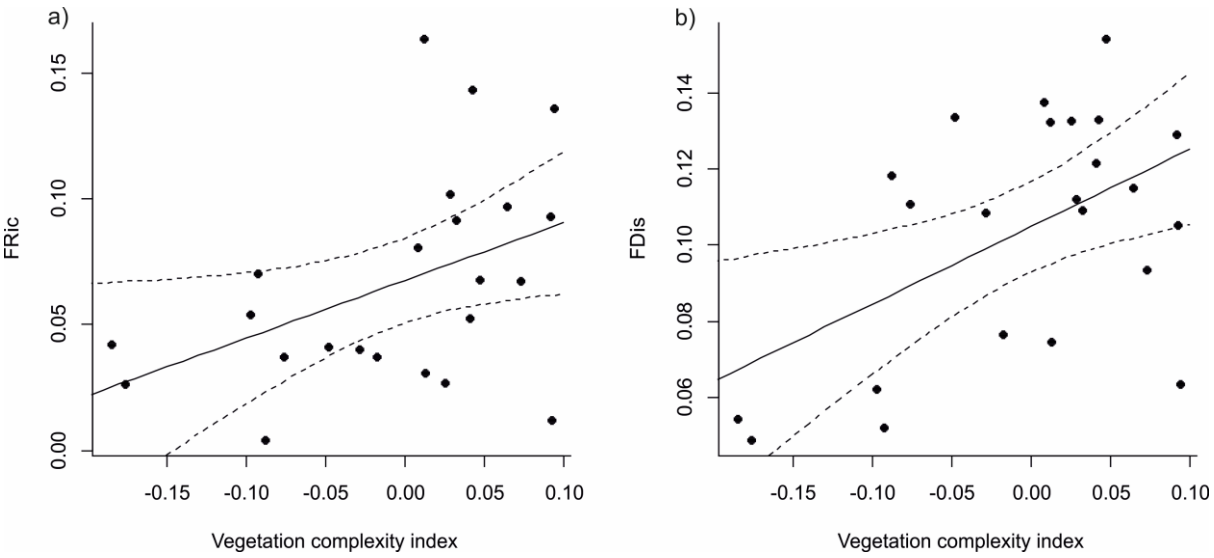


FIG 2

Functional richness (FRic, (a)) and functional dispersion (FDis, (b)) increase with the vegetation complexity within riparian reserves.

There was a significant change in community composition with distance from the nearest logged forest ($F_{1,21} = 2.65$, $p = 0.03$) for all dung beetle species combined (Fig. S2), but no relationship between the composition of the endemics and any explanatory variables ($p > 0.1$ in all cases). The five most abundant species in the forest were (in decreasing order of

abundance) *Onthophagus cervicapra*, *Paragymnopleurus sparsus*, *Onthophagus obscurior*, *Proagoderus watanabei* and *Sysyphus thoracicus*. Combining data for the 5 sites furthest from the forest, the five most abundant species were (in decreasing order of abundance) *Catharsius renaudpauliani*, *Onthophagus cervicapra*, *Proagoderus watanabei*, *Onthophagus incisus* and *Onthophagus obscurior*.

RIPARIAN RESERVES AS CORRIDORS

There was no significant effect of distance to the nearest logged forest, trap side or their interaction on any of the dung beetle community metrics calculated from the FITs (Fig 3).

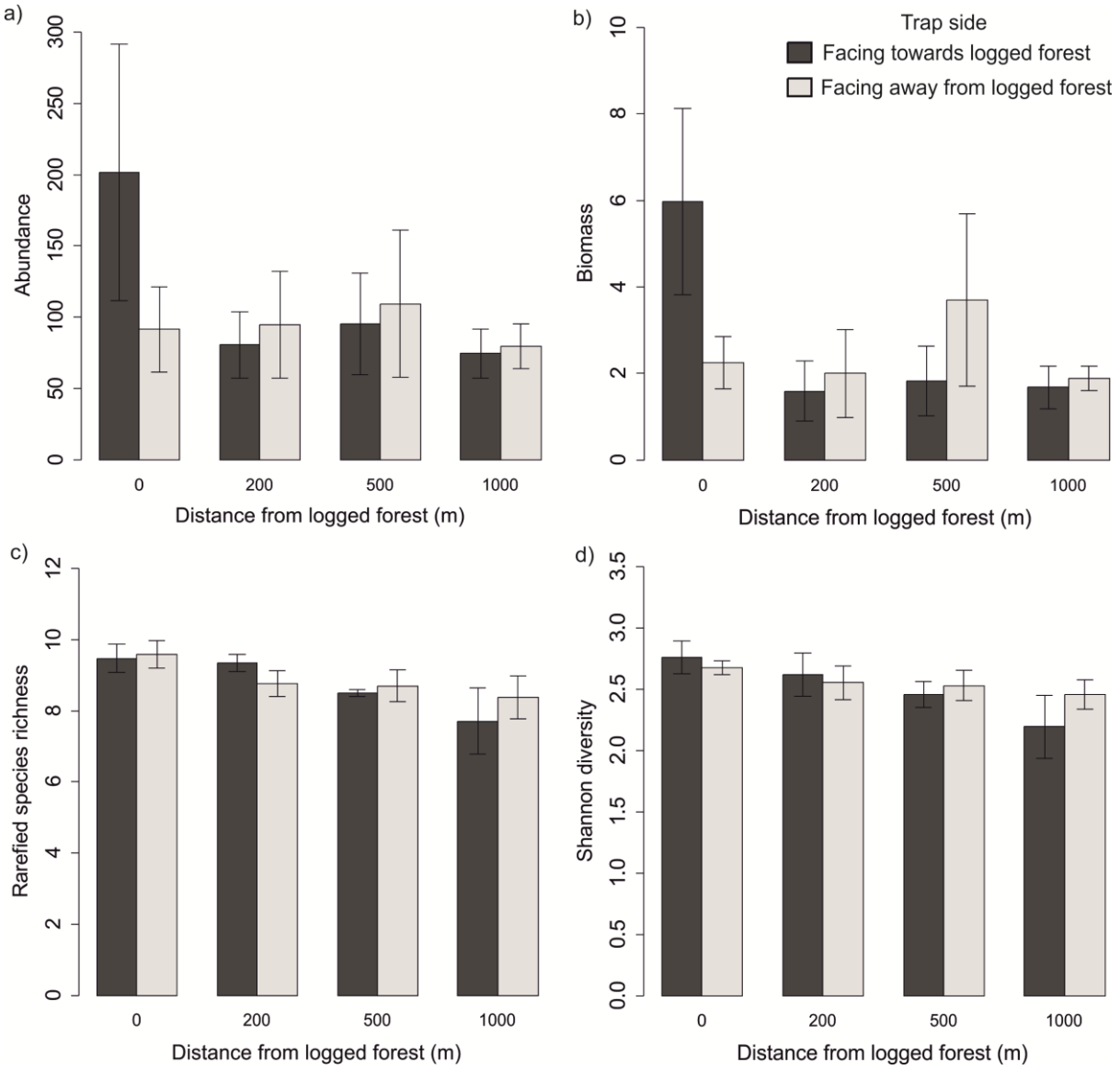


FIG 3

Abundance (a), biomass (b), species richness (c) and diversity (d) of dung beetles (± s.e). caught in FITs at increasing distances from logged forest along the riparian corridor.

COSTING DIFFERENT POLICY SCENARIOS

For a landscape with a similar distribution of rivers to our study area, an increase from 30 m to 50 m native vegetation protected on each side of the river could result in a yield loss of 2.1% to 2.7 %. An increase up to 150 m protected vegetation on each side of the river could result in a yield loss of 3.5% – 17.3%. Table 2 gives the amount of land area and possible yield loss (mean, lower and upper 95% CI bounds) resulting from increases in riparian reserve width from 30 m to 50 m, 80 m and 150 m. Table 3 shows the model predicted gains in overall species richness that correspond to these changes; the mean predicted species richness for 30 m reserves was only 10% lower than the value found in logged forest.

Total oil palm area (km 2)	**Area in 30 m buffer (km 2)**	**Area in 50 m buffer (km 2)**	**Area in 80 m buffer (km 2)**	**Area in 150 m buffer (km 2)**
325.72 (290 plantable)	10.31	17.37	28.41	54.98

upper 95% CI yield loss	4.0%	6.7%	11.0%	21.3%
percentage yield loss	3.6%	6.0%	9.8%	19.0%
lower 95% CI yield loss	3.1%	5.3%	8.6%	16.6%

additional % loss compared to 30m buffer (upper 95% CI)	0%	2.7%	7.0%	17.3%
additional % loss compared to 30m buffer	0%	2.4%	6.2%	15.4%
additional % loss compared to 30m buffer (lower 95% CI)	0%	2.1%	5.5%	13.5%

TABLE 2

Estimates of the economic consequences (% yield loss) of expanding riparian reserves based on the river network and percentage plantable land in the oil palm landscape surrounding the SAFE project, combined with crude palm oil profit estimates for Malaysia from 2012.

	30 m width	50 m width	80 m width	150 m width	Logged forest
upper 95% rarefied species richness	9.66	9.98	10.43	11.28	10.79
rarefied species richness	8.85	9.38	9.86	10.50	9.83
lower 95% rarefied species richness	8.05	8.78	9.29	9.71	8.86
% gain in species compared to 30m buffer (upper 95% CI)	0.0%	3.3%	8.0%	16.9%	
% gain in species compared to 30m buffer	0.0%	6.0%	11.4%	18.6%	
% gain in species compared to 30m buffer (lower 95% CI)	0.0%	9.1%	15.4%	20.6%	

TABLE 3
Biodiversity consequences of expanding riparian reserves. Estimates are derived from the model given in Fig 1 a) so the values given here also correspond to species richness rarefied to 33 individuals (the minimum number of beetles that occurred at any site).

DISCUSSION

As oil palm plantations continue to expand across the tropics, it is important that these agricultural landscapes retain biodiversity and ecosystem functions as best as possible. Our results reinforce the growing body of evidence that the isolation of forest fragments by oil palm has negative impacts on biodiversity but also show that riparian reserves retain many of the species found in logged forest areas. Our data indicate that increasing width specifications wherever possible will be beneficial for biodiversity conservation, although we recognise that enforcing existing legislation and introducing the protection of riparian zones where absent are key preliminary steps. Minimising the distance to other remaining fragments and increasing

vegetation complexity will also help to maximise the conservation value of riparian reserves. The extent to which riparian reserves increase movement through the oil palm landscape remains unclear, and deserves further investigation.

Effects of riparian reserve structure and landscape context

Our results reinforce the importance of continuing to enforce the 30 m protected zone where it is already present in legislation, and introducing similar legislation in countries or regions where it is absent. However, our data suggest that increasing the protected area to 50 – 80 m on each side of the river is necessary to retain levels of species richness and diversity found in logged forest. Whilst our data suggest that riparian reserve widths of 150 m are desirable to retain the mean value of alpha diversity seen in logged forest, in landscapes similar to those we studied there is potentially a high yield loss associated with this level of riparian protection (up to 17.3%). Therefore, we suggest that multiple tiered recommendations for rivers of different sizes will be most appropriate, so that wider reserves are maintained in the most critical locations. Similar multi-tiered approaches have been suggested for riparian zone protection in Canada based on evidence from birds, small mammals and amphibians (Darveau et al. 2001; Hannon et al. 2002). In addition, specifications for a minimal basal area or percentage canopy cover may also be productive, as our results indicate that the vegetation complexity of the reserves can increase the functional diversity of dung beetles and may therefore also affect the important ecological functions they support.

Our recommendations for the lower bound of required reserve width are likely to be conservative, as our “desirable” level for riparian reserve communities is based on the observed variation across only five forest sites. We would expect the confidence intervals on these estimates to decrease if we included more sites, which would correspond to higher width recommendations. Thus, the lower 95% confidence interval is an indication of the very

narrowest riparian reserves in which might expect to find communities with a similar species richness or diversity to those in logged forest.

Our results also indicate that the landscape context of the riparian reserves, in terms of distance from large areas of forest and proximity to other forest fragments, influences their conservation value. The positive relationship between dung beetle (alpha) diversity and the amount of forest in the area surrounding riparian reserves is consistent with evidence from the neotropics that the surrounding matrix impacts dung beetle communities in forest fragments (Barnes et al. 2014). Retaining connections between riparian reserves and forest left on steep slopes could provide synergistic benefits to the communities of both types of forest fragment. Community composition changed with distance from large areas of logged forest, as has been found for both birds and dung beetles in riparian forests within neotropical plantations (Hawes et al. 2008; Barlow et al. 2010b). However, we found that many forest dependent species were still present >14 km from a large forested area. All of the species found in the five logged forest sites were also found in at least one of the five riparian reserve sites furthest from the forest. Moreover, even though abundance, biomass and functional diversity were lower in the riparian reserves than in the logged forest, distance from logged forest did not have further negative impacts on these aspects of the dung beetle community. If the reserves were acting as ecological sinks, a decline in abundance over distance might be expected; the absence of such a trend suggests that the riparian reserves could be supporting permanent populations rather than transitory individuals. However, longer term studies are needed to confirm this. The lack of a significant relationship between distance from forest and either the abundance or richness of endemic species also suggests that these groups of higher conservation concern are not strongly affect by distance to the nearest forest.

We were not able to collect data on the extent to which a direct connection to a large area of forest affects the conservation value of riparian reserves, as this landscape is at the edge of the

expanding area of oil palm and all riparian corridors were still connected to the logged forest. However, connectivity to larger areas of forest has been shown to impact the communities within riparian reserves in the neotropics (Lees & Peres 2008) and may well have a similar effect in Southeast Asia. Studying riparian reserves in a more homogenous landscape (e.g. at lower elevations where the flatter terrain means that there are fewer forest fragments remaining), where corridors do not directly connect to larger forest areas, would allow us to further study the effects of forest connectivity on the conservation value of riparian reserves.

As our study area is part of a relatively newly converted landscape on the frontier of conversion to oil palm it is possible that the riparian reserve communities are still changing in response to the initial land conversion. We were not able to obtain precise measures of the time since the reserves were isolated as parts of the landscape were previously timber plantations under different management. However, data from satellite images indicates that the majority of deforestation occurred in the 15 years preceding our study (Hansen et al. 2013). As it can take > 25 years for extinction debts to be paid (Stouffer et al. 2011; Gibson et al. 2013) the riparian reserves may therefore still be declining in richness. Obtaining data on how these communities change will be critical in order to properly take extinction debts and lags in population changes into account when assessing the impact of land use change and the conservation of forest remnants (Wearn et al. 2012). If our study landscape has extinction debts yet to be paid, it is possible that wider reserves may be required to retain forest like communities than our current data suggests.

We found some disturbance adapted species (those previously found in high abundances in oil palm and not in logged forest, e.g. *Onthophagus trituber* see Chapter 3) at riparian reserve sites furthest from logged forest, suggesting a possible monitoring strategy for the quality of riparian reserves. It would be possible to set levels of abundance for these species, above which a riparian reserve could be considered to require restoration or widening in order to

retain forest-communities. Similar indicators, based on monitoring non-native dung beetles in riparian corridors in Australia (Gollan et al. 2011), and forest specialists in riparian reserves in the Amazon (Viegas et al. 2014) have been suggested. This approach could be a useful monitoring tool for plantation managers and also a metric for auditing plantations undergoing sustainability certification.

These considerations of landscape design and riparian zone management are of clear importance for countries across the tropics where oil palm plantations are expanding, but also of increasing importance as much of the oil palm industry in Southeast Asia is reaching a replanting phase (Snaddon et al. 2013). In addition to ensuring that existing reserves are maintained during the landscape disruption that occurs during replanting, there is also a huge opportunity to put in place restoration plans to rehabilitate riparian zones that were not previously sufficiently protected, or were planted before riparian zone protection became a legal requirement.

Riparian Reserves as Corridors

Our FIT data suggest that there is no net flow of beetles from forest into the reserves. However, the general trend in the results suggests that dung beetle abundance is higher at the boundary between the logged forest and the riparian reserve. The lack of difference between beetles sampled on different sides of the FITs could be because there are equal numbers of beetles moving in and out of the reserves. However, this result may also merely indicate that beetles in riparian forest have complex flight paths, resulting in equal captures on both sides of the FITS and masking an underlying net flow of individuals out of the forest. Mark-release-recapture studies would be a more effective method for assessing the movement of individuals into the corridors (Macneale et al. 2004).

COSTING DIFFERENT POLICY SCENARIOS

Our calculations of the percentage land area lost and corresponding profit loss, from extending the riparian reserves indicate that even an increase from 30 m to 50 m over a large landscape could cause a drop in yield of up to 2.7%; an increase to 80 m could cause a yield loss of up to 7%. For plantation owners, this may be a serious barrier to extending the width of reserves. However, this estimate is based on a relatively high elevation, marginal landscape with many tributaries and a large number of steep "unplantable" areas, so the losses would be lower in landscapes further downstream. In addition, our cost estimate assumes that the yield from oil palm is constant across all locations, and in reality the land near rivers is often less productive (Hai et al. 2001). In areas where a large area of land either side of the river is frequently flooded, the costs of extending riparian reserves would also be lower, although the majority of low yielding land was already included in the riparian reserves in our study landscape. To better calculate the cost:benefit ratio of each additional meter of riparian reserve, and therefore provide a more economically inclusive and robust width specification, we would need more data on the yield from marginal riparian land, and the value of riparian reserves in terms of other ecosystem services (e.g. carbon storage, hydrological benefits) and disservices (e.g. crop raiding by species found in the riparian reserves).

It is also important to emphasise that even though the species richness in the reserves can achieve levels comparable to that in logged forest, the levels of beetle abundance still remain much lower than in logged forest. Whilst we can provide recommendations for maximising the biodiversity within riparian reserves, this strategy is valuable only where plantations are a necessity, and is not comparable to the conservation of larger areas of logged forest which can support animal communities and functions much more similar to undisturbed forest (Edwards et al. 2010, 2011; Slade et al. 2011).

CONCLUSIONS

Overall, it is apparent that riparian buffers of only 30 m can retain many of the species found in large areas of native forest, and should be enforced where relevant legislation exists. Similar legislation should be introduced in countries where it is not currently present, and wherever possible reserves of 50 – 80 m should be protected. In addition, it is evident that larger scale landscape design can influence the conservation value of riparian forest corridors. Identifying synergistic interactions between fragments of non-crop habitat is therefore important for ensuring that management practices prevent biodiversity loss as much as possible. Our results suggest that the cost of protecting riparian forest of this width could be 2.1 – 7 % of total yields, and a more detailed cost benefit analysis incorporating a wider range of services and disservices supported by the reserves would be very informative. We show that by increasing riparian reserve width and vegetation complexity, retaining additional forest fragments in the landscape, and limiting the length of riparian reserves between larger forest fragments, oil palm plantations can be made much more biodiversity friendly, with reasonably limited costs to the industry.

SUPPLEMENTARY MATERIAL

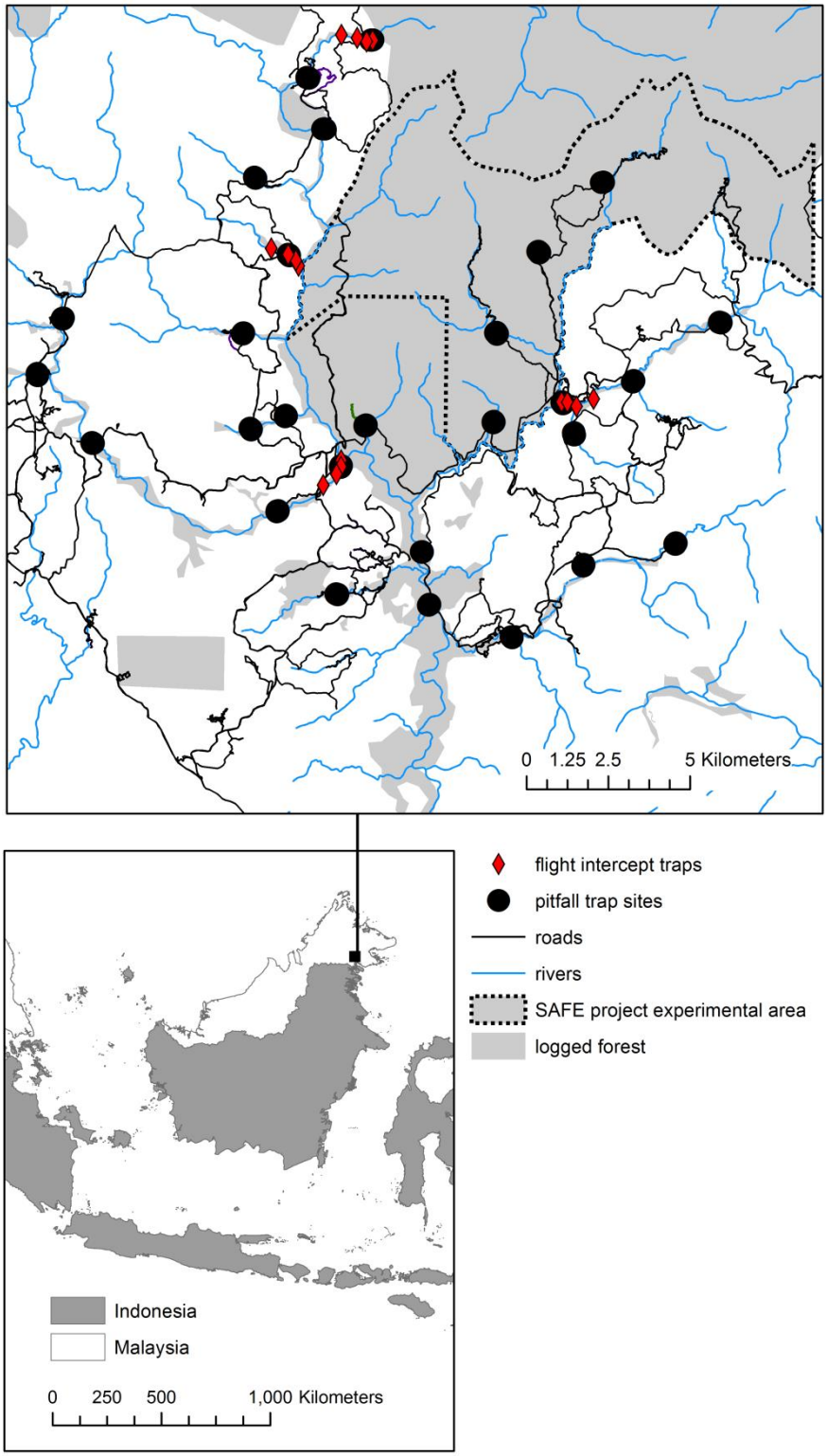


FIG S1

Map showing location of FITs and pitfalls traps within the SAFE project area and surrounding oil palm dominated landscape

