Ecology and conservation of bat species in the Western Ghats of India

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The candidate confirms that the work submitted is her own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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The lesser dog faced fruit bat *Cynopterus brachyotis* eating a banana.

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Abstract

The Western Ghats of India are a globally important biodiversity hotspot, but around 90 % of the land has been converted to agriculture. Little is known about how bats respond to the conversion of native rainforest to different plantation types in the Western Ghats. This thesis examines the response of bats to coffee and tea plantations, and to riparian habitats, in the southern Western Ghats.

Most bat assemblages in the tropics have been studied by catching bats, but many studies have shown that catching alone can give biased and incomplete results. In order to use acoustic data as well as catching data in this landscape I made a library of the echolocation calls of fifteen echolocating species in the landscape. Comparisons of the data from each method showed that combining catching and acoustic data gave the most complete picture of the assemblage, but that acoustic data alone detected more species than catching data alone.

Acoustic and catching data were used to build habitat suitability models for ten species. Scales of 100 m – 500 m were the most important for predicting bat presence. Several species showed a positive response to habitats containing native trees and habitat richness, and a negative response to tea plantations and distance to water.

Coffee plantations did not differ significantly from forest fragments in terms of bat species or abundance, but did differ in species composition. Bat assemblages in coffee plantations were functionally very similar to those in forest fragments. Tea plantations had the lowest bat species richness of all habitats and differed in species composition from all other habitats. Bat assemblages in tea plantations had lower functional richness and specialisation than other habitats, and the bats remaining were open-adapted species.

Rivers with riparian corridors did not have significantly greater bat species richness than rivers without corridors, but differed functionally in several ways. Rivers without riparian corridors had reduced functional specialisation and functional divergence. Rivers with riparian corridors supported more forest adapted species than rivers without riparian corridors.

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Chapter One: General Introduction

1.1 Scope

This research is focussed on describing a previously unstudied bat assemblage in the biodiversity hotspot of the Western Ghats of India, and understanding the response of this assemblage to forest fragmentation and conversion to agriculture. This research will inform our understanding of the relative conservation value of different modified land uses for bats, and identify which bat species may be at risk of population decline. This introductory chapter briefly describes issues around tropical forest loss and conservation in agricultural areas. It discusses the importance of bats in ecosystem function and reviews the literature on the response of bats to habitat loss and fragmentation in the tropics. The methodological biases in the study of bats are described, and how these biases have particularly affected tropical studies. The primary methods used in this thesis are examined; echolocation call libraries, habitat suitability modelling and functional diversity. Finally, the study area is introduced and the thesis aims stated.

1.2 Tropical forest loss

Tropical forests cover only around 7% of the land area of the planet, but are thought to contain in the region of two thirds of all species (Laurance 1999, Dirzo and Raven 2003). This makes them one of the most important habitats on Earth for biodiversity and ecosystem services and thus a focal habitat for conservation studies. These forests are under great threat from growing human populations and the pressures these create (Gardner et al. 2010). Estimated annual rainforest loss was an average of 9.34 million hectares per year between 2000 and 2010 (FAOSTAT 2014), and deforestation rates are proportionally highest in Asia where it is estimated that over 40% of rainforests have already been destroyed (Wright 2005).

Habitat loss and degradation were considered by the IUCN to be the greatest threat to biodiversity worldwide, predicted to pose a greater threat to terrestrial ecosystems even than some of the worst case global warming scenarios, especially in the tropics (Sala et al. 2000, IUCN 2010). Threats were analysed for a sample of threatened mammals, birds and amphibians, and habitat loss/degradation affected 86%, 86% and

88% of each sample taxa respectively (IUCN 2010). Predictions inevitably vary, but only 5-10% of original tropical forest may survive the next 50 years, causing the loss of potentially 75% of forest species, 90% of which are probably unknown to science (Dirzo and Raven 2003). Habitat loss, degradation and fragmentation in the tropics are a serious matter, and ways to mitigate the effects of these threats are needed.

1.3 Conserving biodiversity outside protected areas

Protected areas have long been a key strategy in conservation, and have had some notable successes in protecting biodiversity. As of 2003, 11.5% of the land surface of Earth was covered by protected areas (PAs), outstripping the 10% target set in 1993 for 9 out of 14 terrestrial biomes (Rodrigues et al. 2004). While protected areas clearly play an important role in biodiversity conservation, there are many species that fall through the ‘gaps’ and do not occur in any of the current PAs (Rodrigues et al. 2004). In a detailed analysis of South East Asia 52-59 % of mammal species were not adequately represented in protected areas (Catullo et al. 2008). Bats were one of the two orders least well protected by PAs – only a third of bat species, and only 16% of threatened bat species, receive adequate protected area coverage in South East Asia (Catullo et al. 2008). Even for species that fall within protected areas extinction debt could come into play, where species will go extinct in the future due to current or previous events such as land clearing reducing population sizes to below critical thresholds. This has been recognised as a major factor in the ongoing extinction crisis (Cardillo et al. 2006).

Furthermore, the effectiveness of conservation measures and law enforcement varies greatly. Very few protected areas receive the highest levels of protection, and many protected areas are almost certainly too small and isolated to contain viable populations of many species (Dirzo and Raven 2003, Rodrigues et al. 2004). Designating PAs can exacerbate deforestation in surrounding areas, which can affect the health of the protected area itself (Ewers and Rodrigues 2008, Laurance et al. 2012). According to a reserve-health index calculated by Laurance et al. (2012), about four fifths of all tropical forest reserves were declining in overall health, and for half of these the decline was relatively serious. With human populations expanding and requiring more land for urban areas and agriculture, it is unlikely that enough new PAs can be created or that existing ones can be expanded; indeed, the rate of creation of new tropical protected areas has been falling since the 1980s (Dirzo and Raven 2003). Evidently new strategies must be tested and implemented.

One such strategy is the ‘silver bullet’ approach of conserving the areas of the world with the highest biodiversity: ‘biodiversity hotspots’ (Myers et al. 2000). Twenty five hotspots were identified that between them contain 44% of vascular plants and 35% of mammals, birds, reptiles and amphibians, and in terms of remaining natural vegetation, cover 1.4% of the Earth’s land surface (Myers et al. 2000, Dirzo and Raven 2003). The Western Ghats of India are one of the eight ‘hottest’ of these hotspots, but, like most of the hotspots, little original vegetation remains – on average each hotspot has lost over 85% of primary vegetation (the Western Ghats has only 6.3% primary vegetation) (Bawa et al. 2007, Sloan et al. 2014). Only 38% of natural vegetation across the world’s hotspots is protected to some degree – often more in theory than in practice (Myers et al. 2000).

The biodiversity hotspot approach is certainly a useful way of prioritizing action and resources, and more evidence based than previous approaches focussing on saving charismatic fauna, but it misses several key points (Bradshaw et al. 2009). Chief among them is the importance of ecosystem services and ecosystem function; most areas of the Earth are now modified by humans to a greater or lesser extent and much biodiversity exists in agricultural or even urban areas. Functioning ecosystems need to be preserved not just in the protected 11.5% of the world’s land surface, but across all of it; not only for their own sake but for the sake of food and water security, climate regulation, flood and drought control, disease regulation and clean air - among many others (Kareiva and Marvier 2007). Maintaining a healthy environment is considered by the UNEP (United Nations Environment Program) to be key to reducing global rural poverty (Kareiva and Marvier 2007). Yet the Millenium Ecosystem Assessment found most ecosystem services to have declined, and stated that they are being used unsustainably (Millennium Ecosystem Assessment 2005). We cannot realistically return to a world of pristine wilderness, so, while we should certainly protect what wilderness is left, maximising the ecosystem function and biodiversity of fragmented and agricultural areas and even urban areas is going to be an increasingly important conservation strategy (Kareiva and Marvier 2007, Bradshaw et al. 2009).

Much remains to be learnt about the potential for biodiversity in different agricultural landscapes, but there is work underway to change this (Daily 2001, Benton et al. 2003, Faria et al. 2006, Barlow et al. 2007). There is a slow move away from seeing all converted habitat as completely destroyed, especially as it becomes that clear even large habitat patches are not extinction proof if they are isolated (Ferraz et al. 2003). Indeed, some of the major drivers of how well protected tropical forest areas protect biodiversity are environmental changes occurring immediately outside the reserve. Among the worst offenders are decreased forest cover, increased logging and increased fires outside protected areas, with 85% of tropical forest reserves experiencing a decline in forest cover in the surrounding area over the past 2-3 decades (Laurance et al. 2012). This can seriously affect reserve health, and points to the need for increasing the biodiversity potential of areas adjacent to reserves. To have any hope of averting local and regional extinctions, there needs to be an understanding of how different species can utilise the agricultural matrices between habitat fragments (Vandermeer and Perfecto 2007).

Focussing on these modified habitats does not replace the need for protected areas, but complements them; working out how to maintain more biodiversity and better ecosystem functioning in unprotected areas means greater connectivity between protected areas and more potential source populations of species which will act as buffers against extinctions, as well as providing ecosystem services in agricultural land. There is great debate about ‘land sparing’ (leaving some areas pristine while intensively farming others), versus ‘land sharing’ (less intensive farming in a more heterogeneous, wildlife friendly landscape, on a regional scale). It seems that both protected areas and connecting areas of permeable matrix are needed to support meta-populations and give biodiversity any hope of moving with a changing climate. While primary forest is irreplaceable (Gibson et al. 2011), an agricultural landscape with many forest fragments and agroforestry plantations can support a lot of biodiversity (Mendenhall et al. 2014). Evidently, not all human modified landscapes will have the same potential for biodiversity conservation, and different landscape changes will be to the benefit or detriment of different species, so a careful assessment needs to be made for different areas as to their current conservation value and how this may be improved (Melo et al. 2013). As agricultural landscapes increasingly dominate the earth, understanding species, assemblage and ecosystem level responses to agricultural systems will be critical in developing strategies to avoid ecosystem collapse (Mendenhall et al. 2014).

1.4 Why are bats important in tropical ecosystems?

1.4.1 Pollinators and seed dispersers

Bats are the second most species rich order of mammals, and represent up to 40% of mammals in many tropical ecosystems (Emmons 1997). They undertake a range of ecosystem services, including seed dispersal, pollination and insect control. A variety of ecologically and commercially important plants rely on bats to some degree as a pollinator or seed disperser, including durian, mangoes, bananas, shea butter, *Coffea arabica*, figs and *Agave tequilana*, the source of commercial tequila (Kunz et al. 2011). In neotropical rainforests, many of the plant species that bats pollinate and disperse are pioneer species (Arteaga et al. 2006); it is estimated that 12-30% of native rainforest plant species may lose their seed dispersers in fragmented landscapes, with serious consequences for the ecosystem (Moran et al. 2009).

In the neotropics, 549 species of plant in 191 genera are known to have their seeds dispersed by bats; pteropodid bats in the palaeotropics disperse seeds of at least 139 genera (Lobova et al. 2009; Mickleburgh et al. 1992). Bats can be even more effective seed dispersers than birds, as they defecate while flying rather than while perching, so spread the seeds more widely, and spit out pellets or ‘spats’ containing fruit seeds (Arteaga et al. 2006). They are critically important pollinators of many Cactaceae and Agave (Rocha et al. 2006).

Fragmentation is likely to impact the ability of bats to provide ecosystem services, which could have serious implications for forest functioning. For example, fewer seed species have been found in *Pteropus rufus* faeces in disturbed or agricultural areas (Jenkins et al. 2007); and the distance that seeds are dispersed may rely on high population densities, such as in *Pteropus tonganus* where intraspecific aggression causes individuals to fly further from the parent tree (McConkey and Drake 2006).

Some species, e.g. *Musonycteris harrisoni* in the neotropics are not adapted for long flights in open areas, with attendant consequences for the plants they pollinate or disperse seeds for (Stoner et al. 2002).

An estimate on the financial value of the pollination and seed dispersal services undertaken by bats has not been made. Many of the plants that bats support have unmeasured economic value, especially those consumed and traded on a local scale, and the degree to which bats are necessary as pollinators/seed dispersers is unknown for many of these species (Kunz et al. 2011).

1.4.2 Pest control

There are over 1,200 species of bat, and of those over two thirds are insectivorous to some degree (Kunz et al. 2011). Bats, especially pregnant and lactating females which have very high energy demands, can eat large numbers of arthropods. At peak lactation, it is estimated that a female *Myotis lucifugus* consumes around 125% of her body mass per night (Kurta et al. 1989); a maternity colony of one million Brazilian free-tailed bats consumes in the region of 8.4 metric tons of insects in a night (Kunz et al. 2011). Many of the species consumed are agricultural pests and disease vectors (Kunz et al. 2011). With insects increasingly developing pesticide resistance, biological controls may become more important (Kunz et al. 2011). The estimated global value of pest control is between $54 billion and $1 trillion annually, of which bats are likely to contribute a substantial portion (Naylor 1997). The contribution of bats to pest control has only recently started to be assessed, but it may have been significantly underappreciated. A recent estimate of the value of insectivorous bats to US agriculture was US$ 22.9 billion per year (Boyles et al. 2011) – about 16 % of the approximately US$ 143 billion earned from crops every year in the US according to the USDA National Agricultural Statistics Service data from 2013.

In a neotropical coffee agroforest, bats had a non-significant effect on arthropod density in the dry season, but in the wet season there was an 84% increase in arthropod density in areas from which bats alone were excluded, a greater effect on arthropods than that of birds (Williams-Guillén et al. 2008). In a neotropical forest a similar system of nocturnal and diurnal exclosures also assessed the relative effects of bats and birds; bats had a stronger effect in reducing both arthropod abundance and herbivory (Kalka et al. 2008). Exclosure experiments such as these are likely to underestimate the effects of aerial insectivores hunting insects outside the exclosures, so these estimates may be conservative (Kunz et al. 2011). In cotton fields in an eight county region in Texas the impact of bat predation on agricultural pests was estimated to be $741,000 annually out of a $4.6-6.4 million annual cotton harvest (Cleveland et al. 2006).

Very little has been published in peer reviewed journals on the importance of bats to ecosystems across India, but both fruit bats and insectivorous bats almost certainly have crucial roles in many environments.

1.5 Threats to bats from habitat loss and fragmentation

Habitat loss and fragmentation affect most species globally, and all respond differently. While there has been some argument that effects of habitat fragmentation on bats are likely to be small, due to their high mobility (Estrada and Coates-Estrada 2002), others suggest that habitat loss and fragmentation may result in the loss of many bat species, primarily forest specialists (Estrada and Coates-Estrada, 2002; Faria 2006; Montiel et al. 2006). Indeed, 25% of bats are threatened with extinction or are already extinct (Jones et al. 2003).

Unusually for such small mammals, bats live a long time, mostly have just one or two young a year and may take a few years to reach sexual maturity; they are a ‘k-selected’ order. This is one of the factors leading to a high ‘latent extinction’ risk for bats– the difference between a species’ current extinction risk and the extinction risk on the basis of its biological traits. Extinction debt is the delay between a threat to a species occurring – such as habitat loss and fragmentation – and the eventual extinction of the species, a delay which can be as little as a few years or many thousands of years, although more usually a matter of decades (Dullinger et al. 2013). In areas of the world that have already been heavily modified by humans such as Western Europe, latent extinction risk is relatively low, but in other parts of the world the extinction debt has not yet been ‘paid’ and thus many species that are currently not threatened may become so in the future (Cardillo et al. 2006, Dullinger et al. 2013). Those areas with high human population density will see the greatest number of species declines and extinctions in coming decades (Cardillo et al. 2006), and thus areas undergoing current modification and experiencing high human pressure are likely to be where bat species will decline or go extinct in the future.

A recent review showed that bats in fragmented, agricultural landscapes do not respond in the same manner as bats on islands (Mendenhall et al. 2014). While bat assemblages on true islands surrounded by water followed typical species-area relationships, assemblages in forest fragments in agricultural landscapes did not, indicating that many bats are able to use the agricultural matrix to some degree. More studies showed the same species richness in forest fragments as compared to minimally disturbed forest than showed a reduced species richness in forest fragments (Figure 1.1). However, species richness may mask changes in species composition and/or the occurrence of trait filtering (Villéger et al. 2008). Most studies comparing minimally altered forest with forest fragments and/or agricultural habitats did show a shift in bat assemblage composition. Mendenhall et al. (2014) caught bats in an island system in the Panama Canal for comparison with forest fragments in a matrix of coffee plantations and pastures in Costa Rica. They found again that bat species richness on islands declined with isolation distance and increased with island size, but in the countryside ecosystem bat species richness and evenness were high across forest reserves and smaller forest fragments. This countryside ecosystem, while highly fragmented, did have around 40 % forest cover remaining. In ‘moderately’ fragmented landscapes there may be more habitats to exploit for generalists, or those that feed on early successional plants, but enough old growth forest to support specialist species. However most of these studies are from the neotropics, which have different ecosystems and different bat species to the palaeotropics, so it is hard to make many generalisations. It is also possible that in some studies the extinction debt for the area has not yet been paid.

Bats adapted to forage in dense vegetation are likely to be the worst affected by habitat loss and fragmentation, but the literature indicates that most foraging guilds rely on having some mature forest habitat in the landscape. Overall landscape composition and configuration are likely to have a larger effect on bat diversity than forest.

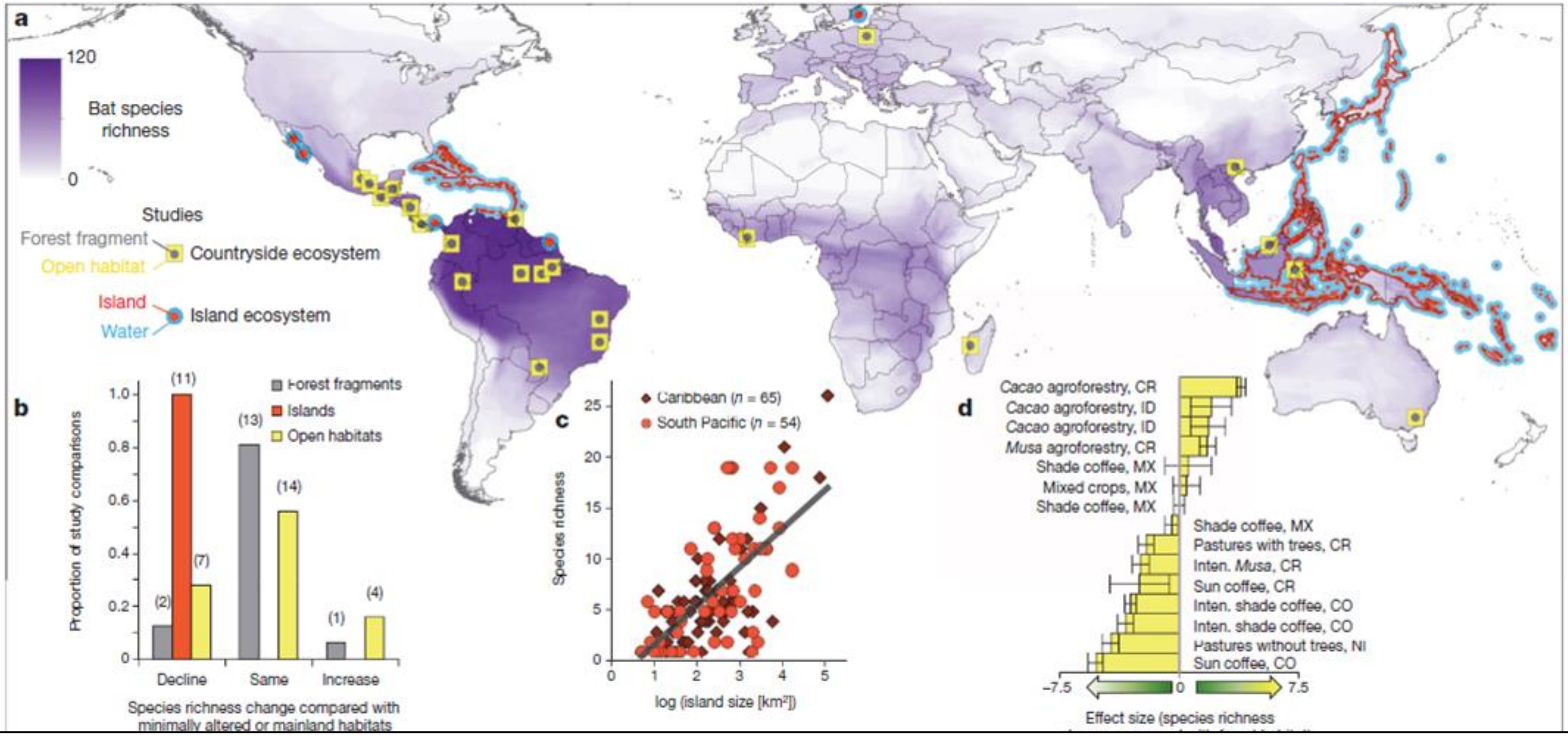

Figure 1.1: Bats in agroforestry and forest fragments globally. From Mendenhall et al., 2014. a) The locations of 52 bat species richness comparisons from 29 studies. In total, the studies represent more than 60% of all bat species globally. b) Island bat species richness always declined relative to the mainland or to larger islands in island ecosystems. In contrast, bat species richness in countryside forest fragments generally had the same number of species as minimally altered forest habitat. Bat species richness in open habitats compared to forest habitat varied. c) Bat species richness on islands in the Caribbean and South Pacific yielded a typical species–area relationship. d) Studies with enough information to calculate effect sizes demonstrated how some agricultural practices, such as agroforestry, support more bat biodiversity than more intensive agricultural practices. Effect size direction indicates species richness decline or increase compared to forest habitat, error bars represent 95% confidence intervals). Country code abbreviations: CR, Costa Rica; CO, Columbia; ID, Indonesia; MX, Mexico.

1.5.1 Forest fragment size

In accordance with island biogeography theory, where smaller islands retain less biodiversity, smaller forest fragments may also support fewer species. Reduced forest fragment size has been proposed to reduce the amount of food available for some species (Struebig et al. 2008), reduce availability of roosts (Struebig et al. 2008), increase human disturbance, e.g. through collecting firewood or grazing animals, affecting proportionally more of a small than a large fragment (Schulze et al. 2000) and increase microclimatic edge effects such as greater light and wind (Klingbeil and Willig 2009).

Some studies have shown that fragment size can affect bat species richness (Happold and Happold 1997, Estrada and Coates-Estrada 2001, Struebig et al. 2008, Meyer and Kalko 2008b, Mendenhall et al. 2014) diversity (Cosson et al. 1999, Struebig et al. 2008, 2009), abundance (Happold and Happold 1997, Cosson et al. 1999, Gorresen and Willig 2004, Montiel et al. 2006, Struebig et al. 2008) and assemblage composition (Cosson et al. 1999, Struebig et al. 2008, 2009, Estrada-Villegas et al. 2010, Meyer et al. 2010). Almost all show that smaller fragments had a more depauperate bat community than larger ones. Mendenhall et al. (2014) however found that while island size predicted bat richness well when the matrix was water, when the matrix was agroforestry and pasture the effect disappeared.

Struebig et al. (2008, 2009) found that some ensembles were more affected by fragment size than others. They found that fragment size was positively correlated with abundance and species richness of cavity/foliage-roosting bats, but not cave-roosting or edge/open space foraging species. The smallest fragments (< 150 ha) varied more in overall species composition than larger fragments or continuous forest, but larger fragments retained bat diversity similar to continuous forest. They found overall that fragment size was the main determinant of diversity and assemblage composition. A later study in the same area showed that bats with high dispersal ability maintained high allelic richness regardless of forest fragment size, but bats with small home ranges (typically < 100 ha around the roost) that do not typically extend beyond the forest edge showed reduced allelic richness with a decline in fragment size, but not with increased fragment isolation (Struebig et al. 2011).

Cosson et al. (1999) found that small islands lost diversity and abundance faster than large islands after a forested area was flooded to create a reservoir; but that changes seen on small islands were not prevented on large (40 ha) ones, merely delayed. This indicates that fragments of this size may be in extinction debt for some time after the initial fragmentation, making an area appear to support more species than it really can. However, bats are far more likely to use an agricultural matrix than a large area of open water, so island studies may have limited applicability to countryside biogeography (Mendenhall et al. 2014).

Some studies found no effect of fragment size on bats (Estrada et al. 1993, Schulze et al. 2000, Faria 2006, Bernard and Fenton 2007, Klingbeil and Willig 2009, Mendenhall et al. 2014). Some, but not all (Schulze et al. 2000), of these studies were conducted in landscapes with high connectivity between fragments (Faria 2006, Bernard and Fenton 2007, Mendenhall et al. 2014), a permeable matrix (e.g. shade cacao plantations: Estrada et al. 1993, Faria 2006) and/or a high proportion of primary forest remaining in the landscape (Klingbeil and Willig 2009), which may indicate that a fragment of any size can sustain rich bat assemblages so long as the functional connectivity to other fragments or suitable habitat is high.

The scale on which the studies were conducted is highly likely to have a strong effect. Faria (2006) classed fragments under 100 ha as ‘small’, and found no effect of fragment size; however some studies that examined fragments under 10 ha found a clear effect of fragment size (Happold and Happold 1997, Cosson et al. 1999, Estrada and Coates-Estrada 2001, Gorresen and Willig 2004, Montiel et al. 2006, Struebig et al. 2008, 2009, 2011, Meyer and Kalko 2008b, Estrada-Villegas et al. 2010). It is interesting to note that Estrada et al. (1993, Estrada and Coates-Estrada (2001) found no effect of fragment size in their study site in Mexico when they looked at a scale of 1-2000 ha, but did when the scale was 3-52 ha. When they ranked forest fragments from small to large an accumulated area of about 100 ha contained 94% of the species recorded for the area. The varied results of these studies demonstrate the difficulty of generalising on the

effect of fragment size on bats. Finding the critical fragment sizes for different species may be highly dependent on other landscape factors and thus only locally applicable, depending on a balance between the contrast between fragments and matrix, the degree of isolation and percentage forest cover in the landscape. In the studies discussed here, matrix varies from water (Cosson et al. 1999, Meyer and Kalko 2008a, 2008b, Meyer et al. 2008, Estrada-Villegas et al. 2010) to shade cacao and coffee plantations (Estrada et al. 1993, Faria et al. 2006, Faria and Baumgarten 2007); fragment size may vary between 2.5 and 5 ha (Meyer and Kalko 2008b, Estrada-Villegas et al. 2010), or 3 and 11,339 ha (Struebig et al. 2008); maximum distance between fragments may be as little as 480 m (Faria 2006), or as much as 11 km (Montiel et al. 2006). Finding a ball park fragment size which supports as much or nearly as much diversity as primary forest is still likely to be useful to conservation planners to inform the development of local studies; a sensible scale to start examining the effects of forest area may be from around 1-300 ha.

1.5.2 Forest fragment quality

Forest quality may affect bats through availability of food and roosts, microclimatic effects and degree of protection from predation. Effects of forest quality on bats can be difficult to compare between studies due to the variety of ways in which it can be assessed. Measures of quality encompass factors including canopy cover, number of tree species and tree density. Some studies have given different areas explicit vegetation scores; others have compared regrowth of differing ages (Bernard and Fenton 2007, Avila-Cabadilla et al. 2012). There is sometimes difficulty in disentangling the effects of area and quality, as smaller fragments are often more disturbed by people in anthropogenically fragmented landscapes and thus score lower on measures of quality (Schulze et al. 2000). Also, it can be harder to catch bats in more complex vegetation (Willig et al. 2007) and bat detectors work less well in cluttered environments, potentially negatively biasing results in more mature habitats (Estrada et al. 2004).

Only two studies showed no effect of forest quality on bats. Bernard and Fenton (2007) found tree species richness and density had no effect on any measure of diversity or abundance. But in this system of naturally fragmented forest and savanna, species richness did not vary between continuous forest and fragments; the savanna appears relatively permeable and isolating distances are low, so many species of bats can easily move between fragments. Also, this is a naturally fragmented system so there has been no human impact on forest quality. Estrada et al. (1993) found no effect on bats of forest age; this may be because the agricultural matrix in the system they studied was quite complex, with many remaining forest trees providing shade for the understory crops.

Several studies found that neither species composition nor richness were affected by successional stage (Castro-Lunaet al., 2007). However, several found strong effects of increased forest age on species richness, indicating that mature forest is the best habitat for maintaining rich bat assemblages (Avila-Cabadilla et al., 2009; Barlow et al., 2007; Estrada et al., 2006; Faria, 2006). Forest specialists – which are often rare - show a preference for primary over secondary forest (Pardini et al. 2009). Two studies found effects only on species composition: Willig et al. (2007) found no presence/absence differences in species between agriculture, regrowth and mature forest, but abundance of many species varied; it could be that the high proportion of forest in this landscape (<10% of this landscape has been deforested for agriculture) acts as a source population for many species. Similarly, Castro Luna et al. (2007) examined four stages of successional regrowth, and found that richness, total abundance and diversity didn't vary between them, but species composition did. Most rare and habitat specialised species were caught in older stands.

Other authors looked less at vegetational successional stage and more at specific vegetation characteristics. Some found higher species richness as number of vegetation strata, height and number of tree species increased (Medellin et al. 2000, Estrada et al. 2006). Others also found greater diversity (Medellin et al. 2000) and more rare bat species (Medellin et al. 2000, Presley et al. 2008), changes in species composition (Estrada-Villegas et al. 2010) and a decline in the relative abundance of the most abundant species leading to greater species evenness (Medellin et al. 2000).

The maturity and complexity of forests have a strong effect on bats, with secondary regrowth and disturbed areas often not containing the same assemblages seen in primary forest. Rarer species in particular appear to favour mature forest, while some of the more common species are abundant in secondary growth. Where large areas of primary forest remain, secondary growth may be recolonised by rarer species as it matures if it is not too isolated; but in areas that have lost a lot of primary forest, rarer and forest specialist bats may be at risk of decline.

1.5.3 Forest fragment shape

Fragment shape has been considered likely to affect bats, as fragments with a higher edge: area ratio are likely to experience greater edge effects. However, only a few studies have addressed this explicitly. Bernard et al. (2007) found that bigger shape indices – i.e. those with more edge to centre – were correlated with fewer captures. Gorresen et al. (2004) found that fragment shape had a low to moderate effect on the abundance of two species, and a strong effect on species evenness, and Klingbeil et al. (2009) in a multivariate analysis found that shape affected the abundance of two species, but did not have ensemble level effects. Some species preferred high shape indices, and others thrived on a low edge: area ratio. Shape of fragment may only be important when the fragment is small; it may have reduced effects if the landscape retains a high functional connectivity for the species in question; or it may be a factor of relatively low importance to bat conservation.

1.5.4 Forest fragment isolation

Despite the high mobility of bats, fragment isolation can still have strong effects. If species do not move through the matrix, due to lack of food, fear of predation or other factors, then populations in some fragments may go extinct and assemblages may change to show a greater proportion of species with greater mobility and more inclination to fly in open space.

Many studies found a strong impact of isolation from other fragments and/or from continuous forest on bat assemblages; indeed, one study found isolation to be the strongest single factor affecting species richness (Estrada et al. 1993), and another found it to be the strongest factor affecting assemblages (Meyer and Kalko 2008a). The effects of isolation appeared to be very prominent where the matrix is water; species richness decreased in one study and species composition changed in two with distance to the mainland (Meyer and Kalko 2008b, Estrada-Villegas et al. 2010). This provides some support for the filter theory, that some species will not cross such an extreme matrix as water – again, Mendenhall et al. (2014) found isolation to be a good predictor of species richness in islands but not in forest fragments in countryside.

In countryside studies in Latin America, abundance was found to decrease with distance from nearest forest fragment (Galindo-González and Sosa 2003, Montiel et al. 2006), and evenness declined with distance to the nearest neighbour (Gorresen and Willig 2004, Klingbeil and Willig 2009). Faria et al. (2006) found that shade cacao plantations bordering forests had higher capture rates, species richness, diversity and evenness than forest tracts, but plantations over 1 km from forest were less diverse than shade cacao near forest and were also the least even habitat. This indicates that proximity to continuous forest is necessary for many species.

A few studies found little or no effect of isolation. Henry et al. (2007) found that distance from continuous forest did not affect the abundance of two frugivores, but these were two of the most common and mobile species in the area. Castro-Luna et al. (2007) found only one species out of ten whose abundance was influenced by distance to continuous forest. In Castro-Luna's study the maximum isolating distances were under 1 km, and the matrix was secondary growth – so the highest levels of isolation were still very low. Isolation had no effect on allelic richness in three species in Malaysia (Struebig et al. 2011).

Overall, isolation from other forest fragments and from continuous forest seem to have a strong effect on bat assemblages in most areas studied. It is important for conservation planners to know how far bats will fly between fragments, but this is also likely to be influenced by what matrix they are flying through. It would be interesting to pursue the effects of isolation at much larger scales, such as large fragments tens of kilometres from the next, and see how bat assemblages changed across these landscape levels.

1.5.5 Effect of forest cover in landscape

Given the high mobility of many bat species, factors in the wider landscape may affect them as much or even more than small scale factors. All studies looking at forest cover in the landscape found some effect, which indicates that this may be one of the strongest factors influencing bat assemblages. Increased forest cover in the landscape was found to increase evenness (Gorresen and Willig 2004), increase richness (Gorresen and Willig 2004, Meyer et al. 2008, Mendenhall et al. 2014) and affect species composition (Meyer et al. 2008). Several species showed a strong positive response to forest cover at scales from 100 - 2000 m, including several understory and canopy frugivores (Gorresen and Willig 2004, Henry et al. 2007b, Pinto and Keitt 2008). However, some of the same species (*Carollia* species, *Sturnira lilium*) showed a negative response to forest cover in another study (Klingbeil and Willig 2009). This may be because in the latter, deforestation was very low (c 10 %), following rivers and roads, so variation in forest cover was not great. In Brazil, shade cacao plantations in a landscape of nearly 70 % forest cover had more bat species than forest fragments – but when the landscape comprised >80 % shade plantations, species richness declined in both forest fragments and shade plantations (Faria et al. 2006).

1.5.6 Agricultural land uses in tropical, human-modified landscapes

In a human modified landscape, the way the land is used will have a large effect on which bat species can persist in the landscape, and how effectively different species will be able to move through it. All studies that have examined treeless pastures or pastures with just a few scattered trees agree that this is a poor habitat for bats, as only a very few species will even move through it (Estrada et al. 1993, 2004, Medellin et al. 2000, Galindo-González and Sosa 2003, Medina et al. 2007). But which agricultural habitats might be suitable for maintaining bat diversity?

In shaded plantations, a crop such as coffee or cacao is grown under the cover of trees, traditionally native forest trees. These plantations can support bat assemblages richer (Faria 2006, Harvey and Villalobos 2007, Pardini et al. 2009, Graf 2010, Williams-Guillén and Perfecto 2011) and more abundant (Faria 2006, Harvey and Villalobos 2007, Pardini et al. 2009, Graf 2010) than forest; however others found a decline in species in these land uses (Estrada et al. 1993, 2006, Estrada and Coates-Estrada 2001). Estrada and Coates-Estrada (2001) found that shade plantations contained 71% of the species found in the landscape (forest fragments had 97%), and Estrada et al. (1993) found that together, five different plantation types contained 77% (compared to 91% in forest fragments).

Species such as small frugivores may increase in agroforestry plantations in the palaeotropics due to the increased light, as they navigate primarily by vision (Graf 2010). Some studies have found that certain rare species were not caught in plantations (Estrada et al. 2006, Faria 2006), which may be a concern to conservationists; however more research is needed on this as rare species are by definition unlikely to be caught in surveys. Many studies showed that guilds considered particularly ‘at risk’ from loss of mature forest, such as gleaning insectivores (Faria 2006, Faria and Baumgarten 2007) and forest specialists (Pardini et al. 2009), were found in shaded plantations, sometimes even in greater number than in continuous forest.

Estrada et al. (2006) noted that insectivorous bats declined as pesticides were incorporated into coffee plantations. In another study, bat abundance was reduced in low shade monoculture coffee plantations compared to less intensively managed coffee, and the proportion of frugivores captured increased with increasing management intensity while the proportions of nectarivores, sanguivores, and gleaning animalivores decreased (Williams-Guillén and Perfecto 2010). Gleaning animalivores were never captured in the most intensively managed sites (Williams-Guillén and Perfecto 2010). Also, the nature of the shade layer is important, since where the shade trees were a monoculture, bat species richness was lower than in plantations with a mix of native shade (Graf 2010).

While some authors have found that shaded, less intensively managed plantations are a better habitat for bats than unshaded (Estrada and Coates-Estrada 2001), others found the two to be comparable (Estrada et al. 1993, Numa et al. 2005). This may be partly – especially in Numa et al. (2005) – due to landscape context, as the results varied between landscapes dominated by shade grown coffee and sun coffee monocultures. Similarly, Faria et al. (2007) noted that shade cacao plantations less than 1 km from forests had greater abundance, species richness, diversity and evenness than forests, but shade cacao more than 1 km from forest had intermediate diversity between the two, and was the least even habitat. Shaded plantations clearly provide a valuable habitat for bats, but they do not replace primary forest. However, a landscape with a high proportion of forest and of shaded plantations will be one that will support a diverse bat assemblage, whereas many other land uses will not.

Most other habitats assessed, from plantain monocultures to orchards and *Eucalyptus* plantations, had bat assemblages that were depauperate and modified compared to continuous forest (Randrianandrianina et al. 2006, Barlow et al. 2007, Harvey and

Villalobos 2007, Loayza and Loiselle 2008, Sedlock et al. 2008). In South East Asia, bat diversity was highest in primary and secondary forest habitats, lower in orchards and lowest of all in oil palm (Fukuda 2009). While nothing is published on the bat assemblages in tea fields, their low, simple structure and lack of native trees suggests that diversity will be relatively low in such habitats.

1.5.7 Effect of riparian habitat

Riparian ecosystems are known to be important for many bat species as they provide water to drink, insect food and different plant resources to dry forest, as well as open flyways and possible navigational features (Lloyd et al. 2006, Avila-Cabadilla et al. 2012, Hagen and Sabo 2012, 2014). The importance of specific riparian habitat features has been well studied in Europe, Japan and North America (Walsh and Harris 1996, Grindal 1996, Hayes and Adam 1996, Carmel and Safriel 1998, Grindal et al. 1999, Zimmerman and Glanz 2000, Holloway and Barclay 2000, Abbott et al. 2009, Lundy and Montgomery 2009, Akasaka et al. 2010, Scott et al. 2010, Akasaka et al. 2012, Goiti et al. 2011, Rainho and Palmeirim 2011, 2013, Salsamendi et al. 2012, Lisón and Calvo 2013, Bellamy et al. 2013). However, these habitats have been less studied in the tropics, despite the fact that there may be greater bat foraging activity over water than in forests (Grindal 1996).

Riparian vegetation is sometimes richer in bat species and abundance than comparable nearby non-riparian vegetation (Monadjem and Reside 2008, Sirami et al. 2013, Taylor et al. 2013), and some species show particular preferences for riparian areas (Avila-Cabadilla et al. 2012). In temperate regions, several studies have found that forest cover, a greater area of natural habitat or more hedgerows around the riparian zone are positively correlated with bat activity (Hayes and Adam 1996, Carmel and Safriel 1998, Holloway and Barclay 2000, Ober et al. 2008, Lundy and Montgomery 2009, Langton et al. 2010).

1.6 Which guilds are most susceptible to habitat loss and fragmentation?

Across most if not all taxa, some species benefit from human induced disturbance while others suffer detrimental impacts (Lewis et al. 2009). A few highly resilient species, popularly classified as ‘winners’, come to dominate disturbed communities, while many disturbance intolerant species or ‘losers’ disappear (McKinney and Lockwood 1999). While ‘winners’ were originally thought of as exotic species with a wide global distribution, it is increasingly clear that native species can be dominating ‘winners’ as well – any biota can potentially contain both ‘winners’ and ‘losers’ (Tabarelli et al. 2012). The differential effects of change on winners and losers can result in locally impoverished assemblages, loss of specialists and reduced ecosystem resilience and function (McKinney and Lockwood 1999, Tabarelli et al. 2012).

In bats, frugivores feeding on pioneer species may be the greatest ‘winners’ and gleaning insectivores and animalivores the most vulnerable ‘losers’. Different foraging guilds of bats have different roles to play in ecosystems, and it is important to understand their responses to habitat loss and fragmentation in order to see where ecosystem function may be affected. Neotropical and palaeotropical forests have different ecologies, and the bat species are also very different in the two regions (Heller and Volleth 1995, Altringham 2011). More work has focussed on bats in the neotropics, so that will form the majority of the discussion. Here I classify bats broadly into insectivores/carnivores and frugivores/nectarivores, then look in more detail at guilds within each.

1.6.1 Insectivores and carnivores

Insectivorous and carnivorous bats are diverse in both morphology and ecology. They are often important predators in ecosystems and in agricultural systems where they control many crop pests (Cleveland et al. 2006). Estrada et al. (1993) showed that insectivorous bats declined from 25.3% of individuals in forest to 4.3% in cacao plantations, although they were relatively successful in some other plantations and in live fences. While two studies found the proportion of individuals that were insectivorous was greater in forest fragments (Estrada and Coates-Estrada 2002), or more insectivorous bat activity in villages (Estrada et al. 2004), than in continuous forest, all report very low numbers of insectivorous bats in pasture habitat (Estrada et al. 2004, Medina et al. 2007). Numbers of some insectivorous species in agricultural landscapes declined as more pesticides were used (Montiel et al. 2006). Carnivores tend to be very rare, and are generally only found in habitats with high tree cover

(Medina et al. 2007). Most of the following examples are from the neotropics, underlining a need for more bat studies in the palaeotropics.

1.6.1.1 Open space foragers and edge specialists

Bats that forage for insects in open space or can use edge environments such as the boundary between forest and fields have been predicted to be more resilient to habitat loss and fragmentation than others. Estrada-Villegas et al. (2010) noted that open-space species were more abundant on small and on isolated islands and at forest edges than on nearby islands or on the mainland, even in this high contrast system of forest islands in a matrix of water.

Pteronotus parnelli is a good example of an edge specialist insectivore that has been documented in many neotropical studies. It was the dominant insectivorous species in a mixed agricultural habitat with forest fragments in Mexico (Estrada and Coates-Estrada 2001). Most studies found this species in more complex habitats such as continuous forest, forest fragments, shaded plantations and older stage secondary growth; but it declined in very open areas such as cornfields and isolated trees (Medellin et al. 2000, Estrada and Coates-Estrada 2001, Galindo-Gonzalez and Sosa 2003, Montiel et al. 2006). So, although this species can use a variety of habitats, complete deforestation would be detrimental to its persistence.

1.6.1.2 Gleaning species

Gleaning species, that pluck invertebrates or small vertebrates from leaves and branches or from the ground, are considered particularly vulnerable to habitat fragmentation and alteration. They are adapted to cluttered forest environments and they are often found in very low abundances even in mature forest, so many are at a higher risk of extinction from habitat loss and fragmentation than more abundant species (Estrada and Coates-Estrada 2002, Faria 2006, Faria et al. 2006, Montiel et al. 2006, Medina et al. 2007, Meyer et al. 2008, Avila-Cabadilla et al. 2009). Many studies found carnivores (typically gleaners) and insect gleaning species to be most abundant in forest habitat (Schulze et al. 2000, Gorresen and Willig 2004, Medina et al. 2007) or not even found in other habitats (Estrada and Coates-Estrada 2001, 2002, Numa et al. 2005, Faria 2006, Willig et al. 2007, Presley et al. 2008). One study noted that large carnivores were caught six times more often in continuous forest than in fragments (Schulze et al. 2000). It appears that these species can use plantations with native shade trees, but the abundance of gleaners in shaded plantations declined with distance from continuous forest (Faria 2006, Faria and Baumgarten 2007). Gleaners may also avoid forest edges (Faria 2006, Meyer et al. 2008).

In the neotropics, *Tonatia silvicola* is like many in its guild, very rare; Gorresen et al. (2004) caught only one individual gleaning insectivore during their 15 month survey. Loayza et al. (2009) noted that it was rare in continuous forest and in fragments, and absent from savanna. Bernard et al. (2003) discovered that it could persist in a naturally fragmented landscape with small isolating distances, with individuals foraging in up to seven fragments separated from each other by no more than 1.6 km of scrubby savanna. Thus, it appears that this species is consistently fragmentation sensitive but can persist so long as isolating distances are very low.

Overall, gleaning insectivores and carnivores appear highly forest dependent; the only other suitable habitat seems to be shaded plantations, which contain many mature trees, but bats using this habitat may need primary forest as well.

1.6.2 Frugivores and nectarivores

Frugivores and nectarivores play crucial roles in pollinating tropical plants and dispersing their seeds. There is a great diversity of sizes and specializations within these guilds. Fruit bats and nectarivores in the palaeotropics all belong to one family, Pteropodidae. In the neotropics all frugivores belong to the Phyllostomidae, which appear to have secondarily evolved to feed on fruits from insect eaters (Altringham 2011). Many are omnivores, and they are typically smaller than Pteropodids. As bats in the palaeotropics have been much less studied than those in the neotropics, we do not know how palaeotropical frugivores and nectarivores are likely to respond to land use changes. It is important to know how well these species cope in fragmented landscapes, and whether they can maintain ecosystem services in the face of change.

1.6.2.1 Nectarivores

Nectarivores in the neotropics are generally less speciose than frugivores, but like frugivores, many nectarivores do seem able to exploit shade plantations. One study found the numbers of nectarivorous bats to be similar between rainforest and shade coffee plantations (Estrada et al. 2006). Others found that nectarivores were more abundant in shade cacao (Faria 2006, Faria and Baumgarten 2007, Harvey and Villalobos 2007), shade banana (Harvey and Villalobos 2007) and shade coffee (Estrada et al. 2006) than in forest. Several studies found that some nectar eating species were rare, found only in forest fragments and continuous forest (Estrada and Coates-Estrada 2001, Faria 2006) (Estrada and Coates-Estrada 2002) or late stage successional growth (Avila-Cabadilla et al. 2009) – this is likely because some species are more effective at exploiting commercial plantations than others.

In Borneo, two species of nectarivorous bats (*Eonycteris spelaea* and *Macroglossus minimus*) were caught at significantly higher rates in orchards than in forest or oil palm, and a third, *Eonycteris major* was only captured in an orchard (Fukuda 2009). All appeared to be feeding on nectar from cultivated crops such as durian, banana and *Parkia* spp. In another study in Borneo *Macroglossus minimus* was found in cacao agroforestry plantations, both with a diverse, original tree cover and with a single species of planted tree as shade, but not in primary or selectively logged forest (Graf 2010).

Some species within this guild appear well adapted to moderately disturbed areas as long as nectar-rich flowers are available, but others require primary forest to sustain viable populations.

1.6.2.2 Frugivores

Frugivores dominate many tropical bat assemblages, often with a few frugivorous species attaining numerical dominance over all other species (Estrada et al. 1993, Pineda et al. 2005, Montiel et al. 2006, Harvey and Villalobos 2007, Medina et al. 2007, Meyer and Kalko 2008b, Graf 2010). Some authors found that overall abundance of frugivores was similar between forest and matrix environments (Estrada et al. 2006, Loayza and Loiselle 2009, Furey et al. 2010), or that the number of frugivorous species was similar between these habitats (Medina et al. 2007). In Borneo, the number of fruit bats was lower in orchards and oil palm than in primary and secondary forest (Fukuda 2009). Others found frugivores to be more abundant in agricultural habitats, such as in shade cacao plantations (Estrada et al. 1993, Faria 2006, Graf 2010), citrus, mixed, allspice, and coffee plantations (Estrada et al. 1993, Fukuda 2009) or even in isolated trees (Galindo-González and Sosa 2003) than in forest fragments. This may be due to the high numbers of fruiting trees used as shade in these plantations.

Some frugivorous species were found only in forest (Faria 2006, Fukuda 2009) or were more common in forest (Montiel et al. 2006, Loayza and Loiselle 2009, Moran et al. 2009), indicating that many frugivores may still rely on this habitat partially or completely. Most frugivores appear to decline severely in monocultures or pastures; unsurprising as there is usually much less fruit in these environments (Harvey and Villalobos 2007, Medina et al. 2007, Fukuda 2009). Species composition of frugivores changes between habitats. In Borneo, *Cynopterus brachyotis* was not common in primary forest, was more common and the numerically dominant species in secondary forest, and was very common and dominant in orchards and oil palm; whereas *Penthetor lucasii* and *Balionycteris maculata* were numerically dominant in primary forest, declined in secondary forest and were not found in orchards or oil palm (Fukuda 2009).

Most of the studies conducted on tropical bat ecology have been undertaken in the neotropics, where all frugivores belong to the Phyllostomidae. Within the frugivores of this family there are two main foraging strategies; canopy feeders and understory feeders. There are fewer data from Asia, but I have categorised the frugivorous Pteropodidae into canopy or understory species based on Francis (1994). Here I will give a brief overview of the effects of fragmentation on each to see how they differ.

1.6.2.2.1 Canopy frugivores

Canopy frugivores feed on mast-fruiting trees, which each provide an abundant but short lived quantity of fruit, with different trees fruiting asynchronously across a wide area. The bats that specialise on these trees must therefore have a high degree of mobility to move between spatio-temporally variable resources (Cosson et al. 1999). There has been some speculation that this makes canopy frugivores better adapted to fragmented landscapes because they make long searching flights between fruiting trees, so are perhaps better adapted to make long flights across disturbed areas in search of food. They also have large home ranges, so may be able to exploit many fragments. However, they also require mature trees to feed on, so too much loss of forest cover may be a serious problem (Cosson et al. 1999).

While many canopy frugivores are naturally abundant and can persist in mature forest fragments and shaded plantations where mature trees remain, they appear sensitive to the change from primary to secondary forest when much of their food resource is lost (Cosson et al. 1999, Medellin et al. 2000, Pineda et al. 2005, Castro-Luna et al. 2007, Willig et al. 2007, Presley et al. 2008, Loayza and Loiselle 2009, Saldana-Vazquez et al. 2010). They are also scarce in open habitats, and some species are more sensitive to fragmentation and habitat modification than others (Cosson et al. 1999, Medellin et al. 2000, Henry et al. 2007a). To conserve this guild a high degree of primary forest in the landscape and shade plantations as the main agricultural use would be recommended.

1.6.2.2.2 Understory frugivores

Unlike canopy frugivores, understory frugivores forage on smaller trees and shrubs that produce a small amount of fruit per night, but whose fruiting may extend over weeks or months (Cosson et al. 1999). Dependence on these predictable, high quality fruits means that understory frugivores minimise foraging time, with foraging bouts interspersed with roosting or sleeping. They do not spend long periods of time on searching flights (Cosson et al. 1999). In the neotropics, understory frugivores of the *Carollia* and *Sturnira* genera feed on the plant genera *Piper* and *Solanum*, often found in secondary growth and at edges.

Where forest was lost in creating a reservoir, understory frugivores on the newly created islands declined (Cosson et al. 1999). However, where the matrix was agricultural or secondary growth, many of the most abundant understory frugivores thrived. *Carollia* and *Sturnira* species were noted as being common in agricultural landscapes in Mexico (Medellin et al. 2000, Estrada and Coates-Estrada 2001, Pineda et al. 2005), Brazil (Faria and Baumgarten 2007) and Bolivia (Loayza and Loiselle 2009). Some of these species even achieved greater abundances in forest fragments (Schulze et al. 2000), shade plantations (Medellin et al. 2000), secondary forest (Willig et al. 2007, Presley et al. 2008) and other agricultural land (Medellin et al. 2000, Willig et al.

2007) than in mature forest, to the point where one author considered very high numbers of these genera to be indicative of forest disturbance (Schulze et al. 2000).

In South and South East Asia, *Cynopterus brachyotis* is one of the species most commonly caught in ground nets (Francis 1994). It feeds on a wide variety of fruit – including *Piper* spp. - and is more common in agricultural habitats than in forest (Fukuda 2009, Graf 2010). However *Balionycteris maculata,* another species found mostly in the understory, was less common in secondary forest than in primary and absent in orchards and oil palm (Francis 1994, Fukuda 2009).

Many understory frugivores can thrive in agroforestry landscapes and in secondary regrowth, where there may be many *Piper* and *Solanum* fruits for them to feed on in the neotropics. However, more mature secondary forest appears to be favoured over younger, and at least some of these species need high forest cover to reach maximum abundances. While this group appears to do well in fragmented landscapes, it is unclear whether or not they can survive in a purely agricultural context.

1.6.3 Other factors affecting vulnerability to fragmentation

The greatest factors affecting extinction risk for bats are small geographic range size and low wing aspect ratios (an indication that bats are adapted to dense vegetation) (Jones et al. 2003). Small range size leaves bats vulnerable to heavy human disturbance within that range; also as the effects of climate change worsen they may struggle if their range experiences adverse changes. Low aspect ratio wings are comparatively short and broad, making for manoeuvrable but slow flight. Bats with low aspect ratio wings tend to be species that glean and hover in cluttered vegetation – forest specialists rather than generalist foragers or bats that can commute long distances across open land to feed. This morphology and ecology is typical of megadermatids, hipposiderids, rhinolophids, and phyllostomids, making them more at risk of extinction than bats with high aspect wing ratios, which tend to forage in more open areas and across larger ranges, such as molossids, many vespertilionids, emballonurids, and mormoopids (Jones et al. 2003). A higher proportion of pteropodid bats – Old World fruit bats - are currently at risk of extinction than other bats, and this appears to be correlated more with reproductive rate than with wing morphology (Jones et al. 2003).

1.7 Functional diversity

Increasingly, it is considered that it is not just the diversity of species that it important to conserve, but the diversity of functions performed in an ecosystem (Tilman 2001, Petchey and Gaston 2002, 2006, Villéger et al. 2008, Mouillot et al. 2011). It appears that functional diversity is more important than species diversity for maintaining ecosystem functions such as productivity and resilience to changes (Tilman et al. 1997, Dukes 2001, Hooper and Dukes 2003, Petchey et al. 2004, Bellwood et al. 2004, Hooper et al. 2005). However, much work in this area has used functional group richness instead of measuring functional diversity itself (Villéger et al. 2008). Grouping species imposes a discrete structure on the functional differences between species, which in reality usually follow a continuous distribution, and information is lost about the differences between species within a group (Fonseca and Ganade 2001). Often the use of functional groups does not include information about the abundance of species, which is problematic as species are likely to have different effects on ecosystem functioning if they differ in abundance (Diaz and Cabido 2001).

Box 1:

Functional space:

A multidimensional Euclidean space where the axes are ecologically relevant traits or multiple traits condensed into principal coordinates.

Functional diversity:

The distribution of species and their abundances in functional space.

Functional group /guild:

A set of species that have similar traits and thus are likely to be similar in their effects on ecosystem functioning.

Functional richness:

The volume of functional space occupied by a species assemblage.

Functional evenness:

How regularly species abundances are distributed in functional space.

Functional divergence:

Variation in species abundances with respect to the centre of the functional space.

Functional specialization:

How functionally unique a community is relative to the available pool of species.

Functional dissimilarity:

The overlap of functional space between multiple communities.

Many alternatives to functional groups have been proposed to measure functional diversity.

These include the use of functional trait axes, hierarchichal classification systems and multivariate functional trait space (Walker et al. 1999, Petchey and Gaston 2002, Mason et al. 2003, Botta-Dukát 2005). Recently, multi-dimensional functional trait space has been used to describe a number of metrics that collectively describe functional diversity; functional richness, functional evenness, functional divergence, functional specialization and functional dissimilarity (Box 1, Figure 1.2, Figure 1.3, Villéger et al. 2008, 2010, 2011). These measures deal with many of the problems of older methods and have been used successfully in studies of changes in communities due to human disturbance (Mouillot et al. 2013, Edwards et al. 2013, 2014). Abundances can be taken into account; multiple traits can be used; there is no trivial link to species richness; and information regarding the relative closeness in trait space of one species to another is not lost (Villéger et al. 2008).

In bats, changes in functional diversity due to changing habitats have not frequently been explicitly addressed. Most studies on bat functional diversity are more properly described as functional group studies (Stevens et al. 2003, 2004). Studies describing changes in bat foraging guilds are very informative, but somewhat hampered by the multiple different classifications of bats into foraging or functional guilds (Schnitzler and Kalko 2001, Denzinger and Schnitzler 2013, Luck et al. 2013). While these studies are particularly useful for practitioners, these groupings lose information about the responses of similar but different species. For example Luck et al. (2013) found that species within the same 'functional group' reacted in very different ways to certain aspects of urbanisation, indicating that even carefully thought out functional groupings can disguise a lot of inter-species variation.

Some studies have taken different approaches. One study did not use statistics to differentiate between species ecomorphology, but simply described changes in ecomorphological groups (Law and Chidel 2002). Another used non-parametric Spearman's rank order correlation to look for associations between a species' proportional activity at a site with morphological traits such as body mass, wing-loading and echolocation call frequency (Jung and Kalko 2011). Again, information is lost by either assigning a

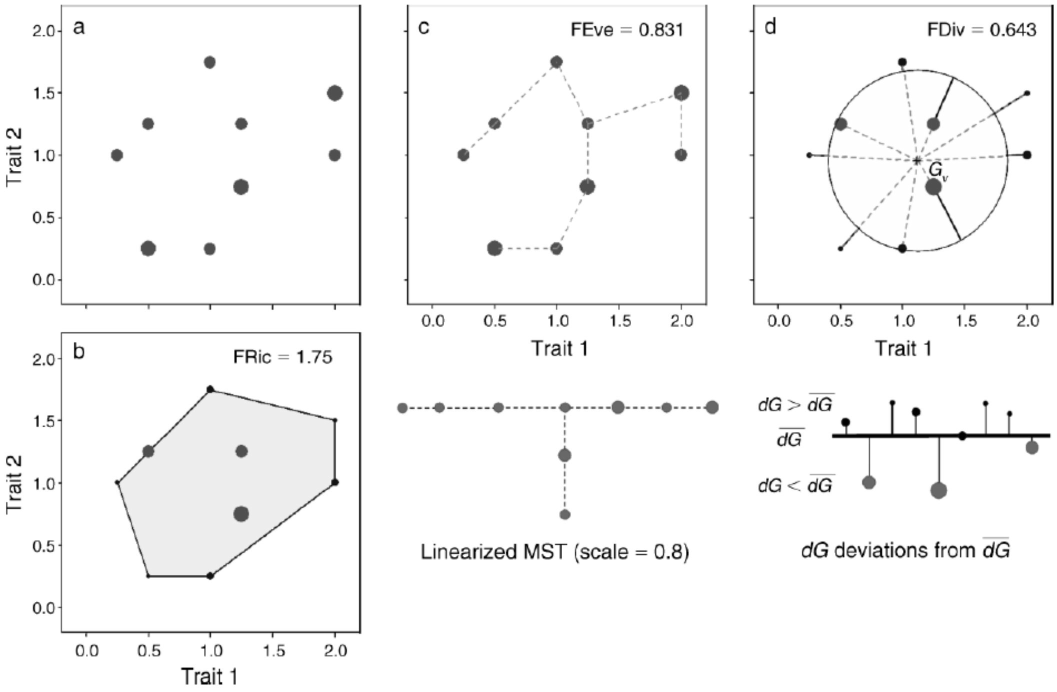

Figure 1.2: From Villéger et al. 2008: Representation of the three functional diversity indices in multidimensional functional space. Two traits and nine species are displayed. **(a)** The species' points are plotted according to their trait values. Larger diameters represent larger abundances. **(b)** The convex hull is drawn around the points by linking the most extreme points in functional trait space, and the convex hull volume is shaded in grey. The functional richness (FRic) corresponds to this volume. **(c)** A minimum spanning tree (MST, dashed line) is used to link each species with its nearest neighbour in functional trait space. Functional evenness (FEve) measures the regularity of species along the MST, and the regularity in their abundances. The stretched tree is plotted under the panel. **(d)** The position of the centre of gravity of the vertices (GV, black cross), the distances between GV and the species in trait space (gray dashed lines), and the mean distance to GV (large circle). The length of the black line linking each species with the large circle represents the deviation of each

species to a functional group or reducing points in multi-dimensional trait space to ranks, with no information about the distances between ranked points.

There have been studies on bats that use a trait based functional space approach, although they have often not explicitly addressed functional questions. RLQ analysis is a powerful method that can be used to assess how the environment filters certain species traits. RLQ takes information on the environment (R), species presences in sites (L) and a species' traits (Q). It then makes an environment X traits matrix, on which an ordination analysis is performed. Thus continuous environmental traits can be compared, but not categorical habitats. This approach has yielded useful information in a number of studies, which broadly supports the results from the work done using foraging guilds. In south eastern Australia, RLQ analysis revealed that species with short, broad wings and linear, medium and high echolocation frequencies were associated with dense tree cover, while larger species with long, narrow wings and low echolocation frequencies showed an association with greater density of grazing livestock (Hanspach et al. 2012). In Indiana in the USA, species with high wing-tip shape index and a broad dietary niche breadth which roosted in tree cavities and crevices were positively related to total forest area and forest aggregation; while species with high wing aspect ratios and wing loadings and species that roost primarily in human structures were more prominent in urban areas (Duchamp and Swihart 2008). Very similarly, near Sydney, Australia bats with low to medium frequency echolocation, larger forearm length, greater body weight, higher aspect ratio wings and greater wing loading were more active at more open and urban sites where species with linear or high echolocation calls were more active in bushland sites (Threlfall et al. 2011).

There is a need for more studies to explicitly address changes in facets of the functional diversity of bats between habitats, due to the great variability in functional roles in bats and their important roles in ecosystems. Understanding the changes in functional diversity of bats in human altered landscapes would provide insights into possible changes in ecosystem functioning in these habitats.

1.8 Methodological biases

1.8.1 Study design

From the studies discussed here we can see that in many cases there are strong effects of habitat conversion and fragmentation on bats. Yet it is still hard to state conclusively what effect habitat fragmentation has on bats, as many studies show conflicting results. This is part due to the varied interpretations of the term ‘fragmentation’, and the magnitude and nature of the fragmentation studied. Future studies could compare landscapes with different degrees of fragmentation in the same geographical region, to try and see how fragmented a habitat can get and still maintain diversity, and which landscape variables are important.

Almost all the work that has been done on the responses of bats to tropical habitat fragmentation has been done in the neotropics. This creates a huge bias in our understanding; more palaeotropical research is urgently needed to identify species and areas at risk, and to develop evidence based strategies for their conservation, especially as bat communities in the neotropics and palaeotropics are not ecomorphologically analogous (Heller and Volleth 1995).

Many studies were able to analyse how different species respond to changes in landscape factors, but were unable to do this with rarer species due to low sample sizes. These are the species of greatest conservation concern; perhaps with sustained use of a variety of catching and ultrasound detection methods, we would be able to discover more about what affects rare and threatened species.

1.8.2 Catching and acoustic studies

There are currently no long-term monitoring programmes for bats in the tropics, and that have not been included in established multi-taxa monitoring programmes such as Conservation International's Tropical Ecology, Assessment and Monitoring (TEAM) network (http://www.teamnetwork.org). If monitoring protocols are to be established it is important to understand the biases inherent in different sampling methods and how they affect bats in different habitats.

Most of the tropical studies discussed used only ground level mist nets to survey for bats. This completely excludes higher flying bats from analysis, and species that can more easily detect and/or avoid mist nets. Using nets at greater heights and introducing methods such as harp traps and tunnel traps, shown to catch some species that avoid mist nets, will give us a truer picture of bat assemblages – as will the use of ultrasound detectors (Sedlock et al. 2008). Also, in some studies species accumulation curve didn't reach asymptotes, indicating that even with the limited methods used more species could have been caught with more replication; this again makes interpretation of data, particularly on rare species, difficult.

This is important because for many bat assemblages we lack even the most basic information on the abundance of different species, their distribution or habitat requirements. The development of comprehensive survey and monitoring methods is critical for understanding the current status of bats and allowing future monitoring of populations (MacSwiney et al. 2008). Ideally the relative roles of different capture and acoustic methods need to be tested in a range of different habitats and different environmental conditions, as different methods may be more or less effective under different conditions (MacSwiney et al. 2008).

All methods for studying bats have potential advantages and disadvantages. Catching bats often allows better species level identification than acoustic methods (although some cryptic species can only be separated by calls), and allows the collection of biometric data, data on sex, reproductive status and the collection of genetic material. However it is also expensive, time consuming, requires skilled labour and disturbs bats, possibly altering behaviour. It can also lead to biases in sampling as some species fly high above nets, are more agile or are better at detecting nets than other species. Harp trapping is less disturbing to bats, but traps are less versatile than nets. Capture success is also likely to decrease on consecutive nights at the same location as bats learn where the nets are and avoid them (Kunz and Brock 1975). Habitats such as open fields, large water bodies or high in the canopy cannot be easily or effectively sampled using mist nets or traps (Kunz and Brock 1975). Nets and traps also sample a very small percentage of the aerospace used by bats, and alert, foraging bats are often able to detect and avoid structures intended to capture them (O’Farrell and Gannon 1999).

These drawbacks have in recent years been compensated for in temperate zones by the use of ultrasound detectors, which detect the high frequency echolocation calls made by bats. Over time, these are often cheaper than catching methods and they are non-invasive. They can help achieve a more complete species list for the area – after decades of intense catching on Barro Colorado Island, Panama, five new species were added to the inventory by using acoustic methods – all species that roost in difficult to reach areas and fly especially high (Kalko et al. 1996). In another study in the neotropics, aerial insectivores that often fly above the forest canopy were only ever recorded using acoustic methods (MacSwiney et al. 2008). They may also give a better idea of bat activity than mist nets do; in one study bat activity data from ultrasound sampling were correlated with insect abundance, and capture data were not (MacSwiney et al. 2008). Ultrasound detectors can sample areas difficult to sample with mist nets such as open areas where bats fly high.

However they are not without issues; some bat species cannot be separated using echolocation calls alone, and again there can be biases in the sample; low intensity echolocators and non-echolocating bats are under sampled or not sampled at all (O'Farrell and Gannon 1999). Sites with dense vegetation may muffle ultrasound calls, high levels of insect noise may mask calls (MacSwiney et al. 2008). Still, in most bat assemblages studied, the use of ultrasound detectors and catching together gave the greatest number of species recorded (Murray et al. 1999, O'Farrell and Gannon 1999, MacSwiney et al. 2008, Furey et al. 2009).

1.9 Habitat Suitability Modelling

Habitat suitability modelling (HSM), also known as species distribution modelling (SDM) or ecological niche modelling (ENM) is a statistical technique that can be used to predict species distribution from environmental data and species presence points. HSM based on GIS data can produce detailed maps that predict the likelihood of species occurrence at given points.

HSM allows us to identify factors driving the habitat choices of species, which is useful in practical conservation (Hirzel and Le Lay 2008) because management decisions need to be made with an understanding of the likely impacts. HSMs with practical value have been successfully built using as few as four or five presence points (Pearson et al. 2007, Catullo et al. 2008) so this technique can be used to model the habitat requirements for rare species for which it is by definition hard to gather substantial amounts of data. It can be used with presence-only data, which is useful as absence data are frequently missing or unreliable, especially for mobile, difficult to detect and rare species (Pearson et al. 2007, Phillips et al. 2009, Rebelo and Jones 2010, Elith et al. 2011). Even models built with low-resolution environmental data may be reasonably good at predicting species occurrence (Becker and Encarnação 2012). These factors make HSM a particularly valuable technique for studying highly mobile, nocturnal species such as bats which can be difficult to survey (McConville et al. 2014).

Habitat suitability maps produced by HSM are able to predict the occurrence of species better than simple presence maps, so can be used to target the search for new locations of rare, cryptic or difficult to detect species and be important in assessing their conservation status (Rebelo and Jones 2010, Razgour et al. 2011, Becker and

Encarnação 2012, Rutishauser et al. 2012). HSMs have been used to assess the likely responses of bats to climate change, and even to understand the risk of zoonotic disease transmission from bats to humans or livestock (Rebelo et al. 2010, Lee et al. 2012, Hughes et al. 2012, Hahn et al. 2014). HSM can identify hotspots for species diversity and potentially important habitat corridors, which makes them useful in understanding the likely consequences of developments or mitigation efforts, in finding suitable reintroduction sites or in assessing the efficacy of current protected area networks (Catullo et al. 2008, Drummond et al. 2010, Roscioni et al. 2013, Bellamy et al. 2013, Lisón et al. 2013). Maps are easy to interpret and thus useful for landowners and conservation practitioners to use on a day-to-day basis, and can form the basis of landscape scale conservation. However they are sometimes interpreted with certainty by recipients of the map where in fact there may be uncertainty in the accuracy of the map, as errors cannot be shown on a single map. Presenting multiple maps may help with this.

1.10 The Western Ghats of India

The Western Ghats mountains run down the western coast of India and support a variety of tropical ecosystems. They cover 182,500 km^2 and, together with Sri Lanka to which they are environmentally similar, form one of the eight 'hottest' biodiversity hotspots in the world (Myers et al. 2000). The Western Ghats contain 30% of all plant, fish, herpetofauna, bird, and mammal species found in India, yet they comprise less that 6% of the country's land area (Bawa et al. 2007). They are isolated from similar moist forested areas and so support a high number of rare endemic species. However, of all 34 biodiversity hotspots in the world the Western Ghats are one of the most densely populated by people and as a result the natural vegetation is destroyed, degraded or fragmented in many places, seriously affecting ecosystem functioning (Bawa et al. 2007, Sloan et al. 2014). Maintaining good ecosystem functioning in the Western Ghats is critical for human health, biodiversity, and ecosystem services such as pollination and insect control. The Western Ghats support many crucial drainage basins that supply water to people in the nearby plains as well as to those in the Ghats themselves (Bawa et al. 2007).

Deforestation and conversion of land to agriculture in the Western Ghats is believed to have started in the 1800s under British colonial rule, and the hills of the Western Ghats are today planted with tea, coffee, cardamom, rubber, eucalyptus and other crops such as oil palm (Bawa et al. 2007). From 1920 to 1990 there was a 40% reduction in forest cover in the region, causing a four-fold increase in the number of forest fragments and a reduction in the size of forest patches of 83% (Menon and Bawa 1997). The most recent estimates suggest that only 6.8% of the land area is now under primary vegetation (Myers et al. 2000), and a major factor in this forest loss and fragmentation is the spread of plantations, predominantly tea, coffee and eucalyptus (Raman 2006).

Around 9% of the Western Ghats hotspot falls within formal protected areas, one of the highest levels of protection of any of the world's biodiversity hotspots. However, the protected areas do not protect all the biogeographic areas evenly (Bawa et al. 2007, Gunawardene et al. 2007). Only 29% of evergreen forests – the forest type with the highest levels of endemism – are protected, yet 61% of high altitude grasslands fall within protected areas, and more high elevation areas are protected than lower elevation areas (Bawa et al. 2007). Even within protected areas there are many threats to biodiversity. Local hunting, illegal logging, invasive species, firewood and fodder collection and livestock grazing all occur in 97% or more of the protected areas, and threat occurrence is independent of the age or size of the protected areas (Bawa et al. 2007). While wages and social services in the Western Ghats are generally better than in the nearby plains of Southern India, many people are still poor, so have little alternative but to extract resources from the forest. There are management plans in place to protect and manage forests, but these are generally not developed or implemented with any scientific input, and community involvement is often negligible (Bawa et al. 2007).

The site chosen for this study, the Valparai plateau, comprises mid-elevation tropical evergreen forest (Raman et al. 2009). The Valparai plateau began to be deforested for agriculture in 1896 and crops such as cardamom, coffee, tea, cinchona, rubber, and vanilla were planted. Initially, about 80% of the cultivated land was growing cardamom or shade coffee, which are sun intolerant crops usually grown under native rainforest trees. Once it was realised that the area was suitable for tea production, much of the remaining native tree canopy was removed to make way for tea monocultures, with tea occupying 75% of the agricultural area of the Valparai plateau by 2000 (Mudappa and Shankar Raman 2007). The Valparai plateau is bordered on all sides by protected areas (the Indira Gandhi Wildlife Sanctuary, Chinnar Wildlife Sanctuary, Eravikulam National Park, Parambikulam Wildlife Sanctuary and the Vazhachal reserved forest) (Mudappa and Shankar Raman 2007). While there are no designated buffer areas for these parks, ecosystem changes in Valparai may have a knock on effect on the protected areas (Laurance et al. 2012).

An Indian evidence-based conservation NGO, The Nature Conservation Foundation (NCF), has been working in the Valparai Plateau since 1991 conducting pure and applied research and local community initiatives. One of their main projects has been the restoration of native tree species in degraded forest fragments on private land to improve landscape level biodiversity and connectivity, with the cooperation and support of plantation owners (Raman et al. 2009).

NCF and their partners have studied how various taxa change in abundance, diversity and assemblage composition between continuous forest and forest fragments, and how they use different areas. Elephants moving through the agricultural area of the plateau were seen to prefer moving in rainforest fragments and riparian habitats to moving in plantations, with the strongest selection being for riparian habitat (Kumar et al. 2010). Although small mammals increased in abundance and diversity in the forest fragments compared to the protected areas of continuous forest, there were more human commensals and a loss of endemics (Mudappa et al. 2001, Kumar et al. 2002). In another study of mammals (excluding bats) four out of 28 species were found in reserve forest but not in forest fragments (Sridhar et al. 2008). Small carnivorous mammals declined in abundance and species composition changed between reserve forest and fragments (Kumar et al. 2002, Mudappa et al. 2007). Smaller fragment area, greater time since isolation and more habitat disturbance all reduced species richness in amphibians, with a similar pattern seen in reptiles except that more disturbed areas had greater reptile abundance (Kumar et al. 2002). Spiders did not change in richness or abundance between fragments and continuous forest, but species composition changed substantially (Kapoor 2008). In birds, community composition was linked to habitat quality and isolation, with less isolated fragments supporting more rainforest species and fewer open forest species than fragments that were more isolated (Raman 2004). Forest fragments in the agricultural area of the Valparai plateau are biodiversity rich, but are not a substitute for continuous forest.

Species diversity in plantations has also been studied for mammals (excluding bats) and birds. In Valparai, coffee and cardamom plantations (both shaded) had lower bird species richness than rainforest fragments and reserve forest (Raman 2006). Overall plantations had 30-50 % fewer rainforest bird species than the reserve forest, and rainforest fragments (all over 18 ha) had about 25 % fewer rainforest species than reserve forest. Plantations and fragments with greater canopy continuity had more rainforest bird species and fewer open forest bird species than more isolated sites. Habitat structure and tree species composition also had strong effects on bird species richness and composition in both rainforest fragments and shaded plantations (Raman 2006). Species richness of rainforest birds declined dramatically in fragments below 10 ha, and species richness overall, and that of rainforest species, was lower in tea and eucalyptus plantations than in shade coffee, with tea plantations overall being the worst habitat for birds (Raman 2001).

Little has been published on how bat assemblages are affected by human modification of the landscape in the Western Ghats, and how those changes compare to birds and terrestrial mammals. The 2002 Status of South Asian Chiroptera workshop report confirms that bats are one of the least studied mammalian groups in the region, with information for many species based only on museum specimens (Molur et al. 2002). Ecological surveys were the primary research recommendation for almost all species in India (Molur et al. 2002). It does, however, appear that bat diversity in human modified landscapes in the Western Ghats is potentially quite low – the only published study in agricultural landscapes records just 13 morphospecies of the 52 species known to live across the Western Ghats, with the greatest diversity in forest fragments and in coffee plantations (Molur and Singh 2009), while a published study from Karnataka records 20 species (Raghuram et al., 2014). 1.11 Thesis aims and outline

This thesis explores the ecology of bats in a heterogeneous agricultural landscape in the southern Western Ghats of India. It aims to describe a previously unstudied bat assemblage and understand the drivers of species responses to habitat changes.

1.11.1 Aims

- To identify the bat species living in the agricultural landscape of Valparai.
- To build an echolocation call library to identify the echolocating bat species in the landscape.
- To identify the responses of bat species to different land uses.
- To use GIS and GPS technology to build a fine scale habitat map of the landscape, and use it to build species-specific, multi-scale habitat suitability models and maps for the entire landscape.
- To understand the key ecological drivers of species, assemblage and functional level metrics of bats in this landscape.
- To understand how biases in different methods for studying bats affect the results of a study, and which biases affect which species within this assemblage.
- To discuss the implications of these findings for bat conservation in the area.

1.11.2 Outline

Chapter Two describes the calls of the echolocating bat species in the study area, and assess the degree to which bats can be identified from their echolocation calls.

Chapter Three describes detailed habitat suitability models for ten species, built from acoustic transect data and catching data. These models aim to give an insight into the autecology of the species and highlight geographical areas of species richness worthy of conservation attention.

Chapter Four compares different habitats within the study area, and different methods of studying bats. The metrics used to compare the different habitats are species richness, diversity, abundance, evenness and composition. The results from catching and acoustic methods are compared.

Chapter Five explores the functional diversity of bats in this assemblage as assessed by functional richness, evenness, divergence and specialisation.

Chapter Six discusses the implications of the results of this thesis for assemblage and ecosystem level conservation and addresses the utility of methods and approaches used in this thesis.

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Chapter Two: Acoustic identification of bats in the southern Western Ghats, India.

2.1 Abstract

Bats play crucial roles in ecosystems, are increasingly used as bio-indicators and are an important component of tropical diversity. Ecological studies and conservation-oriented monitoring of bats in the tropics benefit from published libraries of echolocation calls, which are not readily available for many tropical ecosystems. Here, we present the echolocation calls of 15 species from the Valparai plateau in the Anamalai Hills, southern Western Ghats of India: three rhinolophids (*Rhinolophus beddomei, R. rouxii (indorouxii), R. lepidus*), one hipposiderid (*Hipposideros pomona*), nine vespertilionids (*Barbastella leucomelas darjelingensis, Hesperoptenus tickelli, Miniopterus fuliginosus, M. pusillus, Myotis horsfieldii, M. montivagus, Pipistrellus ceylonicus, Scotophilus heathii, S. kuhlii*), one pteropodid (*Rousettus leschenaultii*) and one megadermatid (*Megaderma spasma).* Discriminant function analyses using leave-one-out cross validation classified bats producing calls with a strong constant frequency (CF) component with 100% success and bats producing frequency modulated (FM) calls with 90% success. For five species, we report their echolocation calls for the first time, and we present call frequencies for some species that differ from those published from other parts of the species' ranges. This highlights the need for more local call libraries from tropical regions to be collected and published in order to record endemic species and accurately identify species whose calls vary biogeographically.

2.2 Introduction

Bats are the second most species rich order of mammals, with great ecological diversity, especially in the tropics. They undertake a range of ecosystem services, including seed dispersal, pollination and insect control. A variety of ecologically and commercially important plants rely on bats to some degree as pollinators or seed dispersers (Kunz et al. 2011). Bats are also increasingly used as bio-indicators to assess the biodiversity of areas and monitor environmental changes (Jones et al. 2009, Pedersen et al. 2012), and there is therefore a need for reliable methods for studying bat assemblages.

For many parts of the tropics we lack even the most basic information on the abundance of different bat species, their distribution and habitat requirements. The development of comprehensive survey and monitoring methods is therefore critical for understanding the current status of bats and allowing future monitoring of populations (MacSwiney et al. 2008). The two main methods used for the study of bats are capturing them with mist nets and/or harp traps, or recording their echolocation calls using ultrasound detectors. The use of ultrasound detectors in the tropics has been hampered by the lack of reliable call libraries, which allow identification of bats to genus or species level from their echolocation calls.

Handling bats directly usually allows better species identification than acoustic methods, although some cryptic species are more easily separated by calls (Fenton 1999), and allows the collection of useful data on the individual bat. However, it is also time consuming and invasive. Further, it can also lead to biases in sampling as many species fly high above nets, are more agile or are better at detecting nets than others (O’Farrell and Gannon 1999, Larsen et al. 2007). Habitats such as open fields, large water bodies or tall canopies cannot be easily or effectively sampled using capture methods.

Ultrasound detectors can be used in areas difficult to sample by capture methods, and detect foraging guilds that catching rarely does (Fenton 1990, MacSwiney et al. 2008). Acoustic transects are easy to standardize and are thus useful for long-term monitoring. However, some species cannot yet be distinguished acoustically, and low intensity echolocators and non-echolocating bats are not accurately represented, particularly in cluttered habitats (Patriquin et al. 2003, Adams et al. 2012). Higher frequency echolocation calls attenuate quickly so are underrepresented; and the type of detector used can also affect which frequencies are recorded, and from what distance (Adams et al. 2012). Ultrasound detectors and catching in combination typically give the most complete inventories and thus they should be used together for surveying and monitoring (Murray et al. 1999, O'Farrell and Gannon 1999, MacSwiney et al. 2008, Furey et al. 2009).

Given the advantages that ultrasound detectors bring to the study of bats, there have been increased efforts to build call libraries for more regions, especially those facing the gravest threats from habitat loss and conversion (Sedlock 2001, Furey et al. 2009, Hughes et al. 2010, 2011). Recording calls from as many different localities as possible is important; new species will be identified and recorded, and biogeographic variation in calls can be assessed (Russo et al. 2007, Hughes et al. 2010).

We are building an echolocation call library for an assemblage of bats from the southern Western Ghats of India. The Western Ghats are a mountain range running along the western coast of India. They form one of the eight 'hottest' biodiversity hotspots in the world, and are home to a large number of endemic species(Myers et al. 2000). The Western Ghats are the most densely populated of all hotspots with high pressures of habitat loss and degradation due to various human activities (Cincotta et al. 2000, Bawa et al. 2007). As a mountainous tropical area with high levels of endemism, they are likely to be subjected to shifting biotic compositions in the future as mid and high elevation specialists migrate upslope due to global warming, endangering many species whose range will probably contract significantly(LaVal 2004). The Western Ghats are in need of rapid conservation action (Feeley et al. 2013).

2.3 Methods

2.3.1. Study site

The study site was the Valparai plateau (c. 220 km^2), located in the state of Tamil Nadu in the southern Western Ghats (N 10.2-10.4°, E 76.8-77.0°). The native vegetation is mid-elevation tropical wet evergreen forest of the *Cullenia exarillata–Mesua ferrea–Palaquium ellipticum* type, with the plateau between approximately 800 and 1600m a.s.l. ((Raman et al. 2009). The Valparai plateau is a plantation-dominated landscape, interspersed with tropical rainforest fragments, streams, swamps and riverine vegetation, adjoining the Anamalai Tiger Reserve and Reserved Forests in Kerala state. This region was forested until the late nineteenth century, but by 2000, 76.3% of the plateau was converted to commercial plantations of tea monoculture, with the remainder as coffee or cardamom grown under mostly native shade trees, scattered eucalyptus plantations, and fragments of remnant forest (Mudappa and Raman 2007). The average annual rainfall is 3,500 mm, of which about 70% falls during the southwest monsoon (June–September; Raman et al. 2009).

2.3.2 Sound recording and analysis

Between 2008 and 2013, bats were captured in mist nets and harp traps in forest fragments, coffee, tea and cardamom plantations, along rivers, and at roosts in tunnels and caves. Bats were caught in accordance with Natural England protocol, and their welfare was of the highest priority at all times (http://www.naturalengland.org.uk/Images/wmlg39_tcm6-35872.pdf). Bats were identified to species (Bates 1997, Srinivasulu et al. 2010) and their echolocation calls on release were recorded using a Pettersson D240X ultrasound detector (www.batsound.com) with a sampling rate of 307 kHz and a range of 10 - 120 kHz recording onto an Edirol R-09 (www.roland.com) digital recorder sampling at 44.1 kHz. The detector was manually triggered 4 seconds after release to capture 3.4 seconds of calls in 10 x time expansion as WAV files.

2.3.2.1 Automatic extraction of call parameters.

We extracted call parameters using custom-written software (Scott 2012, Bellamy et al. 2013). Up to ten clear calls with the highest signal to noise ratio were selected from each individual recording and the call parameters were measured using the same software. For each call parameter, the mean based on up to ten calls for each individual bat was used for further analysis. For each call, the following parameters were quantified: i) start frequency - the point at which a signal 12dB above the background noise estimate was encountered; ii) end frequency - where a drop in energy of over 40 dB from the peak energy of the call was seen; iii) call duration - the time in milliseconds between start and end frequencies; iv) frequency of maximum energy (FMAXE) - the frequency containing the maximum energy on a power spectrum (Scott 2012); and v) bandwidth, obtained by subtracting end frequency from start frequency.

For bats with a strong constant frequency (CF) component to the call (Rhinolophidae and Hipposideridae) only FMAXE and call duration were measured. We use the term constant frequency here to describe a call where the majority of the sound is produced at a single frequency (Fenton 2013). Constant frequency calls are also referred to as high duty cycle calls, and frequency modulated (FM) calls that start at a high frequency and sweep down to a low frequency are also referred to as low duty cycle calls (Bogdanowicz et al. 1999). For bats making frequency modulated (FM) calls all five measurements were used (Table 2.1, Figs. 2.1 and 2.2).

2.3.2.2 Discriminant Function Analyses

We used linear discriminant function analysis (lDFA) to classify bat calls from the southern Western Ghats to the species level (Russo and Jones, 2002). lDFA does not require sophisticated software and is available in a variety of statistical software programs, giving it great scope as a mass identification tool for researchers and conservationists in the field (Papadatou et al. 2008). All statistical analyses in this paper were carried out in IBM SPSS Statistics 19 (Released 2010. IBM SPSS Statistics for Windows, Version 19.0. Armonk, NY: IBM Corp).

Analyses were carried out separately for rhinolophoid bats producing CF calls and for species producing FM calls. All rhinolophoid (CF) bats were analysed using a linear discriminant function analyses with leave-one-out cross validation, based on FMAXE and call duration. Cross-validation is used to ‘test’ a statistical model to reduce overfitting and give insight into how the model will work on an independent datasetn(Stone 1974). Due to small sample sizes we used leave-one-out cross validation, where one sample is removed and the analysis is performed on all the other data, then validated on the removed sample. This is repeated for as many iterations as there are samples (Stone 1974). Bats using FM calls with over five sampled individuals (except *M. spasma*) were grouped and a stepwise Discriminant Function Analysis (DFA) run with the five acoustic variables listed above. As a DFA cannot be performed for groups with fewer individuals than the number of variables, the two variables that had the lowest Wilk’s λ score, and thus contributed the most to the first DFA, were identified and a further DFA run with these two variables, which allowed all species with more than two individuals to be included.

All calls were independent, as they were all recorded from different bats. The tolerance values for all of the independent variables are larger than 0.1, so multicollinearity was not present in either model. All species showed normal distributions of call parameters apart from *Myotis horsfiedlii, Pipistrellus ceylonicus, Rousettus leschenaultii, Rhinolophus indorouxii* and *Scotophilus heathii* which had distributions deviating from normal for one or more parameters, mostly due to skewness (as assessed by the Shapiro-Wilks test). Transforming the variables to make them normal and removing outliers did not increase classification success by more than 2% in the FM model (it could not do so in the CF model as classification was 100% with the baseline model) so we used the baseline FM model of untransformed data with outliers. Box's M statistic was statistically significant on both untransformed and transformed data for both the CF and FM models, so we do not meet the assumption of homogeneity of variance (FM bats F=5.853, *d.f.*=18, 781.984; CF bats F=6.384, *d.f.*=6, 1299.685; P<0.001 for both). We re-ran both analyses using separate covariance matrices for classification. The classification rate did not change by more than 2% so we used the baseline model with a pooled covariance matrix. Sometimes quadratic classification criteria in DFA are used when the assumption of homogenous variance-covariance matrices is violated; but quadratic DFA does not work as well as linear DFA with small sample sizes (Friedman 1989). In our data, the log determinants of the group covariance matrices were very similar indicating that the violation was not substantial. In neither linear model were species misclassified to the species with highest dispersion, the main problem caused by heterogeneous variance-covariance matrices. We therefore considered linear DFA adequate for the classification of these data.

2.4 Results

Table 2.1: Call parameters for all species (mean ± standard deviation, minimum-maximum).

Genera	Species	Start Freq (kHz)	End Freq (kHz)	FMAXE (kHz)	Duration (ms)	Bandwidth (kHz)	Number of recordings
Vespertinilionid	*Barbastella leucomelas darjelingensis**	36.46 ± 1.42 (34.6-39.9)	21.46± 0.4 (20.84-23.1)	29.23 ± 2.2 (25-31.5)	4.37 ± 0.72 (3.4-5.4)	15.62 ± 1.6 (11.82-18.44)	1
	*Hesperoptenus tickelli**	58.16 ± 2.34 (54-60.7)	20.22 ± 1.31 (20.8-26.7)	28.32 ± 1.76 (25.2-31)	5.06 ± 0.7 (4-6.1)	37.94 ± 2.07 (33-37.4)	1
	Miniopterus fuliginosus	93.67 ± 13.86 (54.28-113)	48.29 ± 1.32 (42.88-53)	52.03 ± 1.92 (44.5-62.4)	4.0 ± 1.03 (1.53-9)	44.37 ± 13.08 (6.7-53.3)	31
	Miniopterus pusillus	110.92 ± 10.16 (98.4-125.4)	58.12 ± 1.98 (54.6-58.9)	64.13 ± 3.19 (57.9-68.8)	3.66 ± 1.33 (3-6.6)	52.8 ± 11.2 (40.5-68.3)	4
	Myotis horsfieldii	91.23 ± 15.27 (50.75-126.8)	41.6 ± 2.65 (33.46-57.5)	53.8 ± 5.14 (37.9-101)	2.57 ± 0.6 (1.54-6.7)	23.88 ± 8.55 (6.83-83.9)	59
	*Myotis montivagus**	81.23 ± 14.67 (55.3-99.6)	44.95 ± 1.37 (38.4-49.8)	49.9 ± 2.09 (46.4-55.7)	2.57 ± 0.57 (1.5-4.1)	36.28 ± 14.73 (10.5-54.5)	3
	*Pipistrellus ceylonicus**	59.45 ± 9.11 (40.2-91.3)	35.57 ± 1.62 (31-42.62)	38.64 ± 1.99 (34.9-45.5)	2.57 ± 0.6 (1.5-4.7)	23.88 ± 8.55 (1.9-54.4)	23

	*Scotophilus heathii**	60.12 ± 5.21 (43.2-83.8)	37.65 ± 1.12 (33.8-43)	41.20 ± 1.87 (37.4-59.6)	2.4 ± 0.54 (1.5-5.1)	22.4 ± 5.21 (5.9-46.7)	16
	Scotophilus kuhlii	56.67 ± 2.06) (52.4-61.3)	43.53 ± 0.76 (42.1-44.9)	45.26 ± 0.77 (44-47)	2.96 ± 0.38 (2.2-3.5)	13.1 ± 2.25 (8.9-18.1)	2
Megadermatid	*Megaderma spasma*	99.79 ± 12.37 (65.3-113.1)	38.87 ± 2.30 (34.6-44.3)	55.9 ± 12.3 (38.3-91.4)	2.06 ± 0.32 (1.4-2.87)	60.9 ± 12.06 (30.1-73.3)	5
Pteropodid	*Rousettus leschenaultii*	60.4 ± 22.01 (34.5-184)	13.48 ± 1.8 (8-17.6)	23.29 ± 6.29 (11.7-35.5)	1.9 ± 0.89 (1.5-2.3)	46.93 ± 22.2 (23.1-170.6)	20
Rhinolophid	*Rhinolophus beddomei*			42.81 ± 0.53 (41.7-43.3)	47.70 ± 13.62 (24.7-71.3)		2
	Rhinolophus lepidus			102.31 ± 1.81 (97-106.3)	25.23 ± 11.38 (1.4-51.5)		35
	Rhinolophus indorouxii (prev. R. rouxii)			92.08 ± 1.06 (87.2-94)	24.44 ± 12.1 (2.2-65.3)		41
Hippisiderid	*Hipposideros pomona*			126.337 ± 1.25 (123.7-128.2)	8.13 ± 0.94 (6.1-9.9)		6

*First published calls for these species

2.4.1. Discriminant function analysis

2.4.1.1. Constant frequency calls

Using FMAXE and call duration, DFA classified calls to species with 100% success compared with 25% expected from random assignment (overall Wilk's λ = 0.01, *P*<0.001). A stepwise analysis showed that FMAXE was the most important factor in classification (Figs 2.1, 2.2; FMAXE: Wilk's λ = 0.011, $F_{3, 80}$ = 2377.602, *P* <0.001).

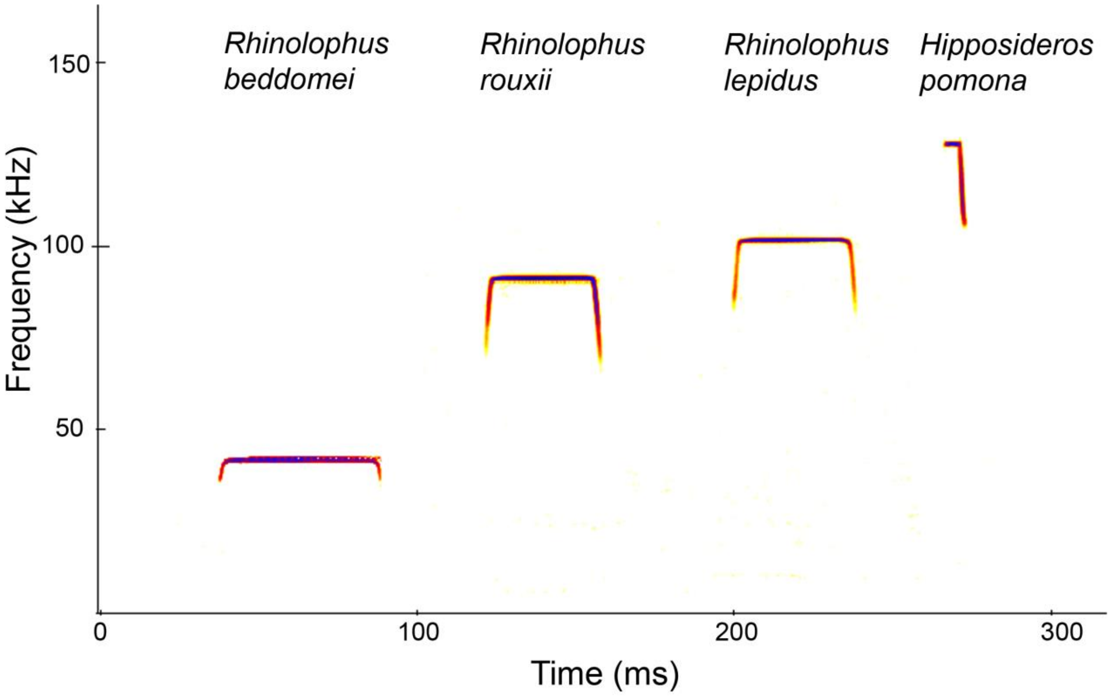

Figure 2.1: Spectrogram of echolocation calls of bats with constant frequency calls (Figure courtesy of E. Foui).

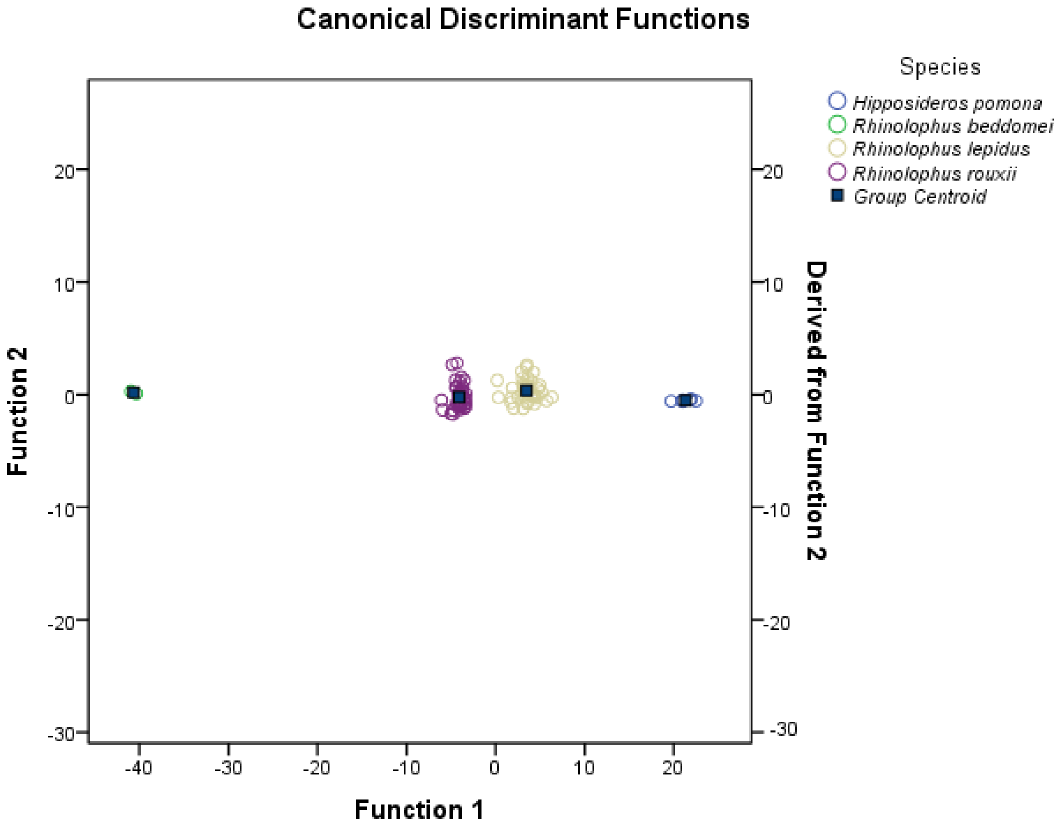

Figure 2.2 Mean calls of Rhinolophoid species plotted by two discriminant functions.

2.4.1.2 Frequency modulated calls

All bats that used a single dominant FM harmonic were grouped for analysis along with *R. leschenaultii,* which uses a low frequency tongue click. This included all non-rhinolophoids other than *M. spasma,* whose calls have an average of four short harmonics, making it easy to separate visually on a spectrogram from other FM bats in the area (Fig. 2.3).

The data for the five species with over five individuals were analysed using a stepwise DFA with cross validation that showed FMAXE and end frequency to be the most useful predictors (end frequency: Wilk's $\lambda = 0.037$, $F_{4,\,144} = 937.80$, $P < 0.001$; FMAXE: Wilk's $\lambda = 0.014$, $F_{8,\,286} = 265.5$, $P < 0.001$). This had 100% assignment accuracy for *M. fuliginosus* and *R. leschenaultii*, >90% accuracy for *M. horsfieldii* and *P. ceylconicus* and 56% assignment accuracy for *S. heathii.* A further DFA was run with just FMAXE and end frequency (Fig. 2.4). This allowed eight species with more than two individuals to be analysed, and classified 89.2% of individuals correctly after cross validation (Wilk's $\lambda = 0.013$, $P < 0.001$) as compared to 12.5% based on random chance. *Myotis montivagus,* *Miniopterus pusillus, R. leschenaultii* and *S. kuhlii* were assigned with 100% accuracy, *Miniopterus fuliginosus* with >90% accuracy, and *Myotis horsfieldii, Pipistrellus ceylonicus* and *Scotophilus heathii* with >80% accuracy (Table 2.2).

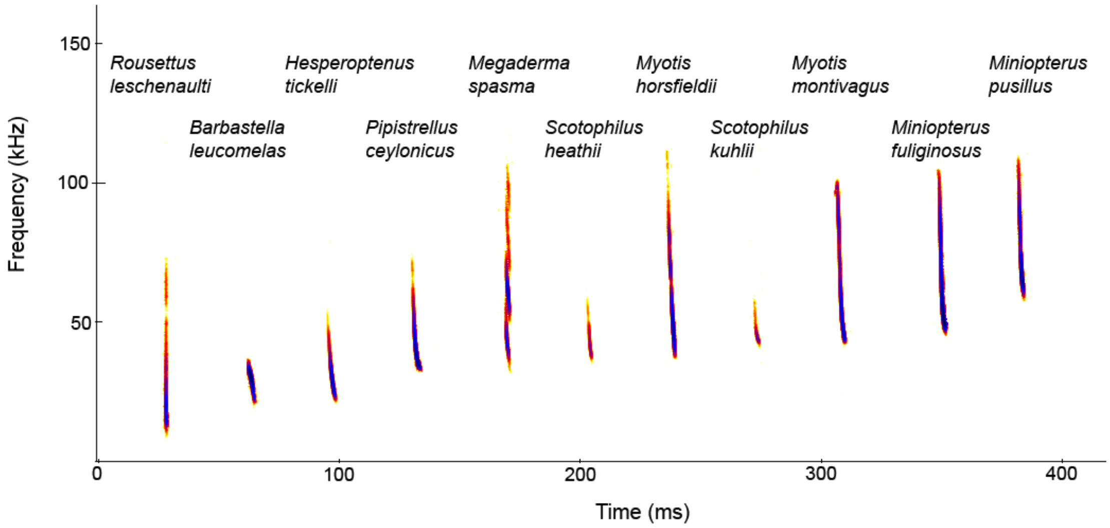

Figure 2.3: Spectrogram of echolocation calls of bats with frequency modulated calls. (Courtesy of E. Foui).

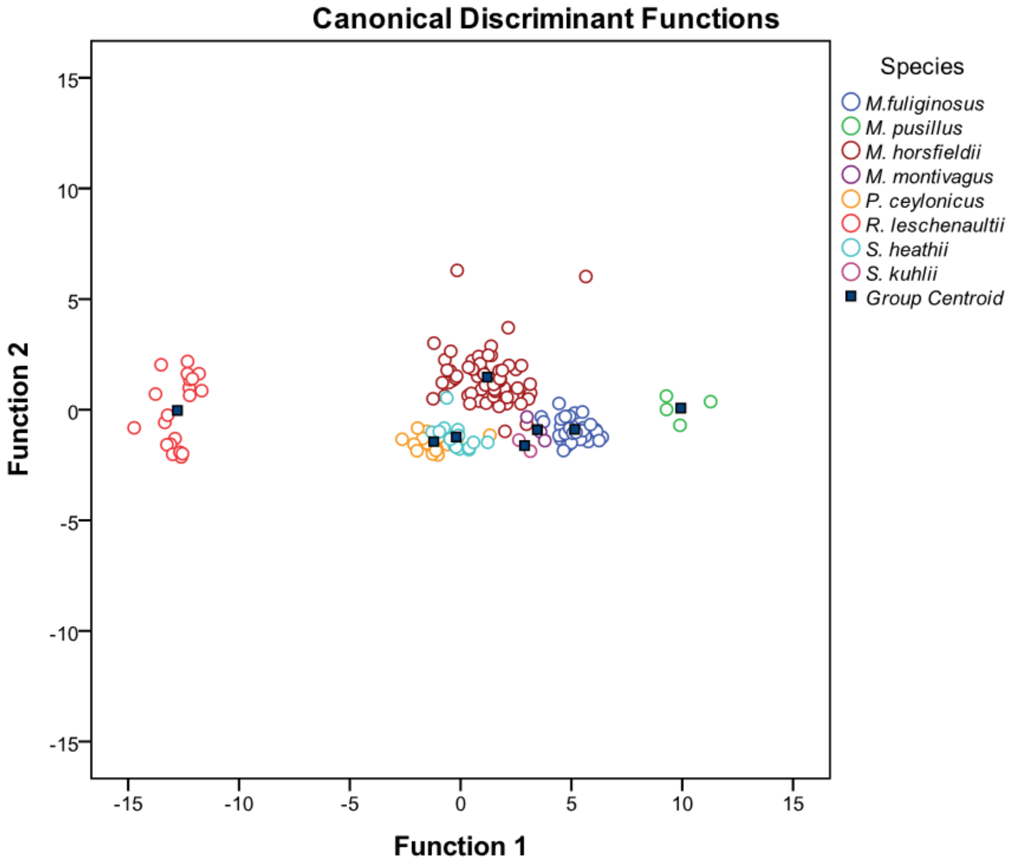

Figure 2.4: Mean frequency modulated calls, plotted against two discriminant

Table 2.2: DFA with cross validation for species with over two individuals. The first part of the table shows the classification success of the lDFA in raw numbers, the second part shows the pecentages. In cross validation, each case is classified by the functions derived from all cases other than that case. 89.2% of cross-validated grouped cases correctly classified.

		Predicted Group Membership								
		M. fuliginosus	*M. pusillus*	*M. horsfieldii*	*M. montivagus*	*P. ceylonicus*	*R. leschenaultii*	*S. heathii*	*S. kuhlii*	Total
Count	*M. fuliginosus*	29	0	0	2	0	0	0	0	31
	M. pusillus	0	4	0	0	0	0	0	0	4
	M. horsfieldii	0	1	50	5	1	0	1	1	59
	M. montivagus	0	0	0	3	0	0	0	0	3
	P. ceylonicus	0	0	0	0	19	0	4	0	23
	R. leschenaultii	0	0	0	0	0	20	0	0	20
	S. heathii	0	0	0	0	2	0	14	0	16
	S. kuhlii	0	0	0	0	0	0	0	2	2
%	*M. fuliginosus*	93.5	.0	.0	6.5	.0	.0	.0	.0	100.0
	M. pusillus	.0	100.0	.0	.0	.0	.0	.0	.0	100.0
	M. horsfieldii	.0	1.7	84.7	8.5	1.7	.0	1.7	1.7	100.0
	M. montivagus	.0	.0	.0	100.0	.0	.0	.0	.0	100.0
	P. ceylonicus	.0	.0	.0	.0	82.6	.0	17.4	.0	100.0
	R. leschenaultii	.0	.0	.0	.0	.0	100.0	.0	.0	100.0
	S. heathii	.0	.0	.0	.0	12.5	.0	87.5	.0	100.0
	S. kuhlii	.0	.0	.0	.0	.0	.0	.0	100.0	100.0

2.5 Discussion

The DFA for species emitting CF calls distinguished 100% of calls correctly. The DFA for the single harmonic FM bats classified calls to species level with ~90% accuracy, however there is the potential for misclassification of some species in this group as some had overlapping call parameters. The most difficult species in this assemblage to locate acoustically are likely to be *H. pomona,* whose very high frequency calls attenuate over short distances and so may be less frequently detected (Griffin 1971); *M. spasma*, which calls very quietly; and *R. leschenaultii*, whose tongue clicks resemble cracking twigs.

For several species – *Barbastella leucomelas darjelingensis, Hesperoptenus tickelli, Myotis montivagus, Pipistrellus ceylonicus, Scotophilus heathii* – the calls reported here are, we believe, the first published calls from these species. This is the first record of *B. leucomelas darjelingensis* in South India. Finding this bat in a tropical location is surprising as its preferred habitat has been described as 'Himalayan moist temperate forest and dry coniferous forest areas', so our record extends the species' known habitat and range considerably – the nearest record is over 2000 km away (Benda and Mlikovsky 2008). *H. tickelli* and *M. pusillus* were also not thought to live in this area (Korad et al. 2007, Bumrungsri et al. 2008, Csorba et al. 2008d). Korad *et al.* (2007) list 16 species found between 10°N and 12°N in the Western Ghats that we did not record from there. IUCN range maps suggest that 10 of these may be found in the Valparai area above 800m asl.: *Pteropus giganteus*, *Hipposideros ater, H. fulvus*, *H. speoris, Megaderma lyra, Harpiocephalus harpia lasyurus, Pipistrellus coromandra* and *P. tenuis* (Bates 1997, Csorba et al. 2008a, 2008b, 2008e, 2008f, Francis et al. 2008, Molur et al. 2008a, 2008b, Srinivasulu and Molur 2008). Other species noted at this latitude by Korad *et al.* (2007) and that have been recorded above 800 m asl. are *Rhinolophus luctus, Falsistrellus affinis, Taphozus theobaldi* and *Tylonycteris pachypus* (Bates 1997, Bates et al. 2008a, 2008b, Csorba et al. 2008c, Walston et al. 2008) The absence of some of these species may be due to the extensive agricultural land use in the area, but we cannot as yet conclusively rule out their presence in the Valparai plateau or surrounding forests. While there is no extensive literature on the habitat requirements of most of these species, *H. ater, H. harpia lasyurus, T. theobaldi* and *R. luctus* have all been associated predominantly with undisturbed forest (Bates et al. 2008a, Csorba et al. 2008e, 2008f, Walston et al. 2008).

2.5.1 Biogeographic Variation

It is important to record calls from as many locations as possible, as call frequencies can vary geographically within a species (Hughes et al. 2010). Knowing the extent of call variability for a species over a wide geographic area can indicate whether or not calls from a species recorded in one area can be used to identify that species with certainty in another. It can also identify populations that might be cryptic species – genetically distinct species with very similar morphological features - or Evolutionarily Significant Units (ESUs), important for conservation decisions (Crandall et al. 2000, Davidson-Watts et al. 2006, Bickford et al. 2007, Frankham 2010).

Each of the rhinolophoid species recorded here vary in call frequency to some degree across their biogeographic ranges, although there are few data for *R. beddomei* or *R. lepidus* (Fig. 2.5, Table 2.3a,b; (Schuller 1980, Neuweiler et al. 1987, Kössl 1994, Francis and Habersetzer 1998, Behrend and Schuller 2000, Pottie et al. 2005, Struebig et al. 2005, Francis 2008, Furey et al. 2009, Zhang et al. 2009, Chattopadhyay et al. 2010, Soisook et al. 2010, Chattopadhyay et al. 2012, Douangboubpha et al. 2010, Hughes et al. 2010). For *R. rouxii spp.* and *H. pomona*, biogeographic variation in call frequency may be due to the existence of cryptic species or subspecies. Cryptic species calling at different frequencies are often found among bats that emit CF calls (Kingston et al. 2001).