Species name	Taxonomic authority	Logged forest sites (n = 5)	Riparian reserve sites (n = 20)
Caccobius (Caccobius) bawangensis	Ochi, Kon & Kikuta, 1997	0	21
Catharsius dayacus	Lansberge, 1886	4	39
Catharsius renaudpauliani	Ochi & Kon, 1996	29	949
Copris (Copris) agnus	Lansberge, 1875	0	1
Copris (Copris) sinicus	Hope, 1842	0	1
Copris (Paracopris) ramosiceps	Gillet, 1921	0	1
Haroldius rugulatus	Boucomont, 1914	0	1
Microcopris doriae	Harold, 1877	3	7
Microcopris hidakai	Ochi & Kon, 1996	0	1
Ochicanthon aff. woroae	Ochi, Ueda & Kon, 2006	0	4
Ochicanthon danum	Krikken & Huijbregts, 2007	1	1
Ochicanthon dytiscoides	Boucomont, 1914	11	16
Ochicanthon masumotoi	Ochi & Araya, 1996	8	10
Ochicanthon woroae	Ochi, Ueda & Kon, 2006	0	2
Oniticellus tessellatus	Harold, 1879	8	9
Onthophagus (Gibbonthophagus) cervicapra	Boucomont, 1914	480	921
Onthophagus (Gibbonthophagus) fujii	Ochi & Kon, 1995	3	4
Onthophagus (Gibbonthophagus) nigriobscurior	Ochi, Kon & Tsubaki, 2009	0	11
Onthophagus (Gibbonthophagus) semipersonatus	Ochi & Kon, 2009	0	1
Onthophagus (Indachorius) aff. cheyi	Ochi & Kon, 2006	0	1
Onthophagus (Indachorius) danumensis	Ochi, Kon & Barclay, 2009	0	1
Onthophagus (Onthophagiellus) aff. falculatus	Boucomont, 1914	0	1
Onthophagus (Onthophagiellus) aff. hidakai	Ochi & Kon, 1995	0	7
Onthophagus (Onthophagus) aff. borneensis	Harold, 1877	0	5
Onthophagus (Onthophagus) aff. variolosus	D'orbigny, 1902	0	2
Onthophagus (Onthophagus) aphodioides	Lansberge, 1883	0	5
Onthophagus (Onthophagus) borneensis	Harold, 1877	1	5
Onthophagus (Onthophagus) deflexicolis	Harold, 1877	6	14
Onthophagus (Onthophagus) incisus	Harold, 1877	79	649
Onthophagus (Onthophagus) obscurior	Boucomont, 1914	169	582
Onthophagus (Onthophagus) ochromerus	Harold, 1877	0	2
Onthophagus (Onthophagus) pacificus agg.	Lansberge, 1895	1	12
Onthophagus (Onthophagus) pastillatus	Boucomont, 1919	0	1
Onthophagus (Onthophagus) pavidus	Harold, 1977	0	3
Onthophagus (Onthophagus) rugicollis	Harold, 1880	114	309
Onthophagus (Onthophagus) rutilans	Sharp, 1875	1	1
Onthophagus (Onthophagus) simboroni	Ochi & Kon, 2006	2	2

Species name	Taxonomic authority	Logged forest sites (n = 5)	Riparian reserve sites (n = 20)
Onthophagus (Onthophagus) vulpes	Harold, 1877	37	211
Onthophagus (Onthophagus) waterstradti	Boucomont, 1914	0	24
Onthophagus (Paraphaenaemorphus) trituber	Wiedemann, 1823	0	11
Onthophagus (Paraphanaeomorphus) aff. phanaeides	Frey, 1956	0	12
Onthophagus (Parascatonomus) aurifex	Harold, 1877	2	4
Onthophagus (Parascatonomus) dux	Sharp, 1875	5	10
Onthophagus (Parascatonomus) rudis	Sharp, 1875	43	80
Onthophagus (Parascatonomus) sarawacus	Harold, 1887	0	3
Onthophagus (Parascatonomus) semiaurreus	Lansberge, 1883	15	113
Onthophagus (Parascatonomus) semicupreus	Harold, 1877	4	7
Onthophagus (Pseudophanaeomorphus) johkii	Ochi & Kon, 1994	1	3
Onthophagus (Serrophorus) laevis	Harold, 1880	2	4
Onthophagus (Serrophorus) muelleri	Lansberge, 1883	66	137
Onthophagus (Sinonophagus) aff. angustatus sp. 1	Boucomont, 1914	0	18
Onthophagus (Sinonthophagus) rorarius	Harold, 1877	2	33
Panelus.sp1		2	3
Panelus.sp3		0	1
Paragymnopleurus maurus	Sharp, 1875	4	19
Paragymnopleurus sparsus	Sharp, 1875	196	409
Paragymnopleurus striatus	Sharp, 1875	2	5
Proagoderus watanebei	Ochi & Kon, 2002	163	723
Sysyphus thoracicus	Sharp, 1875	161	343

TABLE S1

Species names, authorities and total abundance of dung beetles caught in pitfall traps. Borneo endemics are highlighted in bold.

Table S2

Species names, authorities and total abundance of dung beetles caught in flight intercept traps. Borneo endemics are highlighted in bold.

Species name	Taxonomic authority	Total
Anoctus aff. laevis	Sharp, 1875	7
Caccobius (Caccobius) bawangensis	Ochi, Kon & Kikuta, 1997	11
Catharsius dayacus	Lansberge, 1886	2
Catharsius renaudpauliani	Ochi & Kon, 1996	14
Copris (Paracopris) ramosiceps	Gillet, 1921	1
Cyobius wallacei	Sharp, 1875	2
Haroldius aff. borneensis	Paulian, 1993	1
Haroldius rugulatus	Boucomont, 1914	3
Ochicanthon danum	Krikken & Huijbregts, 2007	2
Ochicanthon dytiscoides	Boucomont, 1914	7
Ochicanthon masumotoi	Ochi & Araya, 1996	5
Ochicanthon woroae	Ochi, Ueda & Kon, 2006	18
Oniticellus tessellatus	Harold, 1879	37
Onthophagus (Gibbonthophagus) cervicapra	Boucomont, 1914	249
Onthophagus (Gibbonthophagus) nigriobscurior	Ochi, Kon & Tsubaki, 2009	0
Onthophagus (Gibbonthophagus) subcornutus	Boucomont, 1914	3
Onthophagus (Indachorius) aff. aereopictus	Boucomont, 1914	57
Onthophagus (Indachorius) aff. cheyi	Ochi & Kon, 2006	143
Onthophagus (Indachorius) aff. pseudoworoae	Ochi, Kon & Barclay, 2009	1
Onthophagus (Indachorius) aff. woroae	Ochi & Kon, 2006	127
Onthophagus (Indachorius) danumensis	Ochi, Kon & Barclay, 2009	91
Onthophagus (Onthophagiellus) aff. deliensis	Lansberge, 1885	1
Onthophagus (Onthophagiellus) aff. hidakai	Ochi & Kon, 1995	8
Onthophagus (Onthophagus) aff. borneensis	Harold, 1877	9
Onthophagus (Onthophagus) aphodioides	Lansberge, 1883	7
Onthophagus (Onthophagus) borneensis	Harold, 1877	50
Onthophagus (Onthophagus) deflexicolis	Harold, 1877	96
Onthophagus (Onthophagus) incisus	Harold, 1877	383
Onthophagus (Onthophagus) obscurior	Boucomont, 1914	93
Onthophagus (Onthophagus) ochromerus	Harold, 1877	1
Onthophagus (Onthophagus) pacificus agg.	Lansberge, 1895	81
Onthophagus (Onthophagus) pastillatus	Boucomont, 1919	17
Onthophagus (Onthophagus) pavidus	Harold, 1977	87
Onthophagus (Onthophagus) rouyeri	Boucomont, 1914	5
Onthophagus (Onthophagus) rugicollis	Harold, 1880	121
Onthophagus (Onthophagus) simboroni	Ochi & Kon, 2006	44
Onthophagus (Onthophagus) sp. 6		1
Onthophagus (Onthophagus) sp.F10		1
Onthophagus (Onthophagus) vulpes	Harold, 1877	446
Onthophagus (Onthophagus) waterstradti	Boucomont, 1914	3

Species name	Taxonomic authority	Total
Onthophagus (Paraphaenaemorphus) trituber	Wiedemann, 1823	3
Onthophagus (Paraphanaeomorphus) aff. phanaeides	Frey, 1956	16
Onthophagus (Parascatonomus) aurifex	Harold, 1877	16
Onthophagus (Parascatonomus) brendeli	Ochi, Kon & Barclay, 2009	20
Onthophagus (Parascatonomus) dux	Sharp, 1875	8
Onthophagus (Parascatonomus) fujiokai	Ochi & Araya, 1996	1
Onthophagus (Parascatonomus) rudis	Sharp, 1875	66
Onthophagus (Parascatonomus) sarawacus	Harold, 1887	10
Onthophagus (Parascatonomus) semiaurreus	Lansberge, 1883	169
Onthophagus (Parascatonomus) semicupreus	Harold, 1877	126
Onthophagus (Pseudophanaeomorphus) chandrai	Ochi, 2007	14
Onthophagus (Pseudophanaeomorphus) johkii	Ochi & Kon, 1994	129
Onthophagus (Pseudophanaeomorphus) quasijohkii	Ochi & Kon, 2005	3
Onthophagus (Serrophorus) laevis	Harold, 1880	8
Onthophagus (Serrophorus) muelleri	Lansberge, 1883	59
Onthophagus (Sinonthophagus) aff. rorarius	Harold, 1877	1
Onthophagus (Sinonthophagus) rorarius	Harold, 1877	15
Onthophagus vethi	Krikken, 1977	23
Onthophagus(Onthophagus) batillifer	Harold, 1875	38
Panelus.sp1		34
Panelus.sp2		3
Panelus.sp3		8
Paragymnopleurus maurus	Sharp, 1875	9
Paragymnopleurus sparsus	Sharp, 1875	111
Paragymnopleurus striatus	Sharp, 1875	1
Proagoderus watanebei	Ochi & Kon, 2002	80
Sysyphus thoracicus	Sharp, 1875	99
Yvescambefortius sarawakus	Gillet, 1926	1

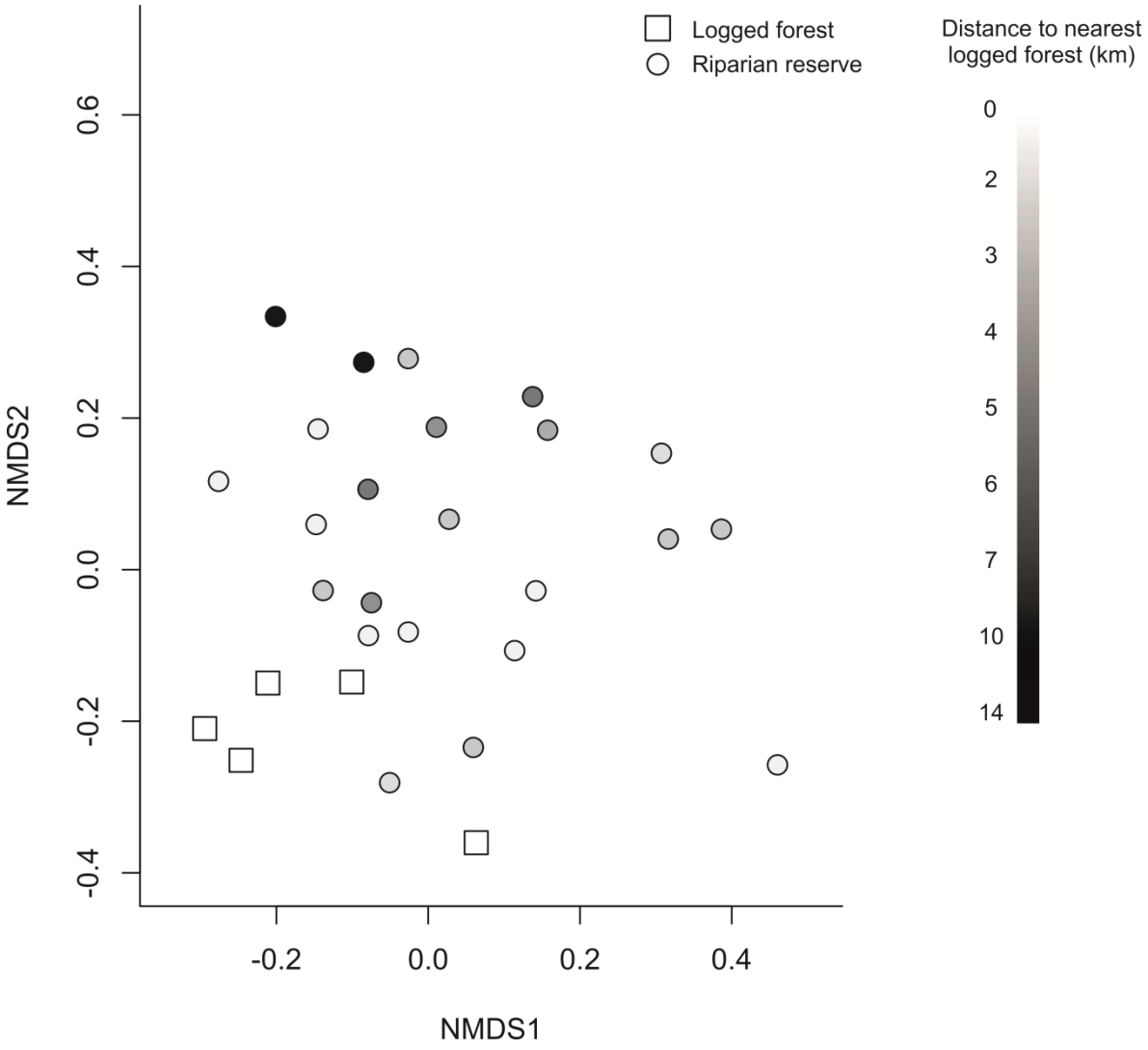


FIG S2

Non-metric multidimensional scaling ordination plot showing that similarity between dung beetle communities in riparian reserve sites and logged forest communities decreases with distance from the nearest logged forest.

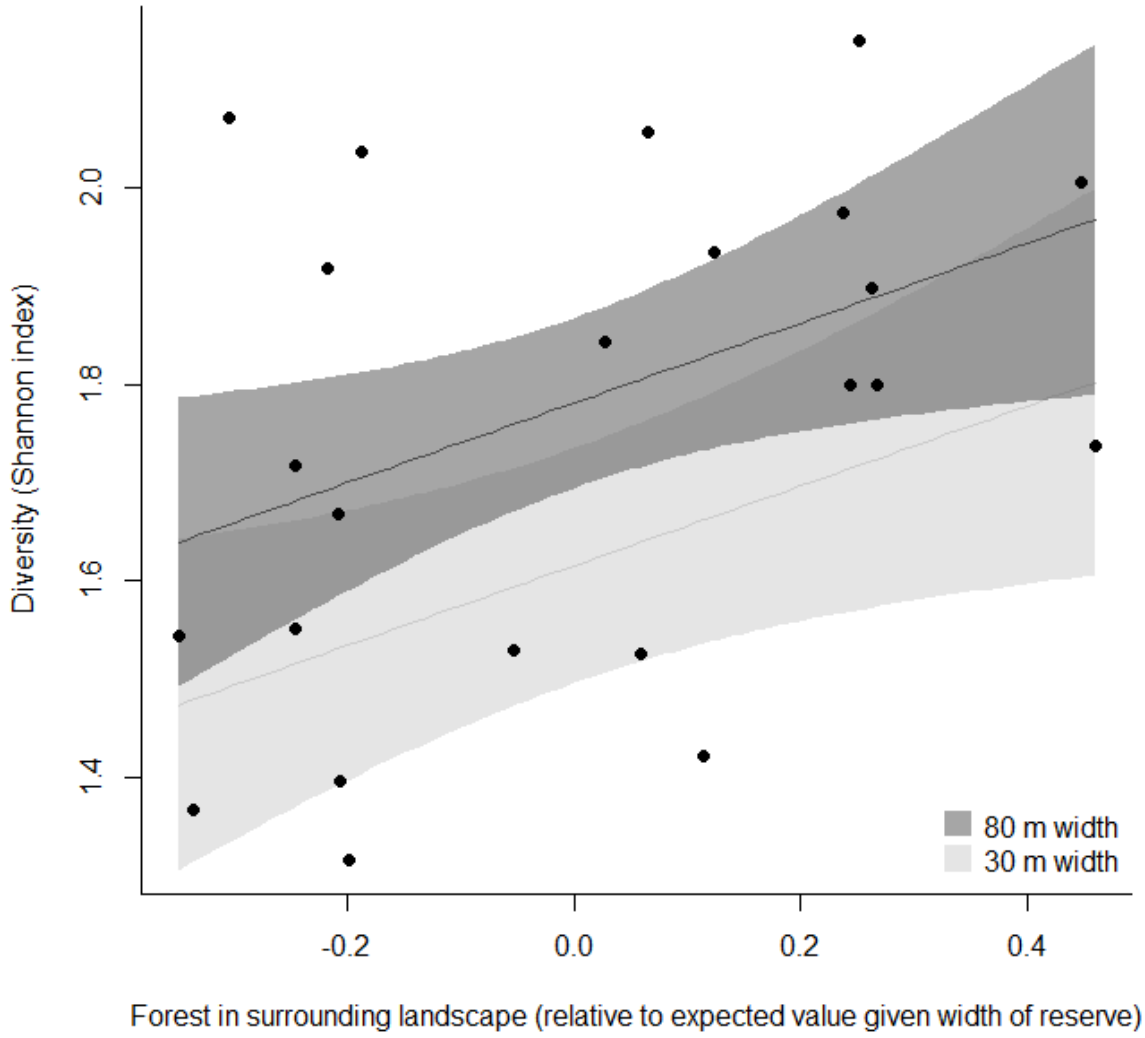


FIG S3

Dung beetle species diversity in riparian reserves increases with the area of forest cover in the surrounding landscape. The solid and dotted lines show the predicted values and 95% confidence intervals from the linear regression for the commonly adopted width (30 m) and the wider recommendation of 80 m; there was no interaction between reserve width and the forest in the surrounding landscape.

CHAPTER 5: RIPARIAN RESERVES WITHIN OIL PALM PLANTATIONS CONSERVE LOGGED FOREST LEAF LITTER ANT COMMUNITIES AND ASSOCIATED NUTRIENT CYCLING PROCESSES

ABSTRACT

The expansion of oil palm plantations in the tropics is causing declines in many species and altering ecological functions. However, the palm oil industry is important for the economy of a growing number of tropical countries. Identifying opportunities to conserve forest dependent species and ecological processes within oil palm-dominated landscapes is therefore important. Protecting riparian vegetation may be one such opportunity; forest buffer strips are protected in many countries to manage hydrological dynamics and water quality. These buffer strips also have the potential to conserve functionally important taxa and the processes they support. We used a bait removal experiment to assess rates of ant-mediated nutrient redistribution (scavenging) and survey leaf litter ant communities within oil palm dominated landscapes in Sabah, Malaysia. Riparian reserves had similar ant species richness, community composition and nutrient redistribution rates to nearby logged forest. Reserve width and vegetation structure did not affect ant species richness significantly, but there was a reduction in the number of foraging individuals with increasing reserve width, and a significant increase in nutrient redistribution with vegetation complexity. Oil palm ant communities were characterised by significantly lower species richness, altered community composition and reduced nutrient redistribution, compared to both logged forest and riparian reserves. Reduced nutrient redistribution in oil palm was not explained by a reduction in species richness, nor a replacement of forest ant species by those with lower nutrient redistribution rates. There was also no significant effect of land use on the nutrient distribution activity of the forest species that persist in oil palm. Rather, changes in the rate of nutrient redistribution were best explained by a reduction in the mean rate of bait removal per individual ant across the whole community. Our results suggest that, in addition to the protection of large continuous areas of primary and logged forest, maintaining riparian reserves is a successful

strategy for conserving leaf litter ants and the functions they support in tropical agricultural landscapes.

INTRODUCTION

Agricultural expansion and intensification continues to cause widespread loss of biodiversity and alters ecosystem functioning (Tilman et al. 2001). For tropical rainforests, the expansion of the palm oil industry is one of the biggest threats. Palm oil is the world's most widely used vegetable oil; it is used for cooking, cosmetics, detergents, and increasingly as a biofuel feedstock. Over the last 10 years, approximately 40% of oil palm expansion in Malaysia and Indonesia (which produce over 80% of global palm oil (FAO 2014)) has been onto forested land (Gunarso et al. 2013). As the palm oil industry is now also expanding in Africa and the Neotropics (Butler & Laurance 2010), tropical forests across the globe are likely to be affected by conversion to oil palm plantations.

Conversion of native vegetation to palm oil plantations has profound negative consequences for biodiversity (Savilaakso et al. 2014), as well as altering both abiotic and biotic processes. For several groups of birds, bats, small mammals and insects, oil palm plantations support less than 40% of the species found in undisturbed or logged forest (Fitzherbert et al. 2008). Oil palm plantations have simplified vegetation structure, as well as higher diurnal temperatures, lower humidity and greater variation in these abiotic variables than forest (Turner & Foster 2006; Luskin & Potts 2011). Carbon sequestration and storage within plantations is lower than in forest (Carlson et al. 2012) and rates of soil erosion and frequency of flash flood events are higher (Obidzinski et al. 2012).

Nevertheless, oil palm plantations are likely to become an increasingly widespread feature of tropical landscapes, so identifying strategies to reduce the negative impacts of the industry are essential. Limiting the expansion of oil palm onto forested land is very important given the high biodiversity value of this habitat (Edwards et al. 2011; Gibson et al. 2011; Woodcock et al.

2011) but there are also promising opportunities for retaining species and processes within plantations. In many countries, the vegetation on river banks is protected to help maintain water quality, reduce sedimentation and limit flood risk downstream (Tabacchi et al. 2000; Mayer et al. 2007). These areas of protected vegetation (also referred to as buffer strips or riparian reserves) can provide non-crop habitat and movement corridors for species that would not otherwise survive in, or move through, agricultural areas (Marczak et al. 2010).

Currently, our understanding of the terrestrial community composition and ecological dynamics of riparian reserves is limited and biased towards temperate regions. As a result, existing policy and legislation guiding riparian zone management in the tropics is based on very little ecological information (Ewers et al. 2011). To guide policy recommendations and maximise the conservation value of riparian reserves, it is necessary to document their terrestrial biodiversity, how this varies with reserve design, and what impact this has on ecosystem functioning.

Ant communities contribute to many ecological processes, including decomposition, predation and seed dispersal, and form a range of symbiotic relationships with other insects and plants (Lach et al. 2010). Furthermore, since ant communities are reasonably robust to multiple rounds of logging (Woodcock et al. 2011), they are a good candidate group for maintaining ecosystem functions in degraded landscapes. However, little is known about how conversion to oil palm affects ant community structure, and nothing is known about how these changes affect ecosystem function. The ant fauna in oil palm plantations is less diverse and has a different species composition and spatial structure to forested areas (Brühl & Eltz 2010; Fayle et al. 2010, 2013; Lucey et al. 2014). As positive relationships have been found between the diversity of leaf litter ant communities and rates of bait removal within tropical forests (Fayle et al. 2011) and urban habitats (Tan & Corlett 2012), it is likely that the functions supported by ant communities are also altered in oil palm. Changes in the foraging activity and nutrient

redistribution carried out by ants could affect the soil structure, soil nutrients and community composition of other soil arthropods or microbes (Frouz & Jilkova 2008).

We used a novel bait removal method to quantify changes in the activity of ant communities and individual species across a land use gradient in Sabah, Malaysian Borneo. Using ecologically relevant baits (crushed earthworm pellets) we were able to answer the following questions:

1) How does ground-foraging ant abundance, species richness and community composition in riparian reserves compare to logged forest and oil palm?

2) How do rates of ant-mediated animal necromass redistribution vary across these land uses?

3) Which changes in the ant community explain observed changes in this ecosystem function?

4) How does reserve design (width and vegetation structure) affect ant communities and function?

METHODS:

DATA COLLECTION

Study sites were located adjacent to rivers (5 - 10 m width) within a 600 km^2 area of twice-logged lowland dipterocarp rainforest, acacia and oil palm plantations (planted between 1998 and 2012) in Sabah, Malaysian Borneo (117.50 N, 4.60 E). Sampling was conducted in continuous twice-logged forest (n = 8), riparian reserves within oil palm (n = 9; mean 48 m ± 26 m s.d. forest on each side of the river), and adjacent to rivers in oil palm without a riparian reserve (n = 8, Fig S1). There is no primary forest within 50 km of these sites, so it was not possible to set up comparison sites in continuous primary forest with adequate spatial interspersion. In addition, as riparian reserves are isolated linear fragments in a previously logged and then converted landscape, riparian zones in continuous logged forest are an appropriate comparison. All data were collected between April and July, the relatively dry half of the year (Walsh & Newbery 1999b), in 2011 (3 sampling points per site) and 2012 (12 points per sampling site), to minimise seasonal influences. All sampling points along the river bank were 30m apart and within 1 m of the high water line.