Chattopadhyay *et al.* (2012) characterized two divergent genetic lineages in the South Indian *R. rouxii*, which they consider sibling species; *R. rouxii* (FMAXE 80 kHz) and *R. indorouxii* (FMAXE 90 kHz) (Fig. 2.5, Table 2.3a,b). The bats we recorded resembled the *R. indorouxii* from Tamil Nadu more than the *R. rouxii* from Karnataka or the Sri Lankan *R.r. rubidus* in echolocation call frequency and forearm length. The mean forearm (FA) length for adult *R. indorouxii* in this study was 51.1mm (range 48.4-55.8mm), which is more similar to the means from the three Tamil sites in Chattopadhyay *et al.* (51.51mm, 51.47mm, 52.16mm) than the two sites in Karnataka (47.75mm, 50.51mm) although there is clearly considerable overlap and FA length alone is not diagnostic for this species group.

FMAXE of *H. pomona* varies from 121-140kHz across its range (Fig. 2.5, Table 2.3a,b; Francis and Habersetzer 1998, Struebig et al. 2005, Shek and Lau 2006, Francis 2008, Furey et al. 2009, Zhang et al. 2009, Douangboubpha et al. 2010, Hughes et al. 2010). Sun *et al.* (2009) found genetic divergence sufficient to indicate cryptic speciation between *H. pomona* they caught in China and *H. pomona* GenBank sequences. More work is needed to see whether this divergence correlates with different phonic types. The mean forearm length of adult *H. pomona* in this study was 40.8mm (range 40-42mm). In China, FA lengths for *H. pomona* were similar to those we found and overlapped across all sites: Yunnan 41.5–44.2 mm, Guangdong 40.6–43.0 mm, Hainan 38–42 mm, Hong Kong 40.4 – 47.1mm (Shek and Lau 2006, Zhang et al. 2009). In Myanmar FA lengths were 38.4-42.8 mm (Struebig et al. 2005) and in Thailand 39.5-44.6mm (Douangboubpha et al. 2010). *H. pomona* varies by nearly 10mm in FA length across its range, but it is currently unclear whether this reflects the presence of subspecies or cryptic species. The degree of biogeographic variability in call frequency for *H. pomona* and *R. rouxii* underlines the need for improvements in local knowledge of rhinolophoid calls across tropical regions.

By contrast the call frequencies of FM species varied little geographically, although there was not much biogeographic data available (Table 2.4; Jacobs 1999, Parsons and Jones 2000, Sedlock 2001, Dietz 2005, Pottie et al. 2005, Zhang et al. 2007, Papadatou et al. 2008, Furey et al. 2009, Furman et al. 2010, Hughes et al. 2010, 2011). The often great intraspecific variability and interspecific overlap in call frequencies means that identifying FM calls may be difficult without prior knowledge of a species' presence. Recording more bat echolocation calls across the tropics would improve our understanding of the biogeography and ecology of species, and assist in the creation and implementation of evidence-based conservation management plans and long-term monitoring programs.

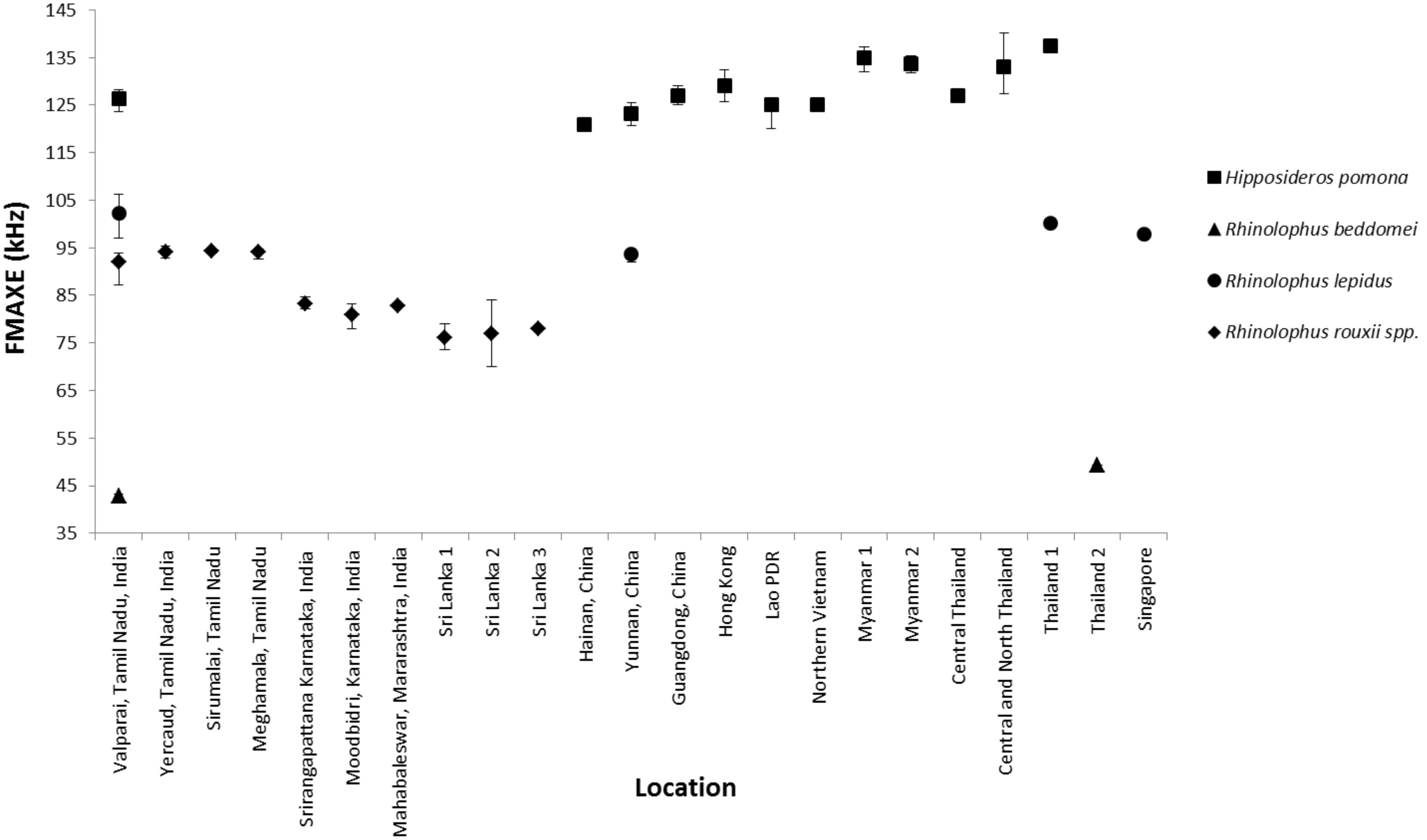

Figure 2.5: Biogeographic variation in the echolocation call frequencies of constant frequency bats.

Table 2.3a: Biogeographic variation in constant frequency bat calls.

Species	Valparai, Tamil Nadu, India	Yercaud, Tamil Nadu, India (Chattopadhyay et al 2010/ Chattopadhyay et al 2012)	Sirumalai, Tamil Nadu, India (Chattopadhyay et al 2012)	Meghamala, Tamil Nadu, India (Chattopadhyay et al 2012)	Srirangapattana Karnataka, India (Schuller 1980/ Chattopadhyay et al 2012)	Moodbidri, Karnataka, India	Mahabaleswar, Maharashtra, India (Schuller 1980)	Sri Lanka (Neuweiler et al 1987/Behrend 2000/Kossl 1994)	Yunnan, China (Zhang et al 2009/Shi et al 2009)	Guangdong, China (Zhang et al 2009)	Hainan, China (Zhang et al 2009)
Hipposideros pomona	126.3 kHz (n=6)								120.8-125.6 kHz	125-129 kHz	121 kHz
Rhinolophus beddomei	42.8 kHz (n=2)										
Rhinolophus lepidus	102.3 kHz (n=35)								92-95.2 kHz (n=3)/91 kHz		
Rhinolophus indorouxii	92 kHz (n=41)	R. indorouxii 93.9 kHz (n=7)/94.1 kHz (n=60)	R. indorouxii 94.3 kHz (n=3)	R. indorouxii 94 kHz (n=12)	*R. rouxii* 85.2 kHz/83.3 kHz (n=13)	*R. rouxii* 80.9 kHz (n=33)	*R. rouxii* 82.8 kHz	R.r. rubidus 73.5-79 kHz (76)/70-84 kHz (n=16)/78 kHz (n=7)			

Table 2.3b: Biogeographic variation in constant frequency bat calls.

Species	Hong Kong (Shek and Lau 2006)	Central and North Thailand (Douangboubpha et al 2010)	Lao PDR (Francis and Habersetzer 1998/ Francis 2008)	Central Thailand (Puechmaille (in Douangboubpha et al 2010))	Myanmar (Streubig 2005)	Myanmar (Puechmaille (in Douangboubpha et al 2010))	Thailand (Hughes et al 2010,2011)	Thailand (Soisook et al 2010)	Northern Vietnam (Furey 2009)	Singapore (Pottie et al 2005)
Hipposideros pomona	125.7-132.5 kHz	127.3-140.2 kHz (mean 133 kHz) (n=36)	125 kHz/120-126 kHz	125.6-128.2kHz	132.1-137.2 kHz (mean 134.9 kHz)	131.8-135.4 kHz	137.4 kHz (n=85)		125.1 kHz (n=7)	
Rhinolophus beddomei								49.3 kHz (n=1)		
Rhinolophus lepidus							100.1 kHz (n=69)			97.8 kHz (n=4)
Rhinolophus indorouxii										

Table 2.4: Biogeographic variation in call frequency of frequency modulated bats.

Species	Valparai, Tamil Nadu, India	Thailand (Hughes et al 2010,2011)	Northern Vietnam (Furey 2009)	Singapore (Pottie et al 2005)	The Phillipines (Sedlock et al 2001)	China (Zhang et al 2007)	Eygpt (Dietz 2005)	Britain (Parsons and Jones 2000)	Romania (Furman et al 2010)	Iran (Furman et al 2010)	Greece (Papadatou et al 2008)	South Africa (Jacobs 1999)
Barbastella leucomelas darjelingensis	29.2 kHz, end freq 20.8 kHz(n=1)					*B. beijingensis* 32.1 kHz, terminal freq 26.8 kHz (n=1)	*B. leucomelas* terminal freq 28 kHz	*B. barbastella* 33.1 kHz, end freq 29.7kHz (n=33)				
Megaderma spasma	56 kHz, end freq 39 kHz (n=5)	73 kHz, end freq 30 kHz (n=44)										
Miniopterus fuliginosus	52 kHz, end freq 48 kHz (n=31)				Min freq 45-46 kHz (n=9)				*M. schreibersi i* 58.8 kHz, terminal freq 48.6 kHz (n=13)	*M. s. pallidus* 56.1 kHz, terminal freq 48.1 kHz (n=20)	*M. schreibersi i* 50.4 kHz to 66.5 kHz (n=61)	*M. schreibersi i* Min freq 37.5 kHz-50.3 kHz
Miniopterus pusillus	64.1 kHz	62.8 kHz (n=11)										

	(n=4)				
Myotis horsfieldii	53.6 kHz, end freq 41.6 kHz (n=59)	56.9 kHz , terminal freq 39.6 kHz (n=8)			Min freq 47.6 kHz (n=14)
Rousettus leschenaultii	20.4 kHz (n=20)		22.9 kHz (n=15)		
Scotophilus kuhlii	46.2 kHz (n=2)			43.3 kHz (n=27)	

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Chapter Three: Habitat suitability modelling of foraging bats at multiple spatial scales.

3.1 Abstract

The landscape of the Western Ghats is being altered by human pressures at a rapid rate. As bats are very poorly known from this biodiversity hotspot, it is unclear how the different species react to different land uses; which species are more and which are less disturbance tolerant, and how the distribution of different species changes with landscape level changes. I used species-specific habitat suitability modelling at multiple spatial scales to address these questions in the southern Western Ghats. I used data from 44 acoustic transects and 43 catching sites for 10 species that were clearly identifiable from echolocation calls, and were recorded in five or more locations. I built a fine scale habitat map for the Valparai plateau and the surrounding 5 km using satellite imagery and on the ground verification. Using habitat data analysed at five spatial scales (100 m – 4000 m) in conjunction with the Habitat Suitability Modelling (HSM) software, MaxEnt, I quantified the predictive power of each habitat layer at each scale on each species. Over-fitting, residual spatial autocorrelation, and sampling bias were addressed by the analysis. Habitat features measured at the 100 m scale and variables quantifying the distance to habitats were generally the strongest predictors of foraging bats. This is likely due to their high mobility, allowing them to find even small or isolated foraging areas within less suitable habitat. Several species were also affected by habitat richness at the 200 m or 500 m scales. The best predictors for multiple species were habitats containing native trees at 100 m scale (positive response), tea plantations at 100 m scale (negative response), habitat richness at 500 m scale (positive response) and distance from water's edge (negative response), which were all in the best fitting model for two or more species. I compared the models for each species to find the best fitting model using a variety of model-testing metrics. The highest scoring models all contained between one and three variables, and models scored better for specialist species confined to specific habitats than for generalist species.

3.2 Introduction

3.2.1 Habitat suitability modelling for bats

As digital maps have become more widely available, more HSM studies of bats in the tropics have been published. Tropical studies have focused on regional scales such as the whole of sub-Saharan Africa (Lamb et al. 2008), Central and South America (Lee et al. 2012) or South East Asia (Catullo et al. 2008, Hughes et al. 2012); or the scale of a large state or a country such as Bangladesh (Hahn et al. 2014), Thailand (Hughes et al. 2010), East Kalimantan in Indonesia (Drummond et al. 2010) or Australia's Northern Territory (Milne et al. 2006). Most tropical habitat suitability models for bats have been built with a cell size of 1 km^2 to 81 km^2 and analysed at a single scale (Milne et al. 2006, Lamb et al. 2008, Catullo et al. 2008, Drummond et al. 2010, Hughes et al. 2010, 2012, Lee et al. 2012). These large scale studies can be used to address wide reaching questions, but conclusions drawn from regional models are not always appropriate at a local scale (McConville et al. 2013).

It is important in species conservation to understand regional patterns of distribution, but is it also important to understand how species respond locally to fine scale changes in habitat and how the strength and direction of responses to variables can change with scale (Bellamy et al. 2013). HSM maps at fine resolutions are likely to be very important for planning mitigation strategies (Hughes et al. 2012), as understanding how individual bats, colonies and populations use local habitat types is crucial for planning at the landscape scale to maximise foraging area and connectivity. In many cases fine scale studies are probably not conducted due to the lack of fine grain habitat data.

Some authors have suggested that as bats are mobile animals, often with relatively large home ranges, fine scale factors are unlikely to drive occurrence patterns (Milne et al. 2006). Other authors have shown that precisely because of their mobility many bats can exploit small, isolated habitat resources and their occurrence is strongly driven by variables from scales as small as 20 m - 500 m (Ober et al. 2008, Pinto and Keitt 2008, Meyer and Kalko 2008, Lookingbill et al. 2010, Fabianek et al. 2011, Razgour et al. 2011, Akasaka et al. 2012, Bellamy et al. 2013, Hahn et al. 2014) and that the strength and direction of a variable's influence can change with the spatial scale at which it is studied. It is therefore important to study bats at multiple scales (Gorresen and Willig 2004, Gorresen et al. 2005, Meyer and Kalko 2008, Klingbeil and Willig 2009, Lundy et al. 2012, Bellamy et al. 2013). The only tropical bat HSM to assess the utility of variables at multiple scales is the study by Hahn et al. (2014) in Bangladesh, although other studies in the tropics (exclusively the neo-tropics) have explored the relationships between bats and scale using other methods (Avila-Cabadilla et al. 2012; Gorresen et al. 2005; Gorresen and Willig 2004; Henry, Cosson, and Pons 2010; Klingbeil and Willig 2009; Meyer and Kalko 2008; Pech-Canche, Moreno, and Halffter 2011; Pinto and Keitt 2008). Many studies describing themselves as multiple scale studies are in fact multiple design, as they include non-scalar factors, typically at the micro-habitat scale.

The study by Hahn et al. is both a multiple scale and a multiple design study, looking at scalar factors (such as percentage cover of habitat type) in 20 m x 20 m grids around *Pteropus giganteus* roosts and also within a 1 km radius of the roost, as well as distance variables and non-scalar variables such as roost tree height, species and diameter at breast height (Hahn et al. 2014). Multiple design studies of bats in the tropics often show that non-scalar variables at a microhabitat level are important predictors of bat presence (Avila-Cabadilla et al. 2012; Meyer and Kalko 2008), as they are in more temperate climates (Zimmerman and Glanz 2000, Loeb and O'Keefe 2006, Yates and Muzika 2006, Ober et al. 2008, Akasaka et al. 2010). These multiple design studies are important and informative, but the variables cannot be measured over multiple spatial scales so they are not in truth multiple scale studies (Bellamy et al. 2013). In order for a study to be considered truly multiple scale, the same independent variables should be used at all study scales, and either extent or grain should be changed, not both (Wheatley and Johnson 2009). Grain refers to the resolution of the study, the smallest 'pixel size' used (e.g. 50 m x 50 m squares); and extent refers to the entire area over which the study takes place (e.g. Central and South America).

An individual bat may respond strongly both to a small scale factor such as a small water body where it drinks or hunts, and simultaneously a larger scale factor such as the area of woodland across its home range that provides roosting sites (Gorresen et al. 2005). Different bat species may also operate predominantly at different scales; the bat *Artibeus jamaicensis* eats the fruit of mature forest trees such as *Ficus* species, which have a scattered distribution. It has a large body mass and home range, and was best predicted by models of forest cover in the 1 km – 1.5 km scale in a study in Brazil (Pinto and Keitt 2008). In contrast, *Carollia* and *Sturnira* bat species feed on plants associated with early successional stages such as *Piper* and *Solanum* species respectively. *Carollia* species were best predicted by forest cover at scales between 100 and 500 m, and *Sturnira* species at the 200 m scale (Pinto and Keitt 2008). Different variables used in the analysis may also be important at different spatial scales. For example, in Gatún Lake islands in Panama area effects were more important at larger spatial scales, and distance effects at smaller scales (Meyer and Kalko 2008). These studies show that although one might have a priori ideas about which spatial scales are influential in a study, it is important to analyse multiple scales to fully disentangle the relationships.

This study took place in the southern Western Ghats of India, in the state of Tamil Nadu. The study area was the cleared agricultural areas of the Valparai plateau and the adjacent Thalanar and Waterfall agricultural areas. These areas are surrounded on all sides by forest reserves, so the levels of biodiversity supported in the agricultural plateau are likely to affect the biodiversity maintained in the reserve forest (Laurance et al. 2012).

3.2.2 Approaches used here in studying bat-habitat associations at multiple scales

In this study I used MaxEnt, a presence-only method of habitat suitability modelling, to quantify the strength and direction of relationships between bats and environmental variables over five spatial scales. Presence-only models use information about variables at known species occurrence points and compare these to values for variables at pseudo-absence points generated by MaxEnt, representing the range of environmental variables available in the study area. I examined how each species responded to a suite of environmental variables at all five spatial scales, and then selected each variable at the best performing scale. The combination of variables with the best predictive power was used to generate a map predicting the likelihood of that species' occurrence across the agricultural landscape. The maps were combined to generate a species richness map across the landscape.

3.2.2.1 Choosing MaxEnt

I followed the methods of recent work on bat HSMs, and used MaxEnt software to build my models (Lamb et al. 2008, Rebelo et al. 2010, Rebelo and Jones 2010, Hughes et al. 2010, 2012, Razgour et al. 2011, 2014, Lee et al. 2012, Roscioni et al. 2013, Bellamy et al. 2013, Buckman-Sewald et al. 2014, Hahn et al. 2014). MaxEnt is a maximum entropy machine learning method (Phillips et al. 2006). The inputs for MaxEnt are occurrence localities as latitude-longitude coordinate points, and environmental variables as a grid of pixels covering the study area (Phillips et al. 2006). MaxEnt works by finding the probability distribution that is closest to uniform for a species (maximum entropy) subject to a set of constraints describing our information about the distribution of that species (Phillips et al. 2006).

MaxEnt offers a range of advantages. It is freely available (http://www.cs.princeton.edu/~schapire/maxent/), user friendly and has been shown to often outperform other methods (Elith et al. 2006, Phillips et al. 2006, Pearson et al. 2007, Rebelo and Jones 2010). As it is a generative approach, not a discriminative one, it performs well even with small sample sizes. It uses presence-only data, important in modelling mobile species where true absence data are rare, and can be used with continuous and categorical environmental variables. It also gives a continuous output, which allows subtle interpretation of the predicted suitability across an area. However, if binary predictions are needed, there is a choice of threshold options. MaxEnt can describe non-linear responses and include interactions between variables, and when using MaxEnt one can formally address sampling bias, spatial autocorrelation and over-fitting to training data. It can be used for a variety of purposes at all scales (Phillips et al. 2006).

While MaxEnt studies have been criticised for insufficient control of sampling bias and not reporting model relationships, these issues can be easily resolved in MaxEnt (Yackulic et al. 2013, Merow et al. 2013). MaxEnt, as a presence only approach, is also often considered unsuitable for situations where absence data exists – such as this study (Yackulic et al. 2013). However, as I was working on highly mobile, often difficult to detect animals – and as some transects points were only briefly surveyed – I decided that adding absence data could severely skew results as there were likely to be a high number of ‘false negatives’ in the data.

Following the methods of Bellamy et al. (2013), I considered the effects of sampling bias, over-fitting and residual spatial autocorrelation in my models and corrected for them. When generating HSMs the presence and pseudo-absence data should be representative of the different environmental variables within the study area. Environmental biases in training data such as extensive sampling at low altitudes and minimal sampling at high altitudes can lead to inaccuracies in the HSM. In presence-only models the MaxEnt software draws randomly selected pseudo-absence points from across the study area to train the model, so using biased presence data with unbiased pseudo-absence data can increase the effects of sampling bias (Phillips et al. 2009). By providing data on the sampling effort across the study area in the form of a bias file and a mask constraining the area that MaxEnt can draw pseudo-absence points from, MaxEnt will factor out biases caused by sampling habitats in different proportions to their prevalence in the study area (Dudik et al. 2005). Bellamy et al. (2013) found that without the bias file test AUC scores were significantly inflated, but that this apparent improvement in test performance was due to the model’s ability to distinguish between over- and under- sampled habitats, rather than truly predicting a species’ presence with greater accuracy.

In ecology, a species’ presence at one point may be used to predict presence at another location simply due to the proximity of the two points – this is known as spatial autocorrelation (Legendre 1993). For example, bats may be unevenly distributed in the landscape due to the configuration and availability of roosting sites. Sites nearby to each other may be more similar in the species that are present or absent than expected by chance, due for example to the presence of a large roost of one species. When generating HSMs, residual spatial autocorrelation can be retained in the model when the distribution of a species is not fully explained by the environmental variables incorporated in the model – this means that the data are not independent, and can affect the accuracy of the HSM (Diniz-Filho et al. 2003, Araújo and Guisan 2006, Veloz 2009, Merckx et al. 2011). Residual spatial autocorrelation can be controlled for when modelling in MaxEnt by manually dividing the data into spatially correlated groups, and using some groups for training and others for testing, so that the model is always tested on data that are spatially independent to the training data (Parolo et al. 2008, Veloz 2009, Bellamy et al. 2013).

Over-fitting to noise in the training data can occur as a result of using complex models with too little information on a species' known presence locations (Merckx et al. 2011). This can cause models to be selected as the best performing model using certain validation techniques, but reduces their ability to make accurate predictions in new locations or conditions (Lobo et al. 2008). In MaxEnt, over-fitting is controlled for using a regularisation parameter (Phillips et al. 2006). This means that the model, rather than fitting exactly to the mean of the data used for model-building, fits to a range of values around the mean (Phillips et al. 2006). This smooths the distribution and makes it more regular, balancing model fit with model complexity (Elith et al. 2006). The regularisation multiplier in MaxEnt has been tuned to a value of one based on the sample size of the modelled species (Anderson and Gonzalez 2011). Bellamy et al. (2013) found in their HSMs on bats that a value of two worked better to reduce overly complex modelled relationships with variables.

3.2.2.2 Choosing spatial scales

The choice of scales should be informed by previous studies and knowledge of the ecology and behaviour of the study species (Wheatley and Johnson 2009). There was little to no information available on the home range size or commuting distances of the particular bat species studied here, so I used scales found to be important in other bat studies. Looking at the results of multi-scale studies such as Akasaka et al. (2010, 2012), Bellamy et al. (2013), Gorresen et al. (2004, 2005) Lundy et al. (2012), Henry et al. (2010), McConville et al. (2013) and Pinto and Keitt (2008), which included a variety of foraging guilds across several continents, I chose five spatial scales at which to study bats. In this study 'scale' refers to the spatial grain of a layer, as the size of the area around a bat presence point over which measurements were taken varied, while the overall size of the study area remained constant. I used two small scales – 100 m and 200 m – as these were found to have the greatest predictive power for most species by Bellamy et al. (2013), and were important in all studies that measured at scales this small (Pinto and Keitt 2008, Fabianek et al. 2011, Akasaka et al. 2012, Lundy et al. 2012). I then used a medium scale (500 m) and two large scales (1,500 m and 4000 m) as several studies found 500 m - 1 km scales to be important (Henry et al. 2010, Fabianek et al. 2011, Lundy et al. 2012), and some studies exclusively studied scales of 1 - 5 km and found that these scales have good predictive power (Gorresen and Willig 2004, Gorresen et al. 2005, Klingbeil and Willig 2009).

The variables at each scale described a habitat feature measured across a square area of a certain size. I refer to each scale as the length of one side of the square in metres, so the 100 m scale refers to a 100 m x 100 m square (0.01 km^2), and the 4,000 m scale refers to a square with an area of 16 km^2. As the precision and accuracy of the GIS habitat map and the locations of foraging bats were high, I was able to construct models and map predictions using a relatively fine resolution (50 m x 50 m). The raster layer was created from polygon layers in ArcMap, and the raster grids for each layer (e.g. habitat) overlayed exactly.

3.3.1 Bat data collection

Bats were caught at 43 catching sites and their echolocation calls recorded (Chapter 2). The locations of bats caught were combined with data from 400 m long transects at 26 sites (Chapter 4) and 18 2 km transects designed to cover habitats not sampled for the purposes of Chapter 4. Data from static bat detectors (Pettersson D500X) at 38 locations were also incorporated into the bat HSMs. A handheld GPS (±3 – 10 m accuracy; Garmin GPSMaps 60 Cx, www.garmin.com) was used to record each sampling location. Catching and recording took place between late January and mid-May 2011, 2012 and 2013. This is the dry season between monsoons, although afternoon and evening storms became generally more frequent from March onwards and work was not done on wet nights.

I attempted to catch bats at four roosts and 39 foraging sites (Fig. 3.1) using one or two harp traps and one to five mist nets, depending on the configuration of the site, and caught bats on at least one occasion in 32 sites. Mist nets were checked every 10 minutes for bats and harp traps every 30 minutes, as being held in a harp trap bag is less disturbing for the bat than being tangled in a mist net. Bats were kept for as little time as possible, and all females carrying young with them were released instantly without measurements or photographs. Pregnant females were processed and released in priority to all other bats. I identified bats using the most accurate field guides for bats in India (Bates 1997, Srinivasulu et al. 2010), categorised them by age and reproductive status, measured body mass and forearm length and photographed the bats for identification purposes and to assess wing morphology, and echolocating bats were recorded on release at the site of capture using a Pettersson D240X bat detector and Edirol R-09 recorder to build the call library (Chapter 2).

The 26 short transects comprised five stationary points 100 m apart. Bats were recorded for 15 minutes each at each point using a Pettersson D240X time expansion bat detector and an Edirol R-09 recorder. These transects were repeated twice, each starting at a different end of the transect, for the work in Chapter Four. These detectors have a maximum range of about 20 m. Recording at stationary points was preferred in this study area to walking and recording due to the noise contamination made by dry leaves, and the steep and uneven terrain and lack of footpaths in many sites, which made it difficult to walk at an even pace.

The 18 long transects were made up of 21 stop points 100m apart, where bats were recorded for 3 minutes at each point using the same equipment as previously. These were only walked once. The longer transects were necessary to encompass all habitats we had permission to sample in limited field time. All transects were started 40 minutes after sunset, by which time the sky was totally dark. This was done to allow for the fact that some bats emerge earlier than others, and also that some will emerge early and commute to their foraging site. In this study I aimed to avoid missing late emerging bats in the first transect points, and I were also more interested in where bats chose to forage then where they were commuting.

Pettersson D500X direct sampling bat detector/recorders were chained overnight in 38 locations and left recording from half an hour before sunset to half an hour after dawn. These were all on transect points, and were initially to be used to compare data from single vs multiple collection points in Chapter Four, but actually generated too much data per night to all be analysed.

Bats were caught at locations designed to sample specific habitats as in Chapter Four, at roosts and in habitats not sampled by catching in Chapter Four. All sites used for sampling for Chapter One were used, such as roosts and over rivers.

3.2.2.3 Choosing habitat features

As the ecology and habitat choices of many of these species were poorly known, especially in relation to the particular habitats found in this study area, I used previous studies to inform the choice of habitat features input into the model. I did not use climatic variables as they are relatively homogenous across this small study area, climate cannot be managed on this scale so these factors are not relevant to the objectives of this study, and high quality fine resolution climatic data were not available for this site. Climatic variables operate at much greater scales than this study does, and have been found by previous studies to be less important than local habitat variables for predicting bat species occurrences at local scales (Razgour et al. 2011). Microclimatic variables may be important – these are likely to correlate with topology and habitat, which are included as variables.

Many bat HSMs have stressed the importance of water bodies to bats, so I included measures of distance to water, percentage cover water and water edge density (Milne et al. 2006, Rainho and Palmeirim 2011, 2013, McConville et al. 2013, Lisón and Calvo 2013, Bellamy et al. 2013, Lisón et al. 2013, Hahn et al. 2014). Habitat coverage is very important in building strong bat HSMs, whether that be grassland or forest (Milne et al. 2006, Rebelo and Jones 2010, Razgour et al. 2011, Lundy et al. 2012, Bellamy et al. 2013, Rainho and Palmeirim 2013). Often habitat variables have greater predictive power when combined and simplified into broad categories (Milne et al. 2006, McConville et al. 2013).

Some species may respond most strongly to landscape composition, such as percentage forest cover, but others may respond more strongly to landscape configuration e.g. edge density. A study in Peru showed frugivores reacting strongly to landscape composition as there were more early successional fruits and flowers in areas with reduced canopy cover. In the same study gleaning animalivore abundance increased as a function of increased edge density, probably because bats used low-contrast edges when foraging and commuting (Klingbeil and Willig 2009). Therefore it is important to have measures of both landscape composition and configuration in models.

Taking into account distance to varying factors has proven to be critical in many bat HSMs. Razgour et al. (2011) found distance to meadows and to suburban centres to be good predictors for the occurrence of grey long-eared bats. In a group of islands, distance to mainland was a strong predictor of species richness and assemblage composition (Meyer and Kalko 2008). Distance to water was important in modelling all species in studies in Ohio (Buckman-Sewald et al. 2014) and in Portugal (Rainho and Palmeirim 2011) and distance to the roost was important for cave roosting bats in Portugal (Rainho and Palmeirim 2011, 2013). All of the final models developed by Bellamy et al. (2013) for seven species contained at least one important distance variable.

Depending on the variation in topography in a landscape, factors such as mean elevation, slope and aspect can be important predictors of bat occurrence (Milne et al. 2006, Lamb et al. 2008, Rebelo and Jones 2010, van Toor et al. 2011, Bellamy et al. 2013, Razgour et al. 2014). The study area in South India used in this thesis varies from 800 m a.s.l. to 1600 m a.s.l., and the plateau is far from flat and homogeneous in topography.

3.3 Methods

3.3.2 Call identification

Acoustic transect data were visualised using BatSound (www.batsound.com). At each site species were marked as present if a clear call attributable to that species was recorded. Due to call overlap between species (Chapter 2) not all species were modelled. *Scotophilus heathii* and *Pipistrellus ceylonicus* overlapped extensively in call frequency, but *S. heathii* calls were clustered towards the higher end of the *P. ceylonicus* range so here I have taken calls under 34 kHz to be *P. ceylonicus* calls, and not attempted to identify *S. heathii* calls. As I only had a recording from a single *Hesperoptenus tickelli* I only classed bats falling within the frequency range seen in this individual recording as *H. tickelli*. I found calls of the same shape falling between 10 and 27 kHz end frequency, but they fell more or less continuously rather than clustering into discrete groups so I am unsure as to how many species these calls represent, and left all bar those calls between 18-22 kHz out of my models. I did not record many *Rousettus leschenaultii* calls on transects, so have not included this species in the modelling. This may be because this species calls relatively quietly, appears to use vision and scent to navigate and find fruit as well as echolocation, and may spend large portions of the night sedentary while feedingEven though end frequencies and FMAXE overlapped, in practice *Myotis horsfieldii* and *Miniopterus fuliginosus* calls could be easily identified by differing shapes, with *M. horsfieldii* showing little or no inflection in their calls and *M. fuliginosus* featuring a prominent quasi-constant frequency 'curve' towards the end of the call as the rate of change in frequency slowed, leading to a 'hockey stick' shape. The calls of *Scotophilus kuhlii* and *Myotis montivagus* were however difficult to distinguish from *M. fuliginosus.* As some *M. fuliginosus* and all *S. kuhlii* calls had end frequencies under 45 kHz, I ignored calls of end frequency 40-44 kHz and classed calls of 45-53 kHz as *M. fuliginosus. M. montivagus* calls were difficult to tell apart in practice from *M. fuliginosus* so I cannot be sure that there are not some *M. montivagus* call misclassified as *M. fuliginosus.* However given the apparent scarcity of *M. montivagus* - I caught three *M. montivagus* compared to 78 *M. fuliginosus* and 71 *M. horsfieldii* – this is unlikely to add many false positive data points.

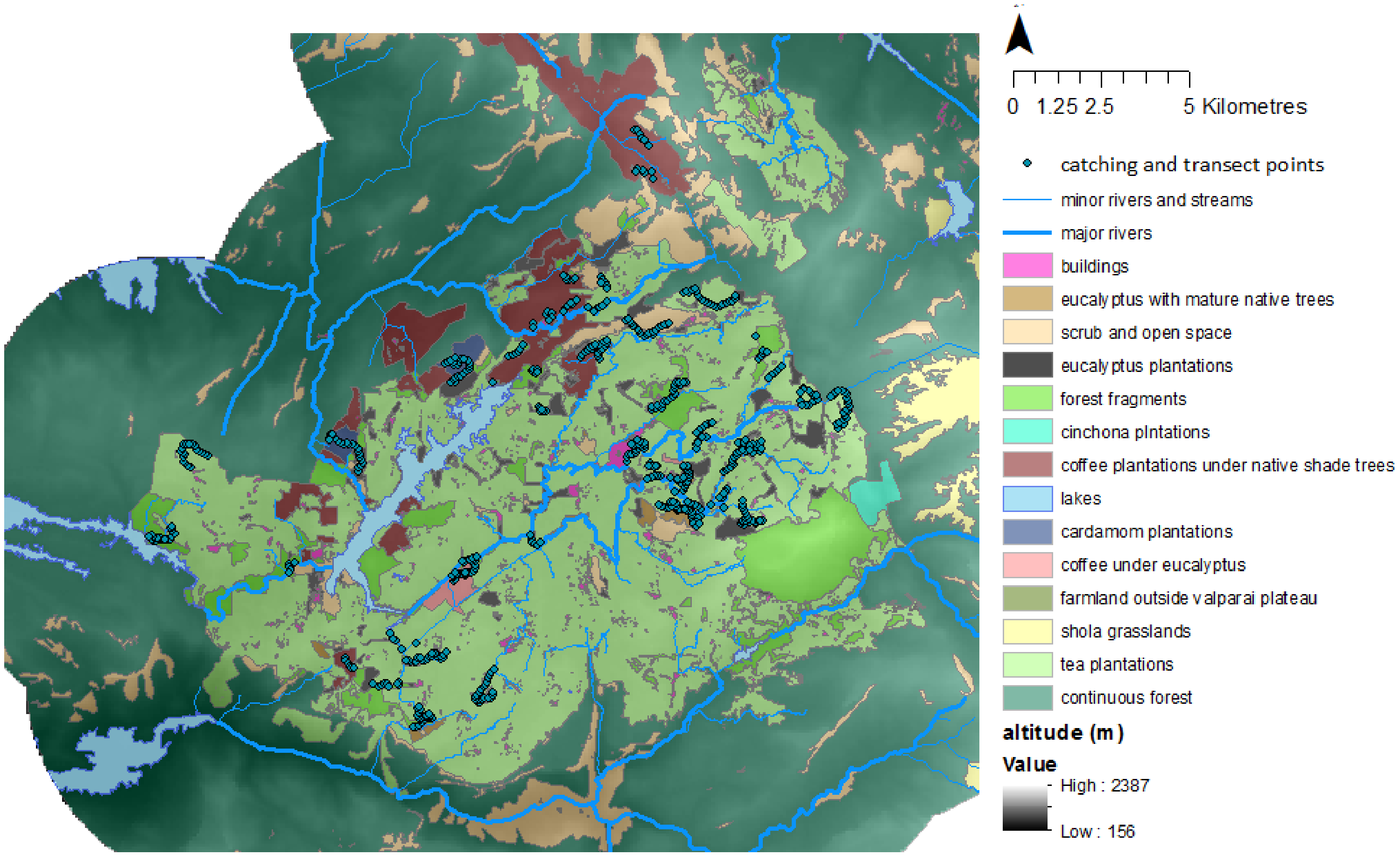


Figure 3.1: Map of the study area and a 5 km buffer. Layers are semi-transparent to allow the altitude to be seen.

3.3.3 Environmental data

3.3.3.1 Building a GIS map

As there were no digital habitat maps available for the study area, I built a map of the Valparai plateau and surrounding 5 km buffer using satellite imagery from Google Earth and on the ground verification using a GPS (Fig. 3.2a). I digitised the edges between tea and any forested habitat by eye using Google Earth imagery, and then walked the edges between different forest cover types – i.e. coffee plantations and forest fragments – recording the track on a GPS. I used a 5 km buffer around the plateau so that measurements at scales up to 5 km at the edge of the study area would be calculated accurately, e.g. percentage cover of habitat containing native trees. The digital terrain model I downloaded from https://earthdata.nasa.gov/user-mgmt/. The map was built in ArcGIS 10.1 using the datum GCS WGS 84 and projected into UTM WGS 84 Northern Hemisphere 43. Polygons were drawn as Keyhole Markup Language files in Google Earth, either directly using the satellite imagery or using tracks imported from the handheld GPS as a guide. They were then converted into shapefiles, and when the map was finished all files were converted to raster for MaxEnt analysis. While I did not have on-the-ground access to all private land, this map is to the best of my knowledge accurate. In the areas I did have access to I found it reliable to within a few metres on the ground.

3.3.3.2 Making environmental variable layers

I used ArcGIS 10.1 to extract the information necessary to build the environmental variables. All variables were built for the study area and buffer together to ensure accurate calculations at the edge of the study area, and then clipped to the study area.

Table 3.1: The 25 environmental variables used in analysis. They were all used at five spatial scales apart from the distance layers.

Layer name	Description of layer
Aspect	Majority aspect (Flat, N, NE, E, SE, S, SW, W, NW)
Cardamom (%)	Percentage cover of cardamom plantations
Coffee (%)	Percentage cover of coffee plantations under native shade trees
Coffee under eucalyptus (%)	Percentage cover of coffee plantations under eucalyptus shade trees

Continuous forest (%)	Percentage cover of continuous forest (forest inside protected areas)
Distance to continuous forest (m)	Straight line distance to continuous forest edge
Distance to forest fragment (m)	Straight line distance to forest fragment edge
Distance to buildings (m)	Straight line distance to buildings
Distance to known caves (m)	Straight line distance to known caves
Distance to water edge (m)	Straight line distance to water edge
Distance to wood edge (m)	Straight line distance to wood edge
Eucalyptus (%)	Percentage cover of eucalyptus at multiple scales
Eucalyptus with native trees (%)	Percentage cover of eucalyptus containing approx. 20-40% mature native trees
Forest fragments (%)	Percentage cover of forest fragments (forest patches outside the protected areas)
Habitat richness	Number of different habitat types present
Habitat containing native trees (%)	Continuous forest, forest fragment, eucalyptus with native trees, coffee and cardamom layers combined.
Buildings (%)	Percentage cover of buildings
Maximum forest fragment size (km^2)	Size of the largest forest fragment
Mean altitude m.a.s.l.	Mean altitude
Mean slope (°)	Mean slope
Scrub (%)	Percentage cover of scrub
Tea (%)	Percentage cover of tea
Water (%)	Percentage cover of water
Water edge density (km/km^2)	Length of water edge per unit area
Wood edge density (km/km^2)	Length of woodland edge per unit area

Topography

The digital terrain model describing altitude had a cell size of 92 m x 92 m. I resampled it to a 32 BIT 50 m x 50 m cell size using bilinear interpolation (Fig 3.2b). This layer was then used to create a slope layer by calculating the maximum change in altitude between any 50 m x 50 m cell and the eight cells directly bordering it. I also measured the aspect or direction of slope. As the values 0 and 360 both signify north, I reclassified the aspect layer into nine classes (-1 = flat; 337.6 – 360°, 0 – 22.5° = north; 22.6 – 67.5° = north-east; 67.6 – 112.5° = east, 112.6 – 157.5° = south-east; 157.6 – 202.5° = south; 202.6 – 247.5° = south-west; 247.6 – 292.5° = west; 292.6 – 337.5° = north-west).

Landcover

Several habitat types as described on the map encompass a range of similar habitats. The category 'forest fragments' includes remnant primary and secondary forest patches experiencing different degrees of degradation, one ex-eucalyptus plantation now dominated by native trees and one ex-vanilla plantation dominated by native trees; but each in 'fragment' approximately 50%-100% of the mature trees are native forest trees .All forest fragments are outside the reserve areas. 'Scrub and open space' describes habitats from bare rocks and earth to low scrub not containing any mature trees. 'Eucalyptus with native vegetation' describes eucalyptus plantations that contain approximately 20-40% native trees, but are still dominated by eucalyptus. All low elevation farm types are grouped together as I was not directly sampling these habitats. The layer 'habitats with native trees' was created by merging continuous forest, forest fragments, coffee under native shade trees, cardamom and eucalyptus with native trees. All layers were built as polygons, converted to raster 10 m x 10 m cell size and then resampled to a 50 m x 50 m raster

Distance, density, maximum patch size and habitat richness

To look at wood edge density and distance to wood edge, I merged all layers describing habitats containing mature trees (whether native or non-native) into one layer to generate woodland structure variables. I used ArcGIS to dissolve the boundaries between adjacent habitat patches containing trees, as these boundaries did not represent a sharp change in habitat structure. I converted this shapefile into a polyline layer representing the edge of all habitats containing trees. I used ArcGIS to calculate the Euclidean distance between each cell and the nearest woodland edge, generating a 10 m x 10 m distance raster which I then resampled into a 50 m x 50 m raster using bilinear interpolation. This avoids some of the inaccuracies that can be produced by measuring Euclidean distances at a coarser resolution. I followed the same protocol with water – I converted polygons of lakes into polyline layers and merged them with rivers, and calculated distance from here. For habitat richness I gave each habitat polygon a unique numerical value and then converted them to raster 10 m x 10 m cells. I merged the layers, then resampled to a 50 m x 50 m cell size, before using the focal statistic tool 'variety' to determine the habitat richness of each cell at each scale. To calculate maximum forest fragment size I used ArcGIS to calculate the area of each forest fragment before converting to raster. To calculate the density of ‘woodland’ edge I took the polyline layer I used to calculate Euclidean distance to woodland edge and used ArcGIS to calculate line density in km/km^2, generating a raster layer describing density. I used the same method to calculate water edge density.

Accounting for sampling bias

I sampled some habitats more than others as I was focussing on comparing them for Chapter Four. Also, some habitats (such as the largest forest fragment and the cinchona plantation) were not sampled for bats as I did not have permission to access that land. In order to account for sampling bias I created a file where the value of each 50 m x 50 m cell represented the amount of time spent sampling in that cell. I used minutes spent on acoustic transects as the

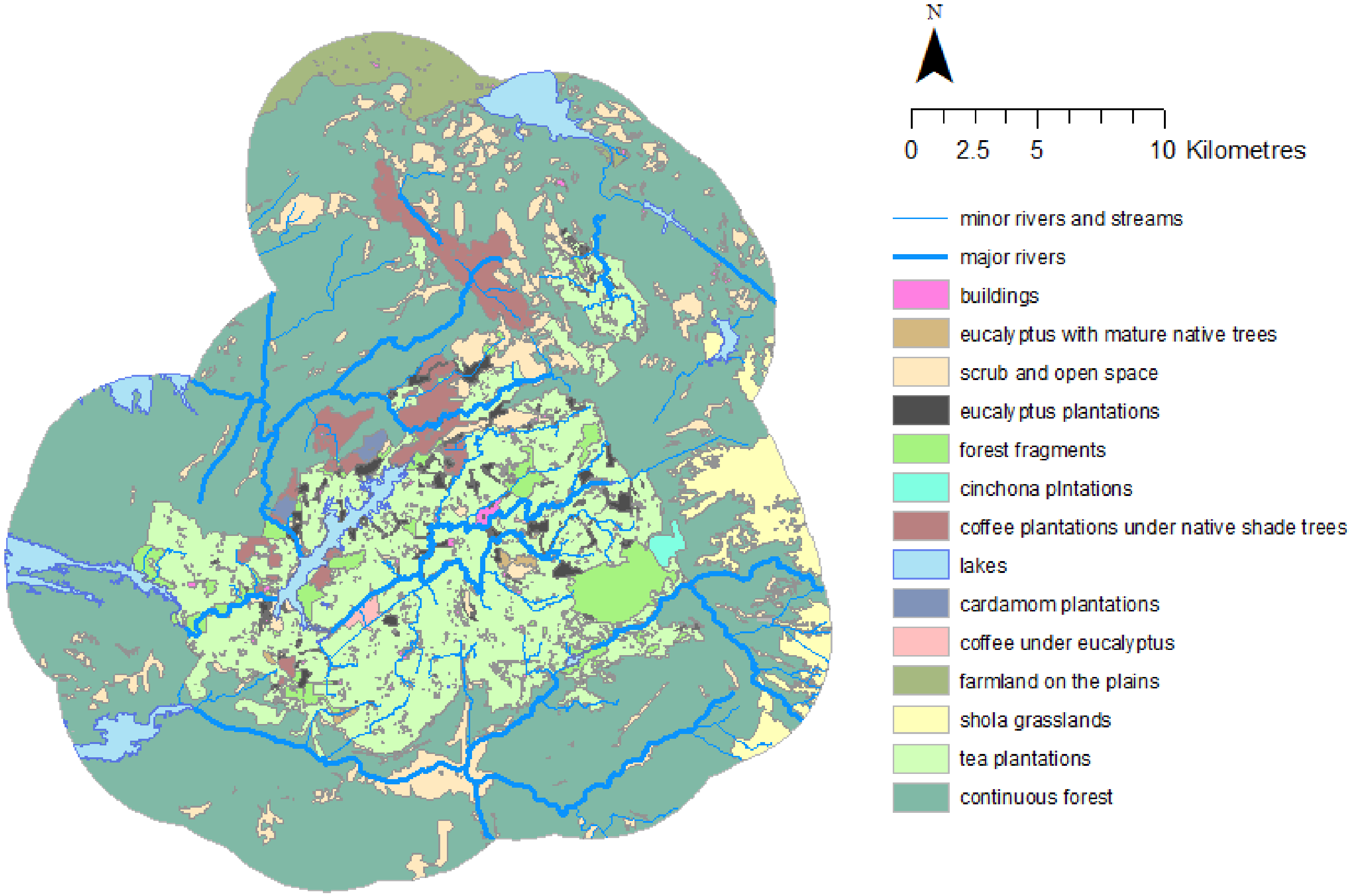


Figure 3.2a: Habitat map of the study area and a 5 km buffer.

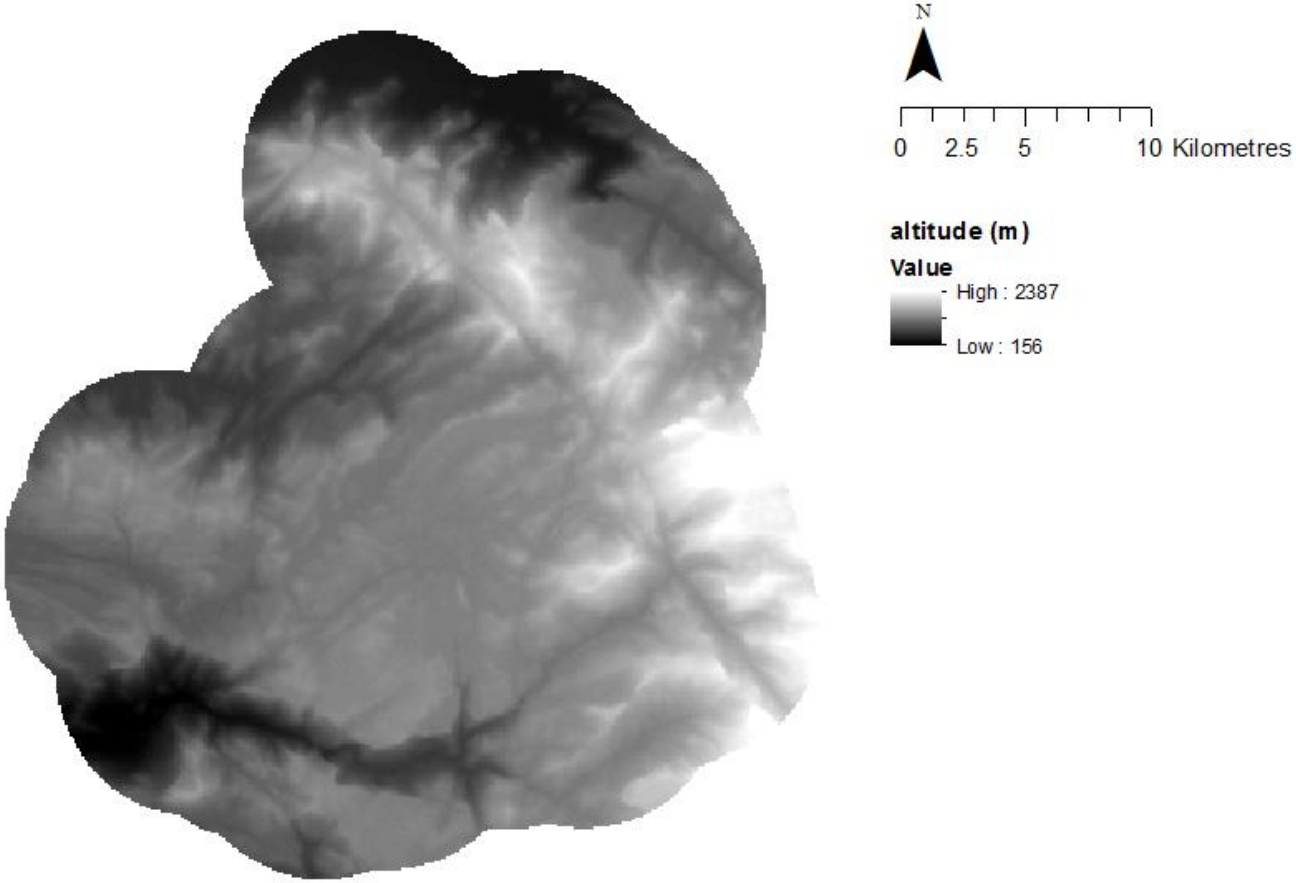


Figure 3.2b: Digital terrain model of the study area and a 5 km buffer.

baseline, so for a cell in which I spent 3 minutes sampling the value would be three. As catching led to fewer recorded bats than acoustic recording I controlled for this by calculating the chance of recording/catching one or more bats in 15 minutes. The probability of detecting a bat by acoustic methods in 15 minutes was 0.97, whereas the chance of detecting a bat by catching one was 0.09. This was equivalent to approximately a 10-fold difference in success rate, so I divided the number of minutes spent at each catching sit by 10 to make catching and acoustic methods more comparable for the bias file.

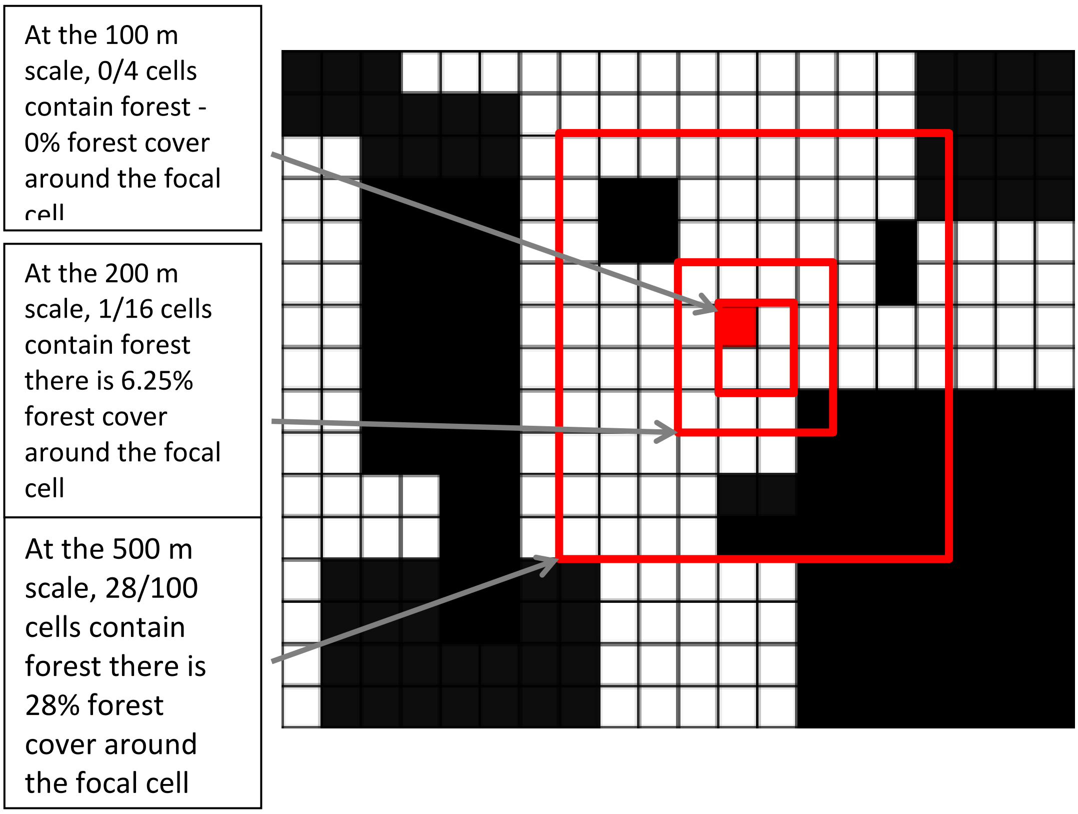
I also accounted for sampling bias by using a mask. I created a raster file of 500 m buffers around every sampling site, and used this to constrain the pseudo-absence points created by MaxEnt to the areas within those buffers.

3.3.3.3 Preparing final layers for MaxEnt

A number of steps were necessary to prepare the original habitat and topography map layers into layers suitable for analysis in MaxEnt. First all layers were converted into 10 m x 10 m rasters, then upscaled to 50 m x 50 m resolution rasters using bilinear interpolation for continuous variables or nearest neighbour assignment for discrete variables. Increasing raster cell size in this way reduces the level of error when describing percentage cover of small, complex shaped habitat patches. I chose 50 m x 50 m as it was the scale used by Bellamy *et al.* 2013, which is based on the potential error associated with each bat location point due to GPS error (max 10 m) and detector range (max 20 m). While I was not using the same GPS track point system as in that study, there are potentially small errors in the map itself caused by working between satellite imagery and using a GPS on the ground to verify the map on rugged, forested terrain, likely to interfere with GPS accuracy.

The distance layers – distance to forest fragment, to continuous forest, to woodland edge, to water and to caves – were all non-scalar, as these variables do not vary in five different spatial scales using the focal statistics tool in ArcGIS. The focal statistics tool uses a moving window analysis to measure the desired statistic across a certain number of cells around each focal cell. Count, sum, variety, range, majority, minimum, mean, medium or maximum can be calculated. If the cell size is 50 m x 50 m, then at the 100 m scale a 2 x 2 cell window would be used, for 4000 m an 80 x 80 cell window.

Using this tool generated a new raster at each spatial scale. The raw numbers were then converted into percentages using the raster calculator tool, using the formula ((layer / total number of cells in window)x 100) – so at the 100 m scale using a 2 x 2 cell window the formula would be ((layer /4)x 100). terms of the scale at which they are measured. All other variables were measured at The final layer was clipped to include the agricultural areas of Valparai plateau, Thalanar and Waterfall only, consisting of 97110 50 m x 50 m cells covering a total area of about 492 km^2.



At the 100 m scale, 0/4 cells contain forest - 0% forest cover around the focal cell

At the 200 m scale, 1/16 cells contain forest there is 6.25% forest cover around the focal cell

At the 500 m scale, 28/100 cells contain forest there is 28% forest cover around the focal cell

Figure 3.3: Assessing the percentage habitat cover around a 50m x 50m focal cell (in red) at three different spatial scales: 100 m, 200 m and 500 m.

Figure 3.4: The percentage forest fragments layer, clipped to the agricultural layer but with the buffer layer in the background for colour contrast, at five different spatial scales. Left- right, 100 m, 200 m, 500m, 1500 m and 4000 m

3.3.4 MaxEnt modelling

3.3.4.1. Model building process

For each species, a single scale model was generated and tested using 5-fold cross validation. To validate an HSM, it is necessary to compare the predictions it makes to separate data not used to build the model. One method of doing this is to split all data for a species into training data and test data. If validating a model like this it is preferable to partition the data so that multiple models can be built and tested from the same data, and an average taken. 5-fold cross-validation if selected on the user interface in MaxEnt puts the data into five random groups, and the four used for training and the one used for testing are different for the five iterations. Using the freeware programme, Spatial Analysis in Macroecology, models were then tested for significant residual spatial autocorrelation (rSAC) using Moran's correlograms based on the residuals of each model (1 – predicted Habitat Suitability Index (HSI)) for each species record) (Rangel, Diniz-et al. 2010). The Moran's index (I) coefficients were plotted against the distance between pairs of recorded locations for each species for distance classes of 1 km. The significance of Moran's I at each distance class was computed by using 9,999 Monte Carlo permutations. The greatest distance at which spatial autocorrelation was observed for a species ranged between 1 km and 6 km, although generally this was around 3-4 km. Typically, although significant, spatial autocorrelation was quite weak. As the study area was small and many transects were close together, it was not possible to ensure that for each species the data was spatially partitioned in such a way as to leave a gap equivalent to the greatest distance at which rSAC was observed between each group. Instead, I split the study area into five roughly equally sized partitions and grouped each species into five spatial groups that corresponded with these partitions. These five groups were used for five-fold, spatially constrained cross validation of every model (Fig. 3.5).

At each scale I used the jackknife procedure available in MaxEnt to find the test area under curve (AUC) and test gain for each environmental variable when a model was built with that variable alone, which showed the importance of each variable at each

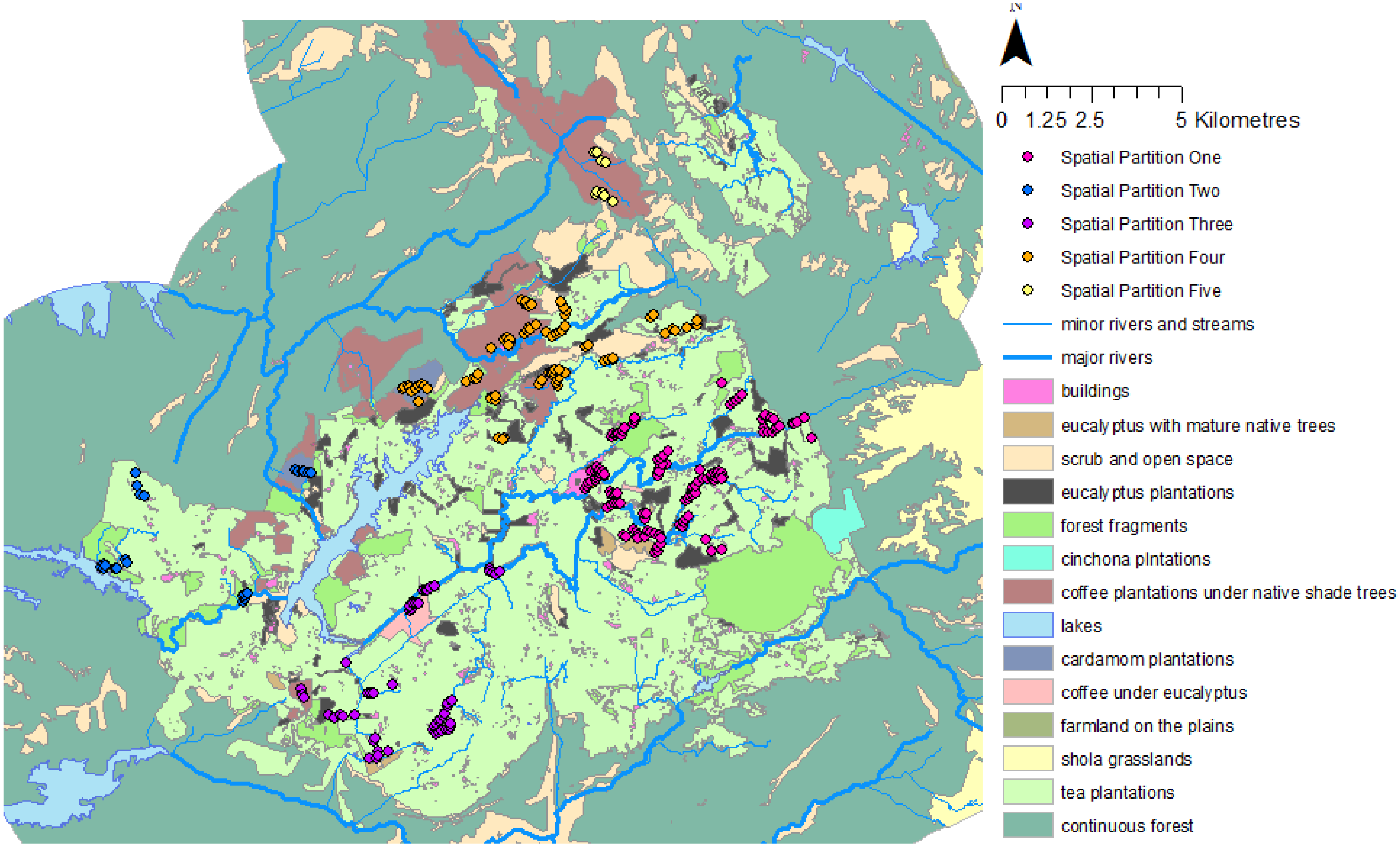


Figure 3.5: The occurrence points for *P. ceylonicus* spatially partitioned into five groups, indicated by different colours.

scale. In conjunction with the jackknife response curves, showing the probability of a species' presence across the range of a variable, it was possible to determine the variables that were most strongly correlated with species' presence locations at each scale and the relationship of each variable to that species. Variables were typically stronger at some scales than at others, and sometimes the relationship between a species and a variable changed with different spatial scales.

Following the methods of Bellamy et al. (2013), I used the variables at the scale at which they were strongest to make the first multi-scale model, known hereon in as the 'full model'. If the average test AUC for a variable from the five-fold cross-validated spatially constrained single scale models was ≤ 0.5 at each scale (equivalent to a random model) then that variable was dropped from the full model. Within the full model all variables were checked for multi-collinearity, and any pairs with a correlation of r ≥ 0.7 were identified (calculated using ENMTools, www.ENMTools.com; (Warren et al. 2008) threshold suggested by (Fielding and Haworth 1995)). Where variables were correlated, the variable with the lowest test AUC was removed.

After this pruning process a model was left with a reduced set of variables. This is hereon known as the 'subset model'. To create a model with the highest predictive power, models were pruned to leave only the strongest variables. Following Bellamy et al. (2013) I removed variables in a jackknife leave-one-out stepwise fashion to remove the variables with the lowest predictive power *(*Parolo et al*. 2008).* Using the jackknife functions in MaxEnt, the mean test AUCs of each five-fold cross-validated spatially constrained model built with one variable removed in turn were compared. The variable that caused the lowest decrease or largest increase in the test AUC when it was removed was pruned. In the models with only five data points, the variables that caused the lowest decrease or largest increase in the test AUC when they were removed were pruned. This process was repeated until only one variable remained – the minimum adequate model. Pruning has been found to make models that perform better on independent test data, which suggests that pruned models may be less prone to overfitting (Parolo et al. 2008).

In a departure from Bellamy *et al.* 2013 I also ran some models with different combinations of variables from the subset model, to see whether test AUC of a model improved when interaction with other variables were added or removed. The models scoring highest on average test AUC for the five-fold cross-validated models were then run with all data from a species at once, to generate a single model that was then used to compare the Akaike's Information Criterion (AIC or AICc) of each model.

While the area under the receiver operating characteristic (ROC) curve, known as the AUC, is often the standard method used to assess the accuracy of predictive distribution models, it is not without its problems, which is why AICc was used to discriminate between the models that performed best on AUC. AUC represents the likelihood that a presence point will have a higher predicted value in the model than an absence point (Hosmer and Lemeshow 1980) regardless of the goodness-of-fit of the predictions (Vaughan and Ormerod 2005, Reineking and Schröder 2006). A poorly fitting model that over or underestimates all the predictions can therefore have a high AUC score; and a well-fitting model can score poorly on AUC, if the probabilities for presence points are only moderately higher than those for absences (Hosmer and Lemeshow 1980). AUC weights omission and commission errors equally, and it does not give any information about the spatial distribution of model errors (Lobo et al. 2008). The far left and right sides of the ROC space correspond to high false positive and high false negative rates, and are therefore not useful in most scenarios (Lobo et al. 2008). Increasing the geographical extent outside the environmental extent used for modelling will inflate AUC scores. For example, a model that over-predicts the presence of a species will have a lower commission error if the number of absences is increased as a consequence of extending the study area (Lobo et al. 2008). The smaller the area of occurrence is compared the whole study extent, the greater the number of absence points. This means it is more likely that absence data are environmentally distant from the presence domain, and this seems to inflate the AUC of rare species and deflate that of more common or generalist species (Lobo et al. 2008). AUC does give some useful information of the relative predictive ability of models created for different species, and is widely used enough for AUC values to be understood, so I shortlisted models for each species based on AUC and also report the AUC scores.

Akaike's Information Criterion (AIC) and AIC corrected for small sample sizes (AICc) can be used to measure the relative quality of a model. AICc has been shown to perform better than BIC (Bayesian information Criterion), training AUC, test AUC and the difference between test AUC and training AUC at discriminating between models produced in MaxEnt (Warren and Seifert 2011). AIC gives a relative estimate for each model of the information lost when that model is used. It captures the trade-off between how well the model fits the data and parsimony in model building, explicitly penalizing unnecessary parameters, which helps to understand exactly which variables are important for a species (Warren and Seifert 2011). AICc is AIC corrected for sample size by adding a penalty for every extra variable in the model – thus it selects even more strongly for more parsimonious models. As the number of individuals gets larger, AICc converges upon AIC, so it is appropriate to use AICc for all sample sizes. The model with the smallest AICc for each species was chosen as the final model. AICc was calculated in EMN tools (Warren and Seifert 2011).

3.3.4.2 MaxEnt settings

Models were run in MaxEnt Version 3.3.3k. Default settings were used except that the regularisation multiplier was changed to two to reduce over-fitting, following Bellamy et al. 2013. MaxEnt then doubles the regularisation parameter it has selected based on the species sample size to ‘smooth’ the response curve (Anderson and Gonzalez 2011). Outputs were logistic with Habitat Suitability Indices (HSIs) varying from 0-1, with zero as the least suitable habitat and one as the most suitable.

3.3.4.3 Niche breadth and overlap

Niche breadth and overlap were calculated for each species. Niche breadth was calculated in two ways. First, it was calculated in ArcGIS for a binary species map which categorised each species into ‘present’ or absent’. As a threshold to determine a species presence or absence I used the option ‘Maximum training sensitivity plus specificity’ in MaxEnt, as this has been shown to be an effective threshold with which to build binary maps (Liu et al. 2013). Secondly, niche breadth was calculated using the threshold independent inverse of Levins metric in ENM tools (Levins 1968, Warren et al. 2008).

Niche overlap was measured in ENM tools using the *I* statistic, Schoener’s D and relative rank (Schoener 1968; Warren et al. 2008). The *I* and D statistics calculate the difference in HSI between two species at each cell, after the HSI map has been standardised to sum to 1 over the entire study area (Warren et al. 2008). Relative rank ranks the HSI scores across the study area and calculates the difference in rank of each cell between two species (Warren et al. 2008). All of these measures range from 0 to 1, with zero indicating no niche overlap between species and one indicating identical predicted distributions.

3.3.4.4 Species richness map

To build a map that gave the estimated number of species at each site, I overlaid the binary prediction maps for all species. To give a map of the summed probability of each species' presence at each site, I overlaid the continuous habitat suitability maps for each species and summed the probability of occurrence for each species, at each site.

3.4 Results

3.4.1 Bat data

For ten species, I could clearly identify their echolocation calls and had ≥ 5 spatial records which were not all spatially clustered. These were the species I chose to model.

Table 3.2: The ten species with spatial record data suitable for modelling.

Bat species	Catching locations	Echolocation call locations	Total locations
Hesperoptenus tickelli	1	32	33
Minioperus fuliginosus	7	186	193
Miniopterus pusillus	2	97	99
Myotis horsfieldii	6	46	52
Pipistrellus ceylonicus	6	284	290
Megaderma spasma	5	0	5
Hipposideros pomona	3	12	15
Rhinolophus beddomei	1	4	5
Rhinolophus indorouxii	7	48	55
Rhinolophus lepidus	10	119	129

3.4.2 The importance of factors at different scales

For five species, the majority of variables were most important at smaller scales (*R. indorouxii, R. lepidus, P. ceylonicus, M. pusillus, M. fuliginosus*); for the other species there was no clear pattern of variable predictive power and scale (Fig. 3.6i-x). However, scalar variables retained in the best performing models were strongest at smaller scales for most species, apart from habitat richness which typically peaked at 500 m. All the factors in the final models were habitat types or density at the 100 m scale or distance variables, apart from habitat richness which was most important for three species (*H. pomona, M. pusillus, M. fuliginosus*) at 500 m and for one at 200 m (*P. ceylonicus*). No topography variables were retained in the best performing model for any species.

Hesperoptenus tickelli

Twelve variables had a predictive power of test AUC ≥ 0.5 at at least one scale (Figure 3.6i). The best performing of these (test AUC ≥ 0.6) were tea at 100 m, distance to wood edge at 500 m and eucalyptus with native trees at 4000 m. Eucalyptus with native trees is quite a scarce habitat and the response of this species in this model may be due to over-fitting, as this model was built on relatively few (n=32) data points. All variable types had good predictive power for this species but distance and habitat type were the strongest predictors. Predictive power did not change in a consistent direction with scale, although the best performing variable (tea) declined sharply as scale increased.

Miniopterus fuliginosus

There were 12 variables with a predictive power of test AUC ≥ 0.5 at any scale for this species (Figure 3.6ii). Only tea at 100 m showed a test AUC ≥ 0.6 for *M. fuliginosus*, and mostly the scalar variables declined in predictive power above 500 m. All variable types affected this species but only habitat richness and one habitat type (tea) remained in the final model.

Miniopterus pusillus

Seventeen variables had predictive power of test AUC ≥ 0.5 at one or more scales (Figure 3.6iii). Distance to wood edge (negative response), tea (negative response) and habitat containing native trees (positive response) all had a predictive power of AUC ≥ 0.6 for at least one spatial scale. Distance variables and habitat type were the best predictors. Predictive power of most variables declined after 200 m, but habitat richness peaked at 500 m. Habitat with native trees (in the final model) declined slowly in power from 100 m – 500 m, then more rapidly from 500 m to 4000 m.

Myotis horsfieldii

While 24 variables had a predictive power of test AUC ≥ 0.5 at one or more scales for this species (Figure 3.6iv), it is clear that the water related variables are the most important. The furthest this species was recorded from water was <30 m and all water variables had a predictive power of test AUC >0.8. The scalar water related variables decreased with increasing scale but the other variables overall did not show a consistent response.

Pipistrellus ceylonicus

Nine variables predicted the presence of *P. ceylonicus* with a test AUC of ≥ 0.5 (Figure 3.6.v). Only one, tea (negative response) had a predictive power ≥0.6. Habitat types, richness and distance appeared to have the greatest predictive power for each species. The power of the predictive variables typically declined after 500 m, with the two variables in the final model showing a strong decline in predictive power with scale – tea declining from 100 m while habitat richness peaked at 200 m then declined.

Megaderma spasma

Nineteen variables had a test AUC of ≥0.5 (Figure 3.6.vi). Several variables had a predictive power of ≥0.8 – forest fragments, altitude, tea, distance to forest fragments, distance to wood edge, and habitat with native trees. The variables did not react in a consistent manner to scale, but the only variable in the final model (habitat with native trees) showed a strong decline at greater scales.

Hipposideros pomona

Few variables had any predictive power for this species - only eight had a predictive power of test AUC ≥ 0.5 at any scale (Fig 3.6vii). Only distance to wood edge and wood edge density had a predictive power ≥ 0.6. The power of the variables did not change consistently with scale. Wood edge density at 500 m, habitat richness at 500 m and distance to wood edge were the best predictors. Habitat richness and wood edge density showed a peak in predictive power at 500 m with lower test AUCs at other greater and smaller scales.

Rhinolophus beddomei

Nineteen variables had a predictive power of test AUC ≥ 0.5 for *Rhinolophus beddomei* (Figure 3.6viii). Only three variables had a test AUC ≥0.5; distance to forest fragment (negative response), forest fragments (positive), and wood edge density (positive). All of these distance, density and habitat type variables are related to forest cover. The predictive power of variables did not change consistently with scale.

Rhinolophus indorouxii

Sixteen variables had a test AUC ≥ 0.5 (Figure 3.6ix). Habitat type and distance variables seemed the most important: habitat with native trees (positive response), distance to water's edge (negative), maximum forest fragment size (positive), forest fragments (positive), distance to wood edge (negative) houses (negative) and water (positive response) all had predictive values ≥0.6 at one or more scales. Predictive power was lower after 500 m for most variables, was lowest at 1500 m and then increased a little at 4000 m. The scalar variables in the final model did not decline dramatically with scale, apart from habitat with native trees which declined hugely at 1500 m then rose in predictive power at 4000 m.

Rhinolophus lepidus

Thirteen variables had test AUC ≥ 0.5 at one or more scales (Figure 3.6x). Habitat with native trees (positive), tea (negative) and distance to wood edge all had test AUC ≥0.6 – habitat type and distance variables appeared the most important. The predictive power of variables generally declined after 200 m. The only variable in the final model – habitat containing native trees – declined gradually in predictive power between 100 m and 500 m, then rapidly between 500 m and 1500 m.

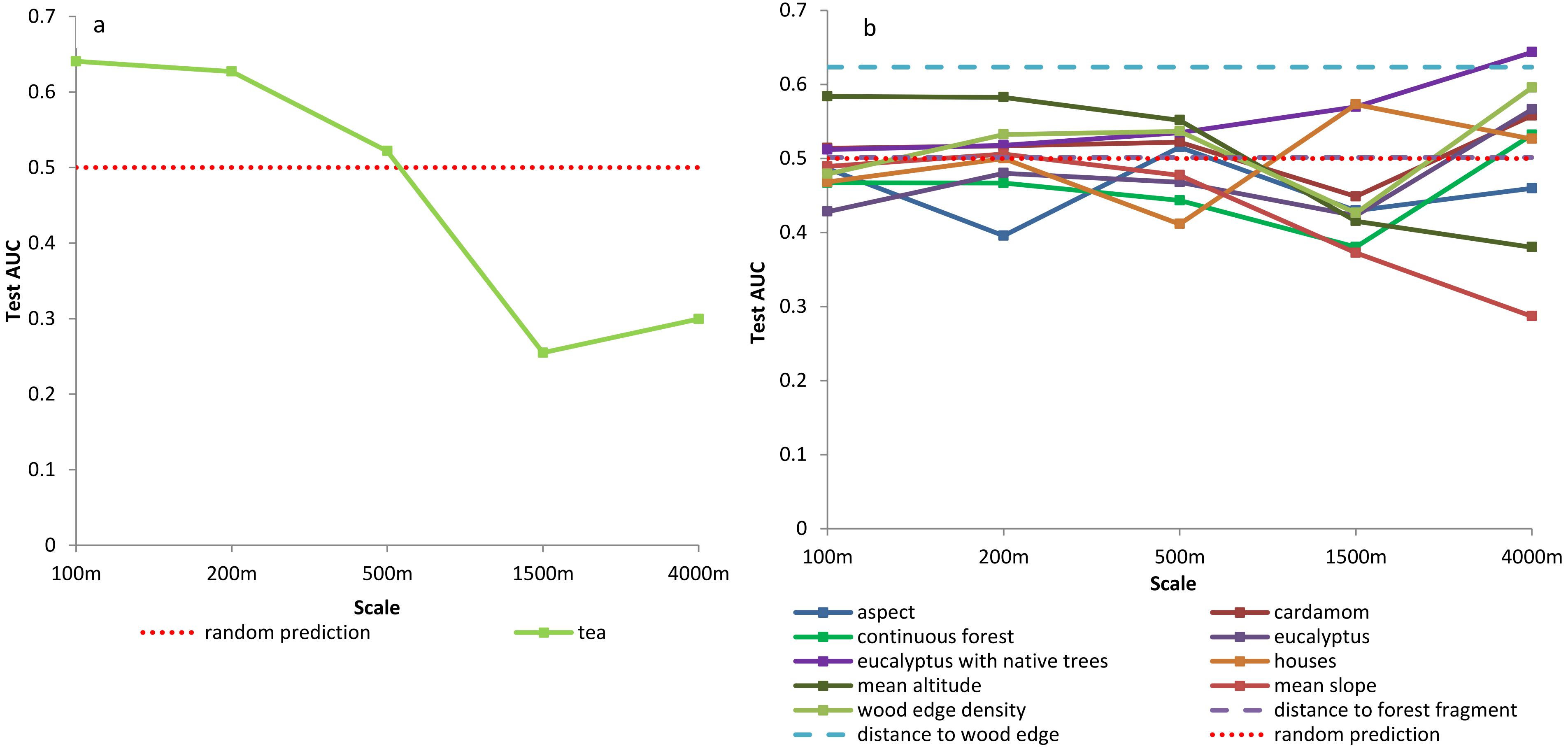


Figure 3.6.i: The strength of relationships between *H. tickelli* presence and environmental variables at five spatial scales. The variables in the final model are shown in (a) and the variables removed in the pruning process are displayed in (b). Distance variables (shown with a dashed line) do not vary with scale. The dashed red line shows the power of a random prediction. Variables which never attained a predictive power of ≥ 0.5 are not included. The X axis is not shown to scale, to improve clarity at smaller scales.

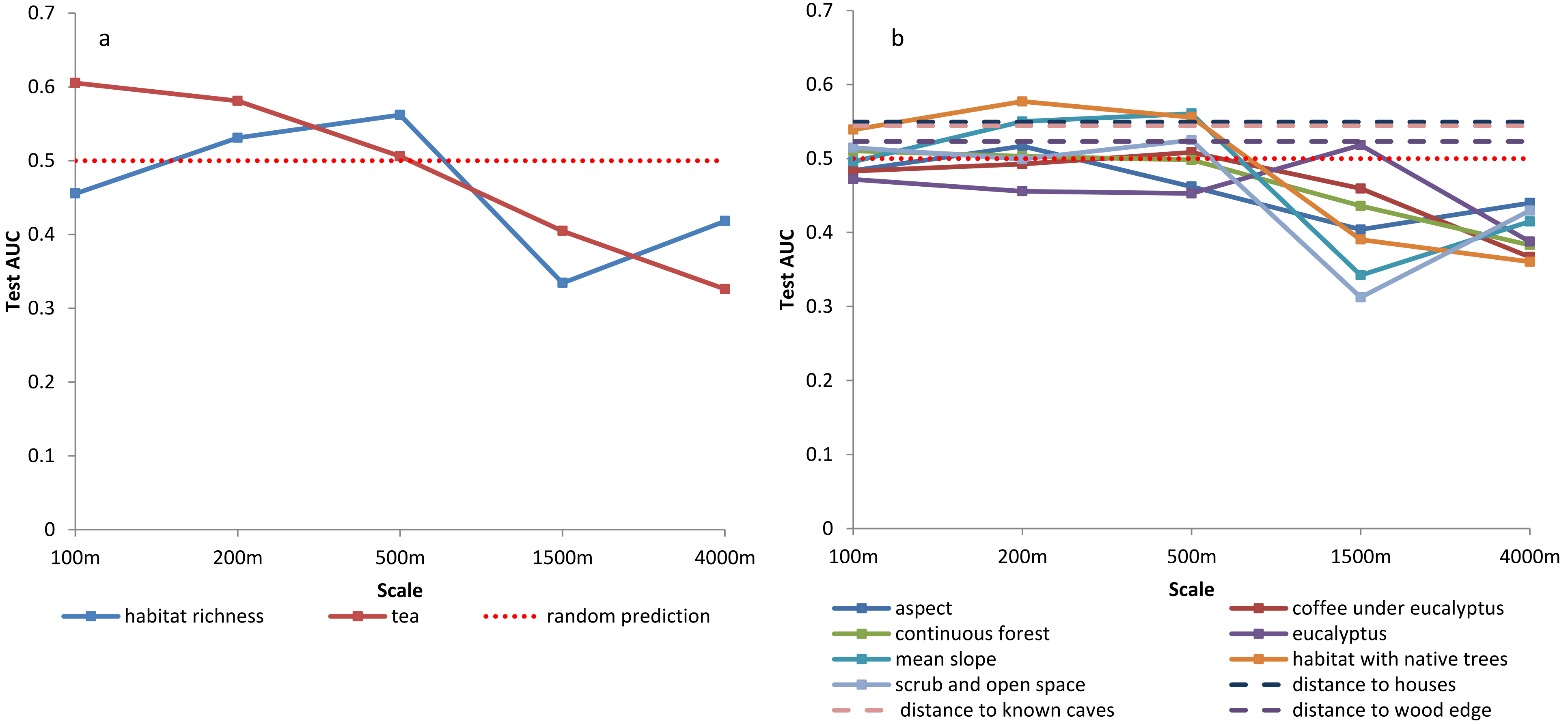


Figure 3.6.ii: The strength of relationships between *M. fuliginosus* presence and environmental variables at five spatial scales. The variables in the final model are shown in (a) and the variables removed in the pruning process are displayed in (b). Distance variables (shown with a dashed line) do not vary with scale. The dashed red line shows the power of a random prediction. Variables which never attained a predictive power of ≥ 0.5 are not included. The X axis is not shown to scale, to improve clarity at smaller scales.

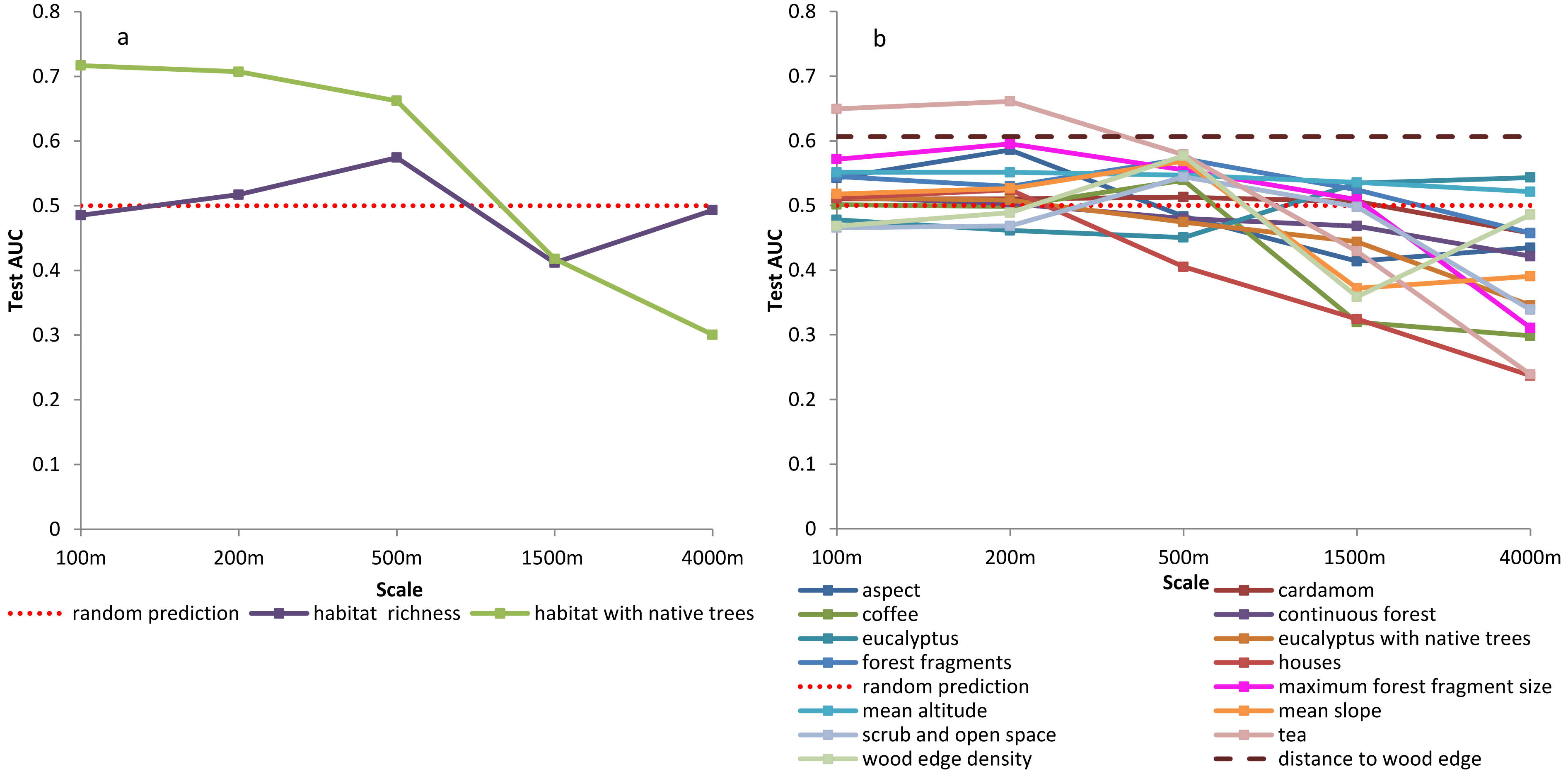


Figure 3.6.iii: The strength of relationships between *M. pusillus* presence and environmental variables at five spatial scales. The variables in the final model are shown in (a) and the variables removed in the pruning process are displayed in (b). Distance variables (shown with a dashed line) do not vary with scale. The dashed red line shows the power of a random prediction. Variables which never attained a predictive power of ≥ 0.5 are not included. The X axis is not shown to scale, to improve clarity at smaller scales.

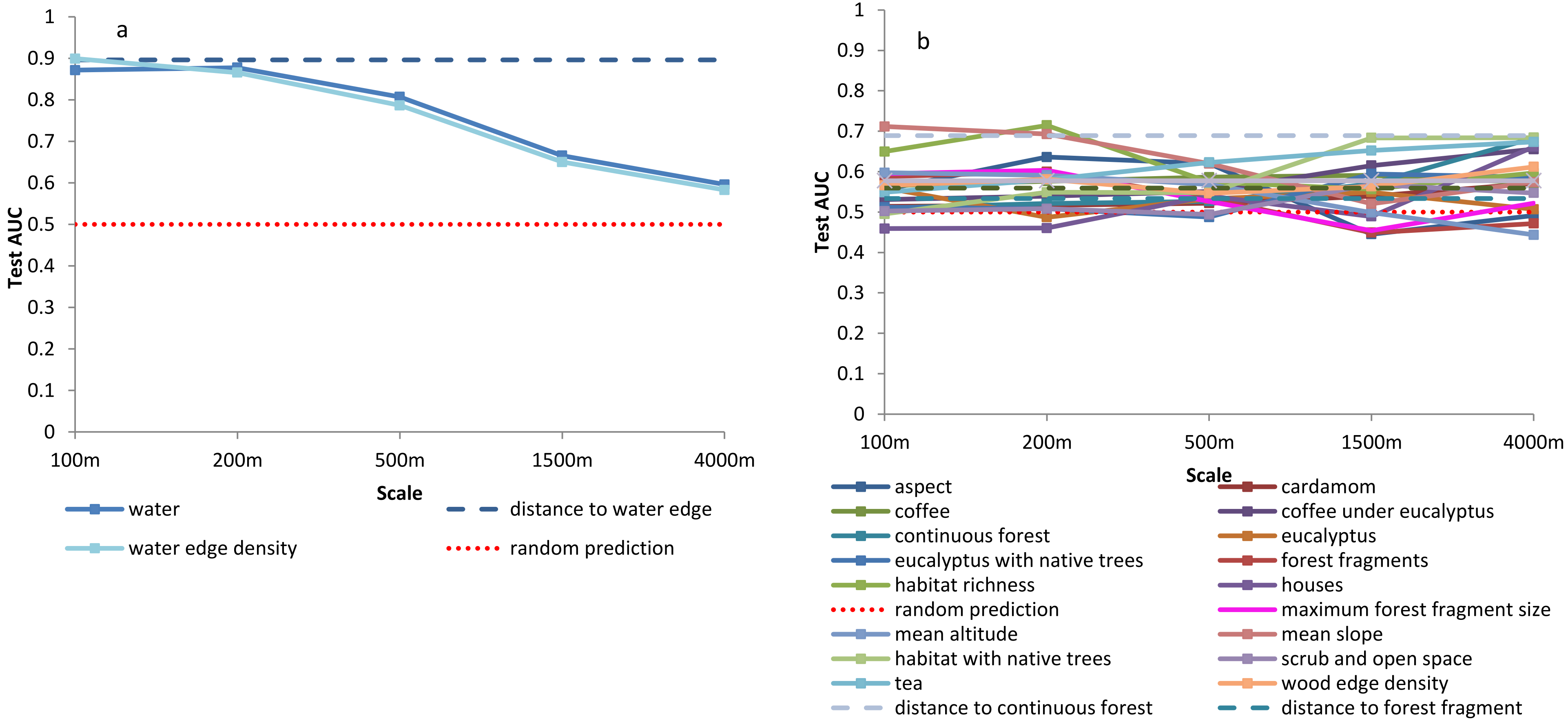


Figure 3.6.iv: The strength of relationships between *M. horsfieldii* presence and environmental variables at five spatial scales. The variables in the final model are shown in (a) and the variables removed in the pruning process are displayed in (b). Distance variables (shown with a dashed line) do not vary with scale. The dashed red line shows the power of a random prediction. Variables which never attained a predictive power of ≥ 0.5 are not included. The X axis is not shown to scale, to improve clarity at smaller scales.

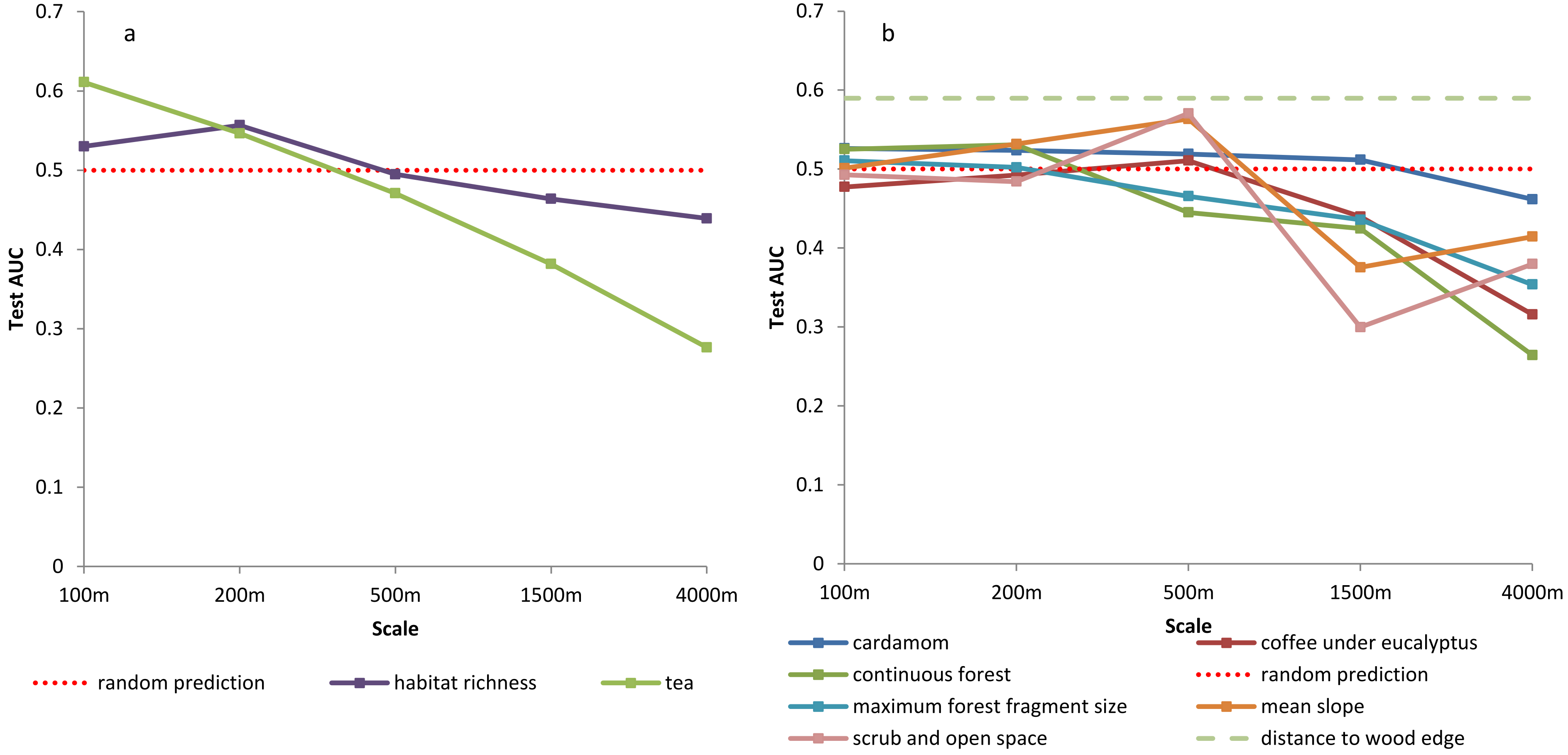


Figure 3.6.v: The strength of relationships between *P. ceylonicus* presence and environmental variables at five spatial scales. The variables in the final model are shown in (a) and the variables removed in the pruning process are displayed in (b). Distance variables (shown with a dashed line) do not vary with scale. The dashed red line shows the power of a random prediction. Variables which never attained a predictive power of ≥ 0.5 are not included. The X axis is not shown to scale, to improve clarity at smaller scales.

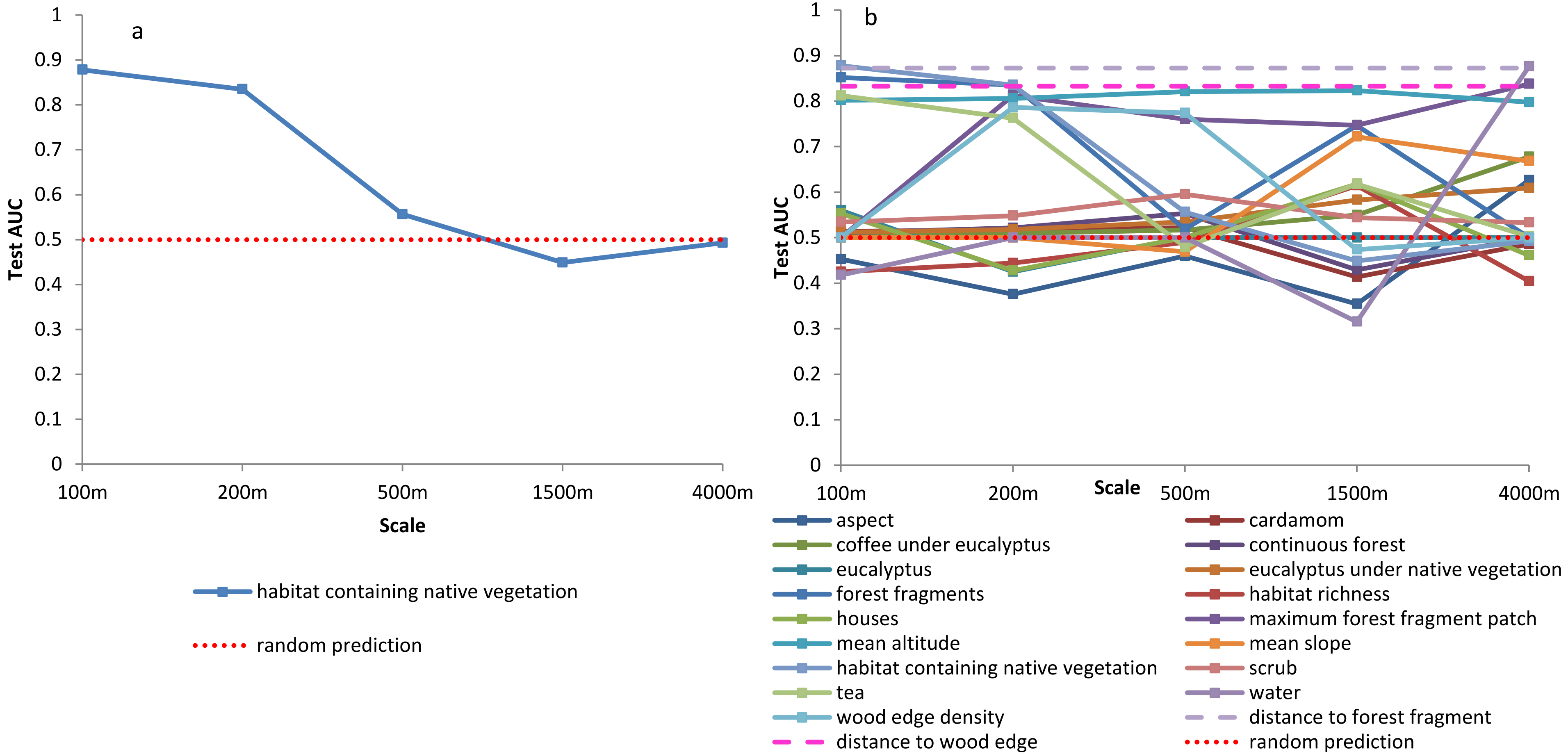


Figure 3.6.vi: The strength of relationships between *M. spasma* presence and environmental variables at five spatial scales. The variables in the final model are shown in (a) and the variables removed in the pruning process are displayed in (b). Distance variables (shown with a dashed line) do not vary with scale. Variables which never attained a predictive power of ≥ 0.1 training gain are not included. The X axis is not shown to scale, to improve clarity at smaller scales.

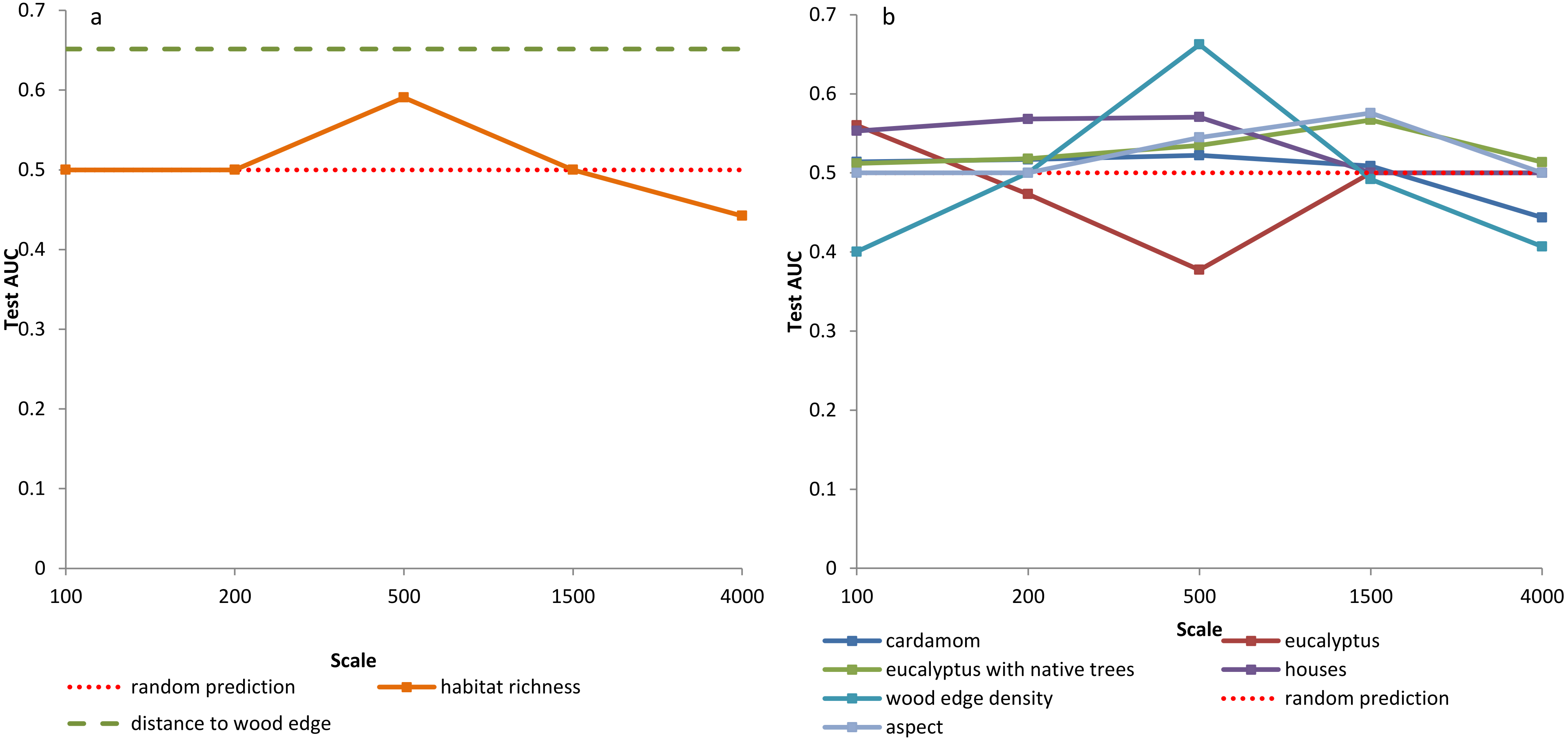


Figure 3.6.vii: The strength of relationships between *H. pomona* presence and environmental variables at five spatial scales. The variables in the final model are shown in (a) and the variables removed in the pruning process are displayed in (b). Distance variables (shown with a dashed line) do not vary with scale. The dashed red line shows the power of a random prediction. Variables which never attained a predictive power of ≥ 0.5 are not included. The X axis is not shown to scale, to improve clarity at smaller scales.

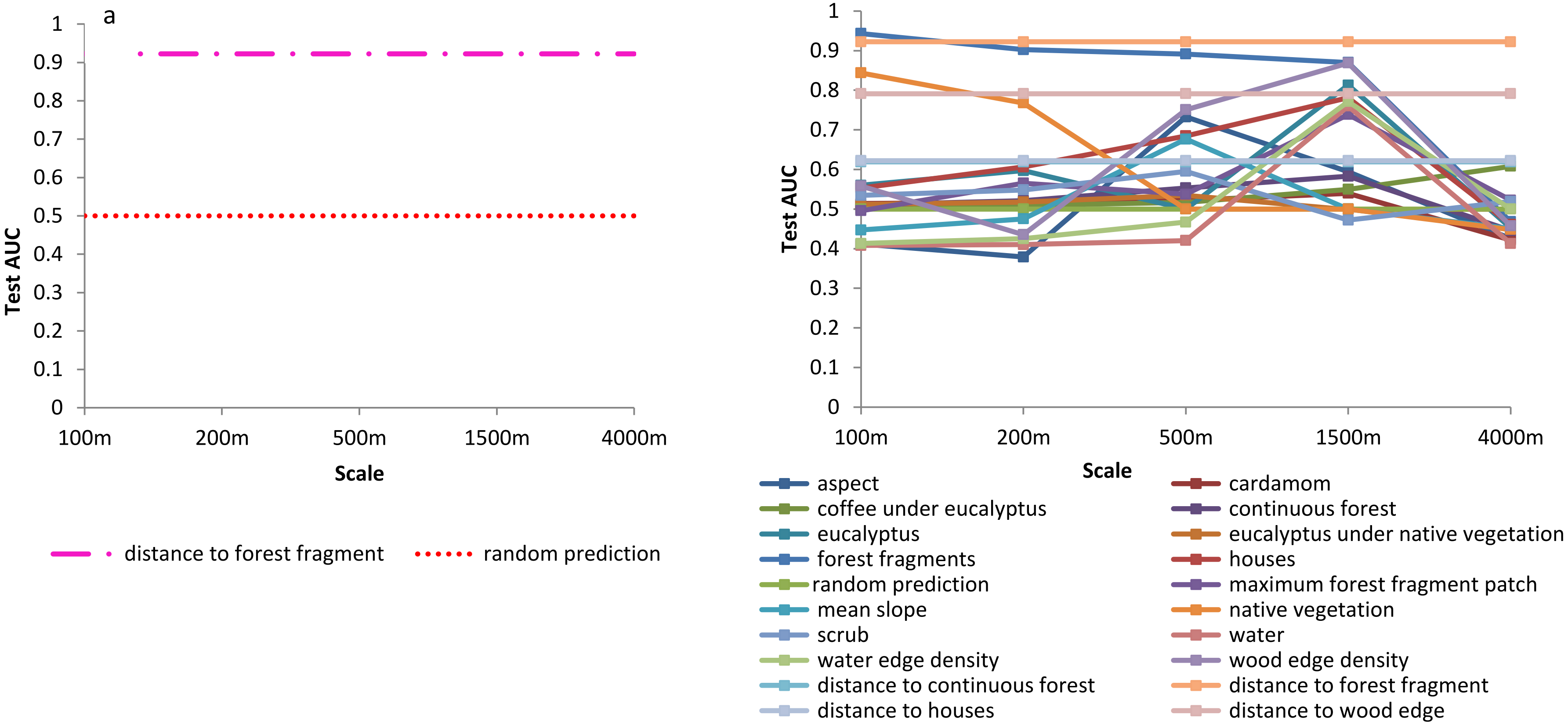


Figure 3.6.viii: The strength of relationships between *R. beddomei* presence and environmental variables at five spatial scales. The variables in the final model are shown in (a) and the variables removed in the pruning process are displayed in (b). Distance variables (shown with a dashed line) do not vary with scale. Variables which never attained a predictive power of ≥ 0.1 training gain are not included. The X axis is not shown to scale, to improve clarity at smaller scales.