At each sampling point we measured nutrient distribution rates with a bait removal observation lasting 30 minutes. In both years, all observations at each site were carried out in one day. Baits were pellets made of crushed earthworm (average mass: 0.017g, maximum diameter: 3 mm; Tropical Fish Food Earthworm Pellets: High Protein, from UK Fishfood). Bait platforms of laminated graph paper were placed with the edge flush with the soil; each with a square grid of thirty baits placed in the centre of 2 cm x 2 cm squares (6 rows, 5 columns). We standardised total bait mass and used four different size classes, randomly positioned on the grid for each trial (2 x whole pellet, 4 x half pellet, 8 x quarter pellet and 16 x eighth pellet) to

ensure that baits were attractive to a range of ant species and also similar to naturally occurring sources of protein (e.g. dead invertebrates).

We recorded the time at which the first ant entered the bait card and the number of individuals arriving during each five minute time period. We also recorded temperature at the beginning of each trial as this can affect the foraging activity of many ant species (Ruano et al. 2000). When a bait item was removed (carried out of its home square) we recorded the position of the bait, the time of removal and the species that removed it. Baits were never broken up by ants. Voucher specimens for each species were either taken at the end of the trial or during the trial (if conspecifics were visible and at least 50 cm away from the bait card). Ant voucher specimens were identified to species as far as possible using keys by (Bolton 1977; Eguchi 2001; Fisher 2010), the online database AntWeb and reference collections held in the Cambridge University entomology collections and British Museum of Natural History, London.

We measured humus depth adjacent to the bait card, canopy density (using a spherical densiometer), tree basal area (using the angle point method (Bitterlich 1984)). We estimated (to the nearest 5 m) the height of the tallest tree within 10 m of the sampling point using a clinometer. Under-storey vegetation density (for an area of 2 m radius around the bait card and up to 2 m height) and mid-storey vegetation density (for an area of 2 m radius around the bait card between 2 m and 4 m height) were scored on an ordinal scale of sparse (fewer than 20 stems or branches) medium (20 – 60 stems or branches) or dense (few patches of light and 60 – 100+ stems or branches).

ANALYSIS

We calculated the following response variables: 1) *Ant abundance*, the total number of foragers arriving at each observation. There were 15 observations in which all bait items were

removed before the trial ended, causing declines in ant abundance. We corrected for this by assuming that ant abundance would have remained at the level observed in five minute period before the last bait item was removed. 2) *Ant diversity* using the Shannon index. This indicates the extent to which any bait card was dominated by one species. 3) *Species count*, the number of species arriving at each bait card. 4) *Species richness*, the number of species observed across all observations at each site. As we were only able to complete 12 (of 15) observations at two of the 25 sites, we calculated the incidences of each species and then applied a coverage-based rarefaction technique using the iNEXT online platform (Hsieh et al. 2013) to account for differences in sampling effort.

We also calculated functional metrics for each observation: 1) time till the first ant reached the bait card, 2) number of bait pellets removed, 3) the proportion of bait mass removed, 4) recruitment rate. We calculated recruitment rate by extracting the gradient of a linear regression on the number of ants arriving in each 5 minute time period following arrival of the first ant.

We analysed the effect of land use, temperature and their interaction on each of our community and functional metrics. For the abundance of ants, diversity of ants, time until the first ant arrived, number of bait pieces removed, proportion of bait mass removed and recruitment rate we ran generalised linear mixed models (GLMMs). We specified site and year as random factors and specified transformations and error families as appropriate (see Results). For site level species richness we used a generalised least squares model with land use as the sole predictor variable, specifying weights to account for heterogeneity of variance across land cover type (varIdent function after (Zuur et al. 2009)). We tested for differences in community composition using a permutational analysis of variance.

There are three non-mutually exclusive hypotheses for the mechanisms underlying changes in the rate of necromass redistribution with habitat conversion: 1) That species are lost (and not

replaced) when habitats are converted, and that this results in reduction in redistribution rates. 2) That there is turnover in species with habitat conversion, and the new species conduct redistribution at a different rate because of a) changes in forager density, b) the new species having different redistribution rates to those they replace, or c) changes in redistribution rates per forager due to abundances of species that rapidly remove baits decreasing, while those that remove baits more slowly increase. 3) That persisting (shared) species alter their rate of redistribution in converted habitats (as with hypothesis 2, this could be due to a) changes in the densities of these species, b) changes in the species distribution rates or c) changes in the redistribution rates per forager).

To examine whether loss of species explained the observed differences in nutrient redistribution (hypothesis 1), we ran a generalised linear model to test for a relationship between the proportion of bait removed (separate analyses for bait pieces and bait mass) and species richness, using data from all sites.

We then tested whether turnover in species could explain differences in nutrient redistribution rates. To ensure that we were only testing for differences between the ant communities responsible for the observed differences in function, we combined data from land uses with no significant differences in either ant community composition or overall bait removal rates. We then isolated data for the species that were unique to each group; these are the species that are "replaced" in the change from land use(s) with higher redistribution rates to land use(s) with a lower nutrient redistribution rate. We then tested whether the abundance of foragers differed between higher and lower function land uses (hypothesis 2 a)). To see if species unique to the lower function land uses had lower bait removal rates than those they had "replaced" (hypothesis 2 b)), we calculated each species' redistribution rate (the mean bait mass removed per individual visiting the card for each species). We then tested whether the species redistribution rates differed between higher and lower function land uses. We also

calculated the mean distribution rate per ant (i.e. combining data across all species) and tested whether this differed between the higher and lower function land uses (hypothesis 2 c)).

To investigate whether observed differences in nutrient distribution could be explained by changes in the persisting species we first isolated the data on the subset of species found in both the high function and low function land uses. We then tested whether the abundance (hypothesis 3 a)) and redistribution rate (hypothesis 3 b)) of these shared species differed between the land uses. We also tested whether the mean bait removal rate per forager (hypothesis 3 c)) differed between land uses.

To investigate effects of riparian reserve width and vegetation structure we first ran a metric scaling analysis on all vegetation and soil measurements to obtain one numerical index summarising the greatest variation in these data at each sampling point. The first axis of the output was negatively correlated with understorey density and positively correlated with canopy density, tree height, humus depth, basal area and midstorey density. Since this axis is therefore capturing variation in the 3-dimensional structure of the vegetation, we refer to it as a vegetation complexity index. We tested for a correlation between vegetation complexity and riparian reserve width, and then used GLMMs to test for the effect of width, vegetation complexity and temperature on each of the community and function metrics calculated for each observation, specifying year and site as random factors. For the data on species richness calculated at the site level and community composition, we ran a linear model and PERMANOVA respectively, with the mean width for each site, the mean vegetation complexity and their interaction as predictors. All analyses were carried out in R (R Core Team 2013) using the packages vegan (Oksanen et al. 2013), lme4 (Bates et al. 2014) and lme (Pinheiro et al. 2013).

RESULTS

ANT COMMUNITY AND FUNCTION ACROSS LAND USES

In total we carried out 366 observations, counted 30,980 individual ants and collected 1906 voucher specimens, from which we identified 51 genera and 149 species and morphospecies. A full list of species is given in Table S1.

There was no significant effect of land use, temperature or their interaction on ant abundance, the number of species at each observation, or the Shannon diversity of ants attending the bait (Table 1). Site level species richness did not differ between logged forest and riparian reserves, but was higher in these land uses than in oil palm (Table 1, Fig 1a). Community composition also varied across land uses (Table 1, Fig 2). Multiple comparisons with Bonferroni corrections confirmed that the community composition of riparian reserves was similar to logged forest and oil palm differed from both of the other land uses.

The time until the first ant arrived did not differ significantly with land use, temperature or their interaction (Table 1). There was a significant effect of land use on the number of bait pieces removed, the bait mass removed and the recruitment rate (Table 1, Fig 1). The bait mass removed was similar in logged forest and riparian reserve, and lower in oil palm (Fig 1 d). Recruitment rate was higher in forest than in oil palm, with riparian reserve sites intermediate between the two and not significantly different from either (Fig 1 f). Since logged forest and riparian reserves did not differ in ant community composition or either measure of nutrient distribution, we combined the two forest habitats (higher function land uses) in analyses partitioning the effects of changes in ant communities on ecosystem functioning.

Model				
Ant community metrics	***χ^2***	***df***	***p***	
Ant abundance ~ land use + temp + land use: temp	7.1	5	0.216	
Species count ~ land use+ temp + land use: temp	5.3	5	0.384	
Ant diversity (Shannon index) ~ land use + temp + land use: temp	5.0	5	0.419	
	F	***df***	***p***	
Site level species richness ~ land use	15.8	2,22	< 0.001	***
Community composition ~ land use†	19.92	2,361	0.001	**
Functional metrics	***χ^2***	***df***	***p***	
Time until first ant ~ land use + temp + land use: temp	0.7	5	0.984	
Number of bait pieces removed ~ land use	16.7	2	0.0002	***
Proportion of bait mass removed ~ land use	10.9	2	0.004	**
Recruitment rate ~ land use	6.4	2	0.041	*

TABLE 1

Results of statistical analyses testing for relationships between land use and ant community or function metrics. χ^2, df and p values are given for likelihood ratio tests of the minimum adequate model against the null model. F, df and p values are given from linear regression ANOVA tables and PERMANOVA(†) tests.

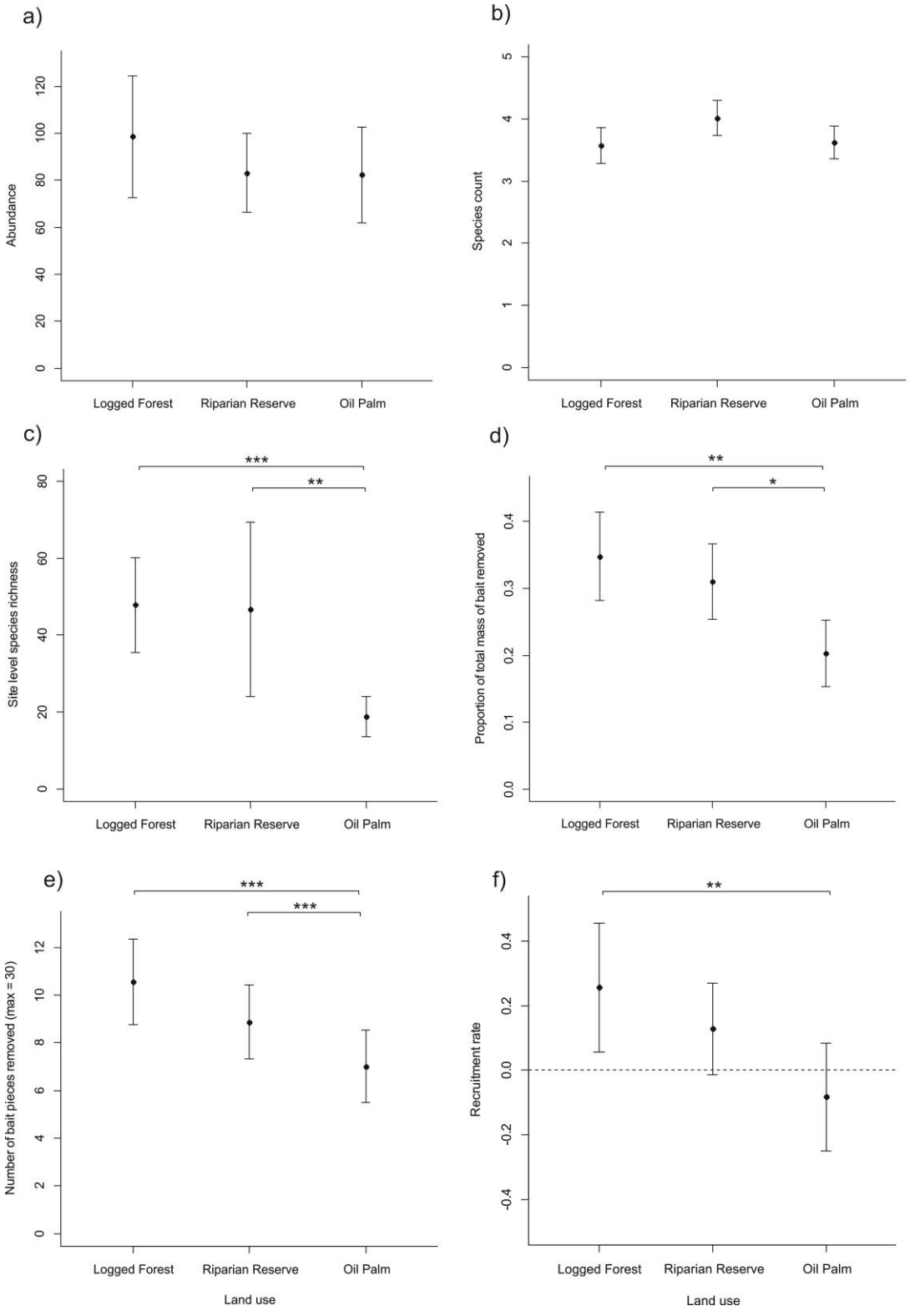


FIG 1

Relationship between land use and a) abundance of ants arriving at each observation, b) number of species arriving at each observation, c) site level species richness, d) the total mass of bait removed, e) number of bait pieces removed and f) the recruitment rate of ants (dotted

line shows no change in number of ants arriving). Plots show mean and 95% CI, stars denote significant differences between groups based on model contrasts (* = p < 0.05, ** = p < 0.01, *** = p < 0.001).

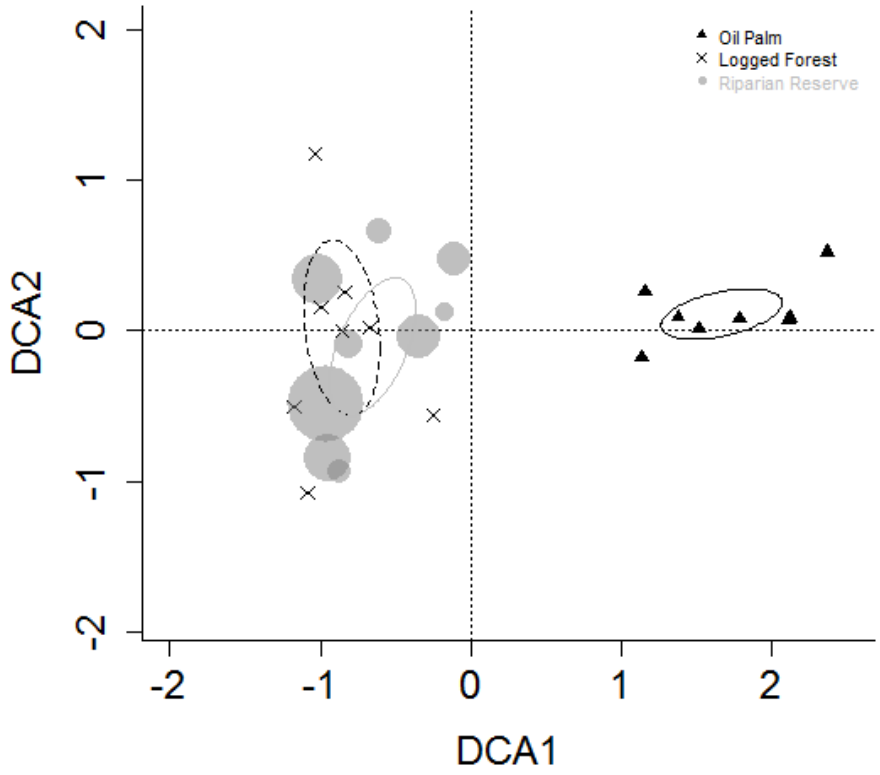


FIG 2

Each point gives the data for incidences of each species across all observations at one site, with the riparian reserve points scaled in proportion to their width (min = 23 m, max = 98 m). The ellipses show the standard error about the mean for each land use type. Riparian reserve ant community composition varies with width, but is not significantly different from forest, whilst both riparian reserve and logged forest differ significantly from oil palm.

BIODIVERSITY-ECOSYSTEM FUNCTION RELATIONSHIPS

There was no significant relationship between the species richness at each site and either measure of nutrient distribution (Table 2, Fig 3). We found no significant difference between the abundance of foragers or the nutrient redistribution rates of the species unique to the higher function land uses (the forest and riparian reserves) versus the species unique to oil palm that replace them, providing evidence against hypothesis 2 a and 2 b (Table 2). Similarly, we found no significant difference in the abundance of foragers or the nutrient redistribution rates of the species that are found in both higher and lower function land uses, providing evidence against hypothesis 3 a and 3 b (Table 2). However, the mean bait removal rate per ant was significantly lower for these shared species when they occur in oil palm sites (supporting hypothesis 2 c), and also significantly lower in the species that are unique to the oil palm and replace those unique to the higher function land uses (supporting hypothesis 3 c, Table 2).

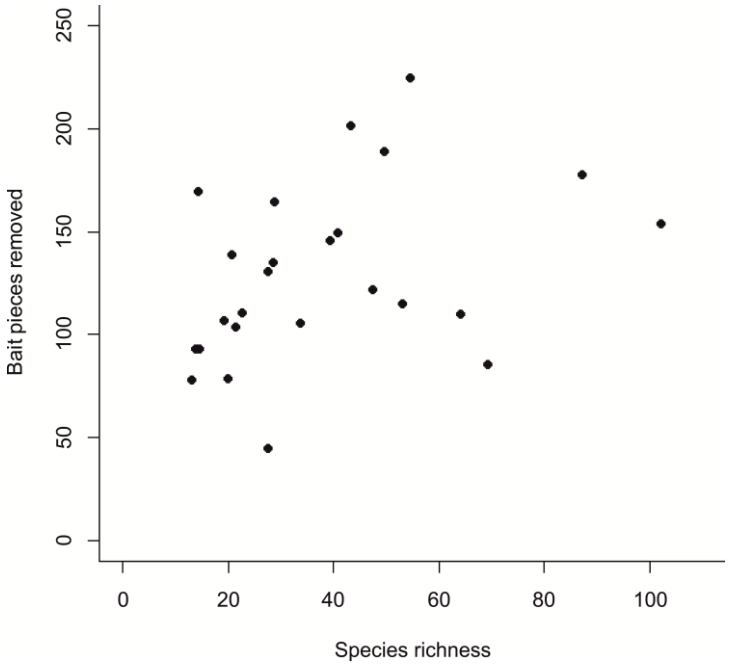


FIG 3
The number of bait pieces removed does not increase significantly with species richness.

STRUCTURAL FEATURES OF RIPARIAN RESERVES

There was no significant relationship between riparian strip width and vegetation complexity ($\chi^2 = 0.60$, df = 1, p = 0.45). Ant abundance declined significantly with riparian strip width, but there were no other significant relationships between reserve width or habitat complexity and the number of species at each observation, the diversity of ants, or the site level species richness (Table 3, Fig 4a). Species composition varied significantly with the width of the riparian reserve, but not with the vegetation complexity (Table 3, Fig 2). There was a significant positive relationship between vegetation complexity and the proportion of bait mass removed, but no other significant relationships between structural features of the riparian reserve and the number of bait pieces taken, the time till the first arrived, or recruitment rate (Table 3, Fig 4 b).

Model

Hypothesis 1 - changes in nutrient redistribution due to loss of species

	F	*df*	*p*	
Bait pieces removed ~ site level species richness	3.4	1,23	0.080	
Bait mass removed ~ site level species richness	2.3	1,23	0.142	

Hypothesis 2 – changes in nutrient redistribution due to turnover in species

	χ^2	*df*	*p*	
Abundance of foragers ~ higher vs lower function land uses	0.32	1	0.561	
Species redistribution rates ~ higher vs lower function land uses	0.24	1	0.627	
		F	*df*	*p*
Redistribution rate per ant ~ higher vs lower function land uses	11.4	1,23	0.003	**

Hypothesis 3 – changes in nutrient redistribution due to changes in species that persist

	χ^2	*df*	*p*	
Abundance of foragers ~ higher vs lower function land uses	0.58	1	0.446	
Species redistribution rates ~ higher vs lower function land uses	0.07	1	0.798	
	F	*df*	*p*	
Redistribution rate per ant ~ higher vs lower function land uses	9.4	1,23	0.005	**

TABLE 2

Results of statistical analyses testing different mechanisms underlying observed changes in function across land uses. χ^2, df and p values are given for likelihood ratio tests of the model described against the null model. F, df and p values are given from linear regression ANOVA tables. Higher and lower function land use groups were designated according to significant differences between bait removal (i.e. forest and riparian reserve combined, versus oil palm). Analyses testing hypothesis 2 used only data on the species only found in one group or the other. Analyses testing hypothesis 3 used only data on the shared species found in both groups.

Model				
	χ^2	***df***	***p***	
Abundance ~ width	98.9	2	0.006	***
Species count ~ width + veg.complexity	0.6	2	0.735	
Ant diversity (dominance) ~ width + veg.complexity	3.7	2	0.156	
Time until first ant ~ width + veg.complexity	2.9	2	0.467	
Bait pieces removed ~ width + veg.complexity	3.3	2	0.195	
Bait mass removed ~ veg.complexity	7.0	1	0.008	**
Recruitment rate ~ width + veg.complexity	1.8	2	0.415	
	F	***df***	***p***	
Site level species richness ~ width + veg.complexity	0.23	2,6	0.805	
Community composition ~ width (†)	3.1	1,129	0.002	**

TABLE 3

Results of statistical analyses testing for relationships between structural features of riparian reserves and ant community or function metrics. Models shown are the full model if no variables were significant, or otherwise the model obtained following model simplification. χ2, df and p values are given for likelihood ratio tests of the minimum adequate model against the null model. F, df and p values are given from linear regression ANOVA tables and PERMANOVA(†) tests.

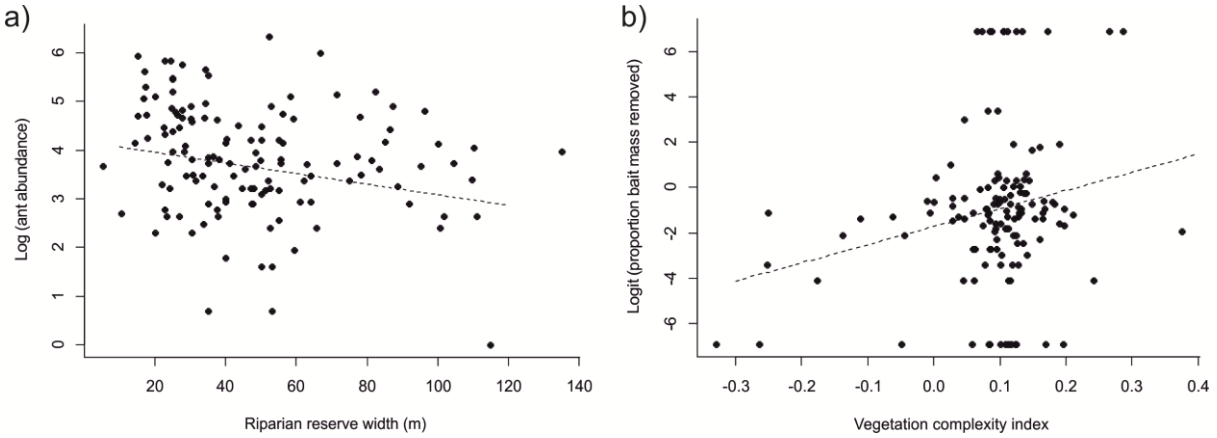


FIG 4

The abundance of individuals (a) visiting the bait card decreases significantly with riparian reserve width and the proportion of bait mass removed (b) increases significantly with vegetation complexity.

DISCUSSION

Oil palm expansion threatens native fauna across the tropics (Savilaakso et al. 2014), but specific management approaches can mitigate the negative impacts of this crop. We found that riparian reserves (strips of native vegetation maintained along rivers) conserve a community of leaf litter ants and level of nutrient distribution very similar to that in riparian zones of logged forest.