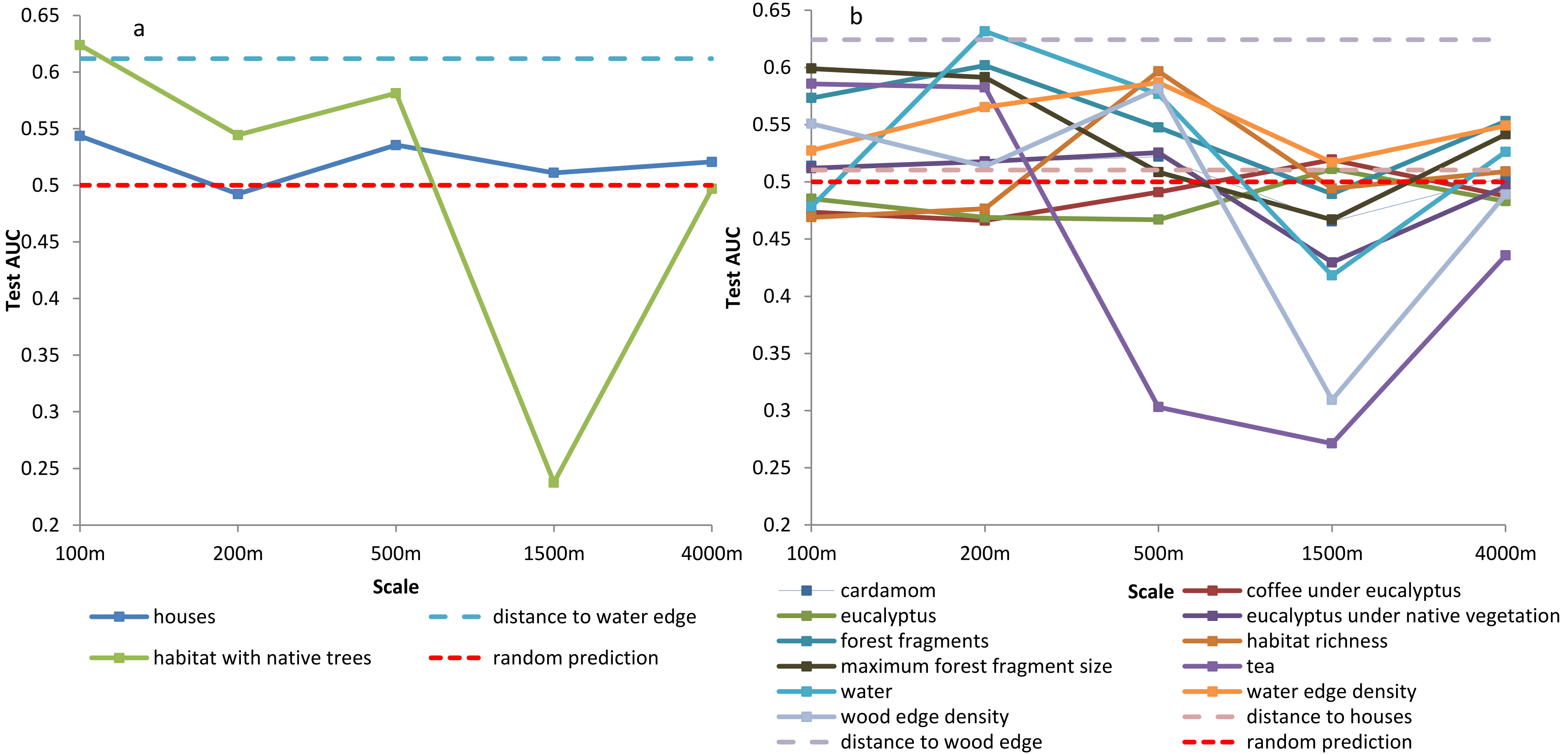


Figure 3.6.ix: The strength of relationships between *R. indorouxii* presence and environmental variables at five spatial scales. The variables in the final model are shown in (a) and the variables removed in the pruning process are displayed in (b). Distance variables (shown with a dashed line) do not vary with scale. The dashed red line shows the power of a random prediction. Variables which never attained a predictive power of ≥ 0.5 are not included. The X axis is not shown to scale, to improve clarity at smaller scales.

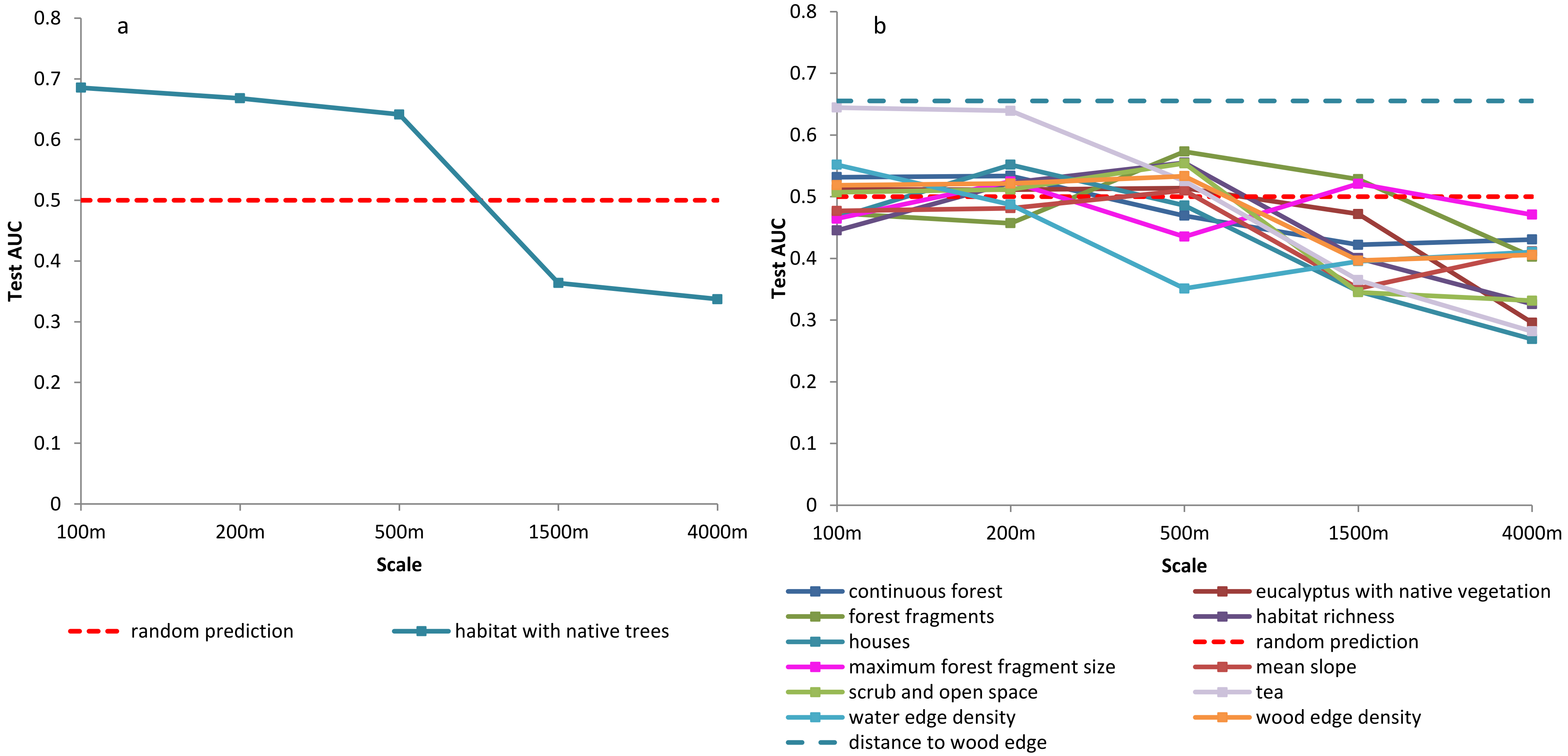


Figure 3.6.x: The strength of relationships between *R. lepidus* presence and environmental variables at five spatial scales. The variables in the final model are shown in (a) and the variables removed in the pruning process are displayed in (b). Distance variables (shown with a dashed line) do not vary with scale. The dashed red line shows the power of a random prediction. Variables which never attained a predictive power of ≥ 0.5 are not included. The X axis is not shown to scale, to improve clarity at smaller scales.

3.4.3 How variables predicted species presence.

The factors which came up in more than two different species models were habitat containing native trees at 100 m scale (positive response), habitat richness at 500 m scale (positive response), tea cover at 100 m scale (negative response) and distance to water (negative response) (Fig 3.28 a-d).

Hesperoptenus tickelli

The best performing model for *H. tickelli* (32 presence points) contained only tea as a variable, to which it responds negatively – the test AUC on spatially constrained data was 0.64 (Fig. 3.7, Table 3.3). This species was found in a range of habitats, including tea, eucalyptus, coffee under either native or exotic shade and forest fragments. It is less common in tea than in wooded habitat but not entirely absent (Fig. 3.8) The HSM distribution map predicts many but not all of the occurrence points.

Table 3.3 – AUC and AICc scores for the best performing *H. tickelli* models.

Model	Test AUC score	AICc score
Distance to wood edge	0.624	733.651
Tea 100 m	0.641	730.555
Tea at 100 m and distance to wood edge	0.626	733.257
Tea at 100 m, continuous forest at 4000m and distance to wood edge	0.606	736.610

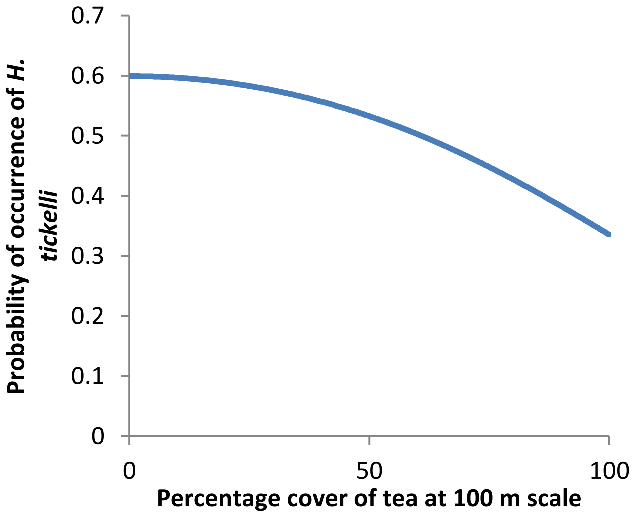


Figure 3.7: The variable in the final model for *H. tickelli*.

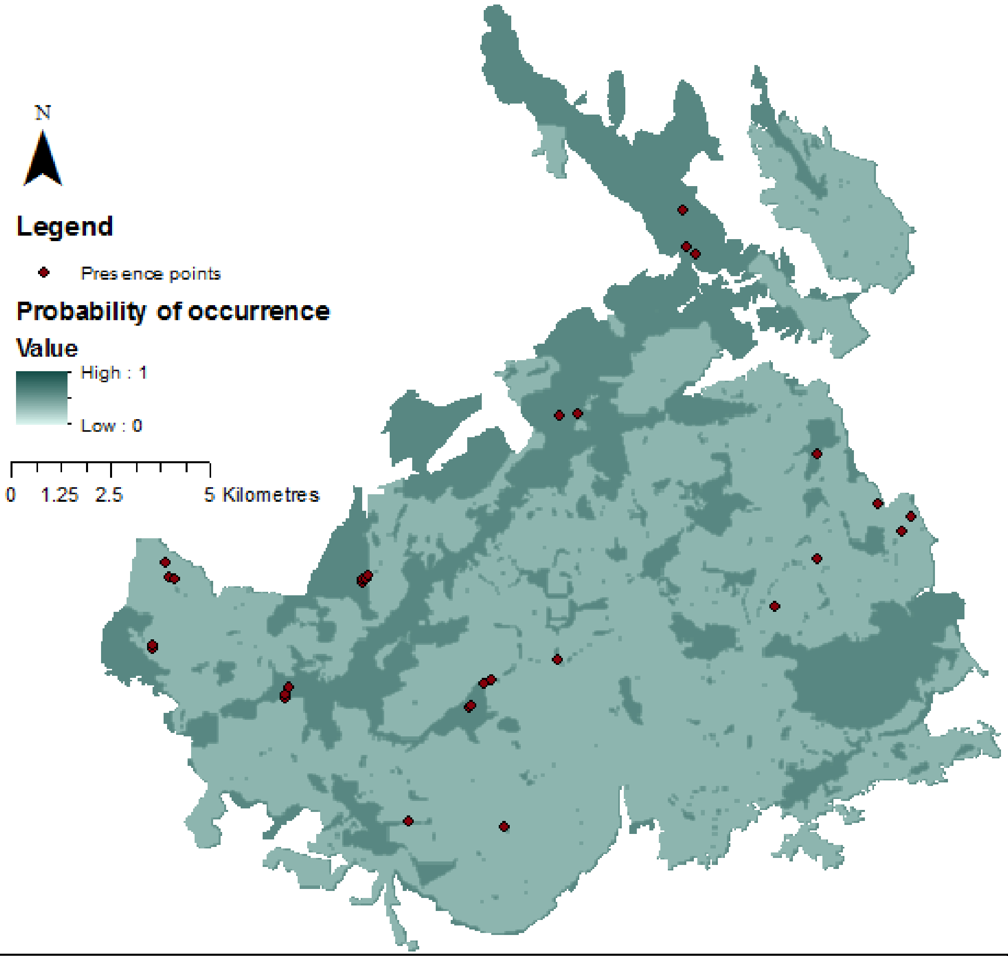


Figure 3.8: Predicted distribution map for *H. tickelli.*

Miniopterus fuliginosus

The final model contained tea at 100 m (negative) and habitat richness at 500 m (positive) and the test AUC was 0.61 (Fig. 3.9). Several models performed very similarly on AUC and AICc, but of these this model performed best on log likelihood and BIC measures (Table 3.4). This species was common (193 presence points) and clearly disturbance tolerant, being found in a variety of plantation habitats including eucalyptus and also in the small urban area. It shows a slight negative response to tea and a strong positive response to habitat richness. The predicted distribution map shows a more or less even occurrence across the study area, which is borne out by the predicted distribution map (Fig3.10). While no areas are outside the training range of these two variables, the lower likelihood of occurrence in the large forest fragment in the south east corner of the landscape is likely to be a spurious result of the habitat richness factor and not biologically meaningful.

Table 3.4 – AUC, log likelihood, BIC and AICc scores for the best performing *M. fuliginosus* models

Model	Test AUC score	AICc score	Log Likelihood	BIC score
Aspect 200 m, distance to houses, habitat richness 500 m, slope 500 m and tea 100 m.	0.605	4489.191	-2219.62	4555.018
Aspect 200 m, distance to houses, habitat richness 500 m and slope 500 m	0.623	4472.829	-2212.71	4535.942
Aspect 200 m, habitat richness 500 m and slope 500 m	0.613	4403.672	-2188.97	4441.091
Habitat richness 500 m and slope 500 m	0.622	4403.599	-2193.41	4428.918
Habitat richness 500 m and tea 100 m	0.607	4403.72	-2197.75	4416.558
Tea 100m	0.621	4432.166	-2215.07	4435.408

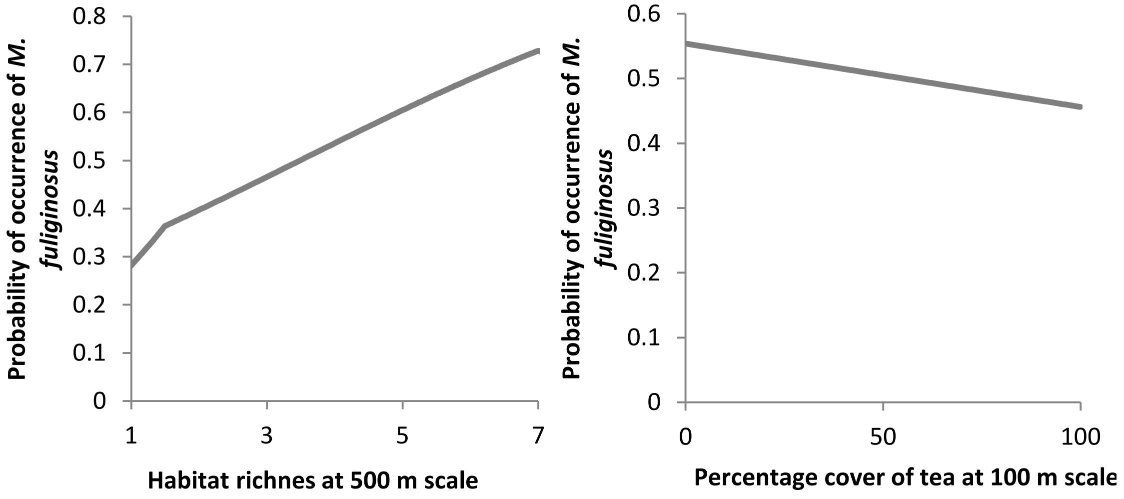


Figure 3.9: The two variables in the best-performing model for *M. fuliginosus.*

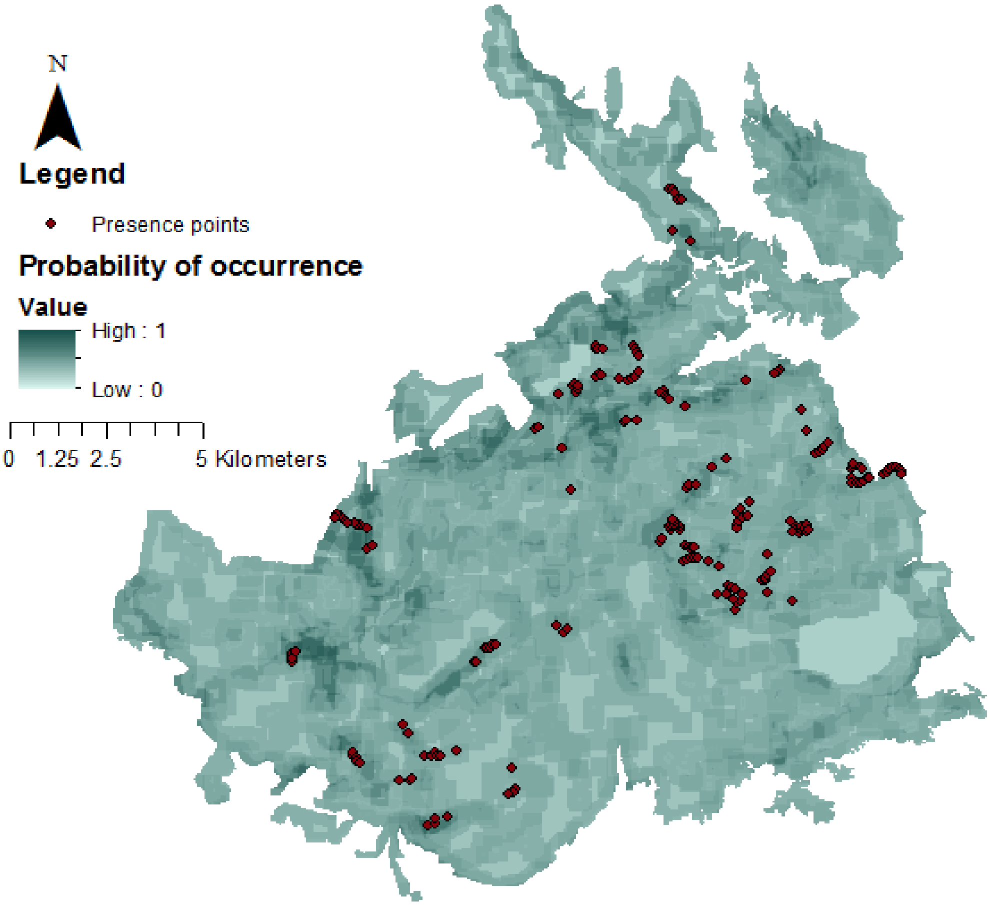


Figure 3.10: Predictive distribution map for *M. fuliginosus.*

Miniopterus pusillus

The final model (based on 99 presence points) contained habitat with native trees at 100 m and habitat richness at 500 m, and had a test AUC of 0.70 (Fig. 3.11, Table 3.5). The next best model scored 0.71 on test AUC but had a higher AICc value. This species was found in various plantation types, on the edge of the small urban area and in forest fragments. The predictive distribution map predicts it is likely to be present in habitats across the landscape but to have the highest probability of presence in areas of forest or agroforestry plantation (Fig. 3.12).

Table 3.5 – AUC and AICc scores for the best performing *M. pusillus* models

Model	Test AUC score	AICc score
Habitat with native trees 100 m	0.717	2252.074
Habitat richness 500 m, habitat with native trees 100 m	0.698	2241.412
Habitat richness 500 m, habitat with native trees 100 m and scrub 500 m	0.683	2247.163

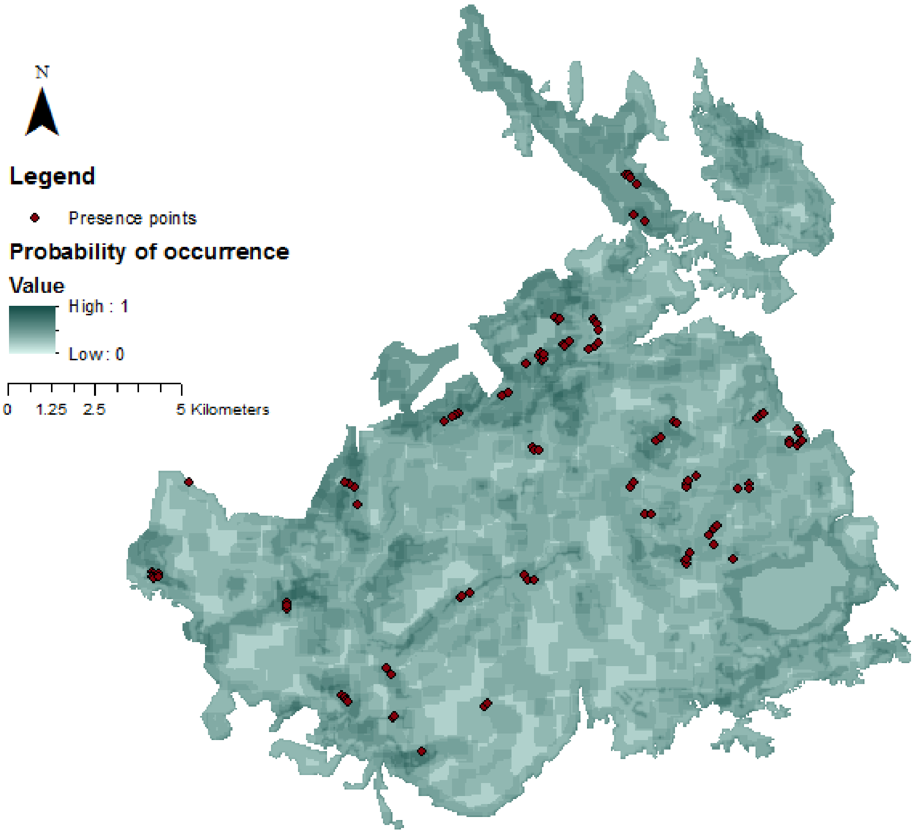


Figure 3.12: Predictive distribution map for *M. pusillus.*

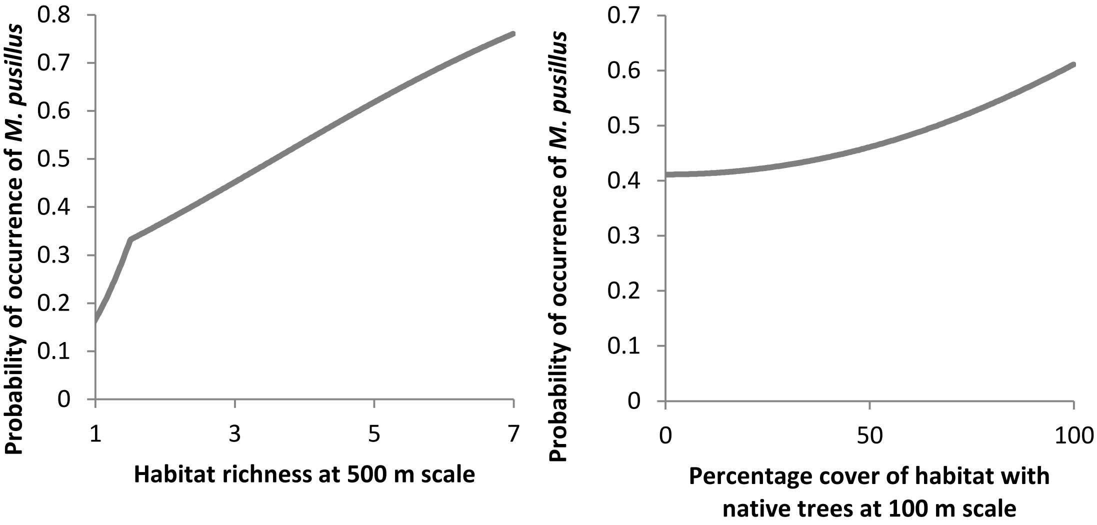


Figure 3.11: The two variables in the best performing model for *M. pusillus.*

Myotis horsfieldii

The final model (based on 52 presence points) with the lowest AICc contained the variables distance to water, water at 200 m and water edge density at 100 m and had a test AUC of 0.89 (Fig 3.13, Table 3.6). The best model on test AUC contained distance to water, water edge density at 100 m and wood edge density at 4000 m (test AUC 0.9) but this scored lower on AICc. This species is quite abundant and is a water specialist. It is disturbance tolerant as it was found on rivers in tea. The predictive map indicates it to be present on all rivers, streams and lakes which seems to be well borne out by the field data (Fig. 3.14).

Table 3.6 – AUC and AICc scores for the best performing *M. pusillus* models

Model	Test AUC	AICc
Water edge density 100 m	0.899	1115.756
Water edge density 100 m and wood edge density 4000 m	0.899	1110.193
Water edge density 100 m, wood edge density 4000 m and distance to water's edge	0.9014	1129.648
Water edge density 100 m and distance to water's edge	0.8991	1119.109
Water edge density 100 m, distance to water's edge and water 200 m	0.893	1101.765

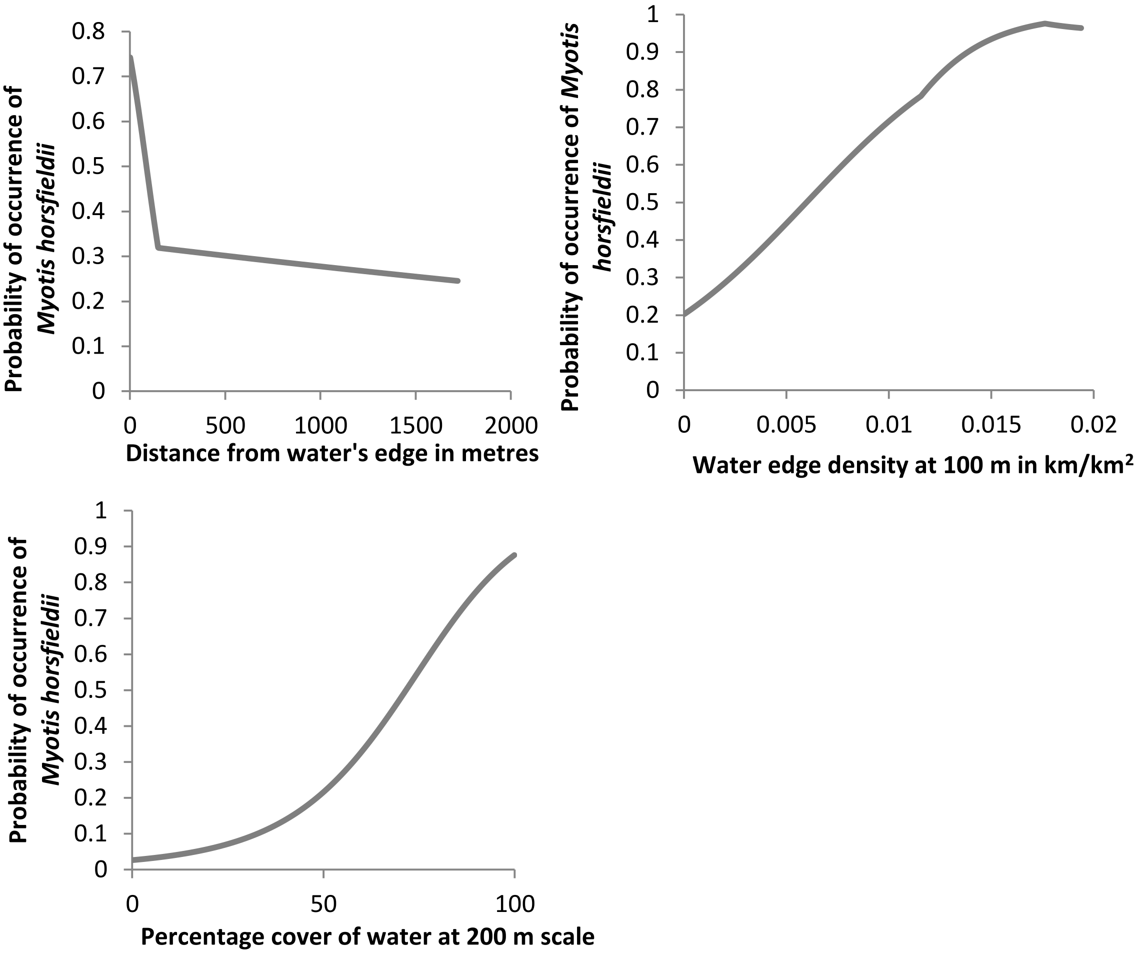


Figure 3.13: The three variables in the best performing model for *M. horsfieldii.*

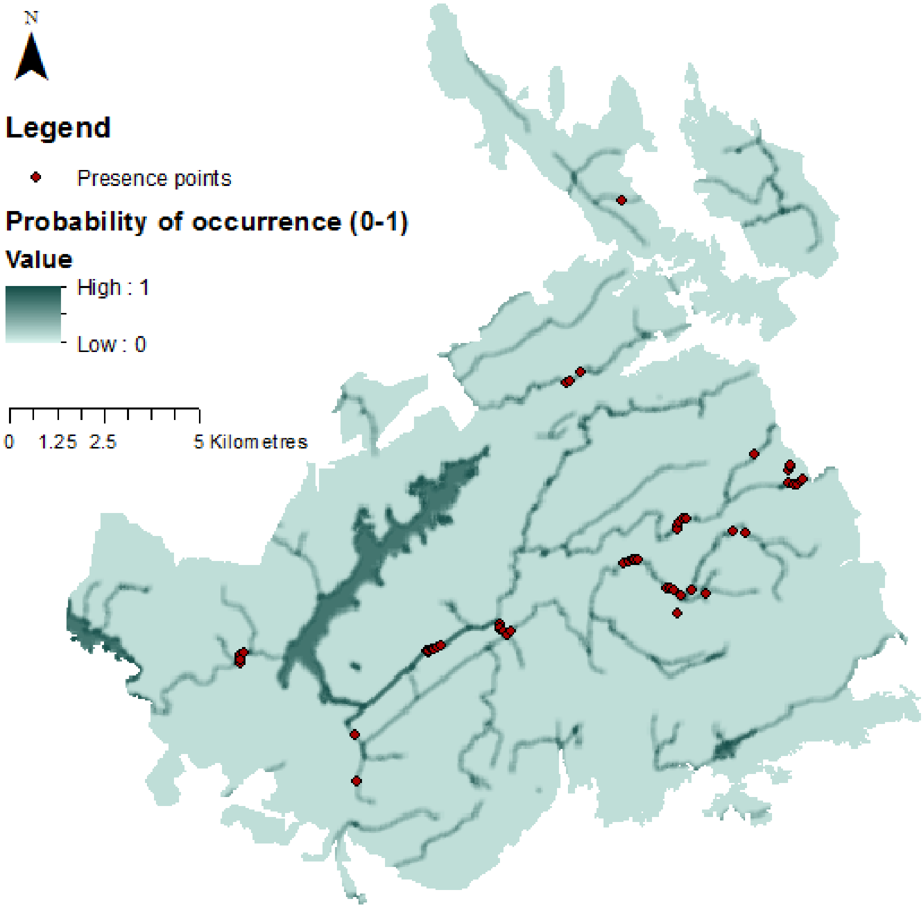


Figure 3.14: Predictive distribution map for *M. horsfieldii.*

Pipistrellus ceylonicus

The final model for this species contained two variables – habitat richness at 200 m and tea at 100 m (negative), which had a test AUC of 0.59. The model containing just tea had a higher AUC value (0.61) but scored worse on AICc (Fig. 3.15, Table 3.7). This species was recorded more than any other: 290 presence points. The habitat suitability map showed that this species was likely to be found in any area but with slightly higher probability in any wooded or water habitat (Fig 3.16).

Table 3.7 – AUC and AICc scores for the best performing *P. ceylonicus* models.

Model	Test AUC score	AICc score
Continuous forest 200 m, habitat richness 200 m, slope 500m and tea 100 m.	0.586	6671.242
Habitat richness 200 m and tea 100 m	0.589	6648.902
Tea 100 m	0.607	6660.502

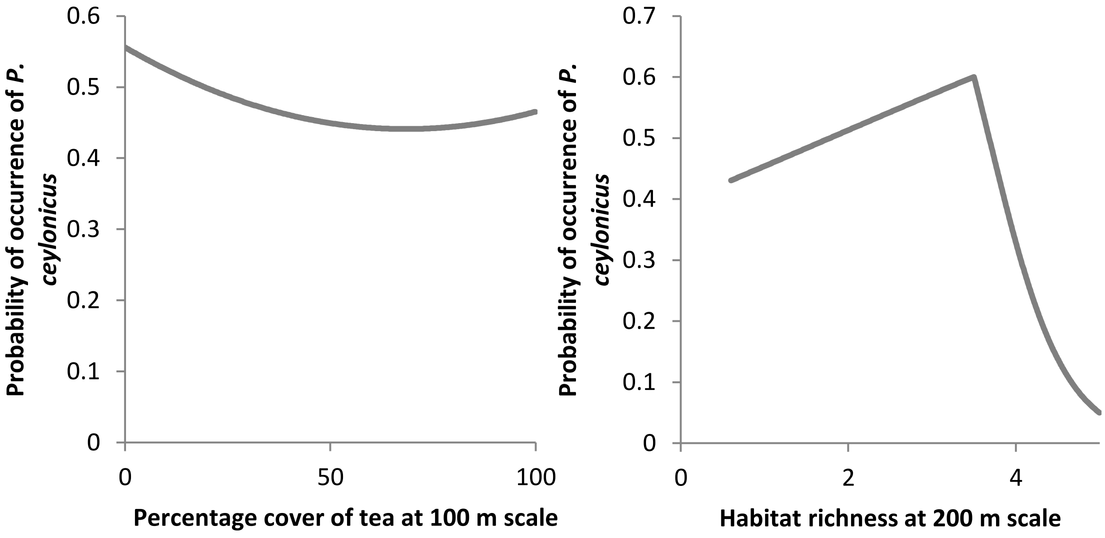


Figure 3.15: The two variables in the best performing model for *P. ceylonicus.*

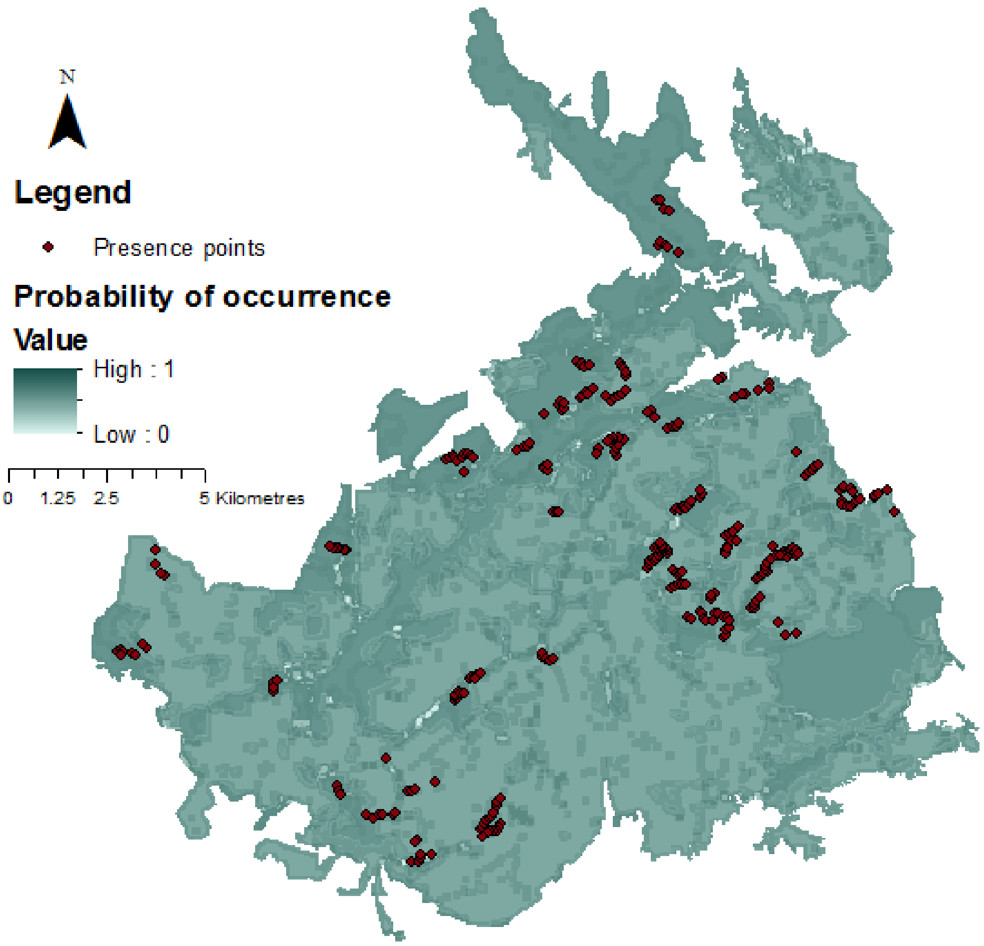


Figure 3.16: Predictive distribution map for *P. ceylonicus.*

Megaderma spasma

The final model (based on five presence points) contained just habitat with native trees at the 100 m scale and had a test AUC of 0.88 (Fig 3.17, Table 3.8). This model scored best on AICc and log likelihood, but worse on BIC and Test AUC than the other models. However, both the other models had large areas where it could not predict accurately due to lack of training data where there were high scores for 4000m water; also, as the model was built with so few points, more complex models are likely to overfit . Despite the low number of presence points the predictive map for appears to be very good (Fig. 3.18, Fig. 3.19).

Table 3.8 – AUC,Log likelihood, BIC and AICc scores for the best performing *M. spasma* models.

Model	Test AUC score	AICc score	Log Likelihood	BIC score
Habitat containing native trees 100 m, water 4000 m and scrub 500 m	0.966	122.838	-46.419	97.666
Habitat containing native trees 100 m and water 4000 m	0.959	102.933	-46.466	96.152
Habitat containing native trees 100 m	0.878	102.693	-49.680	100.970

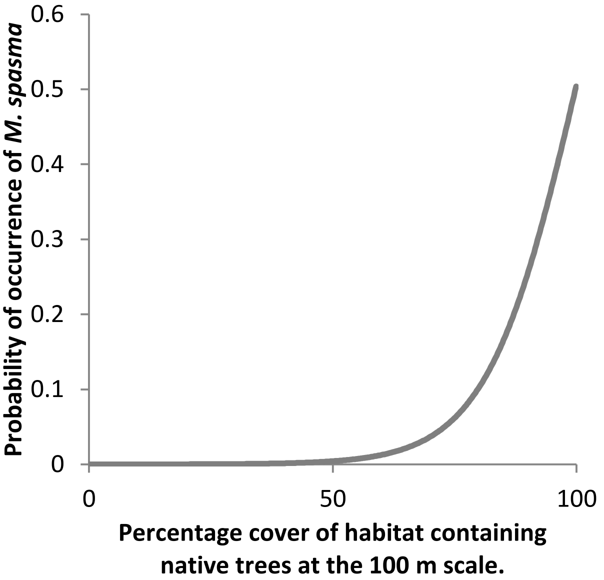


Figure 3.17: The variable in the best performing model for *M. spasma.*

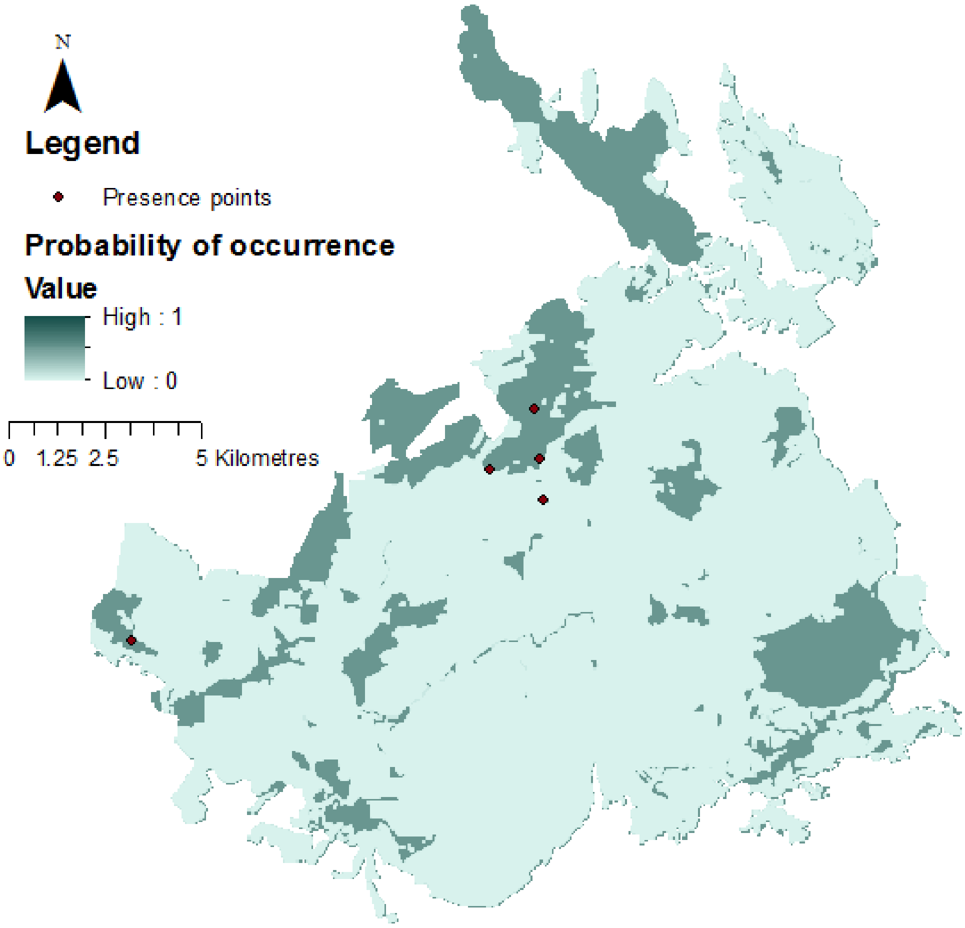


Figure 3.18: Predictive distribution map for *M. spasma.*

Figure 3.19: Close up of predictive distribution map for M. spasma, showing that all presence points are within the predicted area; this presence points falls within a very small forest fragment.

Hipposideros pomona

The final model for *Hipposideros pomona* contained two variables, distance to wood edge (negative) and habitat richness (positive) at 500 m (Fig 3.20), and had a test AUC for the spatially constrained data of 0.67. Several models had similar AICc scores but this was the most parsimonious and thus the least likely to be overfitting to the small number of data points (Table 3.9). The model predicted this species to be present in a large part of the landscape, although not in the areas dominated by tea plantations alone (Fig. 3.21).

Table 3.9 – AUC,Log likelihood, BIC and AICc scores for the best performing *H. pomona* models.

Model	Test AUC	Log Likelihood	AICc score	BIC score
Aspect 1500 m,eucalyptus under native vegetation 1500 m, habitat richness 500 m, buildings 200 m, wood edge density 500 m and distance to wood edge.	0.722	-147.310	317.120	310.868
Aspect 1500 m,eucalyptus under native vegetation 1500 m, habitat richness 500 m, buildings 200 m and distance to wood edge.	0.775	-146.862	310.391	307.265
Aspect 1500 m,eucalyptus under native vegetation 1500 m, habitat richness 500 m, buildings 200 m, distance to water edge and distance to wood edge.	0.769	-147.105	310.877	307.750
Aspect 1500 m,eucalyptus under native vegetation 1500 m, habitat richness 500 m and distance to wood edge.	0.768	-147.221	306.442	305.274
Eucalyptus under native vegetation 1500 m, habitat richness 500 m and distance to wood edge.	0.736	-148.827	305.837	305.779
Aspect 1500 m,eucalyptus 100 m, habitat richness 500 m and distance to wood edge.	0.804	-169.275	346.732	346.674
Aspect 1500 m, habitat richness 500 m and distance to wood edge.	0.700	-148.401	304.984	304.927
Habitat richness 500 m and distance to wood edge.	0.665	-150.029	305.058	305.474

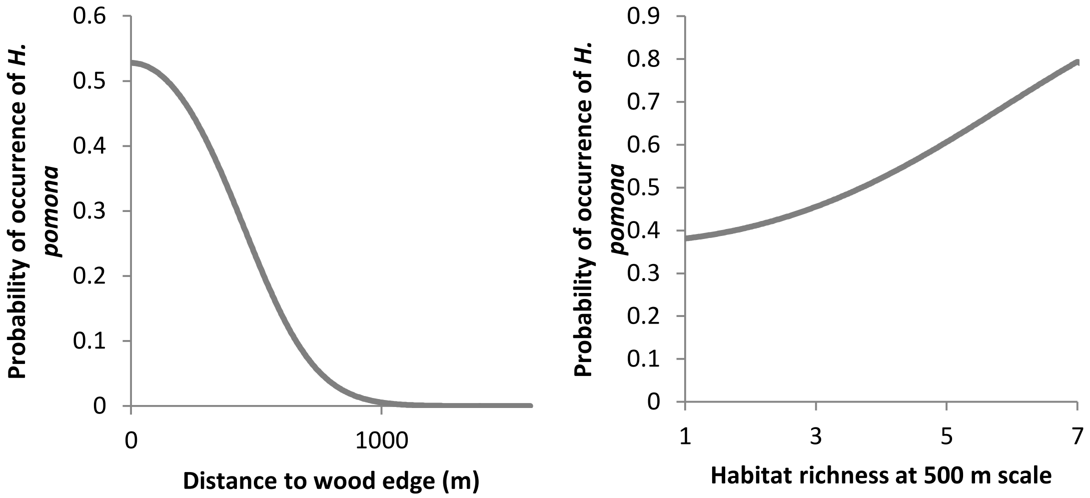


Figure 3.20: The two variables in the best performing model for *H. pomona.*

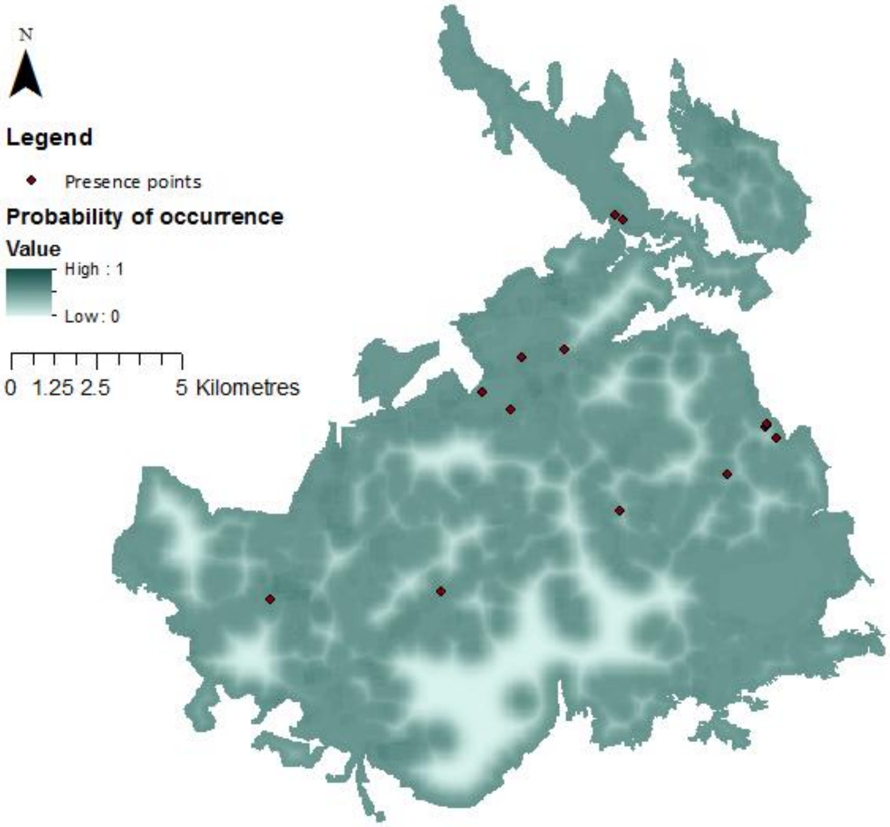


Figure 3.21: Predicted distribution map for *H. pomona.*

Rhinolophus beddomei

The final model for this species contained just one variable (distance to forest fragments) and had a test AUC of 0.92 (Fig. 3.22) based on only five presence points. This was the model with the lowest AICc score (Table 3.10) The distribution map predicts it have to have a more limited distribution than other species (Fig. 3.23).

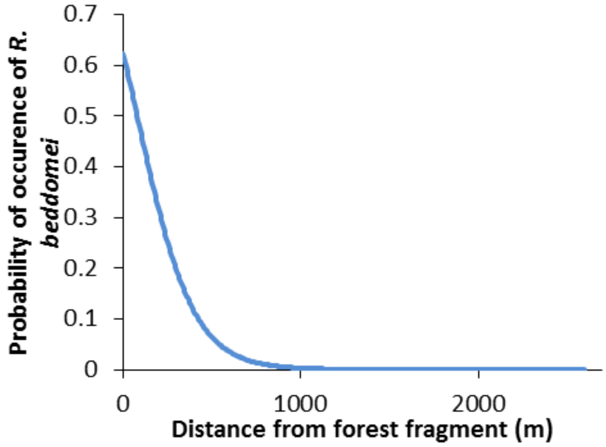


Figure 3.22: The one variable in the best performing model for *R. beddomei.*

Table 3.10 – AUC and AICc scores for the best performing *R. beddomei* models.

Model	Test AUC score	AICc score
Distance to forest fragment, houses 500m, scrub 500m and water edge density 1500m.	0.949	131.141
Distance to forest fragment, scrub 500m and water edge density 1500m.	0.949	131.141
Distance to forest fragment, water edge density 1500m.	0.946	111.780
Distance to forest fragment	0.923	106.283
Distance to forest fragment, forest fragments 100m	0.928	112.156

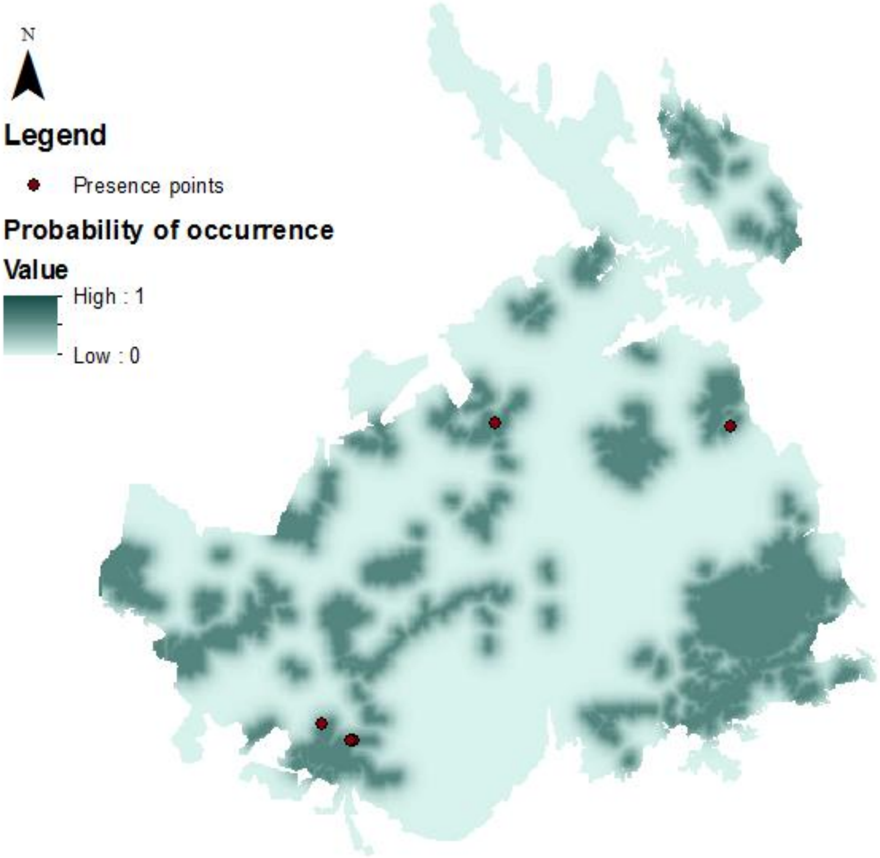


Figure 3.23: Predictive distribution map for *R. beddomei.*

Rhinolophus indorouxii

The final model had three variables; houses at 100 m (negative), habitat with native trees at 100 m (positive) and distance to water (negative), and had a test AUC of 0.65. This model had a lower AICc than other models with higher test AUCs – the best model on test AUC (0.71) was the final model plus tea (Fig. 3.24, Table 3.11).

This species was fairly common with 55 presence points, and was found in tea, coffee under native shade, forest fragments and once in a eucalyptus plantation.

Table 3.11 – AUC and AICc scores for the best performing *R. indorouxii* models.