ANT COMMUNITY AND FUNCTION ACROSS LAND USES

Compared to planting oil palm along the river bank, the protection of riparian vegetation conserved ant communities similar to those in logged forest. Riparian areas of oil palm supported only 26 % of species found in logged forest, compared to 64 % in riparian reserves. These results are comparable to previous studies from Borneo showing that oil palm plantations contain only 5 % to 19 % of the ant species found in primary forest areas (Brühl &

Eltz 2010; Fayle et al. 2010) and that forest fragments have reduced species richness compared to large areas of forest but a higher species richness than surrounding oil palm (Brühl et al. 2003; Lucey et al. 2014). As riparian reserves do not conserve the full complement of logged forest species, we must also emphasise that large areas of logged forest also have high conservation value and should be protected where possible (Berry et al. 2010; Edwards et al. 2011).

Relative to logged forest, the recruitment and nutrient distribution rate of leaf litter ant communities was significantly reduced in the oil palm plantations, but maintained in the riparian reserves. This means that animal necromass and other organic material may remain on the soil surface for longer, or be utilised by other consumers, both of which could impact soil nutrient content and soil fauna community structure. As ground foraging ants can have a strong influence on the removal of organic matter and the structure of soil in tropical habitats (Frouz & Jilkova 2008; Lach et al. 2010), the impact of this change on soil and leaf litter communities and nutrient cycles may be large and deserves further study.

BIODIVERSITY ECOSYSTEM FUNCTION RELATIONSHIPS

Across the tropical land use gradient we surveyed there was no strong relationship between ant species richness and the number of bait pieces removed, suggesting that other aspects of community change drive shifts in function. Fayle et al. (2011) found a slightly stronger relationship between ant species richness and bait removal function, but their study was carried out across a disturbance gradient within primary forest and over a smaller spatial scale; the link between species richness and function may be stronger within land use types. Another factor which could drive changes in function is the abundance of foraging individuals, but we did not find that ant abundance varied significantly with land use. The presence of particular

functionally important species, or "keystone species" in the forest and riparian reserve sites could also explain a higher bait removal function, but we did not find that oil palm specialists had a lower bait removal rate than the forest specialists they replaced. This suggests that a simple sampling effect (increased chance of a functionally important species being present) is not the explanation for the changes in function we observed. In addition, the species which persist in oil palm did not suffer a signification reduction in the amount of bait removed they per individual foraging ant, indicating that the loss of nutrient redistribution function in oil palm is not due to reductions in the foraging efficacy of the individual foragers from species which persist in the plantations following conversion. We did find a significant reduction in the mean mass of bait removed per ant in oil palm communities. Our results suggest that the decline in function was due to species with a lower nutrient redistribution rate making up a higher proportion of the abundance of ground foraging ants.

STRUCTURAL FEATURES OF RIPARIAN RESERVE AND MANAGEMENT STRATEGIES

As riparian reserves can help increase biodiversity and ecosystem function within oil palm plantations, it is important to establish management guidelines that will maximise the conservation value of these reserves. We examined two structural features of riparian reserves that could potentially be specified in management protocols: width and vegetation complexity. The abundance of foraging ants declined with increasing reserve width; this may be because the ant colonies have a larger area over which to forage when the reserve is wider, reducing ant density at individual sampling points. There was also an increase in the mass of bait removed with an increase in habitat complexity. The higher values of the vegetation complexity index correspond to greater leaf litter and humus depth; this increase in ground cover could be necessary for foraging ants to risk taking larger, heavier baits that reduce their speed and increase their vulnerability to predators. As there was no effect of reserve width on

species richness or bait removal function, we can conclude that riparian reserves can protect leaf litter ant fauna that would not be found if oil palm was planted up to the river bank, as well as the functional roles they support, at least within the interior of the riparian vegetation (our sampling sites were restricted to the centre of the corridor). However, our ordination plot suggests that the composition of the wider reserves may be more similar to the logged forest areas, and therefore that widths greater than 30 m may be necessary to improve the conservation value of the reserves. It is also important to note that our results only cover the response of ground foraging species, and it is likely that vegetation structure, and possibly also riparian reserve width, have a much greater impact on arboreal ant species (Widodo et al. 2004).

Although we have demonstrated that riparian reserves retain leaf litter ant communities similar to those in larger areas of logged forest, albeit with slightly lower species richness, there are a number of issues regarding the conservation value of the reserves that require further attention. We were not able to assess the importance of corridor connectivity, as all of the riparian reserves we surveyed are still linked to large fragments of logged forest (>3000 ha). Other studies in tropical landscapes have shown that the connectivity to large areas of forest can be crucial for the persistence of some species (Laurance & Laurance 1999; Lees & Peres 2008). It is possible that the riparian reserves we surveyed are effectively sink populations, dependent on immigration of dispersing reproductives from larger areas of forest. However, we only included non-reproductive individuals in this study, and due to the limited mobility of ground foraging ants, we can be confident that all ant species we observed were from established colonies located within the reserves. In addition, we observed ant alates arriving at several of our bait cards, which also suggests that the riparian reserve colonies are capable of reproducing. However, satellite image analysis indicates our study landscape was converted from forest within the last 15 years (Hansen et al. 2013) and lags in species extinctions as long as 25 years have been documented in tropical forests (Wearn et al.

2012; Gibson et al. 2013), so it is possible that ecological communities within these reserves have not yet reached an equilibrium. Longer-term population studies will be important to determine the extent to which reserves sustain permanent populations.

CONCLUSIONS

Protection of riparian forest can help retain biodiversity and ecological functions within tropical agricultural systems. Our results indicate that the ground foraging ant fauna is less diverse in oil palm plantations than nearby forest and that important nutrient redistribution functions are also impaired. This may have implications for food webs and nutrient cycling in the plantations. Our data suggest that the loss of function is best explained by relative increases in the abundances of species with low nutrient redistribution rates. We recommend that riparian reserves are protected where oil palm expansion is occurring, in order to mitigate the negative impacts of the growth of this industry on tropical biodiversity and ecosystem function.

SUPPLEMENTARY MATERIAL

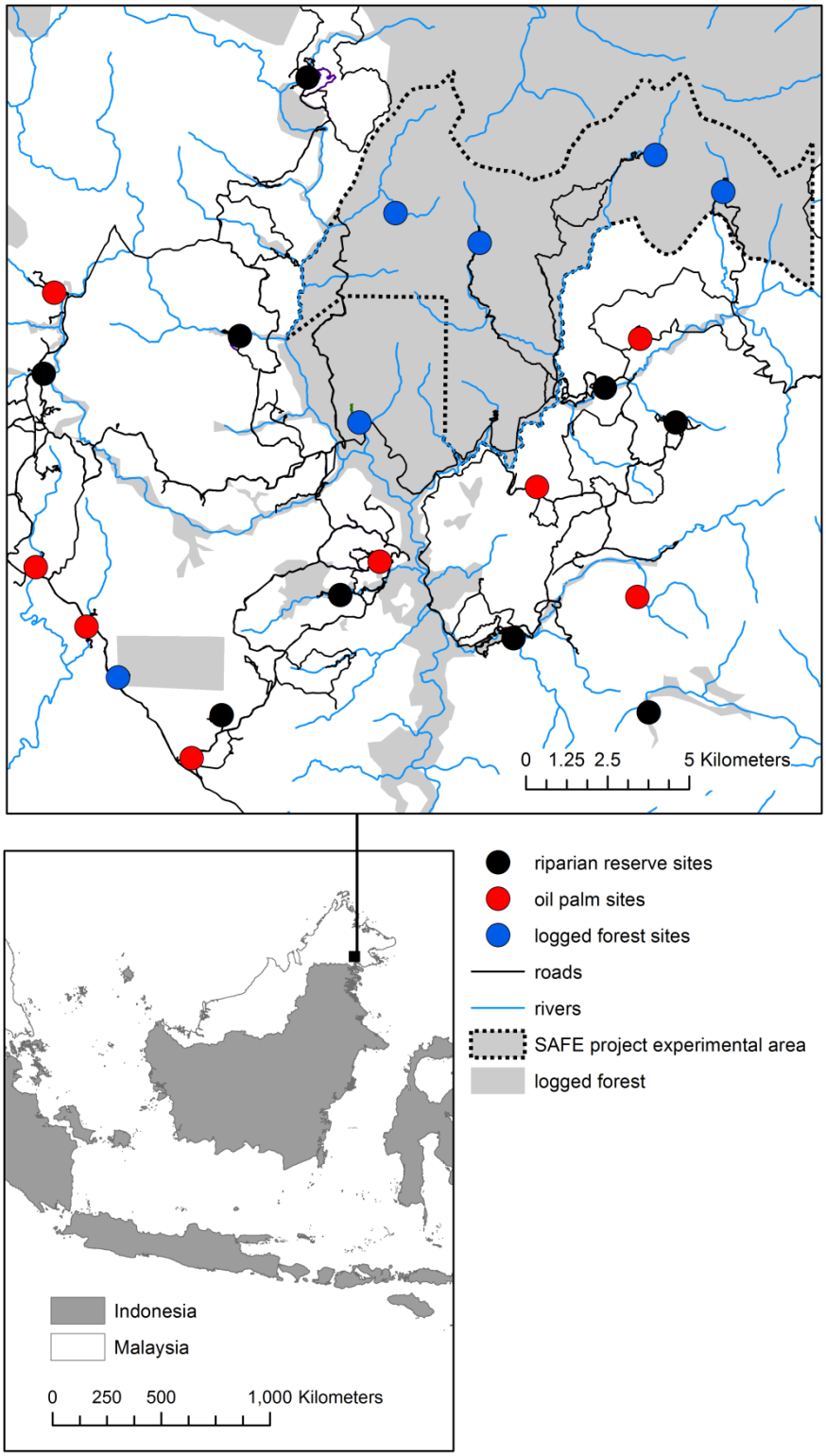


FIG S1
Map of study sites

Species name or code	Taxonomic Authority	Logged Forest	Riparian Reserve	Oil Palm
Acanthomyrmex sp.1		10	8	0
Aenictus sp.1		1	0	0
Anochetus sp.1		7	0	0
Anoplolepis gracilipes	Smith 1857	0	626	2347
Calyptomyrmex sp.1		2	0	0
Camponotus sp.1		1	0	0
Camponotus sp.3		1	1	39
Camponotus sp.4		0	23	0
Camponotus sp.5		0	1	0
Camponotus arrogans	Smith 1858	13	81	0
Camponotus gigas	Leach 1825	39	29	0
Cardiocondyla sp.6		0	0	10
Cardiocondyla tjibodana	Karavaiev 1935	0	0	37
Carebara sp.1		0	1	0
Carebara sp.2		0	0	1
Carebara sp.3		5	0	0
Carebara sp.4		0	1	0
Crematogaster sp.5		3	0	3
Crematogaster sp.6		0	94	0
Crematogaster sp.7		2	0	0
Crematogaster sp.9		0	1	0
Crematogaster aff. fraxatrix	Forel 1911	1	0	0
Crematogaster baduvi	Forel 1912	6	0	0
Crematogaster biroi var.bandarensis	Forel 1911	148	202	55
Crematogaster coriaria	Mayr 1872	4	107	0
Crematogaster difformis	Smith 1857	1	0	0
Crematogaster inflata	Smith 1857	0	1	0
Crematogaster longipilosa	Forel 1907	0	3	154
Crematogaster modiglianii	Emery 1900	2	15	0
Crematogaster rogenhoferi	Mayr 1879	10	21	62
Diacamma sp.3		1	2	0
Diacamma intricatum	Smith 1857	2	17	1
Diacamma rugosum	Le Guillou 1842	0	8	5
Dolichoderus sp.2		2	0	0
Dolichoderus thoracicus	Smith 1860	25	1	0
Euprenolepis sp.3		0	6	0
Euprenolepis procera	Emery 1900	6	26	0
Euprenolepis thrix	LaPolla 2009	32	103	0
Eurhopalothrix sp.1		0	1	0
Gnamptogenys sp.1		2	6	0
Gnamptogenys sp.3		5	1	0
Gnamptogenys aff. binghamii	Forel 1900	6	0	0
Hypoponera sp.1		1	0	3

Species name or code	Taxonomic Authority	Logged Forest	Riparian Reserve	Oil Palm
Iridomyrmex sp.1		0	0	39
Leptogenys sp.1		5	5	0
Leptogenys sp.2		44	42	0
Leptogenys parvula	Emery 1900	0	2	0
Leptogenys peuqueti	André 1887	0	4	3
Lophomyrmex bedoti	Emery 1893	3378	3272	1152
Lophomyrmex longicornis	Rigato 1994	245	0	0
Lordomyrma reticulata	Lucky and Sarnat 2008	3	0	0
Loweriella sp.2		0	0	29
Loweriella boltoni	Shattuck 1992	80	129	59
Mayriella transfuga	Baroni Urbani 1977	2	1	0
Meranoplus sp.1		0	1	0
Monomorium sp.2		0	19	0
Monomorium sp.3		0	3	0
Monomorium sp.7		0	0	1
Monomorium floricola	Jerdon 1851	2	0	99
Monomorium australicum	Forel 1907	0	5	0
Myrmecinas sp.1		0	9	1
Myrmecina sp.2		2	0	0
Myrmicaria sp.1		3	0	0
Myrmicaria arachnoides adpressipilosa	Smith 1857	343	27	0
Myrmoteras sp.1		1	0	0
Nylanderia sp.1		1	15	2206
Nylanderia sp.2		22	27	15
Nylanderia sp.3		147	43	0
Nylanderia sp.4		25	3	0
Nylanderia sp.5		0	45	0
Nylanderia sp.6		86	179	0
Nylanderia sp.7		26	17	0
Odontomachus sp.1		4	59	0
Odontoponera transversa	Smith 1857	402	551	127
Oecophylla sp.1		0	0	3
Pachycondyla sp.3		0	3	0
Pachycondyla sp.4		0	30	38
Pachycondyla sp.5		0	14	0
Pachycondyla pilidorsalis	Yamane 2007	41	33	0
Pachycondyla tridentata	Smith 1858	1	0	0
Paraparatrechina sp.1		76	7	12
Paraparatrechina sp.2		131	30	17
Paraparatrechina sp.4		8	15	0
Paraparatrechina minutula var.buxtoni	Santschi 1928	2	0	0
Pheidole sp.1		4	0	0
Pheidole sp.3		17	140	0

Species name or code	Taxonomic Authority	Logged Forest	Riparian Reserve	Oil Palm
Pheidole sp.4		52	42	0
Pheidole aff.annexus	Eguchi 2001	80	31	0
Pheidole aff.aristotelis	Forel 1911	0	52	0
Pheidole aff.deltea	Eguchi 2001	191	12	0
Pheidole aff.rabo	Forel 1913	6	0	0
Pheidole aff.rugifera	Eguchi 2001	0	0	63
Pheidole aglae	Forel 1913	159	419	47
Pheidole angulicollis	Eguchi 2001	13	23	0
Pheidole annexus	Eguchi 2001	85	12	0
Pheidole aristolelis	Forel 1911	9	36	0
Pheidole bugi	Wheeler 1919	0	0	34
Pheidole butteli	Forel 1913	172	105	0
Pheidole cariniceps	Eguchi 2001	275	394	31
Pheidole elisae	Emery 1900	3	0	0
Pheidole hortensis	Forel 1913	103	94	0
Pheidole longipes	Latreille 1802	1	30	2
Pheidole lucioccipitalis	Eguchi 2001	371	178	0
Pheidole plagiaria	Smith 1860	2	200	538
Pheidole quadrensis	Forel 1900	0	3	0
Pheidole quadricuspis	Emery 1900	4	17	0
Pheidole rabo	Forel 1913	0	1	0
Pheidole sarawakana	Latreille 1802	3	0	0
Pheidole tawauensis	Eguchi 2001	12	3	0
Pheidologeton sp.1		2471	1028	9
Pheidologeton sp.4		1	0	0
Pheidologeton pygmaeus	Emery 1887	0	1	1
Philidris sp.1		17	283	0
Plagiolepis sp.1		1	0	13
Platythyrea sp.1		0	2	0
Prenolepis sp.1		0	70	0
Prenolepis sp.1		68	0	0
Prenolepis sp.1		0	19	0
Pristomyrmex sp.1		0	0	22
Proatta sp.1		0	12	1
Pseudolasius sp.1		10	1	0
Pyramica sp.4		1	0	0
Pyramica sp.5		1	3	0
Recurvidris sp.2		175	7	0
Recurvidris browni	Bolton 1992	15	5	0
Solenopsis geminata	Fabricius 1804	0	0	601
Tapinoma sp.1		4	10	724
Technomyrmex sp.5		1	0	0
Technomyrmex albipes	Smith 1861	0	1	0

Species name or code	Taxonomic Authority	Logged Forest	Riparian Reserve	Oil Palm
Technomyrmex horni	Forel 1912	0	1	0
Technomyrmex kraepelini	Forel 1905	64	55	5
Tetramorium sp.1		27	3	7
Tetramorium sp.11		5	24	0
Tetramorium aff.meshena	Bolton 1976	16	26	0
Tetramorium aptum	Bolton 1977	11	15	2
Tetramorium bicarinatum	Nylander 1846	0	0	271
Tetramorium tortuosum var.eleates	Forel 1913	0	0	13
Tetramorium kheperra	Bolton 1976	0	0	85
Tetramorium lanuginosum	Mayr 1870	0	2	0
Tetramorium longicarinum	Donisthorpe 1941	1	0	0
Tetramorium meshena	Bolton 1976	5	0	0
Tetramorium pacificum	Mayr 1870	49	11	1
Tetramorium parvum	Bolton 1977	0	2	0
Tetramorium simillimum	Smith 1851	0	0	8
Tetramorium smithi	Mayr 1879	0	0	179
Vollenhovia aff.fridae	Forel 1913	1	2	54

TABLE S1

Names of all species observed and the number of foragers counted across all observations in each land use. Twenty-two species were found in all land use types, 31 species were found exclusively in logged forest, 27 exclusively in riparian reserves, and 16 exclusively in oil palm. 41 species were found in both riparian reserve and forest sites, eight species were found in only riparian reserve or oil palm sites, and four species were encountered only in forest or oil palm. The non-native species *Anoplolepis gracilipes, Tetramorium simillimum* and *Tetramorium bicarinatum* were found only in oil palm, but some individuals of the non-natives *Dolichoderus thoracicus* and *Monomorium floricola* were also found in the riparian reserves and logged forest.

CHAPTER 6: DO RIPARIAN FOREST FRAGMENTS PROVIDE ECOSYSTEM SERVICES OR DISSERVICES IN SURROUNDING OIL PALM PLANTATIONS?

ABSTRACT

Agricultural expansion across tropical regions is causing declines in biodiversity and altering ecological processes. However, in some tropical agricultural systems, conserving natural habitat can simultaneously protect threatened species and support important ecosystem services. Oil palm cultivation is the fastest-growing industry in tropical areas, but the extent to which non-crop habitat supports biodiversity and ecosystem services in these landscapes is poorly documented. We investigated whether riparian forest fragments (riparian reserves) provide a pest control service or increase pest activity (disservice) within oil palm dominated landscapes in Sabah, Malaysian Borneo. We assessed the activity of potential predators of pest herbivores using artificial pest mimics and quantified herbivory rates on oil palm fronds in areas with and without riparian reserves. We also manipulated the shape and colour of the mimics to assess the extent to which artificial pest mimics reflect a predatory response. The presence of a riparian reserve increased the attack rate on mimics by arthropods, but not by birds. The width of the riparian reserve had no significant effect on the attack rates of either predator group. Our methodological study suggested attacks on artificial pest mimics provide a better reflection of the predatory activity of birds than arthropod predators. Herbivory rates were also not significantly affected by the presence of a riparian reserve. Overall, we conclude that riparian forest fragments are unlikely to provide a pest control service. Nevertheless, our results provide evidence that riparian buffer strips do not increase the density of defoliating pests and this evidence should reassure managers concerned about possible negative consequences of preserving riparian buffers.

INTRODUCTION

Agricultural production relies on a wide range of ecosystem services; pollination, pest control and decomposition are among the most important. However, recent agricultural expansion and intensification has caused declines in biodiversity, undermining many ecological processes. In some agricultural systems this has caused an increase in production costs and a drop in yields (Power 2010). It is therefore increasingly important that we understand the biological systems underpinning key ecosystem services.

In some tropical systems, the protection of natural habitat can enhance ecosystem services. Pollination and fruit set in coffee plantations increase with proximity to natural habitat (Klein et al. 2003; Ricketts 2004; Ricketts et al. 2004). Positive relationships between pollination rate and proximity to forest have also been found for other tropical crops such as longan (Blanche et al. 2006) and eggplant (Gemmill-Herren & Ochieng 2008). Similarly, forest cover in coffee plantations supports bird and bat species that feed on common pest species (Karp et al. 2013; Maas et al. 2013).

One of the crops expanding most rapidly across the tropics is oil palm (*Elaeis* spp.), but the extent to which non-crop habitats support ecosystem services in oil palm landscapes remains poorly documented. Biological pest control could be among the most economically important services influenced by the presence of non-crop habitat. Many plantations in Malaysia and Indonesia (which currently produce > 80% of the global supply of palm oil (FAO 2014)) practice Integrated Pest Management approaches; they do not routinely apply pesticides and rely on naturally occurring pest predators (Corley & Tinker 2003; Koh 2008b). Parasitoid wasps, predatory hemipterans and ants are recognised as effective pest control agents (Zulkefli et al. 2004; Cheong et al. 2010; Pierre & Idris 2013), and the presence of bird and bats can reduce herbivory on palms (Koh 2008b). However, the extent to which populations of these taxa relies on non-crop habitat is currently unclear.

Forest is commonly retained in oil palm plantations along waterways (referred to as riparian buffers or riparian reserves). Riparian vegetation is primarily protected to maintain water quality, reduce flood risk and prevent soil erosion (e.g. Sabah Water Resources Enactment 1998). However, as riparian reserves can also conserve forest-dependent species that are not otherwise found in areas of oil palm (Chapters 3 and 5) it is possible that they also enhance ecological processes and services. Jirinec et al. (2011) found that riparian strips in coffee plantations increase the density of insectivorous birds and suggested that the strips support pest control services. Similarly, Maisonneuve & Rioux (2001) found that higher tree cover in riparian reserves on Canadian farmland increased the density of insectivores and decreased the abundance of pest species. However, there are also concerns that retaining forest fragments can generate ecosystem disservices by increasing the frequency of crop-damaging species. The Spruce Budworm (*Choristoneura fumiferanas*) can spread rapidly along riparian corridors (Naiman & Decamps 1997), and riparian reserves can also provide habitat for crop-raiding bird species (Deschênes et al. 2003). Overall, there remains very little literature on the role that riparian reserves play in supporting ecosystem services or disservices within agricultural landscapes.

Here, we assess whether riparian reserves affect the activity of defoliating pests and their potential predators within an oil palm dominated landscape in Sabah, Malaysia. We measured leaf herbivory rates and rates of predation on artificial pest mimics in riparian areas of oil palm with and without riparian reserves. Artificial pest mimics were created from plasticine to resemble bagworms (Lepidoptera: Psychidae). Bagworms are among the most important pests of oil palm; outbreaks resulting in defoliation of only 10 – 13 % can reduce yields by up to 43 % (Basri et al. 1995; Kamarudin & Wahid 2010). Plasticine pest mimics have been used to indicate predation rates in both tropical (Loiselle & Farji-Brener 2002; Koh & Menge 2006; Posa et al. 2007; Richards & Coley 2007; Fáveri et al. 2008; Howe et al. 2009; Tvardikova & Novotny 2012) and temperate ecosystems (Skoczylas et al. 2007; Lluch et al. 2009). This method avoids the

problems associated with rearing large numbers of prey items and difficulties in establishing the identity of predators.

In this paper we address three main questions. First, we ask whether the presence of a riparian reserve reduces the attack rate on pest mimics. Second, we test whether the presence of a riparian reserve reduces herbivory on oil palm fronds. Third, we ask how potential pest predators respond to pest mimics of different shapes and colours, to clarify the extent to which attack rates on the mimics reflect true predation rates.