Model	Test AUC	AICc score
Houses 100 m, distance to water edge, habitat containing native trees 100 m and tea 100 m	0.708	1258.008
Houses 100 m, distance to water edge and habitat containing native trees 100 m	0.722	1248.943
Distance to water edge and habitat containing native trees 100 m	0.685	1257.715

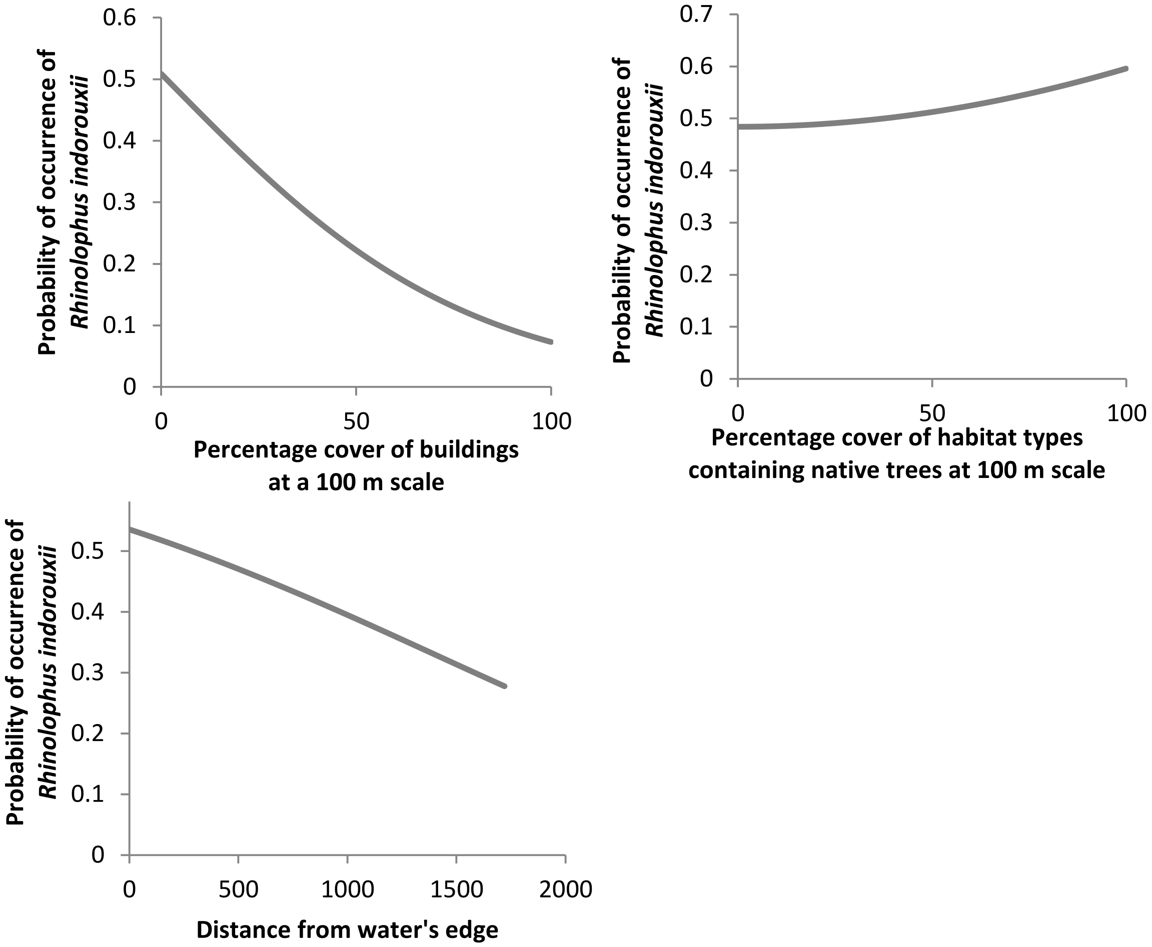


Figure 3.24: The three variables in the best performing model for *R. indorouxii*

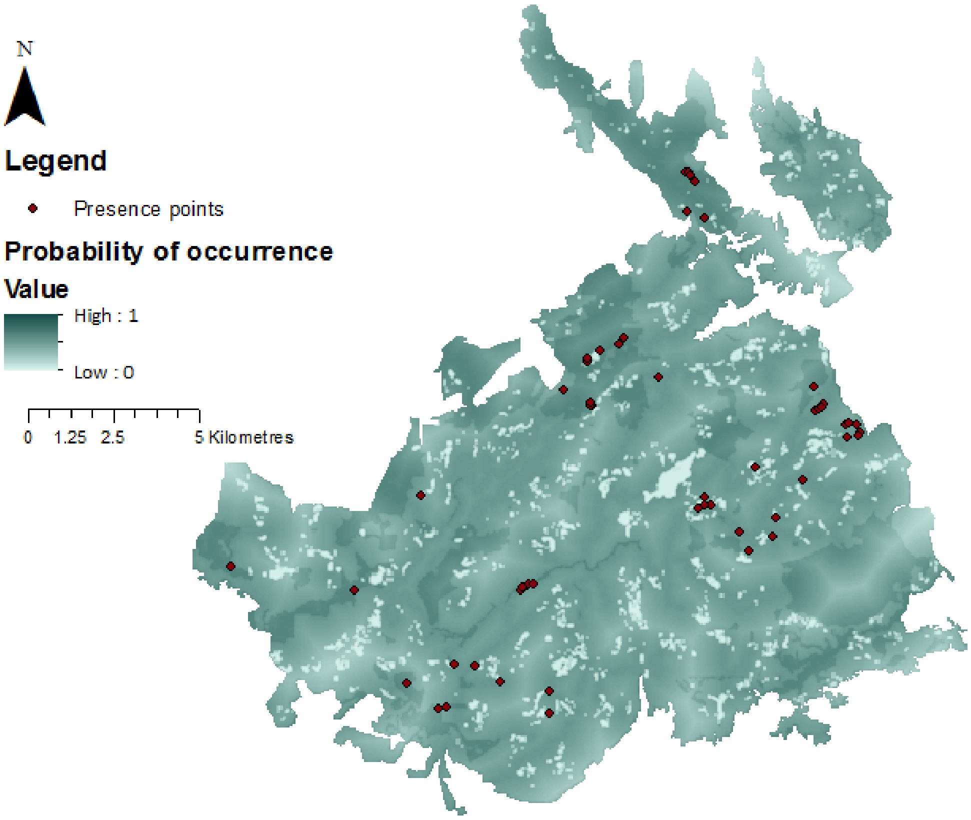


Figure 3.25: Predictive map for *R. indorouxii.*

Rhinolophus lepidus

The final model contained one variable – habitat with native trees at 100 m – and had a test AUC of 0.69, which was the best model both on AICc and test AUC (Fig. 3.26, Table 3.12). This species was common with 129 presence points, and was found in all plantation types (although not in the small urban area). However, once again it showed a negative response to tea plantations (Fig.3.27).

Table 3.12 – AUC and AICc scores for the best performing *R. lepidus* models

Model	AUC score	AICc score
Tea 100 m, habitat with native trees 100 m, continous forest 200 m and water edge density 100 m	0.624	2981.832
Tea 100 m and continous forest 200 m	0.648	2975.023
Tea 100 m, habitat with native trees 100 m and continous forest 200 m	0.630	2992.762
Tea 100 m	0.645	2956.872
Habitat with native trees 100 m	0.686	2945.901

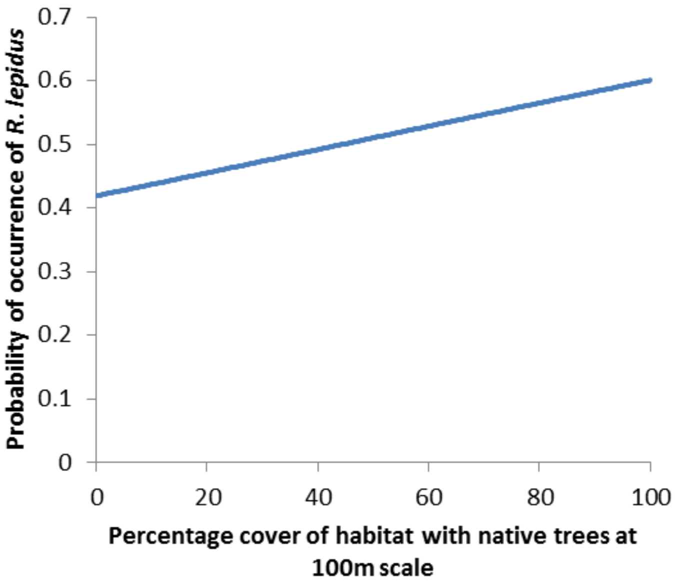


Figure 3.26: The variable in the best performing model for *R. lepidus.*

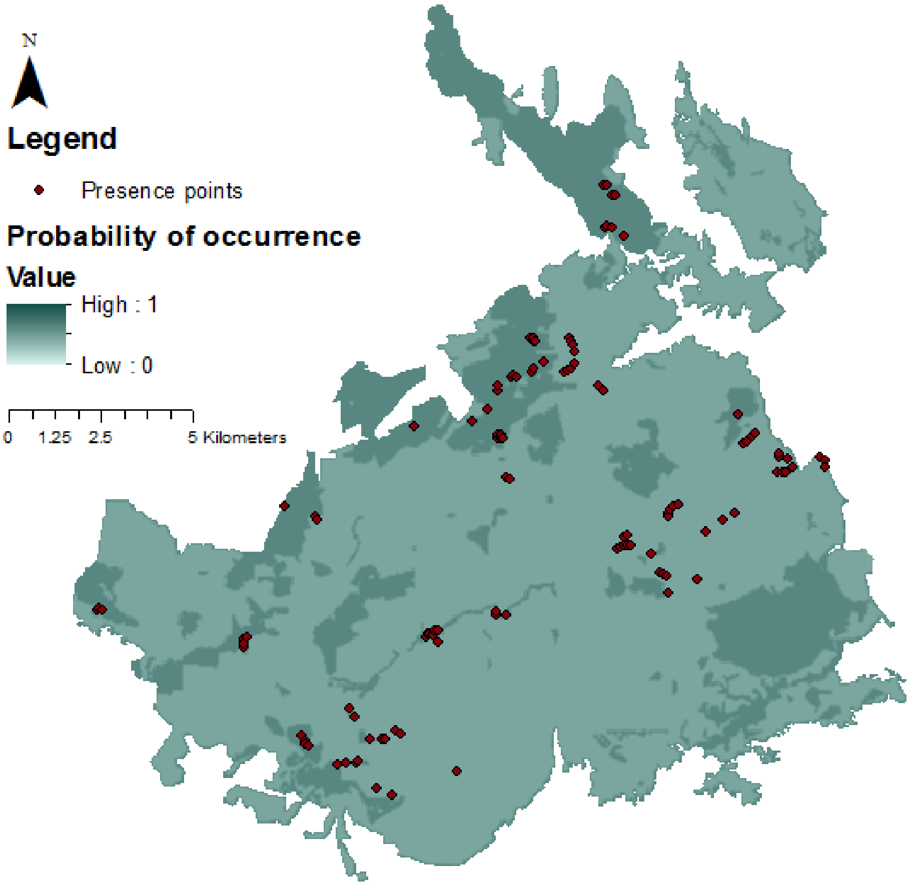


Figure 3.27: Predictive map for *R. lepidus.*

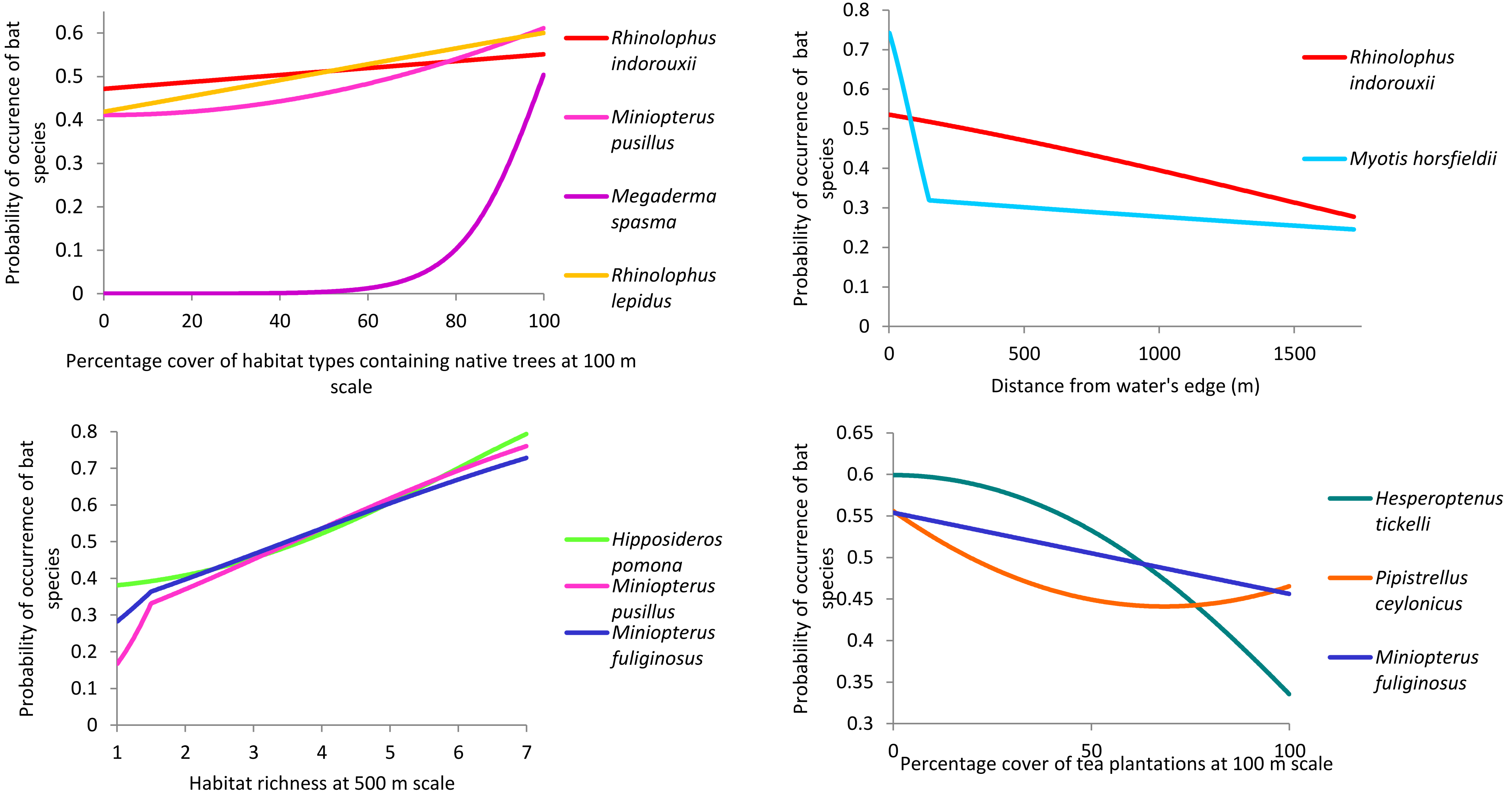


Figure 3.28: The four variables that were in the final model for more than one species, with multiple species' response plotted.

3.4.4 Comparing habitat suitability overlap

The thresholded niche breadth metric results were very different from the non-thresholded niche breadth metric (Table 3.13). Both predicted the forest specialists *M. spasma* and *R. beddomei* and the water specialist *M. horsfieldii* to have very low niche breadths. But in the non-thresholded inverse of Levins' metric all the species other than these three had broad niches of over 0.9. In the thresholded niche breadth metric *H. pomona, H. tickelli* and all three *Rhinolophus* species also had low niche breadths of 0.1-0.29, with *M. pusillus* having a slightly higher breadth (0.4), and the broadest being *M. fuliginosus* and *P. ceylonicus* with measures of over 0.5.

Table 3.13: Proportion of the study area considered suitable for each species. Areas calculation using the binary threshold maximum training sensitivity plus specificity (left), and using the non-thresholded inverse of Levins' metric (right, Levins 1968). Darker shading indicates higher values.

Species	Test AUC	MSS threshold	Niche breadth
H. pomona	0.665	0.109	0.904
H. tickelli	0.641	0.298	0.927
M. fuliginosus	0.607	0.586	0.947
M. pusillus	0.699	0.416	0.926
M. horsfieldii	0.893	0.110	0.553
M. spasma	0.878	0.208	0.217
P. ceylonicus	0.589	0.571	0.980
R. beddomei	0.923	0.139	0.398
R. indorouxii	0.647	0.255	0.975
R. lepidus	0.686	0.286	0.924

The *I* statistic predicted all species to have a niche overlap of >0.9 with all species other than *R. beddomei* and *M. spasma* (Table 3.14). Relative rank scored all niche overlaps as lower overall than the *I* statistic did, other than *R. lepidus* and *M. spasma* which overlapped 100% in niche ranking. This measurement system did not seem to pull out any strong patterns. The D statistic showed *M. spasma* and *R. beddomei* to have the least niche overlap with other species (*M. spasma* 0.2-0.37, *R. beddomei* 0.37- 0.53, Table 3.15). *M. horsfieldii* had the next lowest overall niche overlap with other species, scoring between 0.2 and 0.7 overlap. All other species showed scores over 0.8 in their niche overlap with each other.

Table 3.14: Measuring niche overlap between the best-performing models for all species. Niche overlap metrics are the '*I* statistic' and the non-parametric 'relative rank' Darker shading indicates higher values. (Warren et al. 2008).

I statistic Relative Rank	*H. pomona*	*R. indorouxii*	*H. tickelli*	*M. spasma*	*M. fuliginosus*	*M. pusillus*	*M. horsfieldii*	*P. ceylonicus*	*R. beddomei*	*R. lepidus*
H. pomona		0.965	0.976	0.540	0.977	0.981	0.909	0.977	0.784	0.978
R. indorouxii	0.596		0.981	0.542	0.980	0.980	0.931	0.983	0.752	0.986
H. tickelli	0.411	0.370		0.574	0.988	0.990	0.929	0.993	0.753	0.995
M. spasma	0.396	0.373	0.708		0.502	0.559	0.448	0.520	0.509	0.558
M. fuliginosus	0.662	0.516	0.454	0.357		0.996	0.934	0.993	0.753	0.991
M. pusillus	0.716	0.578	0.480	0.544	0.803		0.929	0.991	0.765	0.993
M. horsfieldii	0.231	0.319	0.411	0.401	0.328	0.305		0.934	0.696	0.928
P. ceylonicus	0.568	0.486	0.654	0.530	0.531	0.561	0.372		0.750	0.997
R. beddomei	0.613	0.535	0.300	0.318	0.487	0.497	0.207	0.425		0.759
R. lepidus	0.394	0.373	0.709	1.000	0.355	0.544	0.400	0.528	0.319	

Table 3.15: Measuring niche overlap between the best-performing models for all species. The niche overlap metric is Schoener's D statistic (Schoener 1968). Darker shading indicates higher values.

D statistic	*H. pomona*	*R. indorouxii*	*H. tickelli*	*M. spasma*	*M. fuliginosus*	*M. pusillus*	*M. horsfieldii*	*P. ceylonicus*	*R. beddomei*	*R. lepidus*
H. pomona		0.859	0.855	0.270	0.884	0.889	0.648	0.893	0.527	0.884
R. indorouxii			0.863	0.275	0.873	0.875	0.689	0.887	0.481	0.897
H. tickelli				0.308	0.877	0.894	0.691	0.901	0.481	0.918
M. spasma					0.240	0.292	0.203	0.252	0.371	0.289
M. fuliginosus						0.935	0.700	0.915	0.485	0.908
M. pusillus							0.689	0.900	0.501	0.915
M. horsfieldii								0.698	0.408	0.686
P. ceylonicus									0.474	0.934
R. beddomei										0.487
R. lepidus										

3.4.5 Overall habitat richness map

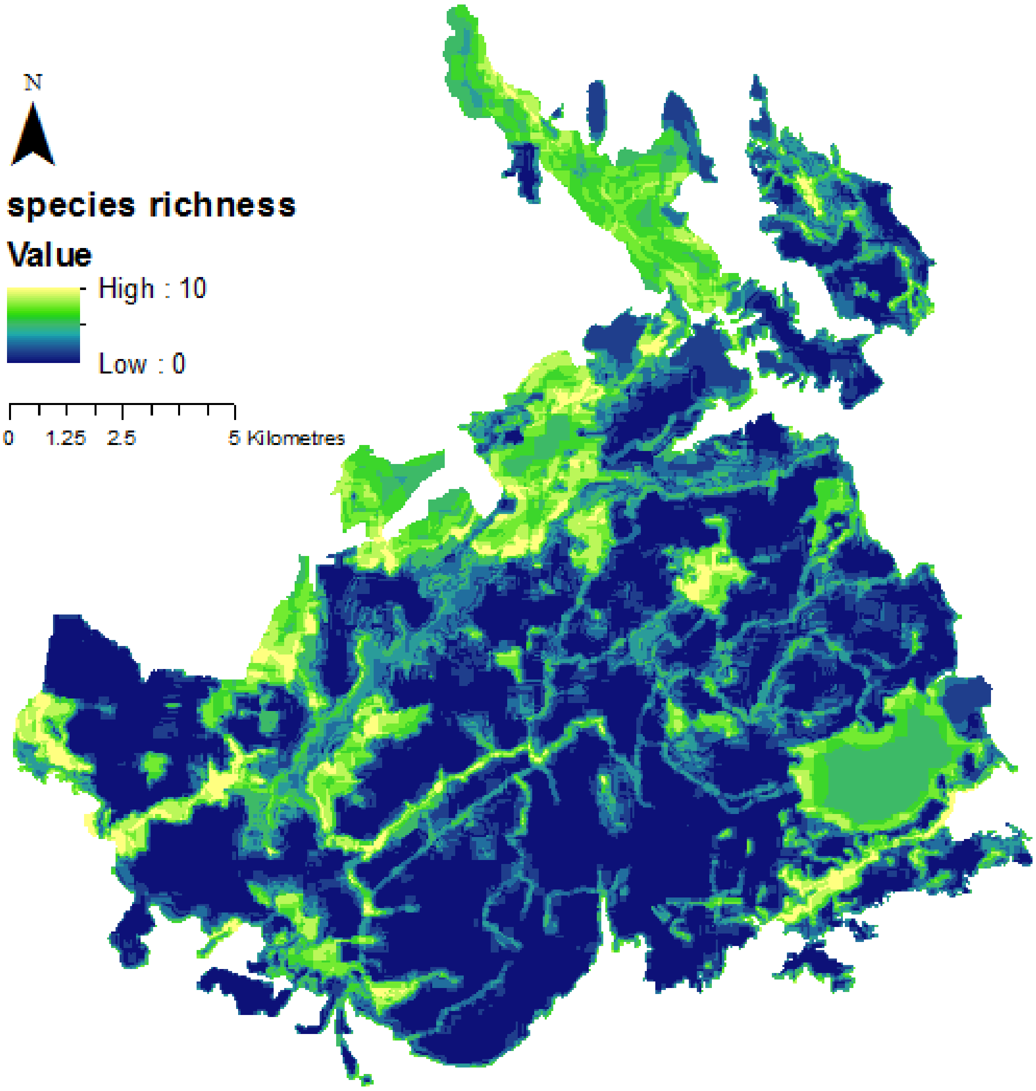


Fig 3.29: Species richness map derived from binary presence/absence scores, indicating the number of species predicted to be present in each pixel.

Both species richness maps made similar predictions, in that waterways and areas with native trees were predicted to have the greatest richness, with the south-west corner that is dominated by tea showing the least richness (Fig 3.29, 3.30). The map made from binary predictions however showed a more exaggerated pattern, whereas the map made from summed HSI scores showed more areas of low, rather than no, suitability for bats overall.

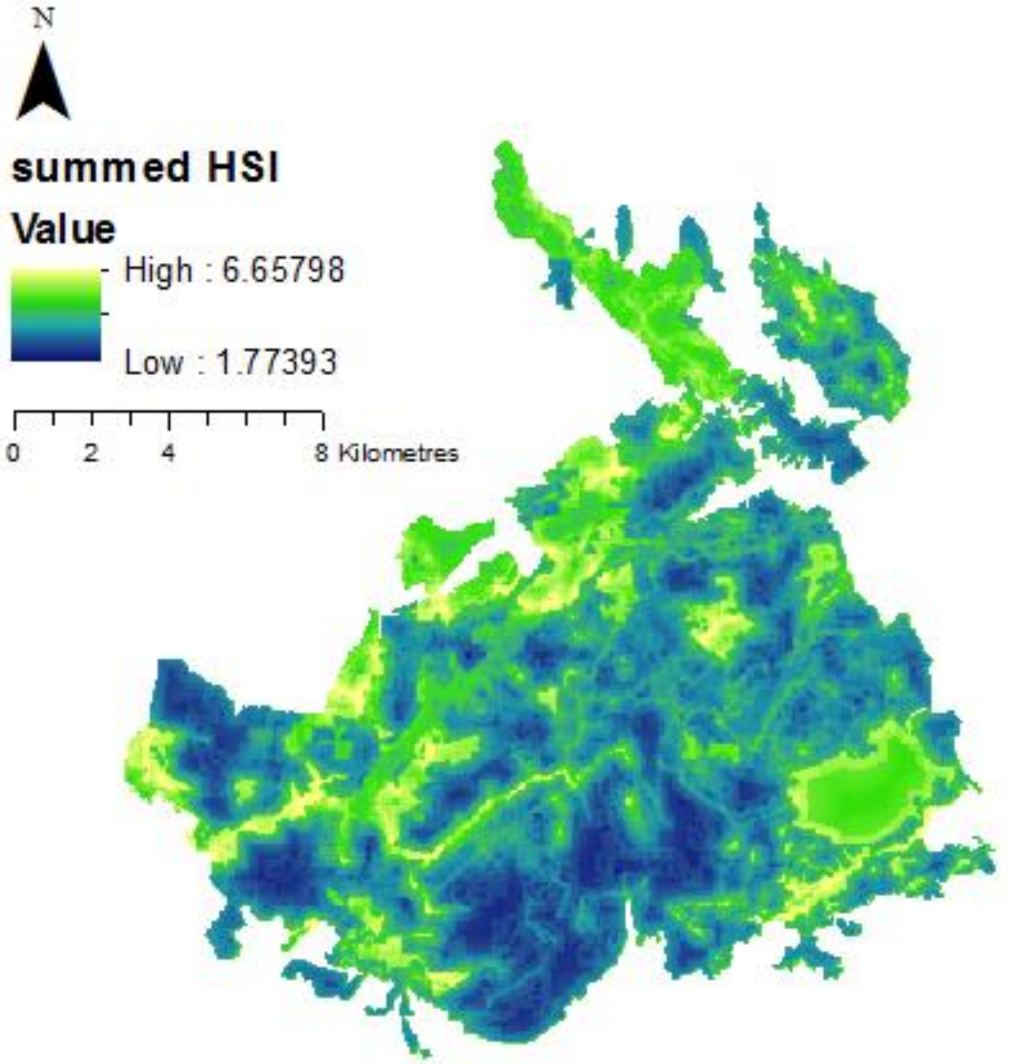


Figure 3.30: Species richness map derived from overlaying all continuous habitat suitability maps and summing the probability of a species presence in each pixel.

3.5 Discussion

3.5.1Multiscale HSM

It is clear from the changes in test AUC at different spatial scales that scale is an important factor in building bat HSMs. Five out of ten species (*M. fuliginosus, M. pusillus P. ceylonicus, R indorouxii* and *R. lepidus*) showed stronger associations with scales of 100 m – 500 m in all the variables that had any predictive power than with scales of 1500 m – 4000 m. These five species were the most abundant and disturbance tolerant species in this study, which may indicate that wider landscape factors are somewhat less important for disturbance tolerant species than they are for less common and more specialist species, as for the other five species many variables were as important at 1500 m and 4000 m as at smaller scales. For all species, however, the scalar variables in the final model showed greater predictive power at the 100 m or 200 m scale, apart from habitat richness, which was strongest at 200 - 500 m for three species and strongest at 200 m for one species.

The stronger associations of bats with smaller scales may be as a result of their great mobility – they can move and exploit small patches of scattered resources (Ober et al. 2008, Pinto and Keitt 2008, Meyer and Kalko 2008, Lookingbill et al. 2010, Fabianek et al. 2011, Razgour et al. 2011, Akasaka et al. 2012, Bellamy et al. 2013, Hahn et al. 2014). Here I saw a bat that appears to be a forest specialist – *Megaderma spasma* – exploiting a forest fragment as small as 2.2 ha, clearly demonstrating bats' ability to use even very small forest patches.

While their immediate surroundings appear to be of primary importance in determining the local occurrence of a species, that habitat richness was important for several species in a 500 m x 500 m square indicates that the wider environment also has an impact on distributions. Milne et al. (2006) also found habitat complexity (measured in the same way as 'habitat richness' here) to be important for many species, albeit at larger scales. They suggested that areas of greater habitat complexity tend to be riparian areas that provide foraging for a range of genera and foraging guilds. This may well be an important factor in this study as well, as I found riparian areas to have high species richness, even in tea plantations. It is also likely that some of these species are using forest fragment or agroforestry edges to forage, or are feeding in tea plantations but not far from the physical cover of trees.

It is apparent that by studying species at multiple scales it is possible to determine the scales most important to each species. All studies should be explicit about the scales they are using, and ideally explore multiple scales; but if time and resources are limited then for a study with a landscape-level extent, a spatial grain of 100 m - 500 m seems to be appropriate for foraging bats (although roosting bats appear sensitive to landscape variables at scales of 1 km – 6 km) (Bellamy et al. 2013). Fine scale maps at the landscape scale are important for local conservation planning, for example finding the best location for a development or a replanted forest patch.

3.5.2. Measuring model performance

All the best-performing models in this study had between one and three variables. As I built the models, those with too many variables tended to underestimate the suitable area for a species, creating omission errors, but some very simple models started to have errors of commission and overestimated the suitable area.

The AUC scores in the best performing models for the generalist species were generally between 0.6 and 0.7. The lowest was *P. ceylonicus* with 0.59. Although there were models with AUC scores >0.6 for this species, they performed worse on AICc, being penalised for complexity. The other more disturbance tolerant species (*H. pomona, H. tickelli, M. fuliginosus, M.pusillus, R. indorouxii* and *R. lepidus*) scored between 0.64 and 0.7 on test AUC, which is fair but not outstanding. The specialist species *M. horsfieldii, M. spasma* and *R. beddomei* on the other hand got excellent test AUC scores of 0.88-0.92. These were the three species with the smallest niche breadth according to the inverse of Levins' metric (Table 3.3, Levins 1968).

Lobo et al. (2008) point out that the smaller the ratio of the extent of occurrence of a species to the extent of the study area, the better predicted a species is likely to be. This is because it is more likely that pseudo-absence data will be environmentally distinct from presence data (Brotons et al. 2004, McPherson et al. 2004, Arntzen 2006, Hernandez et al. 2006). Therefore, AUC values are not an appropriate metric to compare model accuracy between species whose area of occurrence differs greatly.

Errors are also not equivalent between species when they differ in abundance – a commission error of 30 ha of suitable habitat is a different prospect for a rare species predicted in 50 ha and a common species predicted in 500 ha (Lobo et al. 2008). It is clear in this study that, as expected, the species with the smallest niche breadths got the highest test AUC (Table 3.3)

The model accuracy for the three specialist species is clearly very good, because 100% of presence points are predicted but a low area of habitat is predicted to be suitable overall. The models for the less habitat specialist, more disturbance tolerant species had higher commission and omission errors; but these species have weaker associations with any particular environmental variables as they can exploit many habitats, so this is to be expected. The models for disturbance tolerant species are valuable as they draw out habitat associations, but they do not have the same degree of specificity as the models for specialist species.

3.5.3 Species habitat associations.

Different bat species reacted to different environmental variables, and there was a wide range in the strength of the responses. It is clear that *M. spasma* and *R. beddomei* are the species most at risk from the loss of forest fragments and agroforestry plantations, but that the other bat species still respond positively to these habitat features and negatively to monocultures of tea. It is possible that there are some species that are even more sensitive than *M. spasma* and *R. beddomei* that were too rare to model or are restricted to primary forest reserve. *B. leucomelas darjelingensis* was restricted to a single locality near to primary forest so wasn’t modelled, and a rhinolophid bat calling at 80 kHz assumed on the basis of call frequency to be *R. affinis* was recorded in four agroforestry and forest fragment sites, but the sites were so clustered that the data could not be considered spatially independent. As I could not gain permission to work in the protected primary forest area I cannot currently comment on how many forest specialists live in protected areas but not in the agricultural landscape.

Overall tea and distance to water (negative response), and native tree cover and habitat richness (positive response) were the most important factors in the best performing models (Fig. 3.28). These factors are likely to all be surrogates for insect abundance and/or diversity. Tea plantations are very open habitats that can be quite exposed, probably limiting insect numbers, and tea is a monoculture crop meaning that there will be a reduced diversity of insects feeding on it. Many insects have a larval stage in water and insects often congregate over water, providing a good foraging habitat for bats. In agroforestry plantations and forest fragments there is a diverse range of trees, meaning that there will be a greater diversity of insects. Also, the tree canopy provides some shelter from wind and rain for insects and bats. Habitat richness may be important as a variety of different habitats will provide greater beta diversity of insects over an area. Also, as discussed, the rich habitats that bats are using may be those encompassing riparian areas and forest edges – some of these species may be adapted for edge habitats.

Topography was not an important factor predicting bats. This is probably because the study area, while ranging from 800 m to 1600 m asl, does not appear to vary greatly in climatic variables with elevation (pers. obs. – detailed climatic data not available). Many of the species here are associated with mid-elevation forest and are probably not be at the edge of their altitude tolerance (Bates 1997).

Landscape configuration and composition both seem important in predicting species occurrence, with most species having variables related to both in their best-performing model. Most species responded to at least one habitat type (e.g. tea), showing the importance of habitat composition. Almost as many species responded to distance variables, density variables or habitat richness, showing that the configuration of the landscape also affected bat occurrence.

Hesperoptenus tickelli

This species also appears able to make use of open and modified habitats. It was found in forest fragments, coffee under both native shade and eucalyptus, eucalyptus plantations and in tea plantations (near rivers, houses or wooded areas). The best performing model for this species contained only tea at 100 m, to which it had a moderately strong negative response. I caught only one individual of this species, probably because it flies very high. Therefore all calls attributed to this species are those which fell within the range of the single individual recording reported here. I recorded similar calls at lower frequencies which may be attributable to this bat, but did not include them; this species may be more common and disturbance tolerant than this data indicate. This species appears to be quite disturbance tolerant, but the data still suggest it would not do well in a landscape of only tea plantations. The model with only distance to wood edge also performed well on test AUC (0.62), (although not as well on AICc) which further supports this.

This species has previously been recorded in the northern Western Ghats (above 12°N) and in the southern Western Ghats to the east of Valparai, but the IUCN range map does not currently cover this landscape (Korad et al. 2007, Csorba et al. 2008). It is described as being found in lowlands and hills, but here was found in mid-elevation mountains (Molur et al. 2002). It forages in open areas such as paddy fields up to about 12 m in the air, so is rarely caught in mist-nets – probably leading to an under-estimation of its range without the use of acoustic surveys (Bates 1997). It feeds mostly on beetles, termites and other insects (Bates 1997).

Miniopterus fuliginosus

M. fuliginosus catches its prey by aerial hawking, feeding mainly on moths but also on flies and spiders (Chiozza 2008). It is described as foraging in open and semi-open natural and artificial habitats up to 2120m asl (Chiozza 2008). This fits well with the observation that *M. fuliginosus* was very common in this area, being recorded in forest fragments, coffee under native trees and eucalyptus, cardamom plantations, eucalyptus plantations with an without native trees, small urban areas, along rivers and in tea plantations (along rivers, near wooded areas or houses). This species showed a strong positive response to habitat richness within a 500 m x 500 m square, and a weak negative response to tea plantations. While it was observed in tea nearly 2 km from wooded areas, it was always near houses in the tea plantations. In this area people plant both native and exotic trees near houses, and also there are lights around buildings. This species was observed hawking around street lights in the centre of the small town (pers. obs.). This species is clearly successful in an agricultural landscape, but the indications are that it would not thrive as well in a monoculture of tea.

Miniopterus pusillus

The ecology of this species is poorly known, but it has been observed in degraded forest and agricultural areas (Bumrungsri et al. 2008). Its distribution is also poorly known – it has been recorded from further south and further north in the Western Ghats, but not near Valparai (Bumrungsri et al. 2008). High aspect ratio wings and high wing loading mean this species is capable of rapid but not manoeuvrable flight. It has similar morphology to *M. fuliginosus* and is also likely to be an aerial hawker. The very similar *M. australis* (once considered the same species) feeds mostly on moths and beetles, also feeding on spiders and flies, and flies rapidly between the shrub and canopy layers in a forest (Schulz 2000). It seems likely that *M. pusillus* has a similar foraging strategy and diet.

This species was common, although not as abundant as *M. fuliginosus,* and disturbance tolerant; found in forest fragments, agroforestry plantations, eucalyptus plantations, urban areas and tea plantations (generally near rivers, houses or wooded areas). It was best predicted by habitat richness and habitat containing native trees at to which it showed a positive response. Like *M. fuliginosus*, it appears to prefer a mosaic habitat to a monoculture, and again may not do as well in a landscape without patches of native trees.

Myotis horsfieldii

M. horsfieldii presence was predicted exclusively by variables relating to water, and was never recorded or caught more than 30 m from a river or stream. It had a strong positive relationship with water at 100 m scale, water density at 100 m scale and distance to water. It has large feet and may trawl or gaff from the water's surface for insects like the European *M. daubentonii and M. capaccinii*, and indeed it was observed flying very low over the water's surface. It is disturbance tolerant in that it was found along most rivers, including those in tea plantations, but was not found along the polluted river in the small town. Its diet is unknown, although the similar *M. daubentonii* and *M. capaccinii* eat moths, flies and bugs, with maybe a few small fish.

Pipistrellus ceylonicus

This was the most common bat species in the study area, recorded in 290 locations. It was abundant in all habitats. It was best predicted by tea (negative) at the 100 m scale, and habitat richness (positive) at the 200m scale. It showed a negative response until about 70% tea and then a weak increase to 100% tea, and a positive response to habitat richness until nearly four habitats, followed by a steep decline, which is likely to be a result of the relatively few pixels with 4 or more habitats in a 200 m x 200 m square. This species is likely to do better than any other in a landscape of just tea, but even so it is never very far from buildings or wooded habitat. Like *M. fuliginosus,* it is abundant even in the small town of Valparai. This species is probably an aerial hawker, in common with other *Pipistrellus* worldwide.

Megaderma spasma

Megaderma spasma was one of the rarest species in this study, caught in just five locations. However, its agility and ability to avoid/escape from mist nets, and its exceedingly quiet echolocation calls, mean that it was probably under sampled. The model for this species predicts it only in agroforestry plantations and forest fragments, and indeed it was only found in these locations. It may depend on native trees for roosting as well as foraging - I found an all-female roost in a hollow tree, in a forest fragment of <5 ha. It was found in a forest fragment as small as 2.2 ha, 800 m from a larger fragment, indicating that it can survive (but perhaps not thrive) in a fragmented landscape. The high connectivity of this landscape, with low average distances between forest fragments and about 24% of the landscape as agroforestry or forest fragment may facilitate its use of small habitat patches that would not be possible were the patches more isolated. This species flies low, manoeuvring well in clutter (Bates 1997). It is thought to glean from vegetation as over half the moths in its diet were diurnal families (Davison and Zubaid 1992). It feeds on grasshoppers, moths, bush crickets, beetles, and other large flying insects (Phillips 1980).

Hipposideros pomona

Making a model for this species was hampered by the fact that is seems relatively disturbance tolerant but does not appear to be common. The model that scored best on AICc for this species also contained aspect at 1500 m and had a test AUC of 0.8, however I removed aspect for a number of reasons. The difference in AICc was very small – 304.98 for the model with aspect, and 305.06 for the model without. Therefore I did not consider AICc to be useful in differentiating between the two models in this instance. The sample size for this species was relatively low – 15 points. The number of presence points predicted (sensitivity) was the same with both models, but the area predicted to be suitable for *H. pomona* (specificity) was smaller with aspect included and this would increase the AUC value without necessarily being representative of biological significance, a phenomenon which is more likely to occur with lower sample sizes. It seemed extremely unlikely that aspect was having a biologically significant effect over such a large scale as 1500 m when this study landscape has many small rolling hills across it, so aspect is constantly changing over small scales but rarely flat except over the lake, where I did not have access to study– aspect in this model predicted no presence of *H. pomona* over areas where the mean aspect was flat over 1500 m.

This species was found in forest fragments as small as 14.5 ha, riparian corridors as narrow as 20 m, coffee plantations under native shade and tea plantations. Where it was found in tea plantations it was within about 350 m of wooded habitat and/or over a river. Consequently distance to wood edge and habitat richness in a 500 m x 500 m square were the best predictors of this species. It may be that it is only able to use the tea plantations due to the heterogeneous nature of this landscape, where the mean distance of any 50 m x 50 m pixel to a forest fragment is 767 m, with 39% of the agricultural area 500 m or less away from a forest fragment.

While it is able to use a variety of plantations, this bat was not recorded often. This may be a function of its relative scarcity, or of its high pitched echolocation calls which attenuate quickly in air leading it to be under-sampled (Griffin 1971). Little is known of the ecology of this species; it was recorded in several different forest types in Thailand as well as in tree plantations, orchards, fields and around human habitations (Douangboubpha et al. 2010), which fits with this study showing it to be quite disturbance tolerant. The low wing aspect ratio of this species may mean that it is better adapted to forage on spatially closely clustered resources rather than hawking on fast flying prey spread over a wide open area.

Rhinolophus beddomei

R. beddomei was recorded in two forest fragments, a 3.7 ha strip of riparian vegetation near a large fragment and reserve forest, and in a coffee plantation just 40 m from a forest fragment. This species was best predicted by distance from forest fragment to which it showed a strong negative correlation, with no chance of occurrence only 100 m from the fragment. This species calls loudly and so is unlikely to be underrepresented, although the thick foliage in forest fragments may muffle its calls.

This species was thought to be endemic to the Indian subcontinent, being found in the Western Ghats, Eastern Ghats and Sri Lanka (Srinivasulu and Molur 2008), but has recently been found in Thailand as well; always in low numbers (Soisook et al. 2010). This bat flies low over the ground, and hunts in bushes, glades along forest paths or on the forest edge. It feeds on beetles, moths, grasshoppers and flies, although with a preference for Scarabid beetles, even where there are equal or greater availability of other prey taxa (Phillips 1980, Girade and Yardi 2014).

Rhinolophus indorouxii

This rhinolophid was relatively common with 55 presence points. It showed a strong negative response to buildings at the 100 m scale, a moderate negative response to distance from water's edge and a weak positive response to habitat with native trees at the 100 m scale. It appears quite disturbance tolerant, being seen in tea plantations (generally close to trees, water or small groups of houses) but was not seen near the urban area. However, it would not do as well in a landscape without agroforestry and/or forest fragments (Fig. 3.25).

R. rouxii species take insects on the wing, and also hunt in a flycatcher style (Bates 1997). They hunt termites, grasshoppers, moths, beetles and flies (Neuweiler et al. 1987, Eckrich and Neuweiler 1988). It is reported to feed on prey more or less in the proportions in which they are available, although flies are somewhat under-represented (Eckrich and Neuweiler 1988). As it hunts in a flycatcher style from a twig for most of the night, it has been reported to feed in dense wooded areas in preference to grassland (Neuweiler et al. 1987). Is it somewhat surprising to see this flycatcher species in tea plantations, but it is clear that it is relatively disturbance tolerant. The strong association with rivers may mean that it also hunts along waterways.

Rhinolophus lepidus

This was the most common rhinolophid with 129 presence points across all habitats other than the small town. The best performing model contained just one variable, habitat with native trees at the 100 m scale, to which it responded moderately strongly and positively. While clearly disturbance tolerant to a degree, its positive relationship with agroforestry and forest fragments indicate it may not thrive in a tea dominated landscape without these habitat features. Found from the near East to South East Asia, it is reported to fly low and slow, and to feed on moths, beetles, flies and termites (Bates 1997).

3.5.4 Niche breadth and overlap

The measure of niche breadth from the maximum sensitivity and specificity threshold (MSS) highlighted different factors to those emphasised by the inverse of Levins' metric. MSS gave overall lower niche breadth scores than did Levin's metric, as for many species the areas where they were most strongly predicted by this binary threshold were not a large proportion of the observed species range. Thresholds can obscure important biological detail about sub-optimal but still useable habitats. MSS highlighted three of the most common species – *Miniopterus pusillus, Miniopterus fuliginosus* and *Pipistrellus ceylonicus* – as having the widest niche breadths, with *M. fuliginosus* and *P. ceylonicus* having a wider niche breadth than the slightly less common *M. pusillus,* and all other species having similar, low niche breadths (Table 3.3). Niche breadth as measured by the inverse of the Levins' metric, on the other hand, highlighted the two forest specialists as having the narrowest niche breadth, the water specialist *M. horsfieldii* as having a slightly greater niche breadth, and all other species having similar, high niche breadths. Both measures are useful in combination.

Schoener's D statistic was designed to compare microhabitats and/or diet, while the *I* statistic was developed from the Hellinger distance which has previously been to compare community composition across sites. Warren et al. (2008) state that 'The similarity between the calculations for *I* and D is such that we rarely see qualitative differences in the results obtained using these two metrics.' Here the only difference betweent the metrics is that Schoener's D statistic shows the two forest specialists as having the most dissimilar niches to other species, followed by the water specialist (Table 3.5). The *I* statistic only highlights the two forest specialists as having differing niches, but not *M. horsfieldii* which feeds over water. Relative rank analysis did not draw out any strong patterns, with most niche overlap being scored quite low. This is probably because this is a non-parametric measure that ranks the importance of each cell for each species and then compares the ranks, and while a lot of habitat is important for all species it might not have the same importance ranking in every model.

In looking at the measures of niche breadth and overlap it is important to remember the small scale of this study. Over a wider scale encompassing more dramatic topographical changes and climatic changes, the niche breadth and overlap of all these species would score very differently – some are found up to 2000 m or more asl. (*R. lepidus, M. fuliginosus, P. ceylonicus*) whereas other have previously only been found up to 1000 m or less (*R. beddomei, M. horsfieldii*, *H tickelli*); some are widespread (*H tickelli, P. ceylonicus, M. fuliginosus, M.spasma*) whereas others have a more restricted range (*R. beddomei, R. indorouxii*). However, in this particular landscape it is clear that most species overlap greatly in niche, and most species use much of the available landscape.

3.5.5 Species richness

Both overall species richness maps predicted higher species richness in areas of native tree cover, whether that be forest fragments, agroforestry or eucalyptus with native trees, and along streams, rivers and lakes. This fits with what is known of most bats, which prefer tree cover and riparian habitats (Lundy and Montgomery 2009, Akasaka et al. 2012, Bellamy et al. 2013). Species richness maps built by overlaying the HSMs of different species don’t take into account biological interactions such as competition, but are still useful to identify areas of conservation importance.

The map built from binary prediction maps showed a high area with no species present, which was not what was seen in the results. Even in the area dominated by tea some species were still present. This is because the MSS threshold was very high for many species, with most of them having a very small niche breadth using this metric. The map built with the summed HSI scores for each species seemed more realistic, with no areas scoring zero and no areas scoring all ten species – all ten modelled species were never seen in the same place in this study. The greatest number of modelled species in any location was eight, which was achieved by a few forest fragments and coffee plantations. This makes sense as a high HSI score for a species doesn’t mean it will be there, just that there is a higher probability of it being there, and the converse. A HSI score of 0.4 – which is below the MSS threshold for most species – indicates that in areas that have the conditions in that pixel, one can expect that species to be present 40% of the time. The summed HSI map is probably more useful for making management decisions.

3.5.6 Conservation implications

For the species modelled here, agroforestry plantations and forest fragments appeared to be of similar importance. The highest number of modelled species recorded in one habitat patch – eight – was achieved by both coffee plantations and forest fragments. Maintaining both of these habitats – rather than conversion to tea - is probably very important for the future of bats in this landscape. About 11.5% of this landscape is covered in forest fragments, 11% by coffee and less than 1% by cardamom (as elephants have a tendency to raid this crop). Together that is just under 25% of the agricultural landscape that has good potential for the ten species modelled here.

Even the smallest fragment that was intensively studied by both catching and recording, which was just 2.2 ha, holds at least six of the species I modelled including the forest specialist *M. spasma,* indicating that all patches of native trees are of importance to bat conservation in this landscape. It has been suggested that for very mobile vertebrates such as bats and birds even small areas of habitat can be used (Gorresen and Willig 2004, Faria 2006, Meyer and Kalko 2008), and this study supports that. However, it is likely that the high levels of connectivity between forest fragments and agroforestry plantations in this landscape support the use of such small habitat patches that might not be seen were the small forest fragments more isolated in an inhospitable matrix. All the species which had a test AUC of >0.5 for maximum forest patch size showed a positive response to increased forest fragment size, but this variable was not in the final model for any species, indicating that at least for the range of fragment sizes seen here size was not the most important variable. However, at a population level it is possible that larger patches are needed to sustain viable meta-populations.

Up to seven of the modelled species were recorded at one site in tea plantations – however this was very near to both a river and reserve forest. Between one and six species were recorded in other areas in tea plantations, indicating that this habitat can be used by many species. While a weak to moderate negative response to tea cover was seen in the best performing models for three species, and no species showed a positive response to tea, so long as tea percentage coverage at the 100 m scale remains low to moderate many species can make use of it for at least some of their foraging. The two forest specialists were however never recorded in tea.

Five percent of this landscape is covered by eucalyptus plantations for firewood. While I did not catch in eucalyptus, I did walk transects – the number of species in a eucalyptus patch varied from zero to five. This habitat may be poorer for bats than tea – eucalyptus trees did not appear to have many potential roost holes, unlike silver oak used as a shade tree in tea where I did see a few bats roosting, and fewer insects in India are likely to be adapted for Eucalyptus (an exotic from Australia) than for tea, many species of which are native to India.

Changes in the composition of this landscape will have strong effects at the local scale. This is encouraging for conservation efforts in the area, which have focussed on replanting small areas with native trees. This modelling exercise shows that they will be locally important for bats, and that if new fragments are planted close enough to existing fragments they may in time be colonised by *M. spasma* and *R. beddomei.* The furthest these two species were seen from the reserve forest was 2 km. This may be affected by our catching sites, because I did not have permission to catch in any fragments further from the forest, and the catching sites in the centre of the landscape were mostly over water with which neither of these species is associated. However I did record along a road in a fragment 2.7 km from reserve forest and along a riparian corridor 5 km from continuous forest and did not record either of these species, so this may reflect a need for connectivity or proximity to primary forest.

The species of greatest conservation concern in this landscape is *R. beddomei*. While I have the same number of location points for it as *M. spasma, M. spasma* is likely to be under-sampled due to its very quiet echolocation calls and agility. I witnessed this species avoid a harp trap outside its roost and extract itself from a mist net – it is likely almost as hard to catch as it is to record, living up to one of its names as the 'Common Asian Ghost Bat'. It is distributed throughout the Western Ghats, Sri Lanka and South East Asia, and probably occurs in other parts of India - it has recently been reported from the Eastern Ghats (P. Jeganathan pers. comm.). *R. beddomei* was until recently considered endemic to the Western and Eastern Ghats and Sri Lanka, although more recently a single individual was found in Thailand (Soisook et al. 2010). It calls very loudly so is likely to be as easy to detect as any of the more commonly recorded species, although its preference for forested habitat does mean that vegetation may muffle its calls in some cases. The low occurrence of *R. beddomei* in this study almost certainly reflects real scarcity.

3.5.7 Summary

With a good echolocation call library and detailed satellite imagery, fine scale bat HSMs can be built for landscapes in the tropics that have been previously little studied by spatial methods. These can be used to improve our understanding of the autecology of these species. These models could be used to predict the impacts of adding or losing forest fragments or agroforestry plantations, such as adding a riparian corridor from West to East across the plateau, which has been proposed to reduce human-elephant conflict (Kumar and Singh 2011). According to these models the best habitats for bats overall in the landscape are riparian habitats, agroforestry plantations and forest fragments.

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Chapter Four: Species Diversity and Composition

4.1 Abstract

Coffee and tea plantations are widespread in the Western Ghats biodiversity hotspot, but little is known about how bats respond to these agricultural land uses. Retaining riparian corridors and forest fragments are often suggested as conservation measures in agricultural areas, but their conservation value for bats in the Western Ghats is also poorly known. In this chapter bat species richness, diversity, evenness and composition were compared across forest fragments, coffee plantations, tea plantations and rivers with and without riparian corridors. The merits and drawbacks of different methods of studying bats have also not been studied in India, where catching alone is the primary method for surveying bats, so in this study I explicitly compare methods.

Acoustic transects detected more species than did catching bats, and at greater abundances; indicating the need to undertake more acoustic work in the tropics. Combining catching and acoustic data led to the greatest detected species richness, however acoustic transects alone would be preferred to catching methods alone.

Species rarefaction curves indicated that while accumulation rates were slowing, asymptotes were not reached. Coffee plantations had similar mean and total bat species richness to forest fragments, but different species compositions. Tea plantations had lower species richness than all other habitats, although this was not significant, and they had significantly a different species composition to forest fragments.

Rivers with riparian corridors had the greatest total number of species, and the greatest abundance of bats of any habitat. They trended towards greater richness and abundance than rivers without riparian corridors but the difference was not significant.

Shade coffee plantations appear to provide a modified but suitable habitat for many bat species, although they do not replace forest. Tea plantations contained fewer bat species than coffee plantations, and the abundance of several species was reduced

from forest fragments and coffee habitats. Shade coffee would be a preferred land use to tea plantations adjacent to national parks in the Western Ghats.

4.2 Introduction

As discussed in Chapter One, bats fulfil important roles in tropical ecosystems. In conserving bats it is important to know whether different habitats support bat assemblages of different species richness, composition and abundance so as to manage habitat change appropriately.

4.2.1 Catching versus acoustic methods

The call library developed in Chapter Two allowed the identification of most bats in this area from acoustic recordings, which enabled the comparison of data from catching and acoustic methods in this chapter. As discussed in Chapter One, both methods have inherent biases, but it is problematic that currently catching alone is predominantly used in the tropics as it is likely to miss many species in a systematic manner. Firm data on the relative biases and merits of each method will hopefully inform future work in the Asian tropics.

4.2.2 Forest Fragments

Much of the world’s tropical forest now exists as fragments, from less than 10 hectares in size to several thousand hectares (Sanchez-Azofeifa et al. 2001, Struebig et al. 2008). The impact of this on bats has been studied in the neotropics (mostly by catching alone, which gives only a partial picture of bat diversity), but the specific responses of bat assemblages in the palaeotropics have been little studied (discussed in Chapter One). Ideally bat assemblages in forest fragments should be compared to undisturbed or little-disturbed primary forest, but I did not receive local permission to work in primary forest until my fieldwork was finished; so for this thesis I will be using forest fragment data alone. I have funding and permission to return and collect primary forest data post-PhD.

In the Western Ghats, between 1920 and 1990, 40% of the original vegetation was converted to plantations and hydroelectric reservoirs (Menon and Bawa 1997). Open plantations accounted for 76% and shade coffee plantations for 16% of the conversion (Menon and Bawa 1997). Much of the remaining forest has since been fragmented and the number of forest fragments has increased fourfold, but the average size of the fragments has decreased by 83%, with corresponding increases in the perimeter/area ratios of fragments (Menon and Bawa 1997). Knowing the conservation value of both forest fragments and agricultural land is important for guiding future development – is more biodiversity conserved by maintaining a few large forest reserves surrounded by intense high yield agriculture, smaller reserves with forest fragments providing 'stepping stone' habitats between them surrounded by high yield agriculture or larger areas of lower yield, less intense agriculture with smaller forest fragments or reserves (Heller and Zavaleta 2009, Phalan et al. 2011, Hulme et al. 2013)? Basic data about biodiversity in different habitat types will inform these decisions.

4.2.3 Coffee Plantations

Understanding how different taxa respond to widespread land use change in the tropics is critical to finding ways for agriculture and biodiversity to coexist. Coffee is one of the most valuable legally traded commodities from the developing world, with production currently expanding in Asia (FAOSTAT 2014). While global coffee area has decreased by 8% since 1990, intensification has occurred in many places leading to greater overall coffee production (FAOSTAT 2014). In India, the area planted with coffee has more than tripled since the early 1960s, with 368,687 ha of the country planted with coffee in 2012 (Fig 4.1, FAOSTAT 2014). About 60 % of the coffee in India is high yield, sun loving *robusta* and 30 % is high quality, shade loving *arabica*, with a trend towards greater *robusta* growth (Indian Coffee Board 2014).

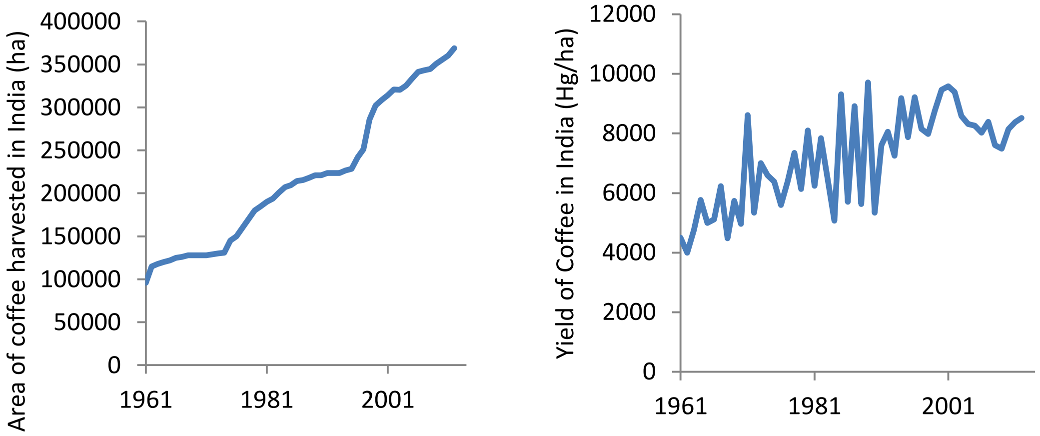

Figure 4.1: Extent of agricultural land planted with coffee in India left, and yield in hectograms per hectare in India, right, from 1961-2002. Data from FAOSTAT 2014.