MATERIALS AND METHODS

DATA COLLECTION

All study sites were located around the Stability of Altered Forest Ecosystems (SAFE) project site in Sabah, Malaysian Borneo (117.50 N, 4.60 E). Further details of the SAFE project area are given in Ewers et al. (2011).

We collected data from a total of 14 riverside sites (Fig 1) between April and November 2012.. Eight sites had a riparian reserve flanking the river (mean forest width measured on one side of the river = 71 m, sd = 52 m) and six sites were lacking riparian forest. All sites were at least 1.5 km apart, and oil palms at all sites were planted between 2006 and 2011.

At each site we attached pest mimics to 29 palms. Each bagworm mimic was a cylinder (diameter 3.5 mm, length 25 mm) of non-toxic brown plasticine (Scholaquip Colorclay). Mimics this size were light enough to attach with a small amount of Loctite gel superglue and also match the average dimensions of early instar bagworms (Mohd Basri & Kevan 1995). Two mimics were attached to each frond, approximately 50 cm apart and on leaflets either side of

the midrib. Two fronds on each palm were baited in this way (i.e. four mimics per palm) and mimics were recovered after 48 hours.

Twenty-five palms at each site were baited with brown caterpillar mimics, two with red caterpillar mimics and two with brown cubes. If the visual cues of the mimics elicit a predatory response, we expected that changing the shape of the mimic (to a cube) or providing aposematic colouring (using red plasticine) would reduce attack rates. Cubes were chosen as a neutral shape that does not resemble any natural prey item, and designed so that the total volume of plasticine was equal to that in the cylindrical mimics.

Attack marks on the mimics were identified under a x20 field microscope using images from previous publications (Koh & Menge 2006; Slade 2007; Howe et al. 2009; Tvardikova & Novotny 2012) and specimens from preliminary exclusion experiments. For each mimic, we recorded the presence or absence of attacks from mammals, arthropods and birds (see supplementary material for examples of each type of attack mark).

At each site we planted three palms to record herbivory rates. All were 14 months old and obtained from the same nursery. Excess fronds were removed so that all palms were approximately 1.3 m tall and only the five youngest fronds remained. The palms were planted 50 m apart at each site, to span the same area over which pest mimics had been set out. Palms were planted 1 – 10 days after the caterpillar mimics had been collected, to retain temporal continuity but avoid interference between the two stages of data collection. We photographed all the new growth on the palms (ensuring that we only recorded herbivory that had occurred after planting) after approximately 5 months (mean = 138 days, sd = 7 days). This period of time was considered sufficient to detect any effects of riparian reserves on herbivore activity as a similar study detected significant differences in herbivory rates on palms of a similar age after only 21 days (Koh 2008b). We calculated the proportion of surface area lost to herbivores using Image J software (Rasband 2012).

All the oil palms used or planted at sites with riparian reserves were located in the first terrace adjacent to the riparian reserve boundary. Due to variation in reserve width we could not also standardise distance from the river across all sites. Instead, we selected/planted oil palms at non-riparian reserve sites so that the distance of focal oil palms from the river did not differ significantly between sites with and without riparian reserves ($F_{1,424} = 1.9$, $p = 0.17$).

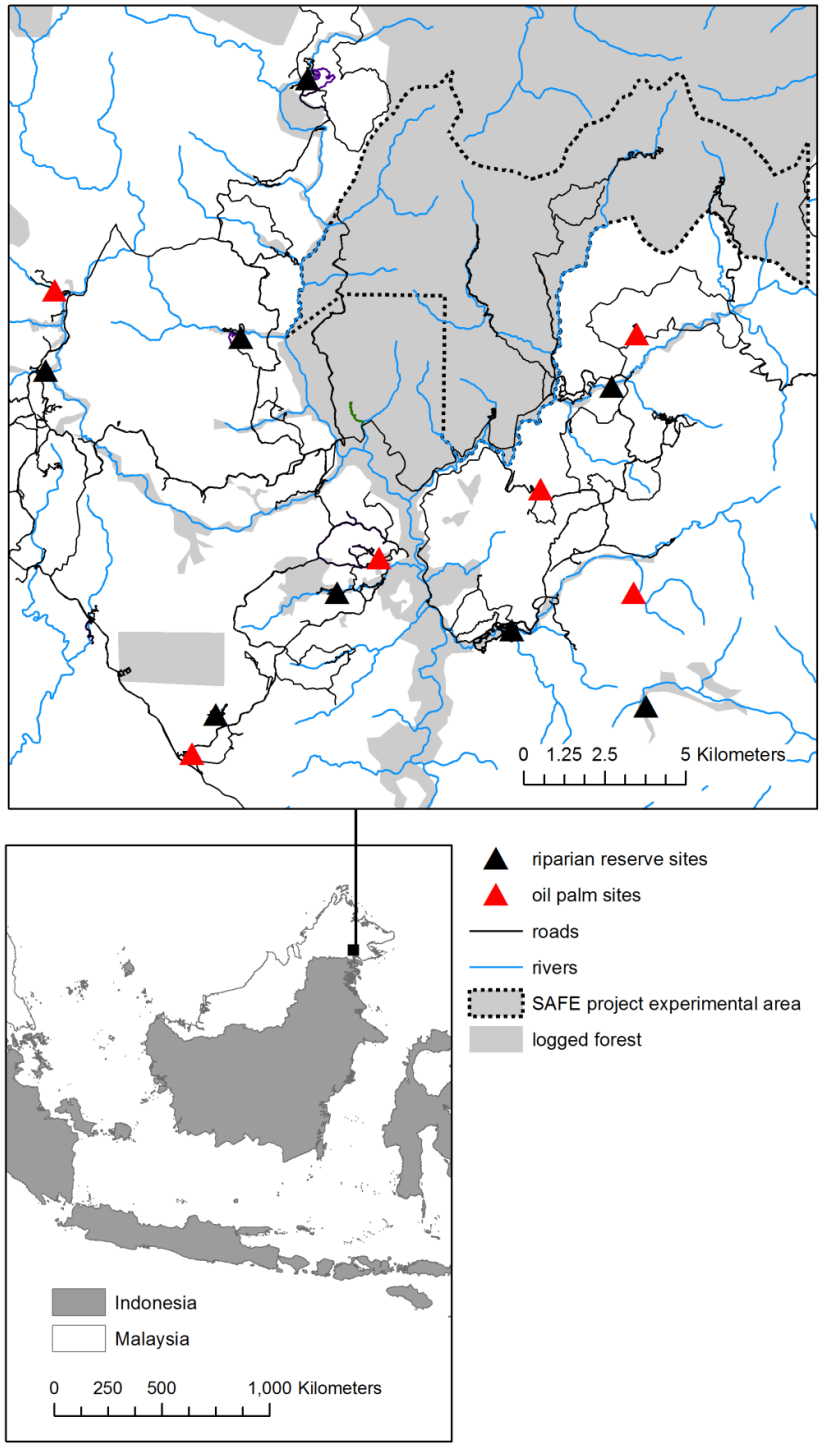


FIG 1.
Location of field sites. Grey shading in top panel indicates logged forest, white indicates oil palm/acacia plantations.

ANALYSIS

All analyses were carried out in R (R Core Team 2013), using the package lme4 (Bates et al. 2014 p. 4)

We analysed the effect of mimic shape and colour on the frequency of bite marks from all potential predators combined, and then each predator group separately. We used binomial GLMMs with oil palm age, riparian reserve presence and site specified as random factors. To retain a balanced design when analysing the effect of shape and colour we used data from the two palms with cubes and red caterpillars and the nearest two palms with brown caterpillar mimics.

We analysed the effect of riparian reserve presence on the frequency of bite marks from all potential predators combined, and then each predator group separately, using binomial GLMMs with oil palm age and site as random factors. We also tested for relationships between riparian reserve width and the frequency of attacks.

We tested whether riparian reserve presence affected herbivory on palm fronds using a binomial GLMM, with palm ID nested within site specified as random factors.

RESULTS

We retrieved 1547 plasticine mimics and 36 oil palms from which we measured the attack rate of potential predators of pests and corresponding herbivory rates. 474 caterpillars were attacked by arthropods, 322 by birds, and only 10 by mammals.

PEST CONTROL SERVICE

53% of mimics were attacked in sites with a riparian reserve, compared to 37% in areas of oil palm without a riparian reserve. However, the difference between these treatments was marginally non-significant (Fig 2 a; Table 1). The proportion of mimics attacked by arthropods was significantly higher in areas with a riparian reserve (Fig 2 b; Table 1). There was no difference in the proportion of mimics attacked by birds between sites with and without a riparian reserve (Fig 2 c; Table 1). There were too few mammal attacks to carry out a meaningful analysis on these data.

There was no significant relationship between riparian reserve width and overall attacks, bird attacks or arthropod attacks (Table 1).

There was no significant effect of the presence of a riparian reserve on the proportion of oil palm leaf area consumed by herbivores (Table 1; Fig 3).

Model	χ^2	df	p
All mimic attacks ~ presence/absence riparian reserve	3.7	1	0.053
Mimic attacks by birds ~ presence/absence riparian reserve	0.0002	1	0.98
Mimic attacks by arthropods ~ presence/absence riparian reserve	5.69	1	0.017 *
All mimic attacks ~ riparian reserve width	0.04	1	0.84
Mimic attacks by birds ~ riparian reserve width	0.04	1	0.83
Mimic attacks by arthropods ~ riparian reserve width	0.05	1	0.83
Herbivory ~ presence/absence riparian reserve * days in field	1.16	2	0.56

TABLE 1
Results of analyses on the activity of different potential pest predator groups and herbivores (tested against null model).

Model	χ^2	df	p
Any attacks ~ shape	2.2	1	0.138
Arthropod attacks ~ shape	0.015	1	0.904
Bird attacks ~ shape	5.01	1	0.025 *
Any attacks ~ colour	0.33	2	0.845
Arthropod attacks ~ colour	2.91	2	0.233
Bird attacks ~ colour	2.21	2	0.331

TABLE 2
Results of analyses on the relationship between mimic shape/colour and activity of different potential pest predator groups (tested against null model).

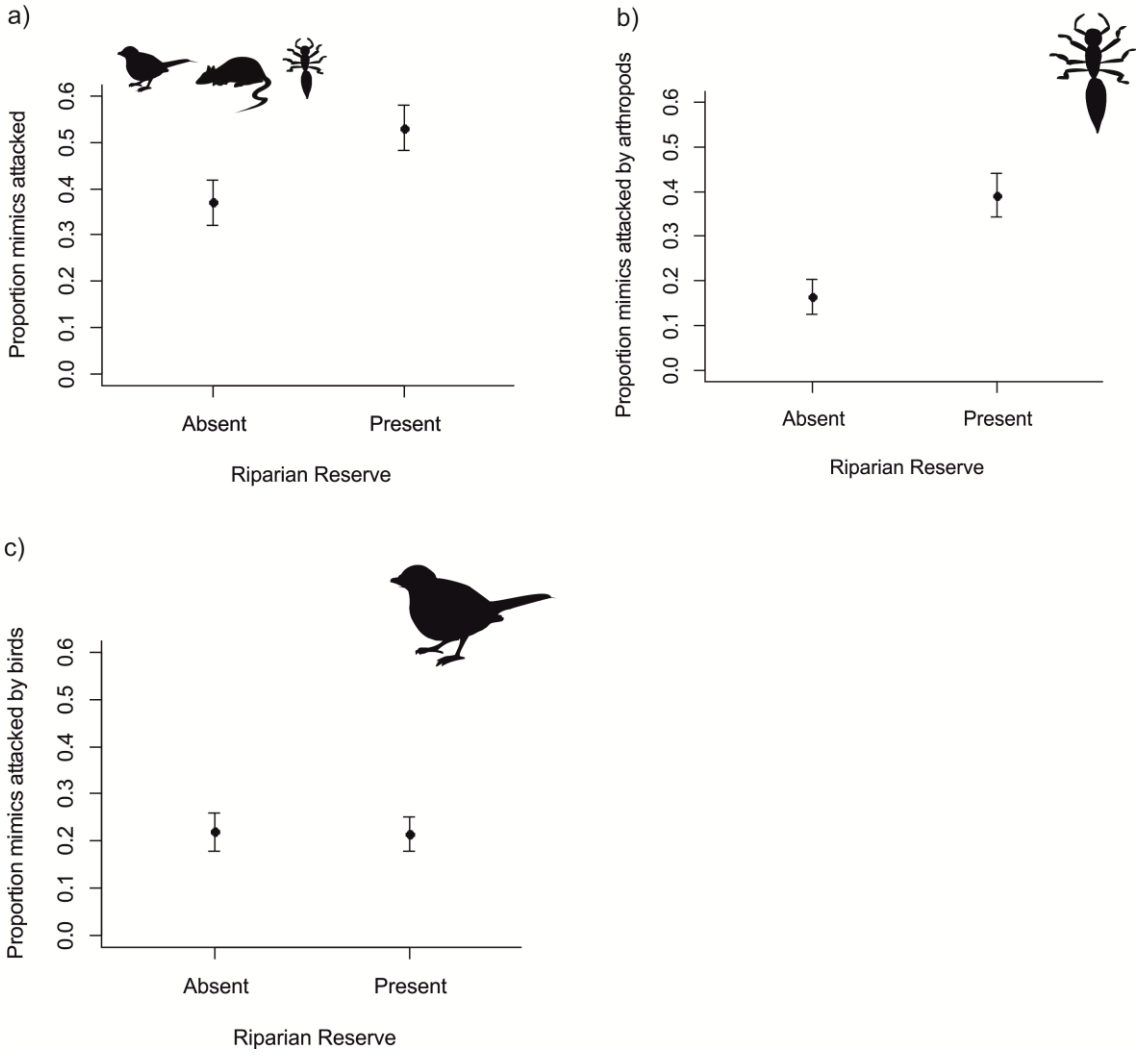


FIG 2

The proportion of caterpillar mimics showing bite marks from a) all potential pest predators, b) arthropods and c) birds on oil palms near rivers with and without riparian reserves. While our analyses used a binary response variable, for clarity we present data here as proportions. Plots show mean ± 95% CI.

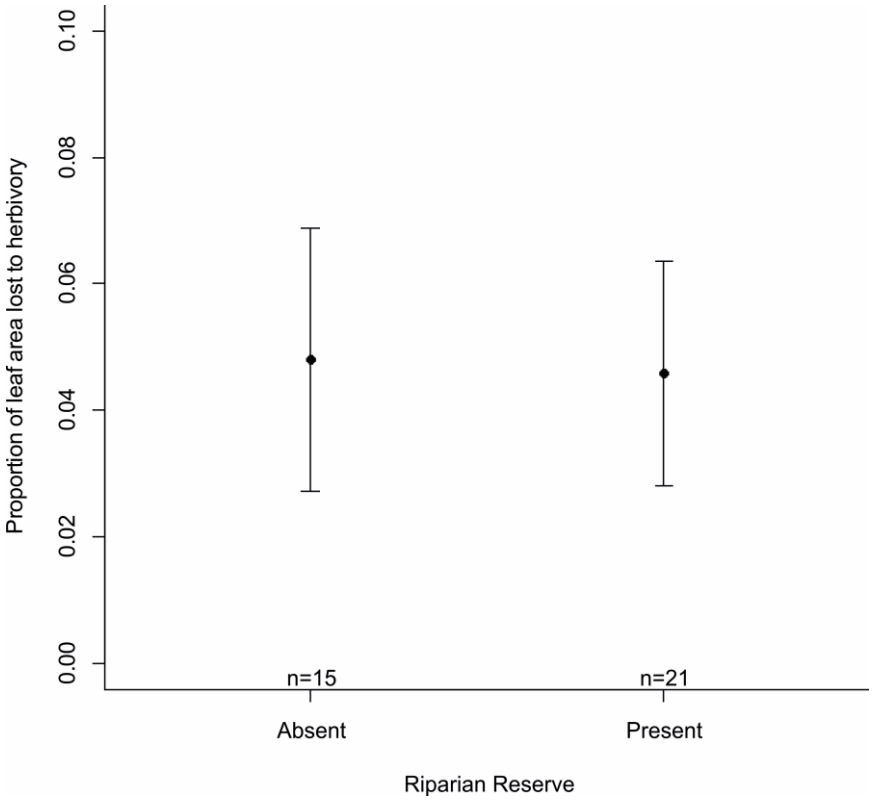


FIG 3
The proportion of leaf area lost to herbivory in sites with and without a riparian reserve. Plot shows mean ± 95% CI.

COLOUR AND SHAPE

We found no significant effect of shape on the overall foraging activity of all predators combined, or on the subset of arthropod attacks. However, bird predation on caterpillar mimics was higher than on cubes (Table 2, Fig 4). We found no significant effect of colour on overall foraging activity, bird attacks or arthropod attacks. There were no mammal attacks on the mimics in these data.

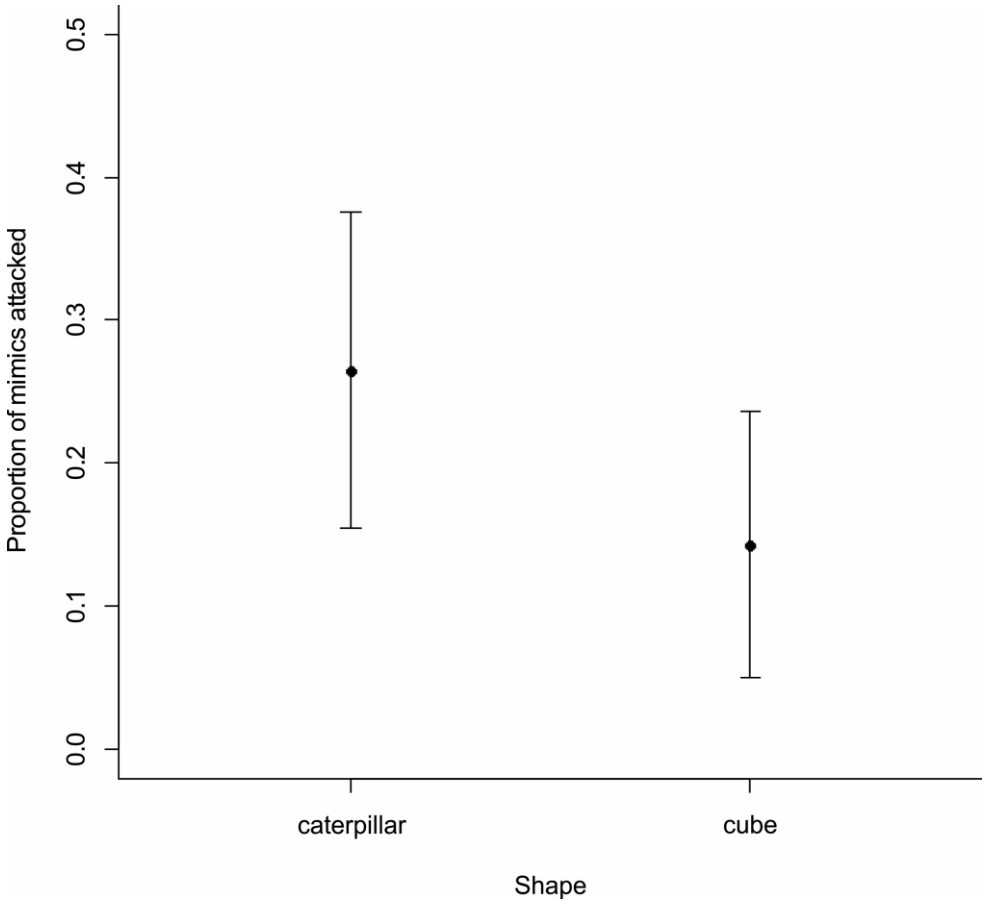


FIG 4.
The proportion of mimics attacked by birds against mimic shape. Plot shows mean ± 95% CI.

DISCUSSION

Oil palm is one of the most rapidly expanding industries in tropical regions, but very little research has examined the extent to which non-crop habitat provides ecosystem services in these landscapes. We found some evidence that riparian reserves increase arthropod foraging activity in oil palm plantations, but this did not correspond to a reduction in herbivory on palm fronds.

PEST CONTROL SERVICE

Our results suggest that retaining riparian reserves increases the foraging activity of arthropods that bite or chew prey (e.g. ants, centipedes, beetles) on oil palms. However, our methodological study (see below) calls into question the extent to which this refects an increase in predation on pests. It is possible that the increase in foraging activity of mobile arthropods we recorded results from spillover from populations in the riparian reserve; other work in Borneo has documented a spillover of insects from forest into oil palm (Lucey & Hill 2012; Lucey et al. 2014).

The proportion of artificial pest mimics attacked by birds was not elevated in the vicinity of riparian reserves. As birds moving out of a riparian reserve would generally be more mobile than arthropods, birds could potentially cover larger areas and provide a more economically significant pest control service. Therefore this lack of any increase in bird attacks in the vicinity of oil palms is likely to be more ecologically informative and economically important than the observed increase in arthropod attacks.

Previous studies have found that increasing the width of riparian reserves in oil palm can increase the species richness or diversity of some taxa (Chapter 3, Chapter 5, Viegas et al. 2014). However, we did not find that the attack rates of any potential predator groups varied with riparian reserve width.

The results from our assessment of herbivory rates provide the strongest evidence that riparian reserves do not provide a pest control service, as there was no significant difference in herbivore activity between sites with and without riparian reserves. However, we were not able to collect data during a pest outbreak. Outbreaks occur infrequently and are economically much more consequential than background herbivory rates (Basri et al. 1995; Kamarudin & Wahid 2010). It is therefore possible that service provision from riparian reserves is only apparent under these conditions, when the population of predators of pests that is supported

by pure oil palm stands becomes saturated with prey. In addition, we were only measuring the impact of defoliating herbivores, and it is possible that the presence of natural habitat in oil palm reserves has a different effect on other pest guilds such as seed predators and stem or root pests. It is also possible that non-riparian fragments of forest provide a pest control service; studies on coffee plantations in Costa Rica have found that the pollination services of riparian fragments were lower than that of non-riparian fragments (Ricketts 2004).

Our results also indicate that there is no pest "disservice" created by conserving riparian forest, and this should be incorporated into a fuller assessment of the costs and benefits of conserving riparian habitat. The extent to which riparian reserves provide other ecosystem services aside from hydrological services also deserves further attention. For example, in our study area in Borneo, aboveground biomass is higher in riparian reserves compared to adjacent areas of oil palm (Singh 2012). Similarly, soil carbon is higher in riparian buffers than agricultural fields in Ohio, USA (Marton et al. 2013). Combining all the possible costs and benefits of conserving riparian reserves, particularly the ecological impacts of different width and vegetation structure specifications, will be necessary to properly informing management guidelines and policy.

COLOUR AND SHAPE

The results of studies using artificial mimics should be interpreted with caution, as the extent to which attack marks on artificial caterpillars correlate with real predation rates remains unclear (Fáveri et al. 2008; Howe et al. 2009). We found that bird attacks dropped when the mimic no longer resembled a prey item, but that there was no change in arthropod attacks, suggesting that attack marks from birds are more likely to correspond to predatory behaviour. This is probably because birds rely more on visual cues than the other predator groups. Arthropods rely much more on olfactory cues and are unlikely to be mistaking the mimics for

potential prey, as highlighted by (Tvardikova & Novotny 2012). Therefore, we suggest that attack rates on plasticine pest mimics are indicative of density or activity of foraging arthropods rather than an actual predation rate, although there may well be a positive correlation between the two.

We did not find lower attack rates from either birds or arthropods on aposematic (warning) mimics. The dependence of arthropods on olfactory cues is also likely to be a reason why a change in mimic colour did not elicit a change in their attack rate. The lack of an effect of colour on bird attacks may be because frugivorous species mistook the mimic for the red colour of the ripe oil palm fruits; several bird species within oil palm plantations are known to feed on palm fruit (Chenon & Susanto 2006). It is not possible to determine whether the attacks on brown and red mimics are similar because they both attract the attention of the same bird species, or those with different feeding behaviours.