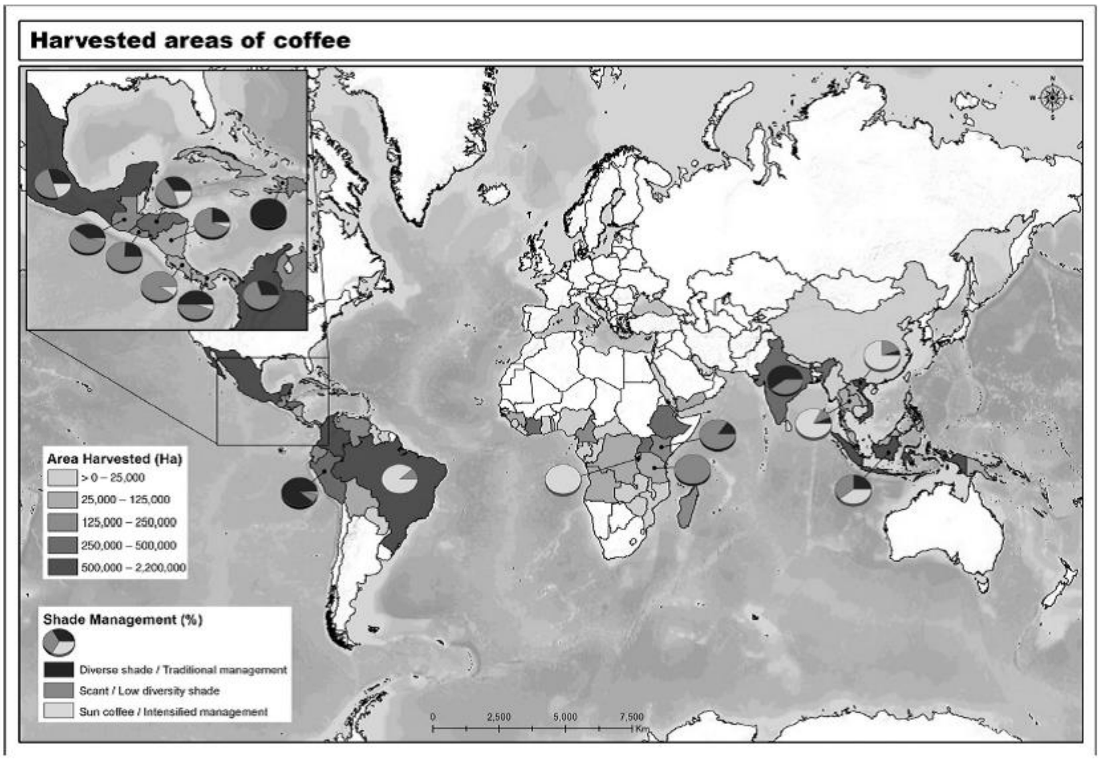

Figure 4.2: Patterns of coffee shade management globally, from Jha et al. 2014. In the pie charts the lightest shade indicates sun coffee/ intensive management, the medium shade indicates scant/low diversity shade and the darkest shade indicates diverse shade/traditional management. Shading of the countries indicates area of coffee harvested, with darker colours indicated greater coffee production area. Data from FAOSTAT 2014.

Since the 1990s, coffee grown under the shade of local rainforest trees has been noted for contributing to the conservation of many diverse taxa (Perfecto et al. 1996, Donald 2004, Jha et al. 2014). Across 19 countries globally for which 2010 data were available just 24% of all coffee was still produced using traditional diverse shade, 35% was managed under sparse shade and 41% was managed with no shade, with an increase in higher yielding, lower quality *robusta* coffee to supply emerging coffee markets (Jha et al. 2014). This indicates that the global shade coffee cultivation is about 20% lower than in 1996 (Jha et al. 2014). In India between 1996 and 2012 there was a 24% reduction in the area grown under traditional diverse shade (Jha et al. 2014). Yields per hectare have also been increasing in India as more *robusta* is grown, but the majority of the coffee in the country (60%) is grown under a dense shade canopy and the rest is grown under sparse shade (Figs. 4.1, 4.2, Jha et al. 2014).

There is a global trend towards increased intensification of coffee growing, and, while India maintains relatively low-intensity coffee management methods, it is still following this trend. While higher yields are cited as the main reason for reducing or removing shade in coffee plantations, intermediate shade levels of 35 – 50 % have been shown to be optimal for increasing yields of *Coffea arabica* (the species of coffee grown in Valparai) (Soto-Pinto et al. 2000). There can be many benefits to farmers of maintaining shade in the long term, especially in the context of climate change - shade appears important for quality, particularly in heat-stressed regions, and shade trees can also reduce crop damage from extreme events such as hurricanes (Muschler 2001, Philpott et al. 2008). Shade trees also provide habitat for pollinators of coffee and predators of coffee pests – predation services were worth US$44–US$310 per ha per year in neotropical agroecosystems (Williams-Guillén et al. 2008, Kellermann et al. 2008, Karp et al. 2013), and enhanced insect pollination improves fruit set (Ricketts et al. 2004). Despite these benefits, the short term perceived yield increases of removing shade may be more important to low-income farmers without a guaranteed buyer for their crop.

Coffee growing regions and biodiversity hotspots overlap, and coffee farms are often located close to protected areas (Hardner and Rice 2002, Jha et al. 2012)**.** While shade coffee plantations may be important in terms of connectivity for biodiversity between protected areas, the effects of climate change mean that under a warming scenario of 2 °C coffee farms are likely to move upslope by 300-400 m, which may bring coffee farmers into conflict with conservationists protecting higher altitude forest reserves (Läderach et al. 2013, Jha et al. 2014). Increased temperatures are also likely to lower yields, which may lead to increased areas of cultivation or conversion to other land uses such as cattle pasture (Läderach et al. 2013). Understanding how best to resolve these conflicts will involve detailed analyses on the effects of different shade regimes on biodiversity, optimum shade to maximise yield and quality, and the potential for using shade for alternative incomes such as timber.

In the Western Ghats almost all coffee is shade grown, often intercropped with pepper (*Piper nigrum*), citrus (*Citrus* spp.), areca nut (*Areca catechu*) and vanilla (*Vanilla* spp.). Coffee is generally planted at 500 – 1500 m asl in the moist-deciduous and wet-evergreen forest zone (Anand et al. 2010). More recently, traditional diverse shade has been replaced in many areas with monocultures of exotic silver oak (*Grevillea robusta*), to bolster income by selling silver oak timber (Damodaran, 2002).

4.2.4 Tea plantations

Over 18% of the tea grown in India is grown in the Western Ghats, in the southern states of Kerala, Tamil Nadu and Karnataka (Daniels 2003). In the Western Ghats tea grows between 300 and 2,300 m asl. in areas with rainfall of 90-750 cm annually (Muraleedharan 1991). The area covered by tea plantations has doubled since the early 1960s, to cover an area of 605,000 ha in 2012 (Fig. 4.3, FAOSTAT 2014). Yield has also increased during this time, indicating greater intensity of cultivation (FAOSTAT 2014).

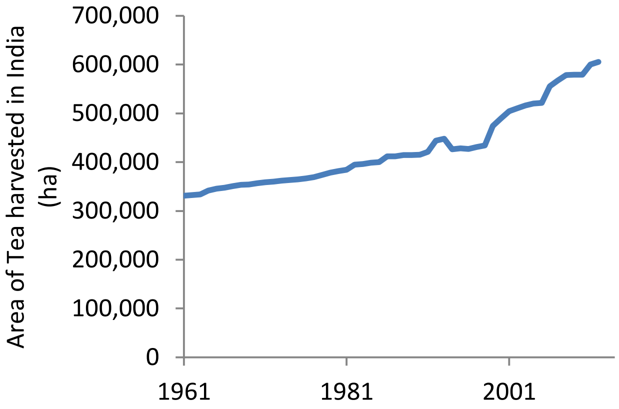

Figure 4.3: Area of India planted with tea from 1961-2012. Data from FAOSTAT 2014.

While little has been written about how palaeotropical bat species respond to coffee plantations, nothing has been written about how bats anywhere respond to tea plantations – in fact there are few quantitative studies on the diversity of any taxa in tea. Unlike coffee, tea is grown in clipped bushes with a few heavily pollarded imported Australian silver oak trees providing a little shade for the young bushes (Fig. 4.4). Up to 30 different pesticides are used in tea, making it a very intensively managed crop, although research is under way to reduce pesticide use (Muraleedharan and Selvasundaram 1996, Tea Board of India 2014).

Few quantitative studies compare biodiversity in tea to other habitats, although some authors consider tea plantations to be a serious threat to tropical biodiversity (Daniels 2003). One study showed lower bird species richness in tea plantations than in shade coffee (Raman 2001), and another showed species richness of frogs to be highest in rivers in forest fragments but not significantly different between rivers in shade coffee and tea plantations (Murali and Raman 2012). Species composition of amphibians in coffee plantations was more similar to forest fragments than was species composition in tea plantations, although there was a high level of inter-site variation (Murali and Raman 2012). A qualitative study found that all medium and large terrestrial mammals living in the area at least passed through the tea plantations (Kumara et al. 2004). Some mammals, such as sambar deer (*Rusa unicolor*), sloth bear (*Melursus ursinus*), barking deer (*Muntiacus muntjak*) and mouse deer (*Moschiola indica*), were at least partially resident in the tea plantations, finding shelter in streamside vegetation, and elephants are also reported to use the riparian corridors in the area for shelter (Kumara et al. 2004, Kumar and Singh 2011). All of these studies were done in the Valparai area, but do not give a clear picture of the overall biodiversity maintained in tea plantations.

Fig. 4.4: Coffee plantations grown under native shade, left, and tea plantations, right.

4.2.5 Riparian Areas

Riparian buffers/corridors of mature habitat are often used in logging concessions to reduce erosion of river banks, intercept fertilisers before they reach the water to reduce eutrophication, and provide habitats for biodiversity (Sweeney et al. 2004, Mayer et al. 2007). As discussed in Chapter One, many studies (mostly in temperate regions) found that bankside vegetation significantly increased bat activity over rivers (Hayes and Adam 1996, Carmel and Safriel 1998, Holloway and Barclay 2000, Warren et al. 2000, Lloyd et al. 2006, Ober et al. 2008, Lundy and Montgomery 2009, Langton et al. 2010). Riparian corridors are increasingly becoming legal requirements in certain land uses (Lees and Peres 2008, Marczak et al. 2010, Gray et al. 2014). Apart from some work in Borneo (Gray et al. 2014), all the studies in tropical regions evaluating riparian corridors focus on the neotropics or north-western Australia (Hill 1995, Lima and Gascon 1999, Laurance and Laurance 1999, Graham and Blake 2001, Galindo-Gonzalez and Sosa 2003, Harvey et al. 2006, Medina et al. 2007, Lees and Peres 2008, Gillies and St Clair 2008, Norris and Michalski. 2010, Barlow et al. 2010, Rodríguez-Mendoza and Pineda 2010, Gillies et al. 2011, Viegas et al. 2014). Very little ecological data has influenced current guidelines for the creation of riparian reserves (Barlow et al. 2010, Ewers et al. 2011).

4.2.6 Aims

In this chapter I aim to assess:

- The relative merits and drawbacks of catching and acoustic techniques for the study of bats in South India.
- How bat assemblages in coffee and tea plantations compare to those in forest fragments.
- How bat assemblages vary between rivers with and without riparian corridors.
- The effects of forest fragment and riparian corridor size on bat assemblages.
- How each bat species in the area changes in abundance between tea plantations, coffee plantations, forest fragments and rivers with and without riparian corridors.

4.3 Methods

4.3.1 Field methodology

Bats were studied in five sites per habitat in five habitats - forest fragments, rivers in tea with riparian corridors of mature native trees along at least one bank of the river (henceforth ‘riparian corridors’), rivers in tea without riparian corridors (henceforth ‘tea riparian’), coffee plantations and tea plantations. All tea sites were ‘paired’ with tea riparian sites, and were c200m from the tea riparian site. It was not possible to do this with forest fragments/riparian corridors. All rivers were fourth or fifth order, at least 4 m wide at the point of study. Forest fragments and riparian corridors were remnant forest patches, or secondary forest/overgrown plantations dominated by mature native trees. All forest fragments were studied in previous work in the landscape (Raman 2001, 2006, Mudappa 2007, Kapoor 2008, Joshi et al. 2009, Kumar et al. 2010).

Between January and May 2010 to 2013, I spent two non-consecutive nights both catching and recording acoustic transects at each site. At every site I caught with five mist nets, and recorded at five points 100 m apart for 15 minutes per point, using a Pettersson D240X ultrasound detector (www.batsound.com) with a sampling rate of 307 kHz and a range of 10 - 120 kHz recording onto an Edirol R-09 (www.roland.com) digital recorder sampling at 44.1 kHz. There was a total of 12.5 hours recording per habitat. Nets were opened at sunset and closed after 2.5 hours, as the peak of bat activity was in the first hour after sunset. There was a total of 25 hours mist netting with five 6 m nets per site, so 125 mist net hours. Bats were identified to species using the best guides for India (Bates 1997, Srinivasulu et al. 2010). Recording started 40 minutes after sunset at which point the area was dark, to reduce recordings of emerging bats circling outside the roost or commuting, as the focus was on recording foraging bats.

In forests, existing animal or human trails were used and recordings made in slight clearings wherever possible. Nets were always set in clearings as the understory of the forest was so dense elsewhere that it was not possible to put mist nets up. In riparian habitats the nets were set over the river in all locations, and the recordings were taken at the river banks, pointing at the river, so only species using the river would be recorded. Detectors had a range of up to 20 m for the loudest species.

4.3.2 Sound analysis

Using ‘BatSound’ (www.batsound.com), calls were identified to species using the call library in Chapter Two. As discussed in Chapter Three, not all species were distinguishable based on call, so any unidentifiable calls were not used in analysis. One ‘morphospecies’ were detected based on calls. Another species, a rhinolophid bat calling at 80 kHz, was thought to be *Rhinolophus affinis* based on the distribution of rhinolophids in India, and this has since been confirmed by catching work (Heller and von Helverson 1989, Robinson 1996, Korad et al. 2007, Jiang et al. 2007, Walston, Kingston & Hutson 2008). The other three are probably vespertilionid bats based on the call structure.

Some bats call more loudly than others so are disproportionately likely to be recorded, and hawking bats calling constantly are more likely to be recorded than fly-catching species. For every 15 minute recording each identifiable species was scored as ‘present’ or ‘absent’, rather than scoring the number of calls attributable to a species in every recording, to reduce bias in relative abundance.

4.3.3 Size effects

Area of forest fragments and riparian corridors was calculated from maps in ArcGIS. Corridor width was measured at each acoustic transect point and the mean taken per corridor. Linear regression analyses were performed separately in R to look at the effects of forest fragment size, riparian corridor size and riparian corridor width on bat species richness.

4.3.4 Species rarefaction curves

Species rarefaction curves were drawn using the total data for each habitat, by plotting the number of individual records (hereafter referred to as ‘individuals’) against the mean number of species accumulated by sampling that number of individuals using the R packages ‘picante’ and ‘vegan’, using the formula ‘rarefaction’ (http://www.jennajacobs.org/R/rarefaction.html) (Kembel et al. 2010, Oksanen et al. 2013, R Core Team 2014).

4.3.5 Species richness

A generalized linear mixed model would not converge for these data; I simplified the model in different ways but as long as there was a random effect in there the model failed to reach convergence. This can occur due to very low variance for the effects. Looking at the output from the full model that failed to converge, fixed effects together explained 83.6% of the variance, with 3% of the variance explained by ‘Site’, 2.4% by ‘Night’, 0.5% by ‘Year’ and 10.4% residual variance not explained by any of the effects used in the model. Therefore very little variation is taken up by random effects. As I could not account for ‘Night’ as a factor I combined the data from each night for each site to avoid pseudo-replication. I ran a poisson generalized linear model (GLM) with Method and Habitat as the predictor variables. I compared models with and without every factor to the full model using a ‘χ^2’ test. I then ran pairwise comparisons using the false discovery rate multiplicity adjustment method in the ‘lsmeans’ package in R, using a model with only the significant variables included (Lenth 2014, R Core Team 2014).

4.3.6 Estimated species richness

Estimated species richness per habitat and per site was calculated for both methods combined using the ‘vegan’ package in R (Oksanen et al. 2013). Estimated species richness was compared between habitats using a linear model in the ‘lme4’ package in R (Bates et al. 2014, R Core Team 2014).

4.3.7 Relative abundance

The total number of ‘records’ of bats per method and per site were counted. I measured every bat caught as one record, and every 15 minute transect recording where a bat was recorded as one record. A generalized linear mixed model would not converge for these data; I simplified the model in different ways but as long as there was a random effect in there the model failed to reach convergence. This can occur due to very low variance for the effects. Looking at the output from the full model that failed to converge, 2.6% of the variation was attributed to ‘Night’, 2.2% to ‘Site’, 0% to ‘Month’ and 0.2% to ‘Year’. Therefore very little variation is taken up by random effects. As I could not account for ‘Night’ as a factor I combined the data from each night for each site to avoid pseudo-replication. I ran a poisson generalized linear model (GLM) with Method and Habitat as the predictor variables. After running a poisson GLM, over-dispersion was detected, and errors were corrected using a quasi-GLM model with the variance given by the mean multiplied by the dispersion parameter. I compared models with and without every factor to the full model using a ‘χ^2’ test. I ran pairwise comparisons using the false discovery rate multiplicity adjustment method in the ‘lsmeans’ package in R (Lenth 2014).

4.3.8 Species diversity and evenness

I measured species diversity using Simpson's Index of Diversity, which accounts for both species richness and evenness and gives a score between 0 and 1 where higher scores have greater richness and evenness. Simpson's Index of Diversity is calculated as:

$$1 - \left(\frac{\Sigma \mathrm{n}(\mathrm{n}-1)}{\mathrm{N}(\mathrm{N}-1)}\right)$$

where ‘n’ is the number of individuals of a particular species and ‘N’ is the total number of individuals of all species.

I calculated species evenness using Shannon's diversity index "H" by using the formula:

$$\mathrm{H} = -\Sigma\left[\left(\frac{\mathrm{n}}{\mathrm{N}}\right) * \ln\left(\frac{\mathrm{n}}{\mathrm{N}}\right)\right]$$

where ‘n’ is the number of individuals of a particular species and ‘N’ is the total number of individuals of all species.

The distributions of the diversity and evenness data were unsuitable for a GLMM, as the data were over-dispersed. As I could not account for ‘Night’ as a factor I combined the data from each night for each site to avoid pseudo-replication. I ran generalized linear models with Diversity/Evenness as a factor of Habitat and Method. After running a binomial GLM, over-dispersion was detected, and errors were corrected using a quasi-GLM model with the variance given by the mean multiplied by the dispersion parameter. I ran pairwise comparisons using the false discovery rate multiplicity adjustment method in the ‘lsmeans’ package in R (Lenth 2014).

4.3.9 Species Composition

Using the ‘vegan’ package in R, I calculated the Bray-Curtis distances between every site based on species composition, and plotted these using non-metric-multidimesional scaling (NMDS) (Oksanen et al. 2013). I then used the ‘ADONIS’ method in the package ‘vegan’ with 9,999 permutations to test for differences in species composition between habitats, and ran pairwise comparisons using the false discovery rate multiplicity adjustment method.

I used Kruksal-Wallis on site level data to test for changes in abundance in different habitats of each species with >35 records in total, using the ‘agricolae’ package in R (de Mendiburu 2014).

4.4 Results

4.4.1 Size effects

Fragment size, riparian corridor size, and riparian corridor width did not have any significant effects on the total species richness ($F_{1,3}$=0.048, adjusted R^2=-0.312, *P*= 0.84;

$F_{1,3}$= 1.198, adjusted R^2= 0.048, *P*= 0.354; $F_{1,3}$= 0.7, adjusted R^2= 0.149, *P*= 0.283) (Figure 4.5).

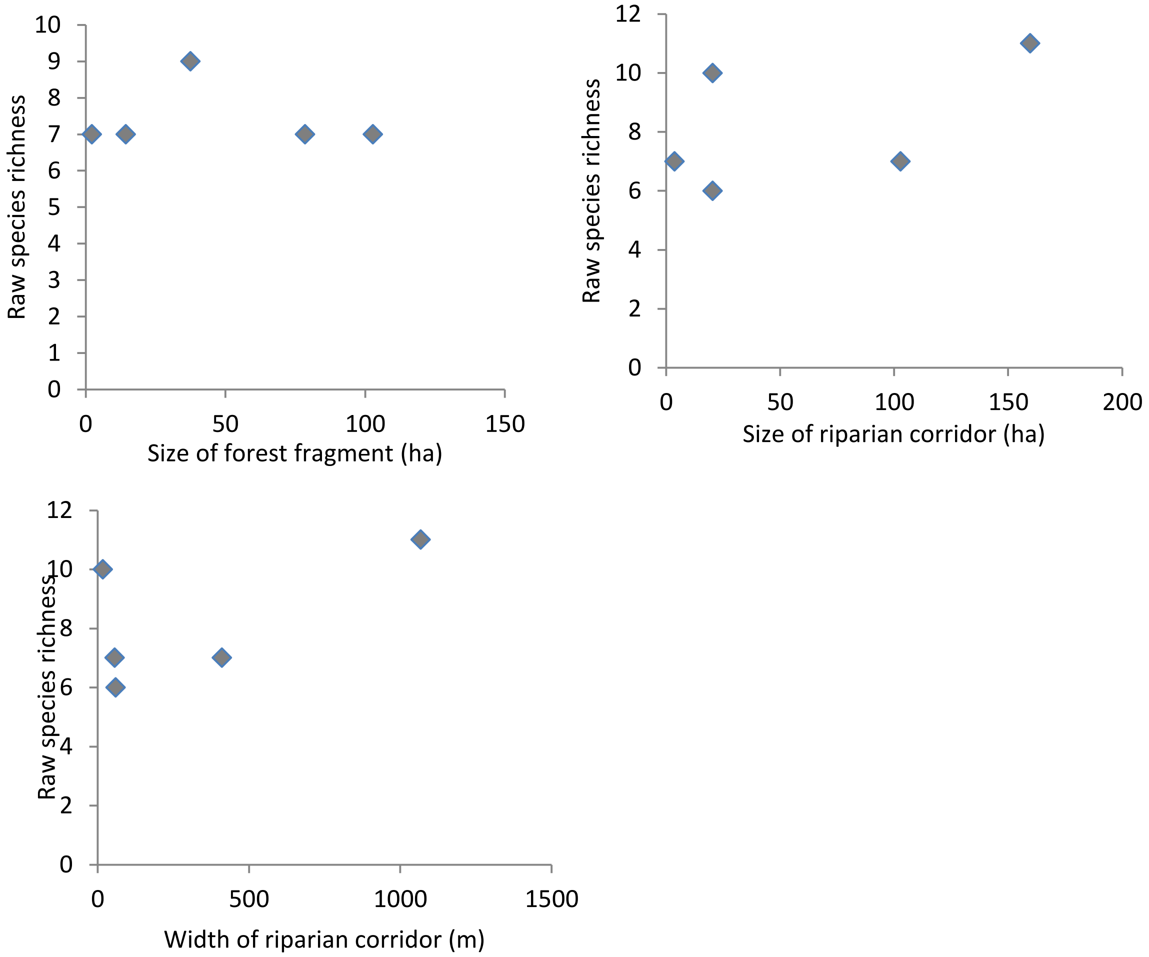

Figure 4.5: Size of forest fragment and species richness, top left; size of riparian corridor and species richness, top right; and mean width of studies section of riparian corridor and species richness, bottom left.

4.4.2 Species rarefaction curves

The species rarefaction curves using both methods combined showed that rivers with riparian corridors, coffee plantations and forest fragments accumulated more species per number of individuals than tea and rivers in tea, with 95% confidence intervals ceasing to overlap at around 50 individuals (Fig 4.6, 4.7). Riparian corridors accumulated the most species, with confidence intervals ceasing to overlap at around 130 individuals (Fig 4.7) The transect data showed a very similar pattern but catching data did not; riparian corridors still had the greatest number of species, then forest fragments and tea riparian followed similar trajectories, coffee was poorer than forest fragments and tea riparian, and tea plantations had so few individuals that any trend is difficult to detect (Fig. 4.7).

The species accumulation curves do not stop increasing for any method, however they were slowing in all habitats for acoustic data and in some for catching data too (Figs 4.6, 4.7). Acoustic transects accumulated more species than did catching in all habitats in total, and at a faster rate than catching in most habitats (Figs 4.6, 4.7).

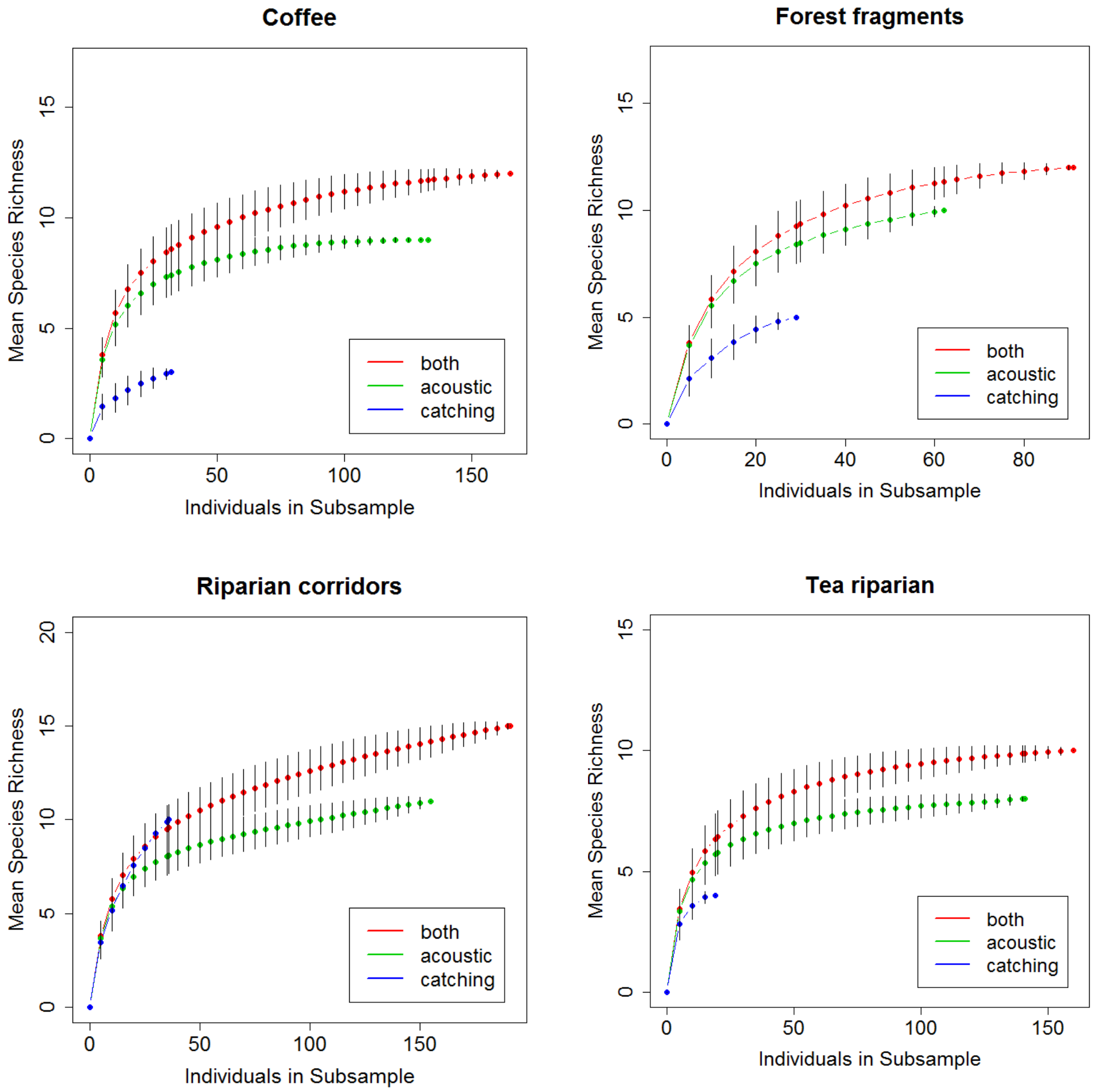

Figure 4.6: Species rarefaction curve for habitats with catching data, acoustic data and both methods combined.

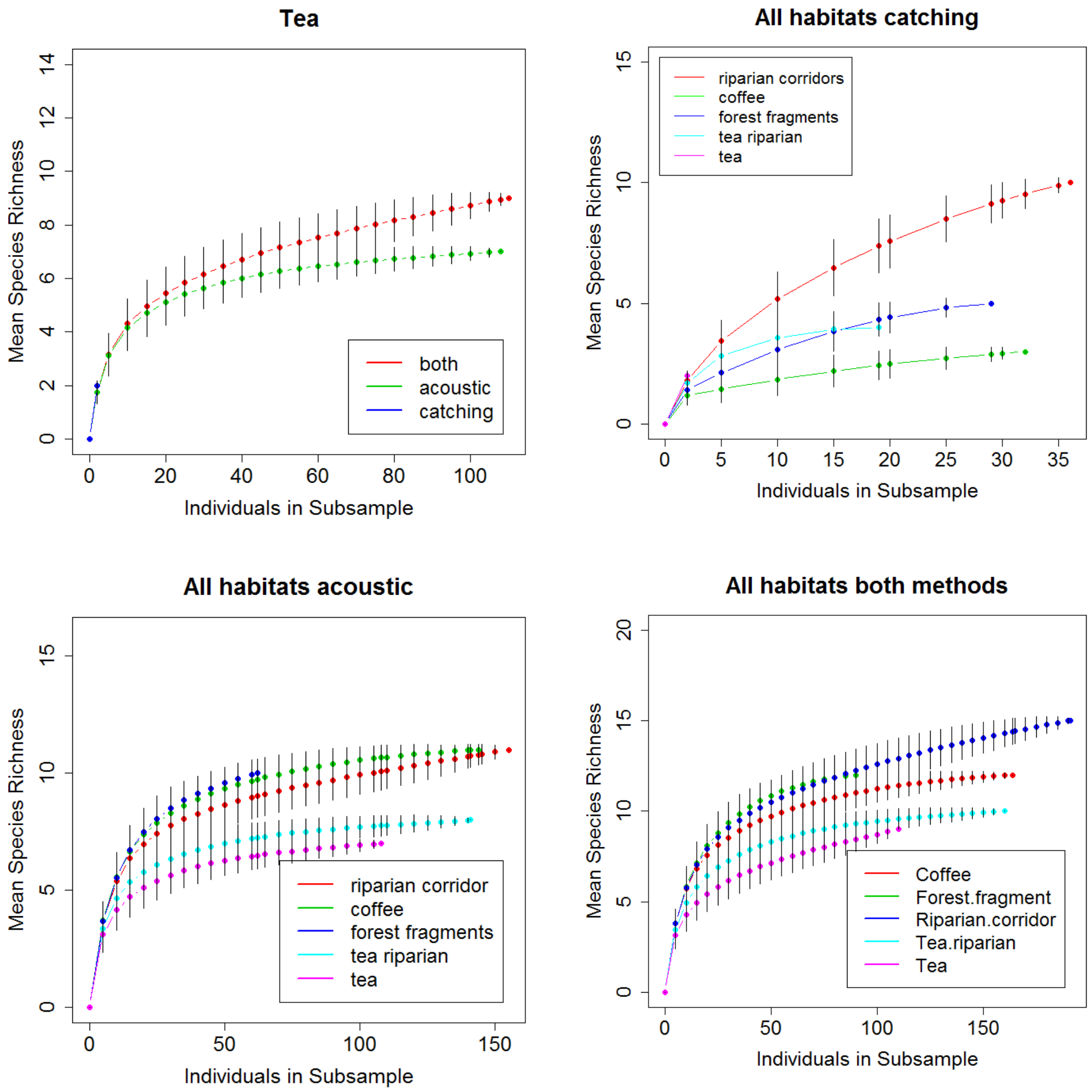

Figure 4.7: Species rarefaction curve for habitats with catching data, acoustic data and both methods combined.

4.4.3 Species richness

Bat species richness differed between habitats (deviance= 568.75, d.f.= 5, *P* <0.0001) and the sampling methods used (deviance = 659.52. , d.f.= 3, *P* <0.0001), although there was no significant interaction (deviance= 6.9, d.f.= 8, *P* =0.548). Richness was highest in riparian areas and lowest in tea, although the difference was borderline significant before multiple comparison corrections and not afterwards (Fig 4.8, Appendix 1). Using catching alone, forest fragments and riparian corridors had significantly greater richness than tea plantations, but these effects were not significant after correction for multiple comparisons (Fig 4.8, Appendix 1). Catching

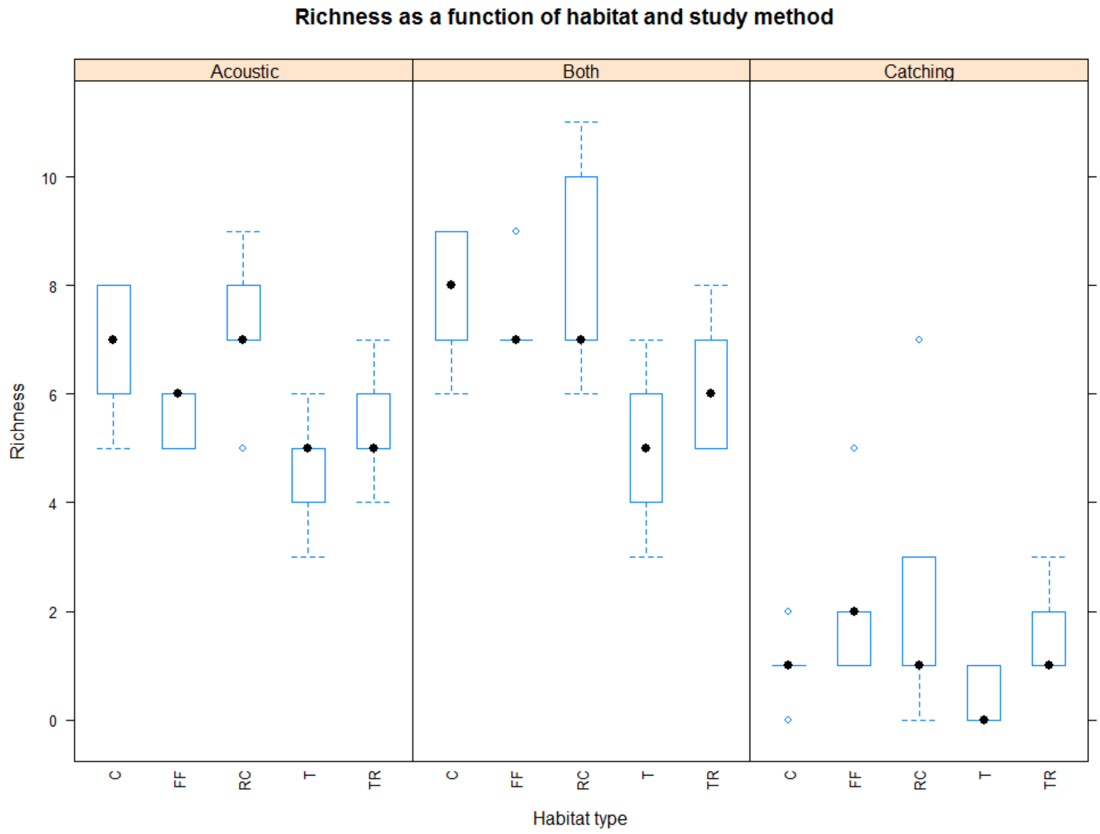

Figure 4.8: Species richness variation between habitats using different methods, using per site data. (C= Coffee, FF= Forest Fragments, RC= Riparian Corridors, T= Tea, TR=Tea Riparian).

recorded significantly fewer species than did acoustic transects for every habitat, before and after correction for multiple comparisons (Fig 4.8, Appendix 1).

The greatest total number of species as assessed by catching and transects together was recorded in riparian corridors (15 species, Fig 4.9). Forest fragment and coffee had the same number of species (12), while tea riparian had 10 species and tea had 9 species. A very similar pattern was seen when looking at transect data alone, where riparian corridors had the greatest number of species, coffee and forest fragments the next greatest, and tea riparian and tea the least. From catch data, riparian corridors were by far the richest, and tea the least rich, with forest fragments and tea riparian having more species than coffee (Fig 4.9).

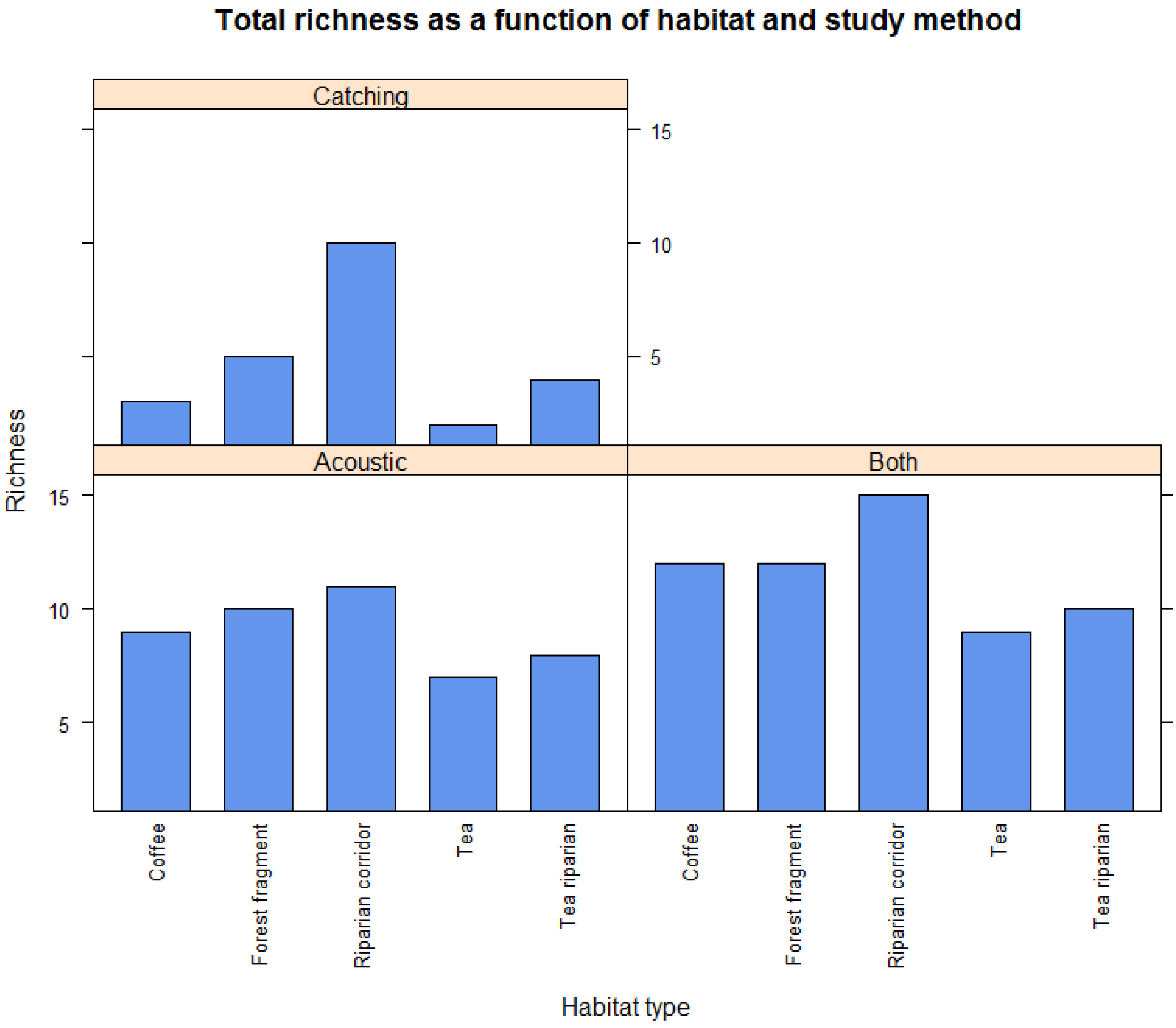

Figure 4.9: Total species richness variation between habitats using different methods.

4.4.4 Estimated species richness

Bat estimated species richness did not differ between habitats when both methods were used together ($F_{4,20}$= 2.149, *P* =0.112).

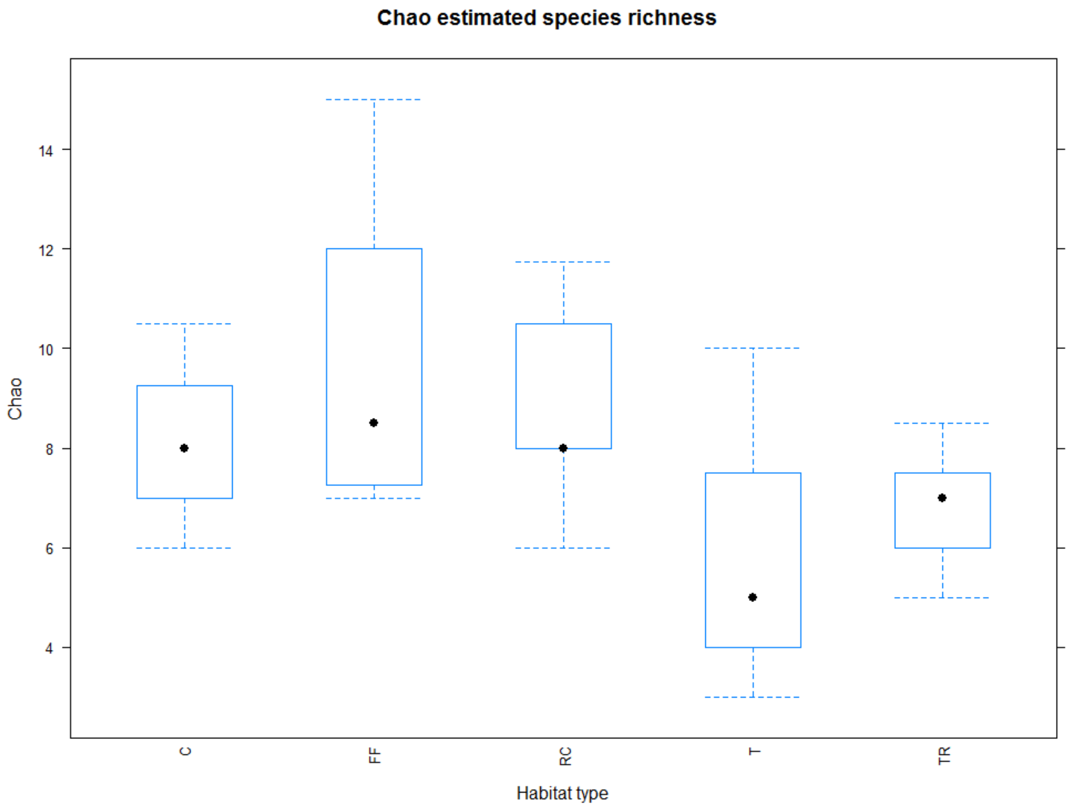

Figure 4.10: Estimated species richness for both methods together.

Table 4.1: Observed and estimated richness at the habitat and site levels.

	Coffee	Forest fragment	Riparian corridor	Tea riparian	Tea	Total
Observed total species richness	12	12	15	10	9	18
Chao estimated total species richness	12	12	17	10	12	19.5
Observed mean species richness	7.8±0.58	7.4±0.4	8.2±0.97	6.2±0.58	5±0.71	NA
Chao estimated mean species richness	8.15±0.8	9.95±1.55	8.85±1.01	6.8±0.6	5.9±1.27	NA

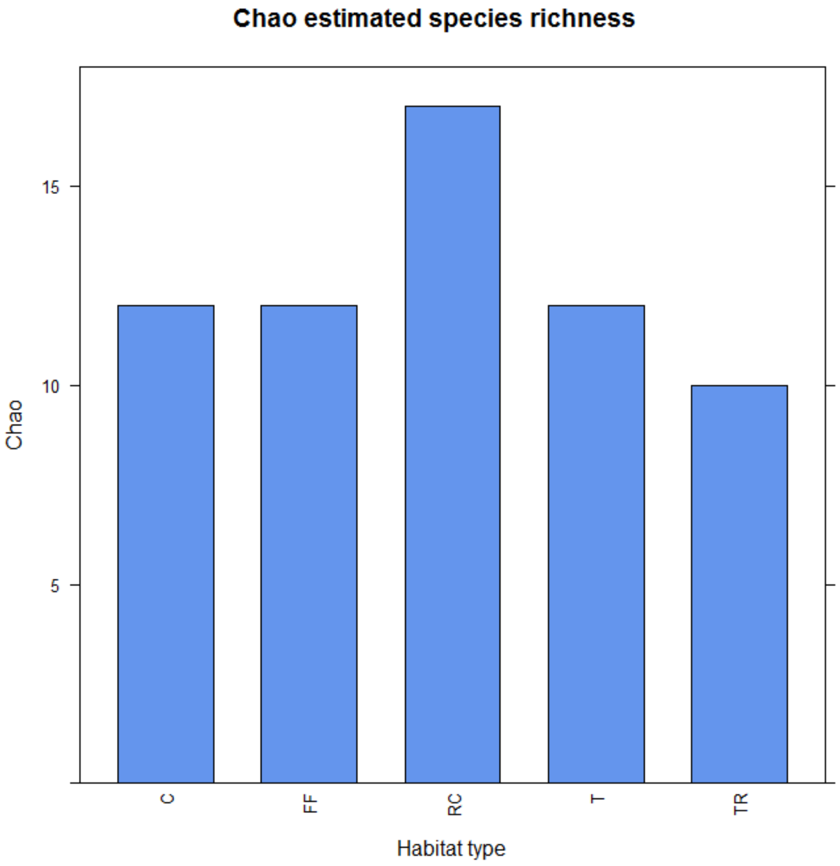

Figure 4.11: Estimated total species richness per habitat for both methods together

4.4.5 Relative abundance

Habitat had a significant effect on bat relative abundance (deviance = -143.48, d.f.=-12, *P*<0.0001), as did the method used (deviance = -565.41, d.f.=-10, *P*<0.0001), but there was no interaction between the two (deviance = -42.152 , d.f.=-8, *P* = 0.138). In all methods, bats were more abundant in coffee plantations and riparian corridors than in forest fragments and more abundant in riparian corridors than in tea plantations (Fig 4.12, Appendix 1). These differences remained significant after correction for multiple comparisons (Appendix 1). When the abundance was summed across sites, riparian corridors had the greatest overall abundance, followed by coffee plantations and tea riparian (Fig 4.13).

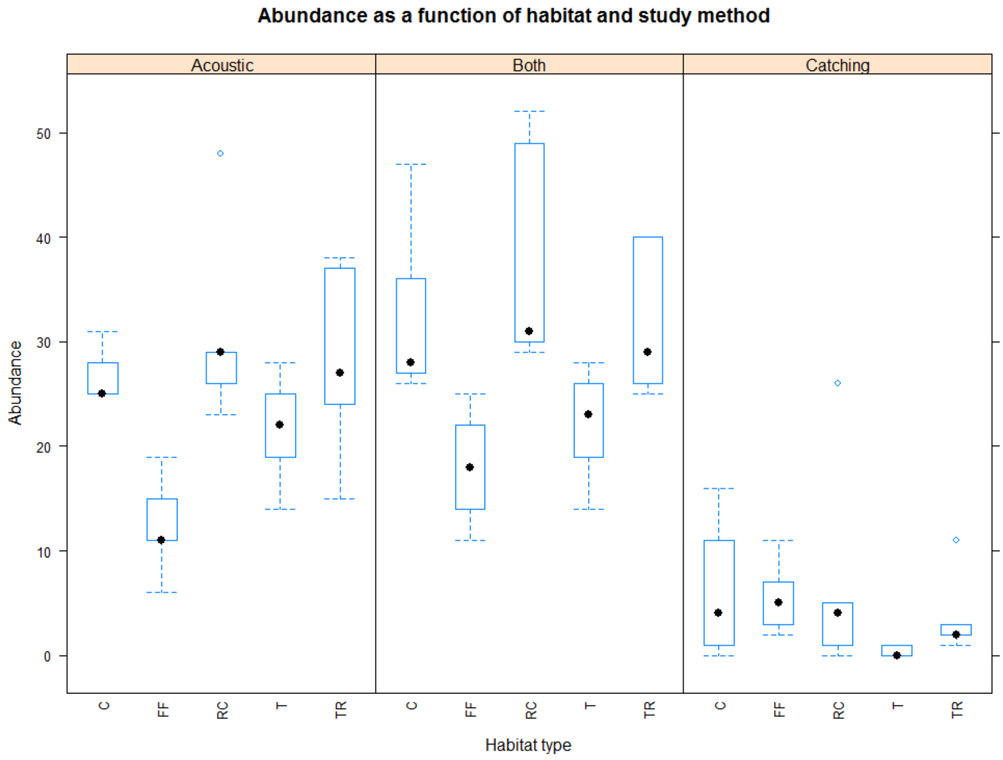

Figure 4.12: Variation in total number of bat records between habitats using different methods based on per site data. (C= Coffee, FF= Forest Fragments, RC= Riparian Corridors, T= Tea, TR=Tea Riparian).

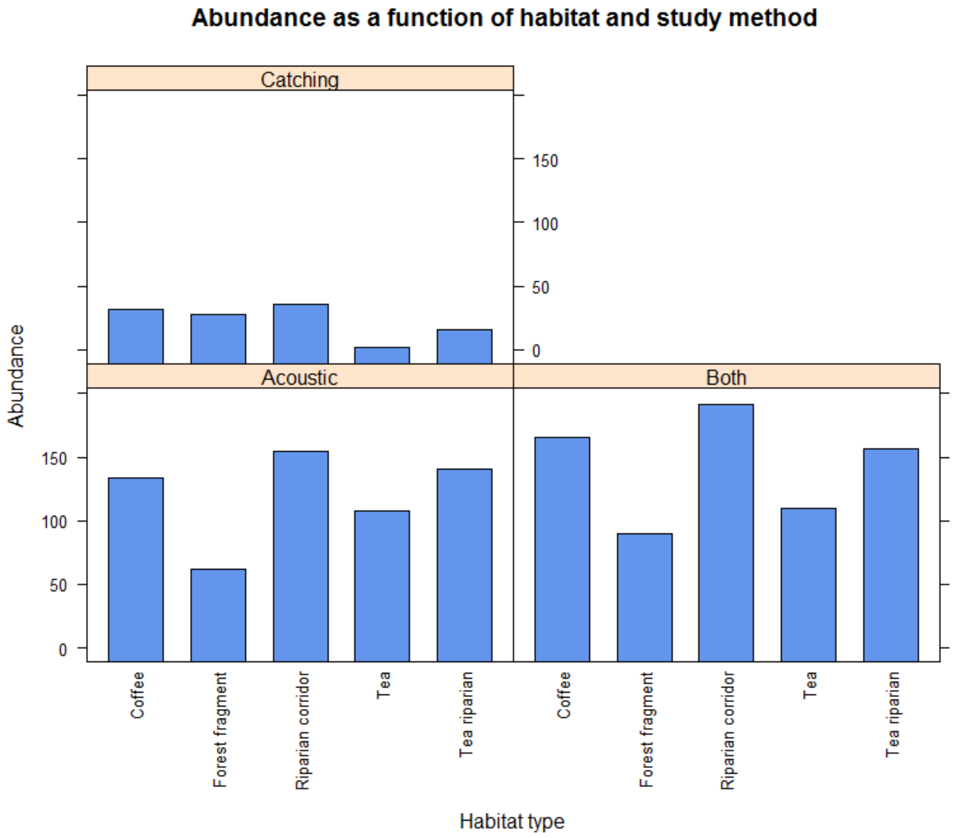

Figure 4.13: Summed bat records between different methods and different habitats.

4.4.6 Species diversity

A linear mixed effects model failed to converge for species diversity but showed that Night accounted for 0% of variation in the model, Site for 0.8%, Month for 0%, Year for 0.15%, residual variation for 19.3% and the fixed effects for 79.8%. Habitat, method and the interaction between the two significantly affected bat species diversity (Habitat: deviance =-5.639, d.f. = -12, *P* = 0.017; Method: deviance = -22.453, d.f. = -10, *P* <0.0001; Interaction: deviance = -3.502, d.f. =-8, *P* = 0.055). The method used altered the diversity for most habitats, but the only between-habitat difference was coffee and tea riparian as measured by catching, and this was not significant after correction for multiple comparisons (Fig 4.14, Appendix 1).

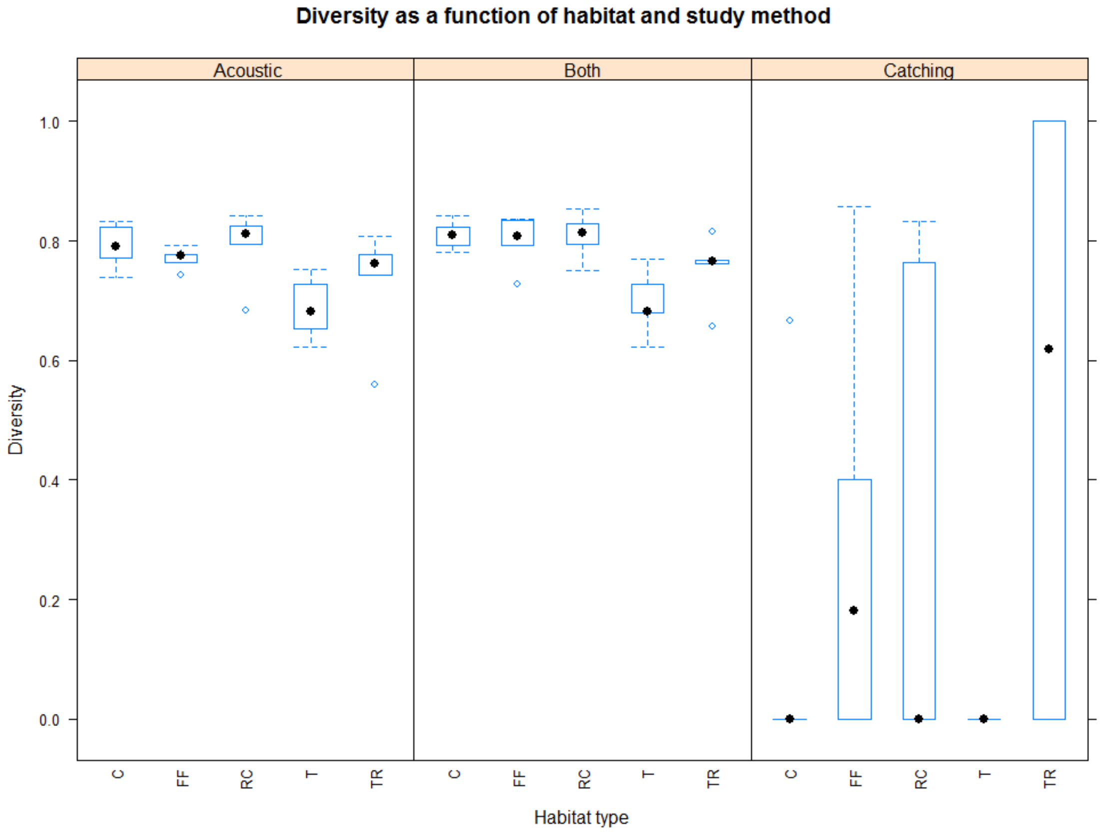

Figure 4.14: Variation in species diversity between habitats using different methods using per site data. (C= Coffee, FF= Forest Fragments, RC= Riparian Corridors, T= Tea, TR=Tea Riparian).