We hope that this methodological assessment will provide useful insight for future studies using this method. We also emphasize that comparative studies with live bait and temporally matched data on the densities of foraging arthropods will be very valuable to clarify what information is obtained from attack marks on plasticine mimics.

CONCLUSIONS

Riparian reserves may affect the foraging activity of arthropods and mammals in adjacent areas of oil palm, but our results do not suggest that this corresponds to a reduction in herbivory on palm fronds under normal pest densities. Our data suggest that the use of artificial pest mimics is likely to be more informative about the predatory behaviour of birds than arthropods, and this should be taken into account by future studies using this method. In addition, our results show that riparian reserves do not increase defoliating pest activity, and this information should be highlighted in circumstances where doubt over pest problems may prevent the protection of this habitat.

CHAPTER 7: GENERAL DISCUSSION

Of all human activities, agriculture may have the largest environmental impact, and managing to meet demands for human nutrition, preserve long term agricultural productivity and protect biodiversity will be one of the greatest challenges of the 21st century. As the human population may reach 10 billion in the coming decades (Lutz & Samir 2010), it is essential that we manage to increase food production sustainably. This is likely to require intensification in areas with large yield gaps, large reductions in food waste, increasing fuel and water efficiency, integrated management of ecosystem services within agricultural landscapes and improvements in food distribution systems (Foley et al. 2011; Godfray & Garnett 2014). Wherever possible, we need to seize opportunities that simultaneously protect soil and water supplies, support essential ecosystem services and protect biodiversity without sacrificing yields. In this thesis, I have evaluated the extent to which one particular management strategy, the protection of riparian reserves, can achieve several of these goals.

IMPACTS OF THE EXPANSION OF OIL PALM ON TROPICAL FORESTS

In tropical regions there is a great overlap between very productive land and highly biodiverse ecosystems (Phalan et al. 2013), and so these areas are often a priority for the development of sustainable agriculture. Oil palm is one of the crops expanding most rapidly in tropical regions; the area planted with oil palm has doubled in the last 20 years, with the majority of this expansion occurring in Malaysia and Indonesia (FAO 2014). Approximately 40 % of the oil palm expansion in this area has directly caused deforestation (Gunarso et al. 2013), and there is a growing body of evidence that the conversion of forest to oil palm has a negative impact on many species (Fitzherbert et al. 2008; Turner et al. 2008; Foster et al. 2011). The results presented in Chapter 2 show that the vegetation structure in oil palm plantations is greatly

simplified compared to logged forest areas, and Chapters 3 and 5 demonstrate that species richness and diversity of dung beetles and ants in oil palm plantations is also much lower than in forested areas. In addition to reinforcing existing evidence that oil palm plantations are species-poor, these results also confirm that secondary or logged forests have considerable conservation value, as has been demonstrated for birds and ants (Edwards et al. 2011; Woodcock et al. 2011). I was only able to make a very limited comparison with primary forest sites due to a lack of primary forest in my study area, but the data presented in Chapters 2 and 3 are consistent with other studies that demonstrate the irreplaceable biodiversity value of primary forests (Gibson et al. 2011); the vegetation complexity and dung beetle diversity of logged forest was much lower than the primary forest reference site I surveyed.

There is much less information available on the functional impacts of converting forest to oil palm. Recent work from Borneo has established that the trait-based functional diversity of birds and dung beetles in oil palm is much lower than in forested areas (Edwards et al. 2013b, 2013d). My comparison of dung beetle communities across a land use gradient (Chapter 3) shows a similar pattern, as the number of functional groups present in oil palm areas was much lower than in the logged forest. I did not explicitly explore the functional diversity of the ant community, as I was already collecting data on a very specific subset of potential functional groups: the diurnal ground foraging fauna. However, Chapters 3 and 5 also provide specific data on how ecosystem functions vary between forest and oil palm. These results suggest that there are contrasting effects of the conversion to oil palm on the functional activity of ants and dung beetles in riparian zones. Dung removal rates did not differ significantly land use, but the nutrient redistribution function of ground foraging ants was significantly impaired in riparian areas of oil palm compared to forest. As discussed in Chapter 3, the consistently low dung removal rates in riparian areas may be because dung beetles avoid building nests near rivers, due to the higher mortality of dung beetle larvae in water logged soils (Sowig 1995). In contrast, even if the survival of ant larvae is also negatively affected by high soil moisture, ant

foragers are able to travel many meters from the colony (Lach et al. 2010), and so the functions carried out by ants can be maintained in riparian zones by colonies further from the river bank. Whilst the ecological properties of riparian zones may be distinct from the rest of the landscape (Naiman & Decamps 1997), my results indicate that the impact of converting forest to oil palm is may vary greatly between different ecological processes.

DO RIPARIAN RESERVES CONTRIBUTE TO THE CONSERVATION OF BIODIVERSITY AND ECOLOGICAL PROCESSES IN OIL PALM PLANTATIONS

Riparian reserves are primarily retained for their beneficial hydrological impact (Lee et al. 2004a), but I have demonstrated that they also increase the biodiversity retained within oil palm dominated landscapes. The species richness of both ants and dung beetles was higher in riparian reserves than in oil palm areas, but more importantly from a conservation perspective, for both taxa the community composition of the riparian reserves was much more similar to the logged forest than it was to oil palm (Chapters 3 and 5). However, the riparian reserves are not a replacement for the conservation of large areas of forest; only 86 % of the dung beetle species found in forest sites (data from Chapters 3 and 4 combined) and 64% of the ant fauna in forest sites (Chapter 5) were also found in riparian reserves. The community composition of dung beetles was still distinct from that of logged forest (Fig 3, Chapter 3) and the similarity decreased as riparian reserves became increasingly distant from the point at which they joined the logged forest (Chapter 4). The conservation value of the riparian reserves should certainly be emphasised in order to increase the number of countries that enforce the protection of vegetation along river banks, and to improve enforcement of legislation in those that already have it, but not at the expense of protecting large areas of remaining forest.

There are also important issues regarding the conservation value of riparian reserves that remain unresolved, particularly concerning the long term sustainability of populations within

the reserves. Further research is needed to assess the extent to which riparian reserves are acting as ecological sinks (i.e. experience population growth rates for any particular species that are <1 in the long term (Dias 1996)), and whether they still are experiencing a local extinction debt. For example, in one temperate study, Roslin (2000) found that *Aphodius* species could move 500 m within 15 days, and suggested that some species could potentially cover distances over 2 km in their lifetime. Whilst very little information on dispersal is available for Bornean species, similar levels of dispersal could result in riparian reserves receiving an influx of individuals from larger forest fragments over a period of months or years. If this is the case, the riparian reserve communities may be entirely dependent on nearby forest areas as sources. Without better data on the dispersal of insects in these environments and their population dynamics, it is difficult to establish the extent to which the riparian reserve populations are self-sufficient.

A number of other studies on the terrestrial communities in riparian reserves have highlighted the issue of riparian reserves being ecological sinks (e.g. Donovan et al. 1995; Conner et al. 2004; Rykken et al. 2007), but obtaining data on long term population dynamics, breeding rates and the number of immigrating individuals is challenging. Neotropical riparian reserves have been shown to support breeding population of small mammals (de Lima & Gascon 1999) and birds (Seaman & Schulze 2010), but even this evidence does not rule out the possibility that populations in the reserves are declining slowly over time. Evidence from fragmented forest in Brazil suggests that it may take up to 20 years before colonisations and local extinctions stabilise (Stouffer et al. 2011), Similar evidence from small mammal communities in fragmented forests in Thailand suggests that it takes 25 years for extinction debts to be paid (Gibson et al. 2013). As global maps of forest cover change since 2000 (Hansen et al. 2013) indicate that the riparian forests in our landscapes are most likely to have been isolated in the last 10 – 15 years, it is very possible that the communities I sampled are not representative of those that will persist in the long term. The similarity in vegetation structure between riparian

reserves and logged forest (Chapter 2) and the clear difference between the dung beetle and ant communities in riparian reserves versus oil palm (Chapters 3 and 5) suggests that the reserves will continue to support communities that would not survive conversion to oil palm. However, the extent to which they conserve forest species may decline over the next 5 – 10 years.

In addition, for species that we know cannot survive exclusively within the riparian reserves, more information is needed on the role the reserves play in facilitating movement and dispersal through the agricultural matrix. There is some evidence that remnants of native habitat, including riparian forest, improve dispersal of birds and other mobile invertebrates across agricultural landscapes in both tropical and temperate regions (Haddad et al. 2003; Gillies et al. 2011; Slade et al. 2013). The movement of large vertebrates such as elephants, proboscis monkey, macaques and orang-utan through riparian corridors is also relatively widely documented (e.g. Hai et al. 2001; Venkataraman et al. 2009), and I have observed other species such as gibbons, mongoose, bearded pigs and tree shrews using the riparian reserves. If the reserves are providing connectivity between remaining large forest fragments, this is likely to be important in maintaining metapopulation dynamics and dispersal between local populations in different forest fragments (Beier & Noss 1998; Haddad et al. 2003). The corridors may also facilitate relocation to higher elevation given indications that the smaller thermal niche breadth of tropical species will leave them more vulnerable to increasing temperatures with climate change (Deutsch et al. 2008; Corlett 2012). Further studies on the extent to which other invertebrate and vertebrate species can be found in the riparian reserves would be very valuable.

How can we design riparian reserves to maximise their conservation value?

The width of the riparian reserve is the most common, and often the only, specification for the management of riverside areas made in policy, and is therefore an appropriate feature to evaluate as any conclusions can be directly linked back to existing legislation. My results indicate that reserve width is likely to vary in importance for different components of the communities retained in riparian reserves. I found a positive relationship between reserve width and dung beetle species richness and diversity (Chapters 3 and 4), a pattern that was also found for dung beetles in riparian reserves in Brazil (Viegas et al. 2014). However, I found no relationship between reserve width and ant diversity (Chapter 5). These contrasting results may be due in part to differences in experimental design; the results for dung beetles were obtained using an equal-area grid of traps, of which a varying proportion was covered by riparian vegetation as reserve width increased. In contrast, the data for ants are from traps exclusively aligned along the river bank, a set up that is less likely to detect effects of width as the traps are not positioned close to the reserve edge. However, the experimental design in Chapter 3 used traps exclusively within the riparian reserves (i.e. similar to the ant sampling design) and still picked up a positive relationship between reserve width and dung beetle species richness; and despite the arrangement of ant sampling points I was able to detect a significant relationship between ant abundance and riparian reserve width. Overall, it seems likely that if there was a strong positive relationship between riparian reserve width and the species richness of the ant communities on the river bank, I would have detected it. Thus it seems likely that the width of the reserve has a greater influence on species richness and diversity in the centre of the reserve (next to the river) for dung beetles than it does for ants. Of course, wider riparian reserves would certainly provide more habitat for forest-dependent species of ant, boosting overall population sizes, even though increasing width (at least within

the range of widths I sampled) might not further increase the extent to which leaf litter ant communities at the centre of the reserve resemble those in forest.

Overall, my results suggest that enforcing the 30 m width currently applied in many plantations in Sabah will certainly benefit biodiversity, but that wider reserves would be desirable; and that protection should be given to riparian zones in countries where they are not currently a legal requirements. In Chapter 4 I carried out a specific analysis of the desirable riparian reserve width and found that reserves of 50 – 80 m should enable dung beetle communities at the centre of the reserves to achieve a similar mean value to that in logged forest habitats. However, riparian reserve width specifications have been made in many ways, and it is possible that a different conclusion could be reached with a different method. I followed the approach used by a number of previous studies (e.g. Vesely & McComb 2002), which set the "goal" for riparian reserves at a certain level found in a nearby reference forest. However, I was unable to use primary forest for this purpose, and I expect that this might well result in a practically unattainable goal anyway, given that riparian reserve habitats are almost exclusively edge habitat. Similarly, other studies have used levels of abundance in a reference forest (Hagar 1999); this was not possible as dung beetle abundance did not vary with width. Other studies have set a threshold for the number of species that must be shared with a reference forest (Whitaker & Montevecchi 1999; Pearson & Manuwal 2001; Cockle & Richardson 2003); again, this was less suitable due to relatively high levels of species overlap across all reserve widths, although the absence of oil palm specialists could be a potentially productive approach to setting desirable reserve widths. In essence, difference methods of setting the desirable width may be suitable for different species groups, complicating attempts to create a unified system for indicating the best width for riparian reserves. A quite different approach is to identify the point at which the species richness or abundance of particular species begins to reach an asymptote (Hodges & Krementz 1996; Ives et al. 2011b), which is likely to be more transferable between species, but can also be criticised for being more

arbitrary and disconnected from real forest dynamics. Whilst I have made a very particular, quantified estimate for a desirable reserve width of 50 – 80 m in Bornean oil palm plantations, it is entirely possible that this recommendation will be altered if the community of researchers and policy makers working on riparian areas adopt a more uniform approach to setting guidelines.

It is also very likely that different widths will be necessary under different ecological conditions or for different focal taxa. For example, wider riparian reserves may be required to support species that have large territories, forage over large areas, or require a certain abundance of a particular resource. Existing research on arboreal mammals in riparian reserve in Australia suggests that corridors up to 200 m wide on each side of the river (twice the maximum width of the reserves we surveyed) are needed to preserve all the species found in forested areas (Laurance & Laurance 1999); this is twice as wide as the recommendation derived from my data. Similarly, the agricultural matrix or productive landscape surrounding the riparian reserve may influence the width that is required to reach a certain desired reference level for any focal taxa. Much of the existing literature on riparian reserves has developed in timber landscapes, where trees are clear-felled every few years, and food-crop plantations may have a very different impact on the flora and fauna persisting in riparian reserves. Martin et al. (2006) showed that riparian reserve bird communities in Queensland, Australia, vary with the surrounding land use (grazed woodland vs pasture vs crops) and Rodewald and Bakermans (2006) demonstrated that the degree of urbanisation in the area around a riparian reserve in Ohio (USA) also explained a significant proportion of variation in the bird community within the reserve.

An additional aspect of riparian reserve design which could be detailed in legislation, albeit with slightly more difficulty, is the structure of the vegetation. It is possible to limit the amount of logging that occurs near rivers, or to carry out restoration planting to fill in tree gaps and

restoring canopy cover where necessary. Therefore, I investigated the effects of vegetation structure on the dung beetle and ant communities. However, I found very little evidence that vegetation complexity affects these groups; there was a positive relationship between dung beetle abundance and vegetation complexity in the data obtained in 2011 (Chapter 3) but this relationship did not hold in the larger dataset I collected in the following year (Chapter 4), and there was no significant relationship between the ground foraging ant communities and vegetation complexity (Chapter 5). However, it is very likely that vegetation structure is more important for arboreal species of vertebrate and invertebrates; arboreal ant species, for example, are much more sensitive to canopy structure (Lach et al. 2010). Indeed, other studies have found that the vegetation structure in riparian reserves affects voles (Yletyinen & Norrdahl 2008) as well as the species richness and activity of bats (Lloyd et al. 2006), that tree cover affects bird species richness and density (Stauffer & Best 1980; Henningsen & Best 2005; Hanowski et al. 2005) and that leaf litter depth affects dung beetles (Viegas et al. 2014). Maisonneuve & Rioux (2001) found that small mammal and herpetofauna abundance was higher in more complex vegetation, but the species richness responses of these groups differed. Other components of the plant community may also be relevant to management guidelines; both Ives et al. (2013) and Hudson et al. (2013) have shown that the density of invasive species in a riparian corridor in the USA affected the species richness of butterflies and bees. This may be of particular concern given the high invasibility of riparian areas (DeFerrari & Naiman 1994; Planty-Tabacchi et al. 1996). It is clear from these studies that even though I did not find vegetation structure to be a strong determinant of riparian reserve communities, it may still be very important for other animal groups, and that specifications for canopy cover, or for a particular range of vegetation types, may be a useful addition to riparian reserve management guidelines.

I was unable to investigate very many aspects of the landscape context and spatial design of riparian reserves, and there is also a range of interesting ways in which reserve design could be

specified that deserve additional attention. I showed that the amount of forest cover in the area surrounding a riparian reserve can impact the dung beetle diversity in the reserve (Chapter 4) but I was unable to examine the effect of connectivity; all riparian reserves in my study landscape were still connected to forest. However, comparisons between riparian corridors in Brazil that were either un-connected or connected to larger areas of forest found that the connected corridors had communities of plants, small mammals and amphibians that were more similar to large areas of forest (Lees & Peres 2008). The connectivity of riparian corridors to larger areas of forest is also known to affect ant species (Ives et al. 2011b), arboreal mammals (Laurance & Laurance 1999) and birds (Seaman & Schulze 2010); a larger number of forest dependent species are retained in connected corridors. As discussed above, the extent to which these individuals may only be transients dispersing through the landscape, or immigrants into sink populations within the reserves, deserves further study. Nevertheless, the connectivity of the reserves may well deserve additional consideration within policy; there is often too narrow a focus on width as the only management parameter to be considered (Ives et al. 2011b).

The wider spatial arrangement of riparian habitat could also be managed in a wider variety of ways. In many countries, a range of widths is specified depending on the size of the water body (Lee et al. 2004a; NSW Office of Water 2012). This is practical solution to the variation in riparian ecology and available productive land and has also been recommended by some ecological studies (e.g. Darveau et al. 2001; Hannon et al. 2002). Other ideas that I think may be particularly promising include the introduction of patch, or headwater reserves where streams meet, so that larger forest fragments are present along the corridor network even though the maximum width of the corridors is limited. This approach has mainly been discussed in the context of the Pacific northwest USA (Rykken et al. 2007; Olson et al. 2007) but may well be applicable to tropical regions too. Similarly, (Ives et al. 2011b) highlight that the perimeter to area ratio (i.e. variation in riparian reserve width along one continuous

stretch) can affect the community within the reserve; they found that a higher edge to area ratio increased edge effects and decreased ant and plant species richness in Australian riparian reserves. This aspect of the spatial design of riparian reserves also deserves to be the focus of future research and potentially included in policy.

ECOLOGICAL IMPACTS OF RIPARIAN RESERVES: ECOSYSTEM SERVICES AND DISSERVICES

An important consideration for the management of riparian corridors is whether or not they influence the ecology of the surrounding oil palm area. Beneficial impacts would act as an incentive for managers to conserve riparian forest and negative impacts might indicate that managers of riparian areas should be compensated for any crop damage resulting from the conservation of riparian habitat. I am only aware of two neo-tropical studies (Ricketts 2004; Michalski et al. 2006) that have explicitly addressed whether the presence of a riparian reserve affects ecological processes in the surrounding agricultural landscape, and none from the old world tropics. Overall, my results suggest that riparian reserves have a reasonably limited impact on ecological processes in surrounding areas of oil palm. I did not find any evidence that the greater diversity of dung beetles in riparian reserves results in an increase in dung removal in the surrounding area of oil palm (Chapter 3). The results presented in Chapter 6 suggest that even though predation by arthropods may be elevated in the areas next the reserves, this does not translate to a reduction in herbivory on oil palm fronds. However, this does not mean that the reserves do not provide dung removal or pest control services under any situation; the increased species diversity in the riparian reserves may provide a pool of species that can expand into oil palm if cattle are introduced. Similarly, it may be that when pest densities increase to the extent that the predators supported by the oil palm are saturated (e.g. during an outbreak), the presence of riparian reserves and the different species that they support may help to bring down pest numbers. Of course, the extent to which

riparian reserve structure affects other services, such as water quality, flood dynamics and carbon storage are also a central part of their role in the oil palm landscapes, and should be incorporated into a more complete overview of the benefits provided by these landscape features.

As well as providing ecosystem services, it is also possible that the riparian reserves have a negative effect (ecosystem disservice) and it is equally important to establish whether these dynamics are occurring. If increases in riparian reserve width cause increases in damage to surrounding crops, the managers of agricultural areas may have a good case for seeking compensation for changes in legislation. The delivery of disservices is a valid concern for oil palm managers as riparian habitat is known to increase pest densities in other agricultural areas (Naiman & Decamps 1997; Deschênes et al. 2003). An important conclusion from the results presented in Chapter 6 is that the riparian reserves do not seem to increase the activity of defoliating pests, and that reserve width also has no effect on the activity of herbivores. However, it is still possible that other pest species, particularly frugivorous mammals, increase in density around the reserves. I have observed pig-tailed macaques (*Macaca nemestrina*) emerging from riparian corridors to feed on oil palm fruit. However, the rates of felid predation on livestock in the Brazilian Amazon decreased with proximity to riparian reserve corridors (Michalski et al. 2006) so it is also possible that the riparian reserves may channel potential pest species through oil palm landscapes in a way that reduces the damage they cause. Experts from riparian forest conservation and restoration projects in Sabah have suggested that the pygmy elephants (*Elephas maximus borneensis*) prefer to move along the native vegetation next to river banks, and are less likely to damage oil palm crop if they are available (Néstle RiLeaf project manager, Kinabatangan, personal communication).

RIPARIAN RESERVES IN A WIDER CONSERVATION CONTEXT

Retaining riparian reserves within a predominantly agricultural landscape would be classified as a land sharing, biodiversity-friendly approach to conservation following the definition of Phalan et al. (2011a). Increasing evidence from the humid tropics suggests that as a general strategy, land sparing will retain higher levels of biodiversity for a given yield output in a defined area, because a high proportion of tropical species are very sensitive to any increase in yield (Phalan et al. 2011c; Edwards et al. 2013a). In addition, intensive agriculture may not be the most suitable where species show different responses to yield increases, in all social or political situations or where the required technology is not available, and so a mixture of strategies is likely to be necessary in different locations (Godfray & Garnett 2014). However, a major obstacle for successful land sparing is the difficulty in ensuring that high quality habitat is actually protected, and that intensive agriculture does not spread over the entire area of concern (Laurance et al. 2014). In addition, Edwards et al. (2013a) recommended that areas which are highly ecologically sensitive should be retained even within a broader land-sparing approach, and specifically mention steep slopes and riverine areas as requiring protection in all management scenarios. There is no currently clear answer to the question of whether conservation scientists should or should not recommend the conservation of smaller fragments in tropical agricultural areas. Certainly highlighting the conservation value of riparian reserves should not detract from the irreplaceable value of large primary forest reserves (Gibson et al. 2011), especially when the cost of expanding riparian reserves could be several percent of total oil palm yield (Chapter 4). However, establishing the extent to which riparian reserves can support forest-dependent communities is certainly important information required to come to an evidence-based conclusion on the extent to which non-crop habitat should be maintained in productive tropical landscapes.

GENERAL CONCLUSIONS

The expanding population and increase in land required for agriculture will exert a huge pressure on remaining natural habitats over the course of this century, especially in the tropics. It is therefore essential that we identify strategies for the sustainable intensification of agriculture that maximise the retention of ecosystem services and minimise negative impacts on biodiversity. Oil palm plantations are one of the most rapidly expanding agricultural systems in the tropics, and I have shown that retaining riparian reserves can increase the biodiversity within these landscapes, at least for two key insect indicator groups. Retaining any riparian vegetation will be beneficial, but in oil palm plantations in Southeast Asia reserves of 50 – 80 m are likely to be needed to retain levels of diversity similar to those in larger areas of logged forest. I have also shown that the extent to which riparian reserves maintain key ecological functions found in larger forested areas is likely to vary, as not all ecosystem functions are affected by the conversion to oil palm. I found very little evidence that riparian reserves enhance the provision of dung removal or pest control services in adjacent areas of oil palm, and that the cost of extending the riparian reserves (up to a maximum of 150 m on each side) could reduce oil palm plantation production between 2 and 17%, depending on the width of the reserves and the productivity of the area. However, the role that riparian reserves play in maintaining water quality and hydrological dynamics remains central to their protection and may offset much of this cost. Overall, riparian zone protection needs to be introduced where it is not currently included in legislation and better enforced in places where it is already required and is not occurring. Although large areas of primary forest will remain the most critical conservation strategy, protecting riparian reserves can make a valuable contribution to species survival in the most biodiverse landscapes on the planet.

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APPENDIX A: LOCATION OF ALL SAMPLING POINTS

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.70087	117.57314	0m	1	0	2011	✓		✓	
4.70084	117.57261	0m	1	50	2011	✓		✓	
4.70083	117.57217	0m	1	100	2011	✓		✓	
4.70176	117.57277	0m	2	0	2011	✓		✓	
4.70181	117.57231	0m	2	50	2011	✓		✓	
4.70176	117.57187	0m	2	100	2011	✓		✓	
4.70275	117.57295	0m	3	0	2011	✓		✓	
4.70286	117.57237	0m	3	50	2011	✓		✓	
4.70276	117.57187	0m	3	100	2011	✓		✓	
4.70381	117.57287	0m	4	0	2011	✓			
4.70382	117.57239	0m	4	50	2011	✓			
4.70388	117.57193	0m	4	100	2011	✓			

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.71407	117.63995	120m	1	0	2011	✓		✓	
4.71432	117.63927	120m	1	50	2011	✓		✓	
4.71423	117.63878	120m	1	100	2011	✓		✓	
4.71575	117.64005	120m	2	0	2011	✓		✓	
4.71559	117.63966	120m	2	50	2011	✓		✓	
4.71560	117.63926	120m	2	100	2011	✓		✓	
4.71686	117.64111	120m	3	0	2011	✓		✓	
4.71690	117.64069	120m	3	50	2011	✓		✓	
4.71686	117.64018	120m	3	100	2011	✓		✓	
4.71809	117.64112	120m	4	0	2011	✓			
4.71809	117.64066	120m	4	50	2011	✓			
4.71813	117.64029	120m	4	100	2011	✓			
4.65130	117.57661	15m	1	0	2011	✓		✓	
4.65155	117.57622	15m	1	50	2011	✓		✓	
4.65190	117.57591	15m	1	100	2011	✓		✓	
4.65272	117.57787	15m	2	0	2011	✓		✓	
4.65267	117.57730	15m	2	50	2011	✓		✓	
4.65266	117.57683	15m	2	100	2011	✓		✓	
4.65357	117.57784	15m	3	0	2011	✓		✓	
4.65354	117.57729	15m	3	50	2011	✓		✓	
4.65357	117.57685	15m	3	100	2011	✓		✓	
4.65432	117.57803	15m	4	0	2011	✓			
4.65452	117.57741	15m	4	50	2011	✓			
4.65448	117.57702	15m	4	100	2011	✓			
4.72481	117.62130	30m	1	0	2011	✓		✓	
4.72427	117.62130	30m	1	50	2011	✓		✓	
4.72381	117.62121	30m	1	100	2011	✓		✓	
4.72466	117.62225	30m	2	0	2011	✓		✓	
4.72411	117.62232	30m	2	50	2011	✓		✓	
4.72366	117.62224	30m	2	100	2011	✓		✓	
4.72570	117.62298	30m	3	0	2011	✓		✓	
4.72530	117.62330	30m	3	50	2011	✓		✓	
4.72504	117.62363	30m	3	100	2011	✓		✓	
4.72656	117.62331	30m	4	0	2011	✓			
4.72640	117.62382	30m	4	50	2011	✓			
4.72616	117.62431	30m	4	100	2011	✓			

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.67524	117.57775	camp	1	0	2011	✓		✓	
4.67496	117.57736	camp	1	50	2011	✓		✓	
4.67466	117.57701	camp	1	100	2011	✓		✓	
4.67610	117.57714	camp	2	0	2011	✓		✓	
4.67583	117.57677	camp	2	50	2011	✓		✓	
4.67562	117.57629	camp	2	100	2011	✓		✓	
4.67676	117.57646	camp	3	0	2011	✓		✓	
4.67663	117.57603	camp	3	50	2011	✓		✓	
4.67633	117.57564	camp	3	100	2011	✓		✓	
4.67794	117.57632	camp	4	0	2011	✓			
4.67789	117.57596	camp	4	50	2011	✓			
4.67805	117.57548	camp	4	100	2011	✓			
4.73705	116.95830	maliau	1	0	2011	✓			
4.73765	116.95842	maliau	1	50	2011	✓			
4.73806	116.95841	maliau	1	100	2011	✓			
4.73694	116.95961	maliau	2	0	2011	✓		✓	
4.73738	116.95942	maliau	2	50	2011	✓		✓	
4.73796	116.95928	maliau	2	100	2011	✓		✓	
4.73713	116.96054	maliau	3	0	2011	✓		✓	
4.73764	116.96038	maliau	3	50	2011	✓		✓	
4.73817	116.96036	maliau	3	100	2011	✓		✓	
4.73809	116.96192	maliau	4	0	2011	✓		✓	
4.73836	116.96156	maliau	4	50	2011	✓		✓	
4.73871	116.96123	maliau	4	100	2011	✓		✓	
4.68658	117.45591	OP1	1	0	2011	✓			
4.68608	117.45566	OP1	1	50	2011	✓			
4.68570	117.45545	OP1	1	100	2011	✓			
4.68730	117.45542	OP1	2	0	2011	✓			
4.68686	117.45484	OP1	2	50	2011	✓			
4.68647	117.45463	OP1	2	100	2011	✓			
4.68807	117.45381	OP1	3	0	2011	✓			
4.68765	117.45357	OP1	3	50	2011	✓			
4.68721	117.45358	OP1	3	100	2011	✓			
4.68852	117.45283	OP1	4	0	2011	✓			
4.68809	117.45263	OP1	4	50	2011	✓			
4.68764	117.45247	OP1	4	100	2011	✓			

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.61469	117.54298	OP10	1	0	2011	✓			
4.61503	117.54321	OP10	1	50	2011	✓			
4.61542	117.54346	OP10	1	100	2011	✓			
4.61386	117.54359	OP10	2	0	2011	✓		✓	
4.61425	117.54381	OP10	2	50	2011	✓		✓	
4.61460	117.54408	OP10	2	100	2011	✓		✓	
4.61329	117.54482	OP10	3	0	2011	✓		✓	
4.61370	117.54497	OP10	3	50	2011	✓		✓	
4.61402	117.54519	OP10	3	100	2011	✓		✓	
4.61252	117.54554	OP10	4	0	2011	✓		✓	
4.61288	117.54577	OP10	4	50	2011	✓		✓	
4.61329	117.54596	OP10	4	100	2011	✓		✓	
4.67397	117.61731	OP11	1	0	2011	✓		✓	
4.67398	117.61776	OP11	1	50	2011	✓		✓	
4.67395	117.61820	OP11	1	100	2011	✓		✓	
4.67494	117.61708	OP11	2	0	2011	✓		✓	
4.67496	117.61757	OP11	2	50	2011	✓		✓	
4.67497	117.61803	OP11	2	100	2011	✓		✓	
4.67611	117.61695	OP11	3	0	2011	✓		✓	
4.67633	117.61737	OP11	3	50	2011	✓		✓	
4.67635	117.61785	OP11	3	100	2011	✓		✓	
4.67693	117.61637	OP11	4	0	2011	✓			
4.67725	117.61670	OP11	4	50	2011	✓			
4.67758	117.61705	OP11	4	100	2011	✓			
4.61129	117.45152	OP2	1	0	2011	✓		✓	
4.61081	117.45172	OP2	1	50	2011	✓		✓	
4.61062	117.45210	OP2	1	100	2011	✓		✓	
4.61226	117.45239	OP2	2	0	2011	✓		✓	
4.61203	117.45268	OP2	2	50	2011	✓		✓	
4.61187	117.45311	OP2	2	100	2011	✓		✓	
4.61322	117.45263	OP2	3	0	2011	✓		✓	
4.61307	117.45307	OP2	3	50	2011	✓		✓	
4.61295	117.45346	OP2	3	100	2011	✓		✓	
4.61514	117.45239	OP2	4	0	2011	✓			
4.61502	117.45333	OP2	4	50	2011	✓			
4.61482	117.45401	OP2	4	100	2011	✓			

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.59493	117.46489	OP3	1	0	2011	✓		✓	
4.59466	117.46529	OP3	1	50	2011	✓		✓	
4.59435	117.46567	OP3	1	100	2011	✓		✓	
4.59596	117.46582	OP3	2	0	2011	✓		✓	
4.59576	117.46618	OP3	2	50	2011	✓		✓	
4.59554	117.46659	OP3	2	100	2011	✓		✓	
4.59739	117.46570	OP3	3	0	2011	✓		✓	
4.59723	117.46606	OP3	3	50	2011	✓		✓	
4.59708	117.46652	OP3	3	100	2011	✓		✓	
4.59819	117.46686	OP3	4	0	2011	✓			
4.59798	117.46720	OP3	4	50	2011	✓			
4.59784	117.46757	OP3	4	100	2011	✓			
4.55761	117.49028	OP4	1	0	2011	✓		✓	
4.55721	117.49026	OP4	1	50	2011	✓		✓	
4.55679	117.49002	OP4	1	100	2011	✓		✓	
4.55748	117.49126	OP4	2	0	2011	✓		✓	
4.55713	117.49130	OP4	2	50	2011	✓		✓	
4.55659	117.49141	OP4	2	100	2011	✓		✓	
4.55866	117.49232	OP4	3	0	2011	✓		✓	
4.55829	117.49234	OP4	3	50	2011	✓		✓	
4.55779	117.49243	OP4	3	100	2011	✓		✓	
4.55830	117.49367	OP4	4	0	2011	✓			
4.55788	117.49369	OP4	4	50	2011	✓			
4.55739	117.49376	OP4	4	100	2011	✓			
4.60277	117.61655	OP9	1	0	2011	✓		✓	
4.60306	117.61620	OP9	1	50	2011	✓		✓	
4.60341	117.61606	OP9	1	100	2011	✓		✓	
4.60341	117.61763	OP9	2	0	2011	✓		✓	
4.60363	117.61732	OP9	2	50	2011	✓		✓	
4.60403	117.61705	OP9	2	100	2011	✓		✓	
4.60558	117.61761	OP9	3	0	2011	✓		✓	
4.60569	117.61729	OP9	3	50	2011	✓		✓	
4.60587	117.61677	OP9	3	100	2011	✓		✓	
4.60664	117.61829	OP9	4	0	2011	✓			
4.60670	117.61785	OP9	4	50	2011	✓			
4.60692	117.61742	OP9	4	100	2011	✓			

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.74611	117.52590	RR1	1	0	2011	✓		✓	
4.74567	117.52584	RR1	1	50	2011	✓		✓	
4.74517	117.52597	RR1	1	100	2011	✓		✓	
4.74625	117.52685	RR1	2	0	2011	✓		✓	
4.74572	117.52692	RR1	2	50	2011	✓		✓	
4.74530	117.52690	RR1	2	100	2011	✓		✓	
4.74686	117.52738	RR1	3	0	2011	✓		✓	
4.74687	117.52789	RR1	3	50	2011	✓		✓	
4.74683	117.52833	RR1	3	100	2011	✓		✓	
4.74793	117.52723	RR1	4	0	2011	✓			
4.74784	117.52775	RR1	4	50	2011	✓			
4.74793	117.52821	RR1	4	100	2011	✓			
4.57105	117.61964	RR12	1	0	2011	✓		✓	
4.57155	117.61973	RR12	1	50	2011	✓		✓	
4.57203	117.61986	RR12	1	100	2011	✓		✓	
4.57059	117.62034	RR12	2	0	2011	✓		✓	
4.57083	117.62062	RR12	2	50	2011	✓		✓	
4.57111	117.62102	RR12	2	100	2011	✓		✓	
4.56955	117.62010	RR12	3	0	2011	✓		✓	
4.56945	117.62055	RR12	3	50	2011	✓		✓	
4.56954	117.62104	RR12	3	100	2011	✓		✓	
4.56820	117.62110	RR12	4	0	2011	✓			
4.56835	117.62157	RR12	4	50	2011	✓			
4.56857	117.62196	RR12	4	100	2011	✓			
4.67501	117.50728	RR3	1	0	2011	✓		✓	
4.67452	117.50719	RR3	1	50	2011	✓		✓	
4.67403	117.50710	RR3	1	100	2011	✓		✓	
4.67496	117.50647	RR3	2	0	2011	✓			
4.67454	117.50610	RR3	2	50	2011	✓		✓	
4.67410	117.50599	RR3	2	100	2011	✓		✓	
4.67499	117.50526	RR3	3	0	2011	✓		✓	
4.67455	117.50516	RR3	3	50	2011	✓			
4.67415	117.50493	RR3	3	100	2011	✓			
4.67553	117.50458	RR3	4	0	2011	✓		✓	
4.67520	117.50438	RR3	4	50	2011	✓		✓	
4.67478	117.50414	RR3	4	100	2011	✓		✓	

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.66479	117.44875	RR4	1	0	2011	✓		✓	
4.66524	117.44873	RR4	1	50	2011	✓		✓	
4.66568	117.44895	RR4	1	100	2011	✓		✓	
4.66413	117.45195	RR4	2	0	2011	✓		✓	
4.66456	117.45178	RR4	2	50	2011	✓		✓	
4.66502	117.45163	RR4	2	100	2011	✓		✓	
4.66454	117.45307	RR4	3	0	2011	✓		✓	
4.66486	117.45282	RR4	3	50	2011	✓		✓	
4.66525	117.45262	RR4	3	100	2011	✓		✓	
4.66535	117.45392	RR4	4	0	2011	✓			
4.66568	117.45357	RR4	4	50	2011	✓			
4.66602	117.45327	RR4	4	100	2011	✓			
4.56995	117.50201	RR5	1	0	2011	✓		✓	
4.56960	117.50237	RR5	1	50	2011	✓		✓	
4.56921	117.50272	RR5	1	100	2011	✓		✓	
4.56938	117.50128	RR5	2	0	2011	✓		✓	
4.56897	117.50138	RR5	2	50	2011	✓		✓	
4.56852	117.50140	RR5	2	100	2011	✓		✓	
4.56953	117.50045	RR5	3	0	2011	✓		✓	
4.56910	117.50044	RR5	3	50	2011	✓		✓	
4.56858	117.50042	RR5	3	100	2011	✓		✓	
4.56927	117.49950	RR5	4	0	2011	✓			
4.56890	117.49950	RR5	4	50	2011	✓			
4.56842	117.49944	RR5	4	100	2011	✓			
4.60353	117.53159	RR6	1	0	2011	✓			
4.60310	117.53159	RR6	1	50	2011	✓			
4.60264	117.53147	RR6	1	100	2011	✓			
4.60363	117.53355	RR6	2	0	2011	✓		✓	
4.60323	117.53335	RR6	2	50	2011	✓		✓	
4.60287	117.53319	RR6	2	100	2011	✓		✓	
4.60323	117.53462	RR6	3	0	2011	✓		✓	
4.60287	117.53441	RR6	3	50	2011	✓		✓	
4.60241	117.53434	RR6	3	100	2011	✓		✓	
4.60274	117.53536	RR6	4	0	2011	✓		✓	
4.60226	117.53546	RR6	4	50	2011	✓		✓	
4.60182	117.53544	RR6	4	100	2011	✓		✓	

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.59135	117.58240	RR8	1	0	2011	✓		✓	
4.59185	117.58256	RR8	1	50	2011	✓		✓	
4.59221	117.58271	RR8	1	100	2011	✓		✓	
4.59180	117.58155	RR8	2	0	2011	✓		✓	
4.59222	117.58166	RR8	2	50	2011	✓		✓	
4.59264	117.58177	RR8	2	100	2011	✓		✓	
4.59207	117.58061	RR8	3	0	2011	✓		✓	
4.59250	117.58079	RR8	3	50	2011	✓		✓	
4.59291	117.58086	RR8	3	100	2011	✓		✓	
4.59255	117.57947	RR8	4	0	2011	✓			
4.59311	117.57967	RR8	4	50	2011	✓			
4.59337	117.58002	RR8	4	100	2011	✓			
4.65169	117.62370	RR9	1	0	2011	✓		✓	
4.65204	117.62403	RR9	1	50	2011	✓		✓	
4.65241	117.62434	RR9	1	100	2011	✓		✓	
4.65118	117.62469	RR9	2	0	2011	✓		✓	
4.65159	117.62502	RR9	2	50	2011	✓		✓	
4.65202	117.62528	RR9	2	100	2011	✓		✓	
4.65074	117.62577	RR9	3	0	2011	✓		✓	
4.65117	117.62593	RR9	3	50	2011	✓		✓	
4.65161	117.62609	RR9	3	100	2011	✓		✓	
4.65083	117.62714	RR9	4	0	2011	✓			
4.65135	117.62711	RR9	4	50	2011	✓			
4.65180	117.62712	RR9	4	100	2011	✓			
4.65083	117.53994	VJR	1	0	2011	✓		✓	
4.65122	117.54015	VJR	1	50	2011	✓		✓	
4.65167	117.54042	VJR	1	100	2011	✓		✓	
4.65231	117.53882	VJR	2	0	2011	✓		✓	
4.65265	117.53943	VJR	2	50	2011	✓		✓	
4.65295	117.53969	VJR	2	100	2011	✓		✓	
4.65342	117.53777	VJR	3	0	2011	✓		✓	
4.65365	117.53832	VJR	3	50	2011	✓		✓	
4.65368	117.53878	VJR	3	100	2011	✓		✓	
4.65461	117.53769	VJR	4	0	2011	✓			
4.65482	117.53823	VJR	4	50	2011	✓			
4.65485	117.53874	VJR	4	100	2011	✓			

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.58053	117.47342	VJR2	1	0	2011	✓		✓	
4.58010	117.47371	VJR2	1	50	2011	✓		✓	
4.57977	117.47398	VJR2	1	100	2011	✓		✓	
4.58098	117.47431	VJR2	2	0	2011	✓		✓	
4.58056	117.47467	VJR2	2	50	2011	✓		✓	
4.58016	117.47484	VJR2	2	100	2011	✓		✓	
4.58143	117.47540	VJR2	3	0	2011	✓		✓	
4.58100	117.47549	VJR2	3	50	2011	✓		✓	
4.58059	117.47572	VJR2	3	100	2011	✓		✓	
4.58201	117.47616	VJR2	4	0	2011	✓			
4.58160	117.47636	VJR2	4	50	2011	✓			
4.58114	117.47658	VJR2	4	100	2011	✓			
4.65091	117.57660	15m	C1	25	2012	✓			
4.65082	117.57670	15m	C2	0	2012	✓			
4.65113	117.57663	15m	C3	10	2012	✓			
4.65123	117.57679	15m	C4	0	2012	✓			
4.65102	117.57689	15m	C5	15	2012	✓			
4.71728	117.60697	B	C1	25	2012	✓			
4.71715	117.60700	B	C2	0	2012	✓			
4.71719	117.60678	B	C3	10	2012	✓			
4.71719	117.60663	B	C4	0	2012	✓			
4.71712	117.60640	B	C5	15	2012	✓			
4.67537	117.57784	camp	C1	25	2012	✓			
4.67524	117.57765	camp	C2	0	2012	✓			
4.67549	117.57760	camp	C3	10	2012	✓			
4.67578	117.57753	camp	C4	0	2012	✓			
4.67568	117.57731	camp	C5	15	2012	✓			
4.69766	117.58930	Es	C1	25	2012	✓			
4.69781	117.58944	Es	C2	0	2012	✓			
4.69789	117.58916	Es	C3	10	2012	✓			
4.69808	117.58894	Es	C4	0	2012	✓			
4.69817	117.58907	Es	C5	15	2012	✓			
4.74610	117.52541	RR1	C1	25	2012	✓			
4.74599	117.52536	RR1	C2	0	2012	✓			
4.74597	117.52563	RR1	C3	10	2012	✓			
4.74599	117.52584	RR1	C4	0	2012	✓			

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.74586	117.52590	RR1	C5	15	2012	✓			
4.63899	117.53489	RR10	C1	25	2012	✓			
4.63904	117.53475	RR10	C2	0	2012	✓			
4.63876	117.53479	RR10	C3	10	2012	✓			
4.63853	117.53463	RR10	C4	0	2012	✓			
4.63874	117.53455	RR10	C5	15	2012	✓			
4.73195	117.52979	RR11	C1	25	2012	✓			
4.73184	117.52972	RR11	C2	0	2012	✓			
4.73192	117.52990	RR11	C3	10	2012	✓			
4.73197	117.53014	RR11	C4	0	2012	✓			
4.73187	117.53041	RR11	C5	15	2012	✓			
4.61125	117.60138	RR13	C1	25	2012	✓			
4.61136	117.60130	RR13	C2	0	2012	✓			
4.61150	117.60150	RR13	C3	10	2012	✓			
4.61162	117.60165	RR13	C4	0	2012	✓			
4.61177	117.60155	RR13	C5	15	2012	✓			
4.61774	117.62691	RR14	C1	25	2012	✓			
4.61762	117.62698	RR14	C2	0	2012	✓			
4.61749	117.62673	RR14	C3	10	2012	✓			
4.61734	117.62661	RR14	C4	0	2012	✓			
4.61731	117.62676	RR14	C5	15	2012	✓			
4.64805	117.59874	RR15	C1	25	2012	✓			
4.64816	117.59888	RR15	C2	0	2012	✓			
4.64782	117.59881	RR15	C3	10	2012	✓			
4.64749	117.59886	RR15	C4	0	2012	✓			
4.64746	117.59907	RR15	C5	15	2012	✓			
4.64530	117.46616	RR16	C1	25	2012	✓			
4.64538	117.46626	RR16	C2	0	2012	✓			
4.64511	117.46629	RR16	C3	10	2012	✓			
4.64510	117.46652	RR16	C4	0	2012	✓			
4.64521	117.46661	RR16	C5	15	2012	✓			
4.61524	117.55686	RR17A	C1	25	2012	✓			
4.61508	117.55698	RR17A	C2	0	2012	✓			
4.61528	117.55699	RR17A	C3	10	2012	✓			
4.61529	117.55717	RR17A	C4	0	2012	✓			
4.61519	117.55716	RR17A	C5	15	2012	✓			

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.60078	117.55906	RR17B	C1	25	2012	✓			
4.60071	117.55920	RR17B	C2	0	2012	✓			
4.60059	117.55903	RR17B	C3	10	2012	✓			
4.60051	117.55881	RR17B	C4	0	2012	✓			
4.60045	117.55890	RR17B	C5	15	2012	✓			
4.69737	117.52021	RR18A	C1	25	2012	✓			
4.69724	117.52021	RR18A	C2	0	2012	✓			
4.69718	117.52052	RR18A	C3	10	2012	✓			
4.69701	117.52057	RR18A	C4	0	2012	✓			
4.69690	117.52056	RR18A	C5	15	2012	✓			
4.64885	117.51001	RR19	C1	25	2012	✓			
4.64906	117.51007	RR19	C2	0	2012	✓			
4.64909	117.50996	RR19	C3	10	2012	✓			
4.64926	117.50971	RR19	C4	0	2012	✓			
4.64939	117.50969	RR19	C5	15	2012	✓			
4.65263	117.51936	RR19A	C1	25	2012	✓			
4.65248	117.51935	RR19A	C2	0	2012	✓			
4.65272	117.51952	RR19A	C3	10	2012	✓			
4.65291	117.51951	RR19A	C4	0	2012	✓			
4.65272	117.51973	RR19A	C5	15	2012	✓			
4.75636	117.54293	RR1A	C1	25	2012	✓			
4.75651	117.54305	RR1A	C2	0	2012	✓			
4.75629	117.54316	RR1A	C3	10	2012	✓			
4.75637	117.54344	RR1A	C4	0	2012	✓			
4.75645	117.54352	RR1A	C5	15	2012	✓			
4.71827	117.51126	RR2	C1	25	2012	✓			
4.71834	117.51128	RR2	C2	0	2012	✓			
4.71835	117.51109	RR2	C3	10	2012	✓			
4.71839	117.51097	RR2	C4	0	2012	✓			
4.71859	117.51090	RR2	C5	15	2012	✓			
4.67981	117.45829	RR20	C1	25	2012	✓			
4.67977	117.45833	RR20	C2	0	2012	✓			
4.67972	117.45812	RR20	C3	10	2012	✓			
4.67953	117.45804	RR20	C4	0	2012	✓			
4.67940	117.45818	RR20	C5	15	2012	✓			
4.62625	117.51706	RR21	C1	25	2012	✓			

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.62654	117.51717	RR21	C2	0	2012	✓			
4.62646	117.51721	RR21	C3	10	2012	✓			
4.62645	117.51750	RR21	C4	0	2012	✓			
4.62659	117.51745	RR21	C5	15	2012	✓			
4.67568	117.50799	RR3	C1	25	2012	✓			
4.67556	117.50796	RR3	C2	0	2012	✓			
4.67563	117.50780	RR3	C3	10	2012	✓			
4.67536	117.50761	RR3	C4	0	2012	✓			
4.67529	117.50772	RR3	C5	15	2012	✓			
4.66438	117.45114	RR4	C1	25	2012	✓			
4.66446	117.45121	RR4	C2	0	2012	✓			
4.66419	117.45110	RR4	C3	10	2012	✓			
4.66390	117.45117	RR4	C4	0	2012	✓			
4.66383	117.45123	RR4	C5	15	2012	✓			
4.60353	117.53389	RR6	C1	25	2012	✓			
4.60338	117.53380	RR6	C2	0	2012	✓			
4.60362	117.53369	RR6	C3	10	2012	✓			
4.60371	117.53345	RR6	C4	0	2012	✓			
4.60357	117.53338	RR6	C5	15	2012	✓			
4.65643	117.59552	RR7	C1	25	2012	✓			
4.65668	117.59562	RR7	C2	0	2012	✓			
4.65631	117.59571	RR7	C3	10	2012	✓			
4.65606	117.59584	RR7	C4	0	2012	✓			
4.65627	117.59600	RR7	C5	15	2012	✓			
4.66212	117.61495	RR7B	C1	25	2012	✓			
4.66205	117.61507	RR7B	C2	0	2012	✓			
4.66223	117.61505	RR7B	C3	10	2012	✓			
4.66250	117.61533	RR7B	C4	0	2012	✓			
4.66243	117.61542	RR7B	C5	15	2012	✓			
4.67851	117.63887	RR7C	C1	25	2012	✓			
4.67862	117.63898	RR7C	C2	0	2012	✓			
4.67844	117.63910	RR7C	C3	10	2012	✓			
4.67829	117.63934	RR7C	C4	0	2012	✓			
4.67846	117.63943	RR7C	C5	15	2012	✓			
4.59180	117.58159	RR8	C1	25	2012	✓			
4.59173	117.58180	RR8	C2	0	2012	✓			

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.59162	117.58168	RR8	C3	10	2012	✓			
4.59150	117.58186	RR8	C4	0	2012	✓			
4.59167	117.58185	RR8	C5	15	2012	✓			
4.64991	117.54134	VJR	C1	25	2012	✓			
4.65011	117.54135	VJR	C2	0	2012	✓			
4.64995	117.54161	VJR	C3	10	2012	✓			
4.65018	117.54174	VJR	C4	0	2012	✓			
4.65031	117.54167	VJR	C5	15	2012	✓			
4.75635	117.54347	RR1	0 m	0	2012		✓		
4.75785	117.53485	RR1	1000 m	0	2012		✓		
4.75606	117.54181	RR1	200 m	0	2012		✓		
4.75698	117.53921	RR1	500 m	0	2012		✓		
4.64046	117.53483	RR10	0 m	0	2012		✓		
4.63361	117.52990	RR10	1000 m	0	2012		✓		
4.63874	117.53476	RR10	200 m	0	2012		✓		
4.63670	117.53354	RR10	500 m	0	2012		✓		
4.69411	117.52311	RR18	0 m	0	2012		✓		
4.69896	117.51558	RR18	1000 m	0	2012		✓		
4.69568	117.52232	RR18	200 m	0	2012		✓		
4.69724	117.52021	RR18	500 m	0	2012		✓		
4.65659	117.59544	RR7	0 m	0	2012		✓		
4.65741	117.60426	RR7	1000 m	0	2012		✓		
4.65648	117.59709	RR7	200 m	0	2012		✓		
4.65539	117.59959	RR7	500 m	0	2012		✓		
4.70042	117.57303	0m	A	0	2012			✓	
4.70070	117.57316	0m	B	0	2012			✓	
4.70096	117.57318	0m	C	0	2012			✓	
4.70123	117.57315	0m	D	0	2012			✓	
4.70157	117.57293	0m	E	0	2012			✓	
4.70170	117.57273	0m	F	0	2012			✓	
4.70204	117.57292	0m	G	0	2012			✓	
4.70225	117.57290	0m	H	0	2012			✓	
4.70250	117.57283	0m	I	0	2012			✓	
4.70275	117.57282	0m	J	0	2012			✓	

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.70292	117.57286	0m	K	0	2012			✓	
4.70315	117.57296	0m	L	0	2012			✓	
4.71451	117.64015	120m	A	0	2012			✓	
4.71474	117.64025	120m	B	0	2012			✓	
4.71500	117.64026	120m	C	0	2012			✓	
4.71530	117.64022	120m	D	0	2012			✓	
4.71552	117.64011	120m	E	0	2012			✓	
4.71591	117.64022	120m	F	0	2012			✓	
4.71609	117.64043	120m	G	0	2012			✓	
4.71624	117.64066	120m	H	0	2012			✓	
4.71625	117.64094	120m	I	0	2012			✓	
4.71645	117.64111	120m	L	0	2012			✓	
4.71413	117.63972	120m	Y	0	2012			✓	
4.71422	117.64003	120m	Z	0	2012			✓	
4.65127	117.57651	15m	A	0	2012			✓	
4.72470	117.62145	30m	A	0	2012			✓	
4.72474	117.62171	30m	B	0	2012			✓	
4.72462	117.62203	30m	C	0	2012			✓	
4.72472	117.62236	30m	D	0	2012			✓	
4.72479	117.62272	30m	E	0	2012			✓	
4.72516	117.62241	30m	F	0	2012			✓	
4.72548	117.62242	30m	G	0	2012			✓	
4.72569	117.62256	30m	H	0	2012			✓	
4.72567	117.62283	30m	I	0	2012			✓	
4.72578	117.62307	30m	J	0	2012			✓	
4.72601	117.62317	30m	K	0	2012			✓	
4.72626	117.62328	30m	L	0	2012			✓	
4.72462	117.62189	30m	M	0	2012			✓	
4.72483	117.62174	30m	N	0	2012			✓	
4.72486	117.62144	30m	O	0	2012			✓	
4.70866	117.54985	5m	A	0	2012			✓	
4.70851	117.55005	5m	B	0	2012			✓	
4.70842	117.55045	5m	C	0	2012			✓	
4.70803	117.55026	5m	D	0	2012			✓	
4.70797	117.55051	5m	E	0	2012			✓	
4.70775	117.55066	5m	f	0	2012			✓	

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.70767	117.55091	5m	G	0	2012			✓	
4.70755	117.55118	5m	H	0	2012			✓	
4.70757	117.55140	5m	I	0	2012			✓	
4.70761	117.55165	5m	J	0	2012			✓	
4.70740	117.55192	5m	K	0	2012			✓	
4.70784	117.55207	5m	L	0	2012			✓	
4.68668	117.45583	OP1	A	0	2012			✓	
4.68696	117.45577	OP1	B	0	2012			✓	
4.68715	117.45554	OP1	C	0	2012			✓	
4.68740	117.45535	OP1	D	0	2012			✓	
4.68770	117.45525	OP1	E	0	2012			✓	
4.68788	117.45506	OP1	F	0	2012			✓	
4.68810	117.45490	OP1	G	0	2012			✓	
4.68816	117.45464	OP1	H	0	2012			✓	
4.68819	117.45436	OP1	I	0	2012			✓	
4.68818	117.45407	OP1	J	0	2012			✓	
4.68806	117.45383	OP1	K	0	2012			✓	
4.68818	117.45356	OP1	L	0	2012			✓	
4.68822	117.45326	OP1	M	0	2012			✓	
4.68830	117.45300	OP1	N	0	2012			✓	
4.68852	117.45282	OP1	O	0	2012			✓	
4.61252	117.54553	OP10	A	0	2012			✓	
4.61275	117.54533	OP10	B	0	2012			✓	
4.61290	117.54518	OP10	C	0	2012			✓	
4.61310	117.54501	OP10	D	0	2012			✓	
4.61331	117.54486	OP10	E	0	2012			✓	
4.61339	117.54459	OP10	F	0	2012			✓	
4.61325	117.54437	OP10	G	0	2012			✓	
4.61333	117.54412	OP10	H	0	2012			✓	
4.61347	117.54391	OP10	I	0	2012			✓	
4.61357	117.54366	OP10	J	0	2012			✓	
4.61382	117.54355	OP10	K	0	2012			✓	
4.61388	117.54330	OP10	L	0	2012			✓	
4.67396	117.61728	OP11	A	0	2012			✓	
4.67426	117.61710	OP11	B	0	2012			✓	
4.67461	117.61683	OP11	C	0	2012			✓	

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.67491	117.61706	OP11	D	0	2012			✓	
4.67536	117.61675	OP11	E	0	2012			✓	
4.67575	117.61686	OP11	F	0	2012			✓	
4.67605	117.61692	OP11	G	0	2012			✓	
4.67635	117.61692	OP11	H	0	2012			✓	
4.67657	117.61676	OP11	I	0	2012			✓	
4.67673	117.61652	OP11	J	0	2012			✓	
4.67697	117.61640	OP11	K	0	2012			✓	
4.67710	117.61617	OP11	L	0	2012			✓	
4.61098	117.45071	OP2	A	0	2012			✓	
4.61109	117.45099	OP2	B	0	2012			✓	
4.61116	117.45127	OP2	C	0	2012			✓	
4.61126	117.45154	OP2	D	0	2012			✓	
4.61145	117.45185	OP2	E	0	2012			✓	
4.61163	117.45205	OP2	F	0	2012			✓	
4.61189	117.45217	OP2	G	0	2012			✓	
4.61214	117.45231	OP2	H	0	2012			✓	
4.61239	117.45243	OP2	I	0	2012			✓	
4.61264	117.45254	OP2	J	0	2012			✓	
4.61288	117.45264	OP2	K	0	2012			✓	
4.61314	117.45272	OP2	L	0	2012			✓	
4.59456	117.46469	OP3	A	0	2012			✓	
4.59476	117.46490	OP3	B	0	2012			✓	
4.59498	117.46511	OP3	C	0	2012			✓	
4.59511	117.46539	OP3	D	0	2012			✓	
4.59547	117.46589	OP3	E	0	2012			✓	
4.59576	117.46589	OP3	F	0	2012			✓	
4.59602	117.46592	OP3	G	0	2012			✓	
4.59631	117.46581	OP3	H	0	2012			✓	
4.59648	117.46558	OP3	I	0	2012			✓	
4.59643	117.46533	OP3	J	0	2012			✓	
4.59635	117.46505	OP3	K	0	2012			✓	
4.59660	117.46492	OP3	L	0	2012			✓	
4.55825	117.49368	OP4	A	0	2012			✓	
4.55835	117.49343	OP4	B	0	2012			✓	
4.55844	117.49319	OP4	C	0	2012			✓	

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.55855	117.49292	OP4	D	0	2012			✓	
4.55853	117.49267	OP4	E	0	2012			✓	
4.55859	117.49238	OP4	F	0	2012			✓	
4.55873	117.49215	OP4	G	0	2012			✓	
4.55882	117.49185	OP4	H	0	2012			✓	
4.55872	117.49161	OP4	I	0	2012			✓	
4.55863	117.49136	OP4	J	0	2012			✓	
4.55835	117.49138	OP4	K	0	2012			✓	
4.55810	117.49138	OP4	L	0	2012			✓	
4.63307	117.58886	OP5	A	0	2012			✓	
4.63285	117.58895	OP5	B	0	2012			✓	
4.63268	117.58906	OP5	C	0	2012			✓	
4.63242	117.58912	OP5	d	0	2012			✓	
4.63212	117.58910	OP5	e	0	2012			✓	
4.63186	117.58926	OP5	f	0	2012			✓	
4.63196	117.58956	OP5	g	0	2012			✓	
4.63176	117.58979	OP5	h	0	2012			✓	
4.63161	117.59004	OP5	i	0	2012			✓	
4.63139	117.59019	OP5	j	0	2012			✓	
4.63125	117.59040	OP5	k	0	2012			✓	
4.63102	117.59046	OP5	l	0	2012			✓	
4.60277	117.61654	OP9	A	0	2012			✓	
4.60286	117.61678	OP9	B	0	2012			✓	
4.60304	117.61699	OP9	C	0	2012			✓	
4.60312	117.61724	OP9	D	0	2012			✓	
4.60336	117.61743	OP9	E	0	2012			✓	
4.60345	117.61768	OP9	F	0	2012			✓	
4.60352	117.61794	OP9	G	0	2012			✓	
4.60353	117.61821	OP9	H	0	2012			✓	
4.60355	117.61851	OP9	I	0	2012			✓	
4.60354	117.61895	OP9	J	0	2012			✓	
4.60366	117.61920	OP9	K	0	2012			✓	
4.60387	117.61900	OP9	L	0	2012			✓	
4.74609	117.52560	RR1	A	0	2012			✓	
4.74601	117.52585	RR1	B	0	2012			✓	
4.74592	117.52613	RR1	C	0	2012			✓	

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.74605	117.52639	RR1	D	0	2012			✓	
4.74614	117.52664	RR1	E	0	2012			✓	
4.74616	117.52693	RR1	F	0	2012			✓	
4.74608	117.52718	RR1	G	0	2012			✓	
4.74612	117.52745	RR1	H	0	2012			✓	
4.74637	117.52755	RR1	I	0	2012			✓	
4.74669	117.52751	RR1	J	0	2012			✓	
4.74700	117.52744	RR1	K	0	2012			✓	
4.74720	117.52724	RR1	L	0	2012			✓	
4.57094	117.61968	RR12	A	0	2012			✓	
4.57090	117.61999	RR12	B	0	2012			✓	
4.57072	117.62019	RR12	C	0	2012			✓	
4.57045	117.62029	RR12	D	0	2012			✓	
4.57018	117.62033	RR12	E	0	2012			✓	
4.56989	117.62029	RR12	F	0	2012			✓	
4.56962	117.62012	RR12	G	0	2012			✓	
4.56938	117.62007	RR12	H	0	2012			✓	
4.56909	117.62024	RR12	I	0	2012			✓	
4.56883	117.62021	RR12	J	0	2012			✓	
4.56863	117.62028	RR12	K	0	2012			✓	
4.56853	117.62051	RR12	L	0	2012			✓	
4.67478	117.50697	RR3	A	0	2012			✓	
4.67475	117.50667	RR3	B	0	2012			✓	
4.67486	117.50648	RR3	C	0	2012			✓	
4.67490	117.50615	RR3	D	0	2012			✓	
4.67495	117.50571	RR3	E	0	2012			✓	
4.67490	117.50540	RR3	F	0	2012			✓	
4.67504	117.50520	RR3	G	0	2012			✓	
4.67516	117.50499	RR3	H	0	2012			✓	
4.67530	117.50473	RR3	I	0	2012			✓	
4.67554	117.50458	RR3	J	0	2012			✓	
4.67558	117.50431	RR3	K	0	2012			✓	
4.67567	117.50406	RR3	L	0	2012			✓	
4.66432	117.45293	RR4	A	0	2012			✓	
4.66395	117.45273	RR4	B	0	2012			✓	
4.66380	117.45266	RR4	C	0	2012			✓	

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.66484	117.45342	RR4	D	0	2012			✓	
4.66522	117.45339	RR4	E	0	2012			✓	
4.66398	117.45174	RR4	F	0	2012			✓	
4.66367	117.45161	RR4	G	0	2012			✓	
4.66348	117.45141	RR4	H	0	2012			✓	
4.66369	117.45114	RR4	I	0	2012			✓	
4.66424	117.45199	RR4	J	0	2012			✓	
4.66434	117.45227	RR4	L	0	2012			✓	
4.66471	117.45318	RR4	Z	0	2012			✓	
4.57011	117.50198	RR5	A	0	2012			✓	
4.56983	117.50196	RR5	B	0	2012			✓	
4.56952	117.50173	RR5	C	0	2012			✓	
4.56939	117.50145	RR5	D	0	2012			✓	
4.56941	117.50106	RR5	E	0	2012			✓	
4.56946	117.50083	RR5	f	0	2012			✓	
4.56947	117.50053	RR5	g	0	2012			✓	
4.56960	117.50028	RR5	h	0	2012			✓	
4.56960	117.50004	RR5	i	0	2012			✓	
4.56944	117.49985	RR5	j	0	2012			✓	
4.56926	117.49965	RR5	k	0	2012			✓	
4.57041	117.50189	RR5	z	0	2012			✓	
4.60327	117.53466	RR6	A	0	2012			✓	
4.60334	117.53438	RR6	B	0	2012			✓	
4.60349	117.53402	RR6	C	0	2012			✓	
4.60361	117.53379	RR6	D	0	2012			✓	
4.60371	117.53352	RR6	E	0	2012			✓	
4.60371	117.53328	RR6	F	0	2012			✓	
4.60375	117.53294	RR6	G	0	2012			✓	
4.60375	117.53260	RR6	H	0	2012			✓	
4.60391	117.53237	RR6	I	0	2012			✓	
4.60377	117.53206	RR6	J	0	2012			✓	
4.60370	117.53174	RR6	K	0	2012			✓	
4.60358	117.53151	RR6	L	0	2012			✓	
4.66043	117.60756	RR7	A	0	2012			✓	
4.66046	117.60784	RR7	B	0	2012			✓	
4.66060	117.60808	RR7	C	0	2012			✓	

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.66047	117.60832	RR7	D	0	2012			✓	
4.66017	117.60843	RR7	E	0	2012			✓	
4.65999	117.60862	RR7	F	0	2012			✓	
4.65982	117.60876	RR7	G	0	2012			✓	
4.65979	117.60897	RR7	H	0	2012			✓	
4.65994	117.60918	RR7	I	0	2012			✓	
4.66018	117.60929	RR7	J	0	2012			✓	
4.66040	117.60949	RR7	K	0	2012			✓	
4.66061	117.60969	RR7	L	0	2012			✓	
4.59135	117.58241	RR8	A	0	2012			✓	
4.59158	117.58224	RR8	B	0	2012			✓	
4.59164	117.58198	RR8	C	0	2012			✓	
4.59153	117.58180	RR8	D	0	2012			✓	
4.59143	117.58156	RR8	E	0	2012			✓	
4.59177	117.58151	RR8	F	0	2012			✓	
4.59204	117.58159	RR8	G	0	2012			✓	
4.59216	117.58133	RR8	H	0	2012			✓	
4.59219	117.58112	RR8	I	0	2012			✓	
4.59222	117.58088	RR8	J	0	2012			✓	
4.59210	117.58066	RR8	K	0	2012			✓	
4.59115	117.58249	RR8	Z	0	2012			✓	
4.65086	117.62710	RR9	A	0	2012			✓	
4.65083	117.62680	RR9	B	0	2012			✓	
4.65070	117.62660	RR9	C	0	2012			✓	
4.65063	117.62632	RR9	D	0	2012			✓	
4.65055	117.62608	RR9	E	0	2012			✓	
4.65060	117.62586	RR9	F	0	2012			✓	
4.65077	117.62573	RR9	G	0	2012			✓	
4.65101	117.62532	RR9	H	0	2012			✓	
4.65117	117.62506	RR9	I	0	2012			✓	
4.65122	117.62482	RR9	J	0	2012			✓	
4.65124	117.62453	RR9	K	0	2012			✓	
4.65136	117.62429	RR9	L	0	2012			✓	
4.65089	117.53966	VJR	F	0	2012			✓	
4.65095	117.53932	VJR	G	0	2012			✓	
4.65131	117.53923	VJR	H	0	2012			✓	

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.65136	117.53886	VJR	I	0	2012			✓	
4.65162	117.53877	VJR	J	0	2012			✓	
4.65190	117.53891	VJR	K	0	2012			✓	
4.65216	117.53911	VJR	L	0	2012			✓	
4.65229	117.53890	VJR	M	0	2012			✓	
4.65234	117.53849	VJR	N	0	2012			✓	
4.65225	117.53868	VJR	O	0	2012			✓	
4.65245	117.53839	VJR	P	0	2012			✓	
4.65247	117.53813	VJR	Q	0	2012			✓	
4.58058	117.47339	VJR2	A	0	2012			✓	
4.58081	117.47350	VJR2	B	0	2012			✓	
4.58107	117.47357	VJR2	C	0	2012			✓	
4.58119	117.47373	VJR2	D	0	2012			✓	
4.58133	117.47391	VJR2	E	0	2012			✓	
4.58108	117.47400	VJR2	F	0	2012			✓	
4.58103	117.47422	VJR2	G	0	2012			✓	
4.58108	117.47449	VJR2	H	0	2012			✓	
4.58117	117.47479	VJR2	I	0	2012			✓	
4.58137	117.47491	VJR2	J	0	2012			✓	
4.58138	117.47520	VJR2	K	0	2012			✓	
4.58147	117.47547	VJR2	L	0	2012			✓	
4.67428	117.61745	OP11	1	NA	2012				✓
4.67463	117.61740	OP11	2	NA	2012				✓
4.67496	117.61743	OP11	6	NA	2012				✓
4.60329	117.53277	RR6	3	NA	2012				✓
4.60320	117.53331	RR6	4	NA	2012				✓
4.60303	117.53376	RR6	5	NA	2012				✓
4.74548	117.52573	RR1	7	NA	2012				✓
4.74570	117.52608	RR1	8	NA	2012				✓
4.74569	117.52644	RR1	9	NA	2012				✓
4.67425	117.50773	RR3	10	NA	2012				✓
4.67444	117.50734	RR3	11	NA	2012				✓
4.67431	117.50691	RR3	12	NA	2012				✓
4.68672	117.45511	OP1	13	NA	2012				✓
4.68698	117.45544	OP1	14	NA	2012				✓
4.68682	117.45577	OP1	15	NA	2012				✓

latitude	longitude	site	transect	distance from river	year	dung baited pitfalls	flight intercept trap	ant bait removal observation	palm frond herbivory assesment
4.66435	117.45173	RR4	16	NA	2012				✓
4.66454	117.45212	RR4	17	NA	2012				✓
4.66426	117.45139	RR4	18	NA	2012				✓
4.55837	117.49344	OP4	19	NA	2012				✓
4.55774	117.49257	OP4	20	NA	2012				✓
4.55808	117.49300	OP4	21	NA	2012				✓
4.56884	117.50136	RR5	22	NA	2012				✓
4.56891	117.50092	RR5	23	NA	2012				✓
4.56911	117.50045	RR5	24	NA	2012				✓
4.61275	117.54570	OP10	25	NA	2012				✓
4.61314	117.54545	OP10	26	NA	2012				✓
4.61361	117.54544	OP10	27	NA	2012				✓
4.59248	117.58251	RR8	28	NA	2012				✓
4.59273	117.58205	RR8	29	NA	2012				✓
4.59286	117.58156	RR8	30	NA	2012				✓
4.57139	117.61978	RR12	31	NA	2012				✓
4.57112	117.62018	RR12	32	NA	2012				✓
4.57076	117.62047	RR12	33	NA	2012				✓
4.60028	117.61753	OP9	34	NA	2012				✓
4.60020	117.61800	OP9	35	NA	2012				✓
4.60030	117.61852	OP9	36	NA	2012				✓
4.63095	117.59082	OP5	37	NA	2012				✓
4.63140	117.59072	OP5	38	NA	2012				✓
4.63181	117.59050	OP5	39	NA	2012				✓
4.66019	117.60803	RR7	40	NA	2012				✓
4.65945	117.60860	RR7	41	NA	2012				✓
4.65985	117.60967	RR7	42	NA	2012				✓