4.4.7 Species evenness

An LMM with all variables indicated that the random effects were not very important; Night explained 0% of the variance in the model, Site 0.007%, Month 0% and Year 0%, and residual variance was 0.043%. Habitat and Method between them explained 99.7% of the variance. Only method affected bat species evenness (Deviance = 29.2, d.f. = -10, $P < 0.0001$). Catching had lower evenness than did transects for most habitats (Fig 4.15, Appendix 1).

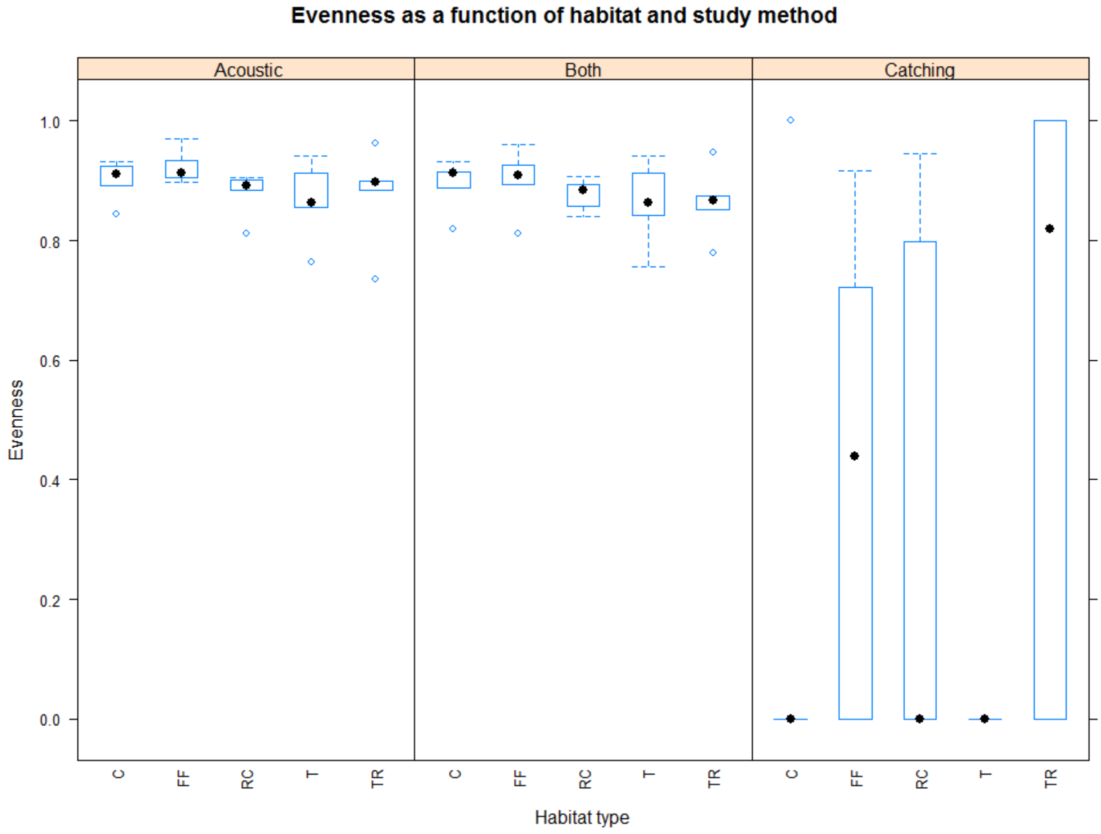

Figure 4.15: Variation in species evenness between habitats using different methods using per site data. (C= Coffee, FF= Forest Fragments, RC= Riparian Corridors, T= Tea, TR=Tea Riparian).

4.4.8.1: Rank abundance graphs

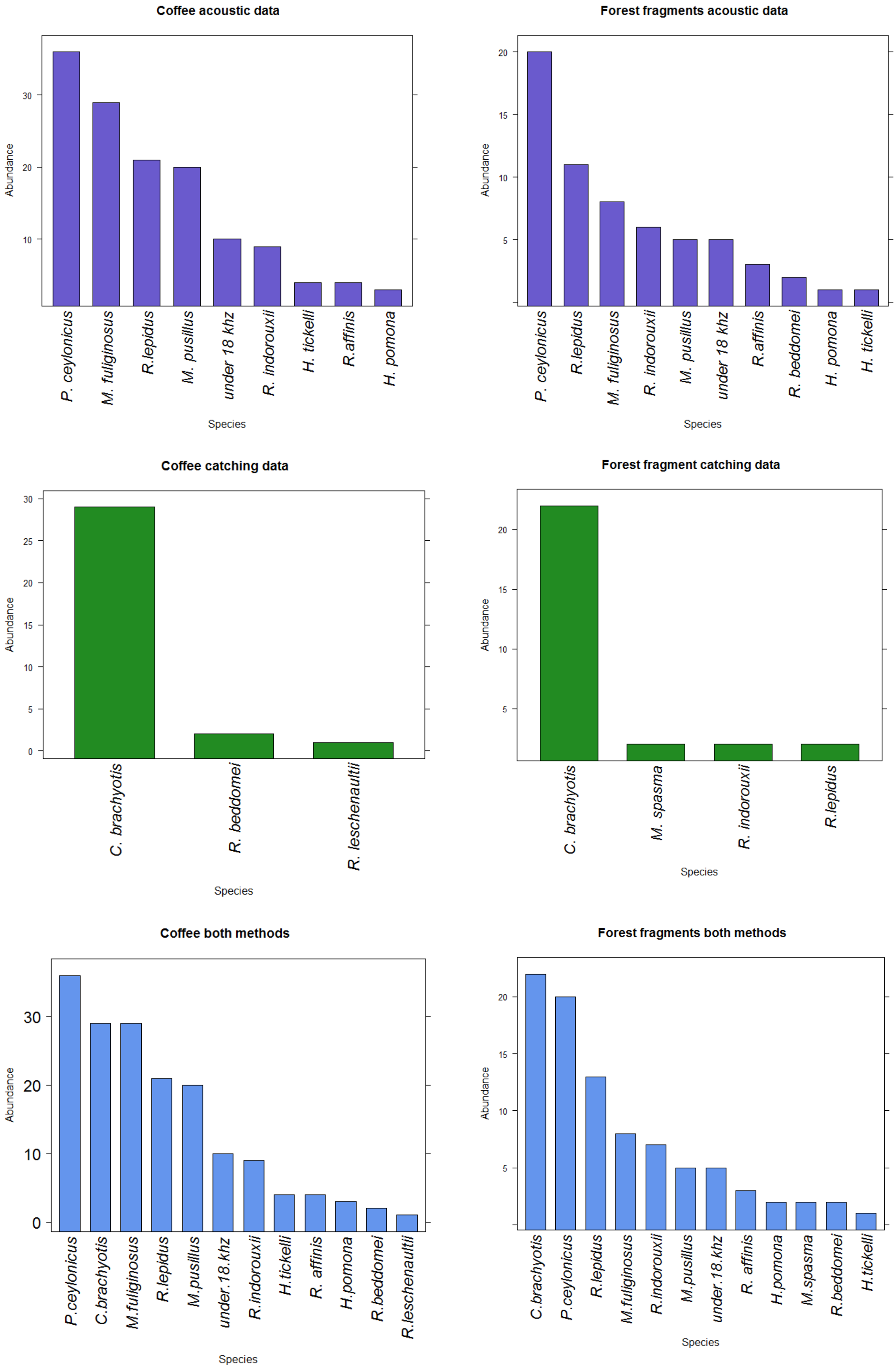

Figure 4.16: Rank-abundance plots showing the species composition of coffee plantations and forest fragments using catching, acoustic transects and both methods together.

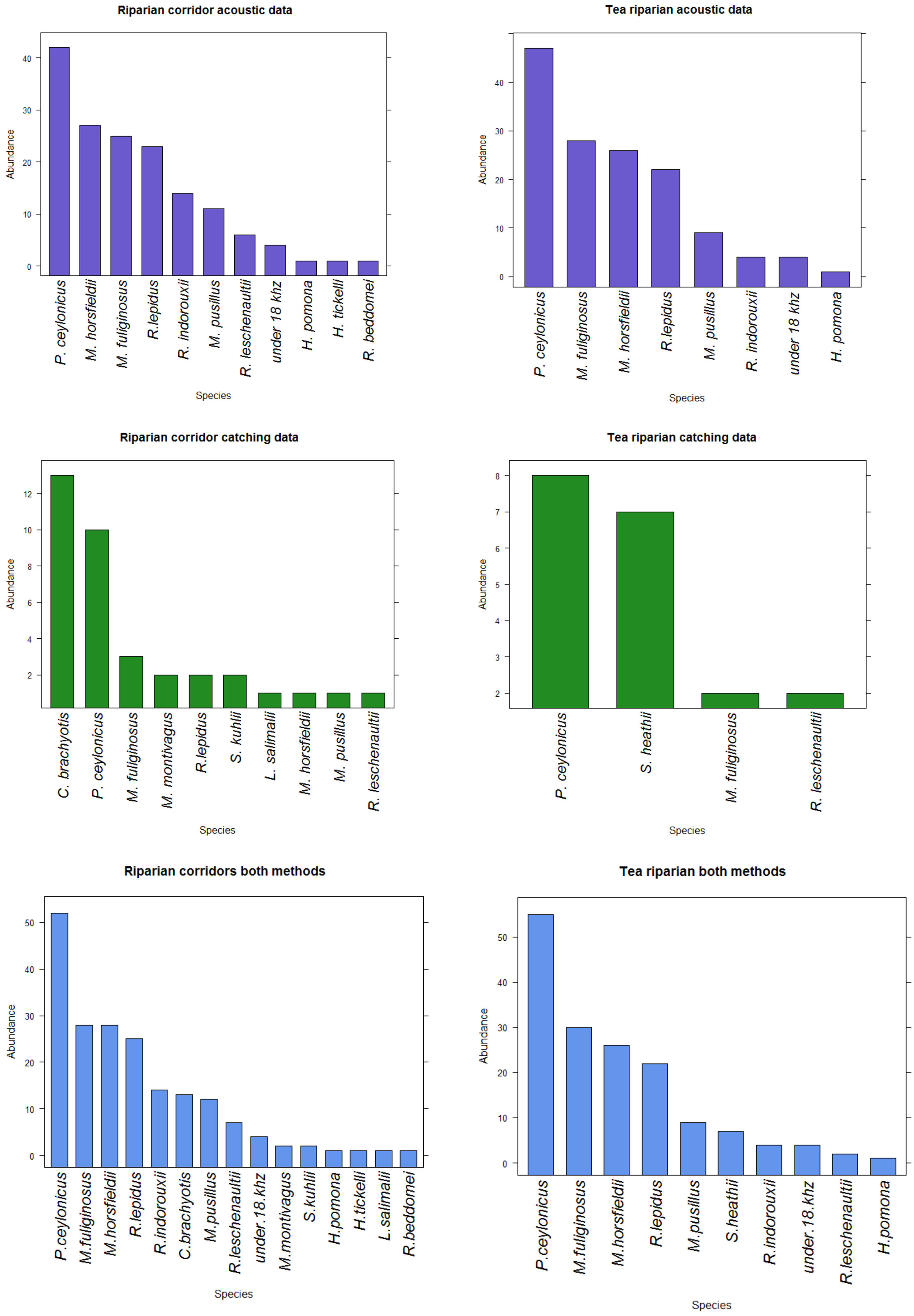

Figure 4.17: Rank-abundance plots showing the species composition of rivers with and without riparian corridors using catching, acoustic transects and both methods together.

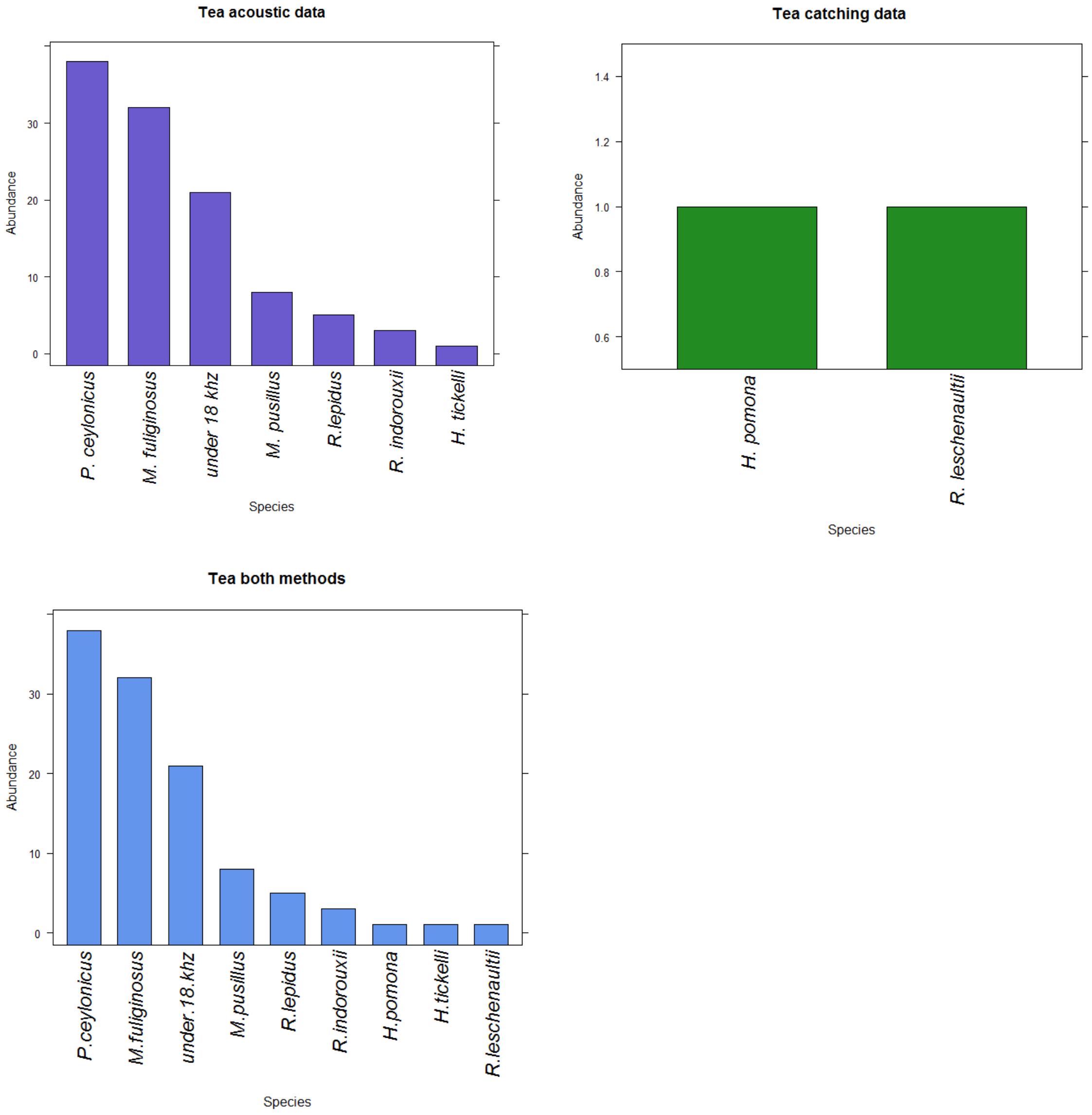

Figure 4.18: Rank-abundance plots showing the species composition of tea plantations using catching, acoustic transects and both methods together.

4.4.8.2 **NMDS** ordination plots of species composition

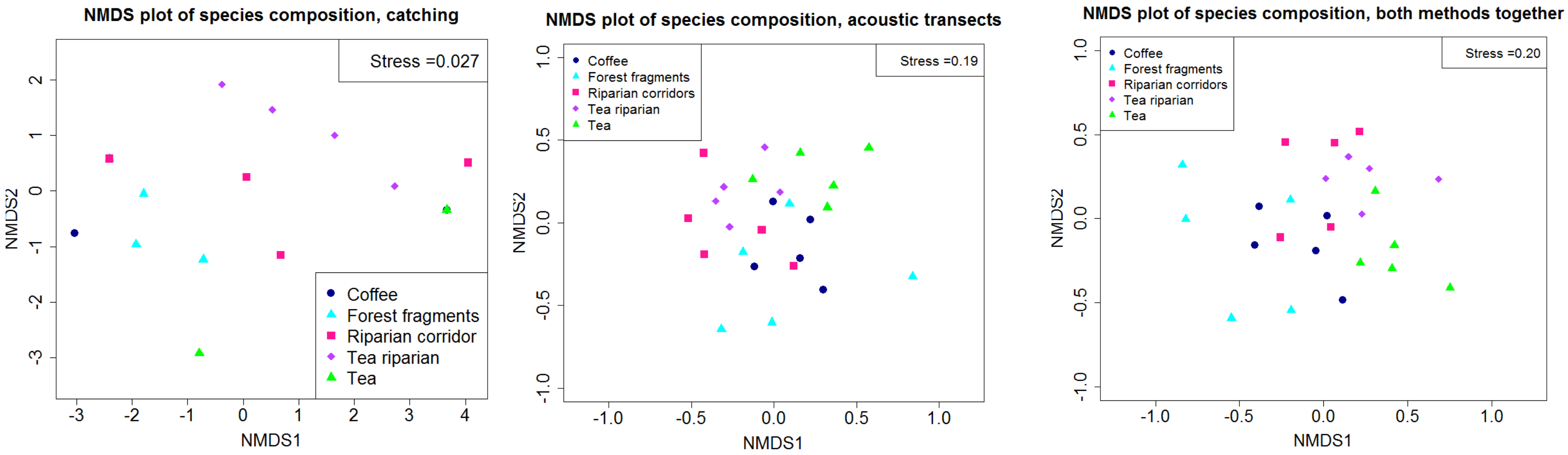

Figure 4.19: Non-Metric-Multidimensional-Scaling (NMDS) plots based on Bray-Curtis distances between sites. L-R – catching alone, acoustic transects alone and both methods combined.

4.4.8.3 Using ADONIS to test for variation in species composition

Species composition differed significantly between habitats when both methods were combined. (ADONIS: $r^2 = 0.49$, d.f. = 4, *P* = 0.001, Fig 4.19). Pairwise comparisons controlled for false discovery rate showed all pairwise comparisons between species to be significantly different other than riparian corridors, which were not significantly different from coffee plantations or tea riparian habitats, and coffee was not significantly different from tea (Table 4.2).

Table 4.2: Pairwise comparisons of species composition assessed by both methods combined using ADONIS, with post-hoc corrections using false discovery rate. <0.05=*, <0.01=, <0.001=*** Greys indicate signficance level after false dicovery rate correction.**

Comparison	F-value	P-value	q-value after FDR correction
Coffee – Forest Fragment	2.789	0.007 **	0.016 *
Coffee – Riparian corridor	1.913	0.109	0.122
Coffee – Tea riparian	3.326	0.008 **	0.016 *
Coffee - Tea	2.302	0.055	0.068
Forest fragment – Riparian corridor	5.488	0.008 **	0.016 *
Forest fragment – Tea riparian	8.617	0.009 **	0.016 *
Forest fragment - Tea	5.934	0.008 **	0.016 *
Riparian corridor – Tea riparian	0.708	0.683	0.683
Riparian corridor - Tea	4.291	0.009 **	0.016 *
Tea Riparian - Tea	3.980	0.015 *	0.022 *

Species composition differed significantly overall between habitats as assessed by catching alone. (ADONIS: $r^2 = 0.36$, d.f. = 4, *P* = 0.007). However pairwise comparisons controlled for false discovery rate showed no pairwise comparisons between species to be significantly different (Table 4.3).

Table 4.3: Pairwise comparisons of species composition assessed by catching alone using ADONIS, with post-hoc corrections using false discovery rate.

Comparison	F-value	P-value	q-value after FDR correction
Coffee – Forest Fragment	1.595	0.149	0.274
Coffee – Riparian corridor	0.633	0.715	0.715
Coffee – Tea riparian	2.300	0.080	0.202
Coffee - Tea	1.242	0.400	0.572
Forest fragment – Riparian corridor	2.024	0.050	0.167
Forest fragment – Tea riparian	6.842	0.008	0.082
Forest fragment - Tea	4.658	0.048	0.167
Riparian corridor – Tea riparian	1.554	0.164	0.274
Riparian corridor - Tea	0.984	0.464	0.581
Tea Riparian - Tea	1.058	0.567	0.630

Species composition differed significantly between habitats as measured by transects alone (ADONIS: r2 = 0.56, d.f. = 4, *P* <0.0001). Pairwise comparisons controlled for false discovery rate showed all pairwise comparisons between species to be significantly different other than riparian corridors with both coffee and tea riparian habitats, and coffee was not significantly different from tea (Table 4.4).

Table 4.4: Pairwise comparisons of species composition assessed by acoustic transects alone using ADONIS, with post-hoc corrections using false discovery rate. <0.05=*, <0.01=, <0.001=***. Greys indicate signficance level after false dicovery rate correction.**

Comparison	F-value	P-value	q-value after FDR correction
Coffee – Forest Fragment	3.096	0.008 **	0.023 *
Coffee – Riparian corridor	2.419	0.070	0.077
Coffee – Tea riparian	3.320	0.023 *	0.035 *
Coffee - Tea	2.487	0.048 *	0.060
Forest fragment – Riparian corridor	4.040	0.007 **	0.023 *
Forest fragment – Tea riparian	5.332	0.009 **	0.023 *
Forest fragment - Tea	3.391	0.007 **	0.023 *
Riparian corridor – Tea riparian	0.206	0.911	0.911
Riparian corridor - Tea	3.857	0.023 *	0.035 *
Tea Riparian - Tea	3.654	0.025 *	0.035 *

4.4.8.4 Species changes in abundance by habitat

Table 4.5: Abundances of bats across habitats.

Habitat	Riparian Corridor	Coffee	Forest Fragments	Tea Riparian	Tea
Cynopterus brachyotis	13	29	22	0	0
Hipposideros pomona	1	3	2	1	1
Hesperoptenus tickelli	1	3	1	0	1
Latidens salimalii	1	0	0	0	0
Megaderma spasma	0	0	2	0	0
Myotis horsfieldii	28	0	0	26	0
Myotis montivagus	2	0	0	0	0
Miniopterus fuliginosus	28	29	8	30	32
Miniopterus pusillus	12	20	5	9	8
Pipistrellus ceylonicus	52	36	20	52	38
Rousettus leschenaultii	7	1	0	2	1
Rhinolophus affinis	0	2	3	0	0
Rhinolophus beddomei	1	2	2	0	0
Rhinolophus indorouxii	14	9	7	4	3
Rhinolophus lepidus	25	21	13	22	5
Scotophilus heathii	0	0	0	7	0
Scotophilus kuhlii	2	0	0	0	0
Under 18.khz	4	10	5	4	21

All species varied in abundance between habitats (Table 4.5). For species with >35 individuals in total, I tested for significant changes in abundance in different habitats using a Kruskal-Wallis test. Of the eight species tested, four varied significantly in abundance between habitats (Table 4.6). Two (*Pipistrellus ceylonicus* and *Miniopterus fuliginosus*) increased in frequency in tea plantations. One (*Cynopterus brachyotis*) decreased in abundance in tea plantations. One (*Myotis horsfieldii*) was only present in riparian habitats. The other species showed non-significant trends in abundance between habitats.

Table 4.6: Mean number of records per habitat with standard deviations and Kruskal-Wallis comparisons of abundances, for species with >35 individuals. Letters indicate differences in adjusted p values of pairwise comparisons between habitats – habitats with the same letter are not-significantly different, habitats with different letters are significantly different a P<0.05. <0.05=*, <0.01=, <0.001=***. Greys indicate signficance level after false dicovery rate correction.**

Species	FF	C	RC	TR	T	χ^2	df	P value (post fdr)
Cynopterus brachyotis	4.4±3.2 a	5.8±7.29 a	2.6±3.71 ab	0±0 b	0±0 b	11.86	4	0.018 *
Myotis horsfieldii	0±0 b	0±0 b	5.6±5.03 a	5.3±4.4 a	0±0 b	16.17	4	0.003 **
Miniopterus fuliginosus	1.6±0.89 b	5.8± 1.92 a	5.6±1.67 a	6±1.73 a	6.4±3.13 a	11.1	4	0.025 *
Miniopterus pusillus	1±1.41	4±2.34	2.4±1.14	1.6±1.81	1.8±1.48	5.9	4	0.2
Pipistrellus ceylonicus	4±2.12 c	7.2±2.95 b	10.4±2.7 ab	7.6±2.07 b	11±2.12 a	14.1	4	0.007 **
Rhinolophus indorouxii	1.4±1.14	1.8±2.39	2.8±2.68	0.8±1.3	0.6±0.55	4.17	4	0.38
Rhinolophus lepidus	2.6±1.9	3.8±1.3	5±2.7	4.4±2.7	1±1.4	8.832	4	0.065
Under 18 kHz	1±0.7	2±1.22	0.8±0.83	0.8±1.7	4.2±3.34	7.142	4	0.133

4.5 Discussion

In this chapter I showed that catching detects fewer individuals and fewer species of bats than acoustic transects do. Bat species richness was similar in forest fragments and coffee plantations and greater than in tea plantations. However, species composition was different between forest fragments and coffee plantations. Rivers with riparian corridors showed greater richness and abundance of bats than rivers without riparian corridors, but the differences were not statistically significant. There was no effect of forest fragment or riparian corridor size on bat species richness. Several species showed significant differences in abundance between different habitats.

4.5.1 Comparison of methods

The data presented here make it clear that catching alone is not a suitable method for describing bat assemblages. The number of individual records of bats and the number of species recorded were significantly lower than on transects, meaning that a lot of species went undetected by mist nets. Catching alone failed to detect differences in species composition between habitats, where transects alone found the same differences as catching and transects combined, albeit separating the data slightly less clearly than the combined data.

There were biases in catching data in relation to where some species were caught, that were contradicted by transect data. For example, *Pipistrellus ceylonicus* was the bat recorded most using acoustic data, and was very common in all habitats; however it was only caught in riparian habitats, where it presumably flies lower to drink or feed along the surface of the water. The rhinolophid bats were only caught in heavily vegetated areas, but they were recorded in all habitats – it may be that these species find it harder to detect mist-nets in more cluttered habitats. There was also a potential detection bias for *Rousettus leschenaultii* as this species was picked up by bat detectors along riparian corridors, but not elsewhere, although it was caught in other habitats. This may reflect genuine greater abundance along rivers, but as this species echolocates quietly it may be easier to detect where there is an open flyway concentrating bat activity. These data show that relying on any one method may give inaccurate results, but that if it is not possible to use both methods in combination, acoustic transects should be chosen over catching alone.

However, catching does still have an important role in bat studies in this region. Some species were only sampled by catching; two of the three fruit bats, *Cynopterus brachyotis* and *Latidens salimalii*, and the low-intensity echolocator *Megaderma spasma*. Three species (*Scotophilus heathii, Scotophilus kuhlii* and *Myotis montivagus*) could not be distinguished by echolocation call alone (see Chapter Three) so their presence could only be confirmed by catching. Many of these species were only caught over rivers – it may be that like *Pipistrellus ceylonicus,* they are present in many habitats but easier to catch over water.

In forest fragments, dense vegetation muffled sound and made it harder to record echolocation calls, however in tea plantations the habitat was so open that it was difficult to catch bats, as the nets stood out more from the surrounding habitat (O'Farrell and Gannon 1999, Patriquin et al. 2003). These factors may have led to the reduced abundances of bats in forest fragments as measured by acoustic transects, and in tea as measured by catching.

In most other studies, using ultrasound detectors and catching together also detected the greatest number of species (Murray et al. 1999, O'Farrell and Gannon 1999, MacSwiney et al. 2008, Furey et al. 2009), and generally acoustic methods alone gave greater species richness than catching alone (O'Farrell and Gannon 1999, MacSwiney et al. 2008, Furey et al. 2009). Acoustic methods are very likely to give a better idea of bat activity than catching does, as bat activity data from ultrasound sampling were correlated with insect abundance while capture data were not; also the bats sampled are undisturbed so data is likely to be more representative of true activity levels (MacSwiney et al. 2008).

In India very few studies have used acoustic detectors, and none that I know of have identified bats to species level using a call library. I encourage bat researchers working in India, and more widely in the tropics, to create call libraries and use acoustic data in conjunction with catch data wherever possible in order to build a clear picture of how different bat species respond to habitat loss and land use change.

4.5.2 Bat assemblages in tea plantations, coffee plantations and forest fragments.

The true importance of the studied habitats can only be assessed by comparing them with little-disturbed or undisturbed rainforest in the same area. Until I have collected that data, however, I will use forest fragments as a 'baseline' habitat to compare with plantations. I can also see how much of the known species assemblage for the landscape is found in each habitat. No habitats contained all of the 19 species and morphospecies recorded from this region. *Barbastella leucomelas darjelingensis* was not found in any of the study sites, although two individuals were caught and calls were recorded at five points near the edge of primary forest when catching for the call library.

4.5.2.1 Shade grown coffee as a 'biodiversity friendly' crop

There was no significant difference in this study in species richness between coffee plantations and forest fragments. No species in this study were seen in forest fragments but not in coffee plantations (*Megaderma spasma* was caught once in a coffee plantation on a night not part of this study). This suggests that coffee plantations may be good at maintaining bat assemblages in the area. However, coffee plantations had a different species composition to forest fragments, and they differed in the abundance of several species. *Pipistrellus ceylonicus* and *Miniopterus fuliginosus* were both significantly more abundant in coffee plantations than in forest fragments.

In the neotropics, some authors found coffee and cacao plantations to have equal or greater bat species richness than forest habitats (Pineda et al. 2005, Faria et al. 2006, Faria and Baumgarten 2007, Harvey and Villalobos 2007, Pardini et al. 2009, Williams-Guillén and Perfecto 2011), but others found shade plantations to be less species rich than forest (Estrada et al. 1993, 2006, Estrada and Coates-Estrada 2001, Faria and Baumgarten 2007). Of the two palaeotropical studies published, one in Indonesia (based on catching) found richer bat species assemblages in shade coffee than in forest (Graf 2010). The other used acoustic transects in India but could only identify bats to family level – activity was higher in forest fragments than in coffee but very few other conclusions could be drawn (Molur and Singh 2009). Only Williams-Guillén and Perfecto (2011) used both catching and acoustic data together to assess species richness and composition – all other studies used just catching data, while Molur and Singh (2009) used only acoustic data. As the data in this chapter show, catching alone is likely to be an unreliable method to assess bat species richness.

Bat species composition was not significantly different between forest fragments and shade plantations of coffee and cacao in several studies (Estrada and Coates-Estrada 2001, Pineda et al. 2005, Faria et al. 2006, Graf 2010, Williams-Guillén and Perfecto 2011). In two, bats described as forest specialists were more abundant in shaded plantations than in forest (Harvey and Villalobos 2007, Pardini et al. 2009) while some nectarivorous and frugivorous bats also showed greater abundance in shade plantations (Faria et al. 2006, Harvey and Villalobos 2007, Graf 2010).

Species richness and composition in shade plantations seem to be affected by local and landscape level factors. Estrada et al. (2006) showed that insectivorous bats declined as more pesticides were used in shade plantations. In the Atlantic forests of Brazil, shade cacao plantations in a landscape of nearly 70% forest cover were even more species rich than forest fragments with a very similar species composition – but when >80% of the landscape was covered with shade plantations, species richness was lower in both forest fragments and shade plantations (Faria et al. 2006). In another study in the area, shade plantations contiguous to forest were richer than forest, with similar species composition; however shade plantations >1 km from the forest showed lower richness and different species composition to forest (Faria and Baumgarten 2007).

Recent papers (Phalan et al. 2011, Hulme et al. 2013) show that in many systems it is more beneficial to biodiversity to boost yields by intensive farming on a smaller area of land, while leaving some land unfarmed for biodiversity - although this can be dependent on the level of yield obtained with low-yield 'wildlife friendly' farming (Hodgson et al. 2010). *Arabica* coffee plantations may be an exception to this, as higher yields are often found at intermediate shade levels, shade improves coffee quality (and thus price), can increase pollination of coffee, and may help in mitigating against some of the worst effects of climate change (Jha et al. 2014). It may also be a suitable crop to grow in the buffer zones of protected areas (Valparai is a landscape adjacent to several PAs) to mitigate edge effects on the primary forest (Woodroffe and Ginsberg 1998, Hansen and Defries 2007, Laurance et al. 2012). However, both *arabica* and robusta coffee plants can becomes invasive in even undisturbed forest, so coffee plants themselves could become a threat to pristine forests (Joshi et al. 2009).

A recent study showed that small scale land sparing robusta (*Coffea canephora*) coffee farming, where an area of land equal to that under cultivation was left to regenerate, had greater bird diversity and similarity of composition to primary forest than robusta coffee grown under commercial polyculture shade (Chandler et al. 2013). While this is an important first step, coffee yields, and perhaps more importantly, the price obtained for the coffee, were not measured; nor were the effects of fertilizer and pesticide application. It would be useful to replicate this study using traditional 'rustic' shade comprised of native rainforest trees, and to look at the lower yielding but more expensive *arabica* coffee as seen in Valparai. Further studies could also look at the yields per hectare and the price for the coffee based on its quality. The freshwater impacts of dumping coffee pulp in waterways have been little examined, as have any potential ways to mitigate effects (Donald 2004).

Our understanding of the best ways to maintain both coffee production and biodiversity remains incomplete, a situation which needs remedying as coffee cultivation is likely to move into protected forest reserves in some parts of the world as climate change takes place (Läderach et al. 2013). The results from Valparai, as from many places elsewhere, suggest that coffee under native shade can have a supplementary role for biodiversity but cannot replace forest. However, it may be beneficial to explore mechanisms for promoting coffee grown under native shade in the buffer zones of protected areas.

4.5.2.2 Tea plantations

Tea plantations cover around 3.28 million ha globally, yet our understanding of how biodiversity responds to this land use is virtually non-existent. Here, I saw a mean of 5 bat species per site in tea, compared to 7.8 species in coffee and 7.4 in forest fragments. The total number of species in tea plantations was 9, compared to 12 in coffee plantations and forest fragments. The species composition in tea plantations differed significantly from all other habitats other than coffee plantations, . Bat abundance was also lower in tea than in all other habitats, significantly lower than coffee plantations and riparian corridors.

The most abundant bat species in tea plantations were *Pipistrellus ceylonicus* and *Miniopterus fuliginosus*, which both increased in abundance in tea plantations compared to other habitats. *Miniopterus pusillus* was one of the more abundant species in tea, yet was not as abundant as it was in coffee plantations and riparian corridors; and two rhinolophid species, *Rhinolophus lepidus* and *Rhinolophus indorouxii*, were detected several times in tea plantations here but at lower abundances than in all other habitats (although the difference was not significant. *Hipposideros pomona, Hesperoptenus tickelli* and *Rousettus leschenaultii* were only seen once in this habitat so may not be well suited to feeding in tea estates. Tea plantations seem to be a good habitat for a relatively few species, a tolerable but not ideal habitat for a few more, and an intolerable habitat for 10 of the 19 species and morphospecies known from the area that were not seen in tea plantations at all.

For bats, tea plantations are a poor substitute for forest, with a reduction in overall bat abundance, a reduction in abundance and diversity of fruit bat and rhinolophids, and a potential decline or loss of hipposiderids and megadermatids. In ecologically important areas such as the Western Ghats it may be worth trying to prevent further conversion of shade plantations such as coffee to tea. Suitable habitat for tea plantations may shift altitudinally and latitudinally due to climate change, potentially leading to habitat loss for mid and high elevation species. Zoning around protected areas, and plans for agricultural changes in the face of climate change, should acknowledge that tea does not appear to be a comparable habitat to forest fragments or even shade coffee for bats, birds or frogs (Raman 2006, Murali and Raman 2012).

4.5.3 Bat assemblages on rivers with and without riparian corridors

Riparian corridors had the most species records of all habitats, with 14 known species and one morphospecies. Nine known species and one morphospecies were seen in tea a river without a riparian corridor.

No significant differences in species richness, abundance, diversity, evenness or species composition were seen in analyses of per site or per night mean data between rivers in tea plantations with and without riparian corridors. This is likely due to insufficient sampling per site, as for the overall habitat data rivers with riparian corridors accumulated more species in total than all other habitats; confidence intervals stopped overlapping at around 150 individuals. As the mean number of individual records using both methods per night was between 12 and 20 depending on habitat, I would need more per site sampling to detect these effects – around 10-15 nights per site to detect the difference between riparian corridors and forest fragments /coffee plantations and 4-6 nights sampling per site to be certain of detecting the difference between riparian corridors, forest fragments and coffee plantations on the one hand, and tea plantations and rivers in tea on the other.

Cynopterus brachyotis, Myotis montivagus, Scotophilus kuhlii, Hesperoptenus tickelli, Rhinolophus beddomei and the endangered *Latidens salimalii*, along with one unidentified morphospecies, were caught or recorded at one or more sites with a riparian corridor, where only one species – *Scotophilus heathii* – was seen at two rivers without a riparian corridor, but not at a river with a corridor. *Rhinolophus indorouxii* was more abundant on rivers with riparian corridors, with 14 records compared to just four on un-vegetated rivers.

On rivers with riparian corridors there were several records of two species of fruit bat, and one record of the endangered fruit bat *Latidens salimalii*; whereas without riparian corridors there were just two records of one species of fruit bat (*Rousettus leschenaultii*). There is less food along rivers without mature native trees on the banks for these species, and it is possible that the smaller *Cynopterus brachyotis* is not as likely to fly long distances in search of food as the larger *Rousettus leschenaultii*.

Some of the species seen over the river by a riparian corridor are among the rarest in this assemblage, such as *Rhinolophus beddomei*, a relatively rare forest specialist bat, apparently restricted to areas with mature native trees in this habitat (Chapter Three). Three species – *Latidens salimalii, Myotis montivagus* and *Scotophilus kuhlii* - were unique to riparian corridors. In this study, I did not attempt to catch or record bats in the interior of the riparian corridors. I was mostly interested in how the presence of riparian vegetation affected the bat assemblage that was using the river, so I may be missing some of the species that live in the interior of the riparian fragment – for example *Megaderma spasma* and the rhinolophid assumed to be *R. affinis* were detected at forest fragment sites but not in rivers with riparian vegetation.

In temperate regions, forest cover, a greater area of natural habitat or more hedgerows around the riparian zone are positively correlated with bat activity (Hayes and Adam 1996, Carmel and Safriel 1998, Holloway and Barclay 2000, Ober et al. 2008, Lundy and Montgomery 2009, Langton et al. 2010). Tropical studies reveal that riparian vegetation can be richer in bat species and have higher activity levels than comparable nearby non-riparian vegetation (Monadjem and Reside 2008, Sirami et al. 2013, Taylor et al. 2013), and some bat species show particular preferences for riparian vegetation (Avila-Cabadilla et al. 2012).

The Indian government has committed US$10.14 billion to planting five million hectares of forest and improving forests quality on another five million hectares (National Action Plan on Climate Change 2011). While the main focus of this reforestation drive is for large scale work (5000+ ha plots), riparian corridors in agricultural land may be a good investment for reforestation due to the hydrological and erosion reducing benefits (Sweeney et al. 2004, Mayer et al. 2007). They may help to restore landscape connectivity and have potential for mitigating human elephant conflict by providing ‘migration corridors’ through the landscape where elephants can drink, feed and rest in the shade rather than venturing into tea estates (Kumar and Singh 2011).

4.5.4 The effects of forest fragment and riparian corridor size on bat assemblages.

Conservation planning at the landscape scale requires an understanding of the effects of landscape composition and configuration on the target species. Additionally, when comparing the species richness, abundance and composition of different habitats, I wanted to address the possible effects of habitat patch size on inter-habitat variation. I had a low number of replicates for forest fragment and riparian corridor size, but a moderately large range in size (2.2 ha-102.8 ha for forest fragments, 3.7 – 159.7 ha for riparian corridors). There was no detectable effect of habitat patch size on species richness for either forest fragments or riparian corridors.

The sample size in this study was small, but the range of fragment sizes was large. This landscape has many small fragments with relatively low isolating distances, low to moderate overall forest cover (if shade plantations are included in forest cover) and is surrounded by several protected areas; so the landscape may be reasonably well connected for many bat species.

As discussed in Chapter One many studies do see changes in bat species richness with fragment size, quality and isolation. Several studies on bats have shown changes in species composition in relation to fragment size (Cosson et al. 1999, Struebig et al. 2008, 2009, Estrada-Villegas et al. 2010, Meyer et al. 2010), successional stage (Castro-Luna et al. 2007, Willig et al. 2007, Pardini et al. 2009) and distance of forest islands to mainland (Meyer and Kalko 2008, Estrada-Villegas et al. 2010). Even if species are present in forest fragments, populations may be isolated, which can lead to reduced genetic diversity within a species (Struebig et al. 2011).

In some countries there is legislation around the minimum width of riparian corridors to protect hydrological functions and biodiversity, however legislation is often not based on ecological data (Codigo-Florestal 2001, Marczak et al. 2010, Barlow et al. 2010, Gray et al. 2014, Barlow et al. 2010, Ewers et al. 2011). Here, width of riparian corridor did not have a significant effect on species richness (range: 17 – 1067.5 m). The richest site did have the greatest width, and but also the only site to have vegetation on both banks which may be important for some species.

While these data will hopefully be compared to rivers in primary forest to assess the true conservation value of corridors, even a riparian corridor with a mean width of just 17 m in the area studied contained 11 species, more than were found in all tea riparian sites together. A meta-analysis on both vertebrate and invertebrate taxa showed that wider buffers did not result in greater similarity between riparian corridors and primary forest (Marczak et al. 2010). More work needs to be done on more taxa on the effects of riparian corridor width, but it appears that even narrow corridors of 20 m on just one bank have some benefit for biodiversity.

This study alone is not enough to draw conclusions for legislation or landscape design. It does however suggest that the efforts of The Nature Conservation Foundation to replant many plots of a few hectares each with forest, and to extend existing forest fragments, are likely to be beneficial for bat species.

4.5.5 Species' reactions to land use change

Many species varied significantly in abundance between different habitats. *Cynopterus brachyotis* was most abundant in forest fragments and coffee plantations, was found at intermediate abundance over rivers with riparian corridors and was not found in either tea plantations or tea riparian areas. This species is heavily dependent upon fruits and flowers, and tea plantations appear to be an unsuitable habitat for this species. Shaded coffee plantations, however, are a suitable habitat for this species. It has been shown in other studies that *Cynopterus brachyotis* is very adaptable, feeding on oil palm (Fukuda 2009) and on very ripe coffee (Huang et al in prep.). *Cynopterus brachyotis* appears to be common in many areas (Francis 1994, Hodgkison et al. 2003, Sedlock et al. 2008), and is reported to be more common in early successional forest, oil palm, orchards and shaded plantations than in old growth forest (Bumrungsri et al. 2007, Fukuda 2009, Graf 2010). This species is considered rare in South India but common across its range, and quite disturbance tolerant (Csorba et al. 2008c). It is apparently restricted to mid-elevation areas in India, so might decline with conversion to non-fruiting crops like tea or eucalyptus in these areas (Singaravelan et al. 2009, Korad 2014).

Several other bats in this assemblage appear to be 'loser' species, which decline in abundance with intensive agriculture. *Megaderma spasma, Rhinolophus beddomei, Myotis montivagus, Scotophilus kuhlii,* the rhinolophid calling at 80 kHz (probably *R. affinis*) and the endangered *Latidens salimalii* (section 4.5.5.1) were not seen in tea plantations or in rivers without riparian corridors, although they occurred too infrequently to test this quantitatively. All of these bar *Latidens salimalii* (only caught once), *Scotophilus kuhlii* and

Myotis montivagus (possibly a riparian specialist, only caught over rivers) however were seen in coffee plantations, indicating that this may be a good agricultural type for conserving species intolerant of large disturbances. (N.B. – *Megaderma spasma* was caught once in coffee, but not on one of the nights included in this analysis).

Consistent with the results of this study, *Megaderma spasma* never appears abundant across its rangeand is not tolerant of major habitat modification, but it is known from many locations. In Indonesia it was seen only in agroforestry systems with a diverse layer of shade trees, not in forest (Graf 2010). It is recorded as locally endangered in Singapore and present but not abundant in forest fragments in Malaysia (Pottie et al. 2005, Struebig et al. 2008), and present but not abundant in primary forest but not present in secondary forest, orchards or oil palm in Borneo (Fukuda 2009). It is considered common by the IUCN in South Asia (Csorba et al. 2008b).

Rhinolophus beddomei appears restricted to forest and shade plantations based on the results of this study. Little is known about the responses of this species to land use changes, but it has been reported as not common in Maharashtra and southern Tamil Nadu, India (Korad 2014, Ponmalar and Vanitharani 2014). Known from a few locations in South India and one in Thailand, it is noted as being very dependent on forest habitat by the IUCN (Srinivasulu and Molur 2008).

Myotis montivagus was only seen in riparian corridors. It appears to roost near streams in evergreen forest – it was only seen in the mountainous Western Ghats in Maharashtra (Korad 2014). It may be a disturbance-intolerant riparian specialist, and more work should be done to see whether it persists in rivers with shaded plantations. It is considered widespread but never locally common by the IUCN (Francis et al. 2008).

Scotophilus kuhlii was only seen in a single riparian corridor site in this study, although it may be under-represented as it was not distinguishable acoustically from *Miniopterus fuliginosus*. This was the most common species in Singapore (Pottie et al. 2005). In Malaysia it was known from a single forest fragment in the study area but not from continuous forest (Struebig et al. 2008). It is known as the 'Oriental House Bat' due to its strong association with human dwellings, and has strong dispersal capabilities so is unlikely to become globally threatened in the near future (Rawlinson et al. 1992, Hisheh et al. 2004).

Scotophilus heathii was only seen in tea riparian sites, mostly at a single site. It may be under-represented as its calls were not distinguishable from low frequency *Pipistrellus ceylonicus* calls. Known as the Greater Asiatic Yellow House Bat, it is widespread and considered tolerant to a degree of habitat modification (Bates et al. 2008b).

The rhinolophid assumed to be *R. affinis* was only recorded from forest fragments and coffee plantations, not in tea plantations. *R. affinis* increased in abundance from continuous forest to forest fragments in Malaysia, and was widespread in the forest fragments there (Struebig et al. 2008). In Vietnam it was rare in both primary forest and agriculture/degraded forest, but was common in disturbed forest (Furey et al. 2010). This species is considered widespread and disturbance tolerant (Walston et al. 2008).

Myotis horsfieldii is, as discussed in Chapter Three, a riparian specialist and was only found in riparian sites. The presence or absence of bankside vegetation did not affect its occurrence. As it is tolerant of this level of disturbance it can be classified as a 'winner' species in this landscape. While considered sparse in Maharashtra, this was based on discovered roost sites alone so may not reflect its true abundance (Korad 2014). It was also considered more water than forest dependent in the Philippines (Sedlock et al. 2008). It is moderately common, widespread and quite disturbance tolerant according to the IUCN (Rosell-Ambal et al. 2008).

Miniopterus fuliginosus was quite abundant in all habitats other than forest fragments, where it was significantly less abundant. This species appears to be a 'winner species', whose abundance increases in disturbed habitats, however *M. schriebersii* (the previous name for this species in Asia) was not considered common based on roost finds in Maharashtra, India (Korad 2014). There appears to be little data for this species in Asia but it is widespread and perceived as disturbance tolerant by the IUCN (Chiozza 2008).

Pipistrellus ceylonicus was the most abundant species overall; it was most abundant in tea and riparian corridors, then in coffee and tea riparian areas, and was least abundant in forest fragments. This species was considered common in Maharashtra in India based on roost sites found (Korad 2014), but although widespread and perceived as disturbance tolerant it there is little information on its responses to specific habitat types (Bates et al. 2008c).

Several species did not show preferences for any habitat – *Rhinolophus lepidus, Rhinolophus indorouxii, Miniopterus pusillus, Hesperoptenus tickelli*, *Hipposideros pomona* and the morphospecies 'under 18 kHz'. Significant differences might be seen if there was more data, increasing the power of the test, especially as most of these species were scarce. Both the *Rhinolophus* species were most abundant in riparian corridors and lowest in tea, so trend more towards being 'loser' species, while the morphospecies under 18 kHz increased in tea plantations and so might be a 'winner' species.

Rhinolophus indorouxii was most frequently found in riparian corridors in this study and least frequently seen in tea, although the differences were non-significant. This species appears to be a sibling species in the *Rhinolophus rouxii* species complex, with different sibling species in neighbouring states in south India (Chattopadhyay et al. 2012). There is not much information on how any on the *Rhinolophus rouxii* species respond to land use change, and each sibling species requires separate analysis. While the species complex is widely distributed and not uncommon, the IUCN consider it to be declining (Molur et al. 2002).

Rhinolophus lepidus was more abundant overall than *Rhinolophus indorouxii*, but showed the same trend of greatest abundance in riparian corridors and lowest abundance in tea plantations. This species was also widespread and common in forest fragments in Malaysia (Struebig et al. 2008, 2009), and was seen in primary and secondary forest and rural fringes in Singapore (Pottie et al. 2005). In Malaysia it was shown to fly up to 11 km from the roost, and there was no effect of fragmentation on allelic richness (Struebig et al. 2009, 2011). It is widespread and common across South and South East Asia (Bumrungsri et al. 2008b).

Hesperoptenus tickelli was rare in most habitats, and *Miniopterus pusillus* was more common; but no significant differences in abundance were seen for either of these species between habitats. *Miniopterus pusillus* was most abundant in coffee and least in forest fragments, so may prefer intermediate disturbance, but the variance in these data is high. Little is known of the specific responses of either species to land use change, but both have been reported from agricultural areas (Bumrungsri et al. 2008a, Csorba et al. 2008a).

Hipposideros pomona was recorded infrequently in all habitats, but trended towards greater abundance in coffee plantations and forest fragments. In Vietnam this species was never common but was more abundant in primary forest and agriculture/degraded forest than in slightly disturbed forest (Furey et al. 2010). Similarly *Rousettus leschenaultii* was recorded infrequently in all habitats but most often in riparian corridors. This species was abundant in both agricultural areas and primary forest in Vietnam (Furey et al. 2010). Both species are considered widespread and disturbance tolerant, but the data from Valparai suggest that tea plantations may be too modified a habitat for these species as there is no fruit present (Bates and Helgen 2008, Bates et al. 2008a).

4.5.5.1 New record of an endangered species

A single adult male *Latidens salimalii* was caught in a riparian corridor. This endemic species is classified as Endangered by the IUCN (Molur and Vanitharani 2008). It is known from a few locations in Kerala and Tamil Nadu from 800 – 1,100 m asl., with a likely extent of occurrence of around 1,100 km^2 (Molur et al. 2002, Vanitharani et al. 2005). Population estimates number in the hundreds, and there has been a significant recent decline in this species (Molur et al. 2002). This is a cave dwelling bat that is sensitive to disturbance, and is threatened by hunting for use in traditional medicine and tree cutting in coffee estates where roosts are found (Molur et al. 2002, Molur and Vanitharani 2008). It is protected under the Schedule I of the Indian Wildlife (Protection) Act, amended in 2006 (Molur and Vanitharani 2008). Its presence in this area justifies maintaining forest fragments and riparian corridors where it may be living.

4.5.7 Summary

Acoustic data detect more species per night than catching, and should be incorporated into more tropical bat studies. Bat species richness, abundance and composition varied significantly between habitats. Coffee plantations retained significantly more species than tea plantations, and rivers with riparian corridors had a greater total number of species than rivers without riparian corridors. Coffee plantations had similar species richness but different species composition to forest fragments. More replicates are needed to better understand the role of riparian corridors in maintaining bat diversity. Size of forest fragment or riparian corridor did not affect species richness.

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Chapter Five: Functional Diversity

5.1 Abstract

Functional diversity of animal and plant communities is increasingly considered critical for maintaining ecosystem functioning. I studied the functional diversity and specialisation of bat assemblages in tea and coffee plantations, forest fragments, and rivers with and without riparian corridors. I aimed to identify where trait filtering was occurring and which traits were filtered. I also compared my results to those derived from a more traditional analysis based on guild richness.

In this study, functional richness and specialisation of bats in forest fragments were significantly greater than expected from random assembly, and functional specialisation in tea plantations was significantly poorer, indicating that specialists had been filtered out of this habitat. The assemblage in tea plantations contained bat species that were on average smaller, had lower frequency echolocation calls, higher relative wing loadings and higher wing aspect ratios than bat species in coffee plantations and forest fragments, as well as more bat species that used frequency modulated calls with a quasi-constant frequency tail. These are all characteristics of open-air foragers with large home ranges that feed on a wide variety of smaller insects. There were more frugivores in coffee plantations and forest fragments than in tea plantations.

Rivers with riparian corridors did not differ from patterns of random assembly but rivers without riparian corridors had lower functional specialisation and functional divergence than expected. Rivers with riparian corridors contained more frugivores than rivers without riparian corridors, and had larger bat species with lower wing aspect ratios than did rivers without riparian corridors.

Functional diversity and specialisation metrics based on a functional space approach captured more information than guild based comparisons between habitats. Quantifying changes in the values of functional traits between habitats revealed significant trait filtering, especially in the most open habitats, with changes in the mean size, wing morphology, diet and echolocation call type and frequency of bats.

5.2 Introduction

Protecting the range of functions performed in an ecosystem is an increasingly important component of conservation biology (Tilman 2001, Petchey and Gaston 2002, 2006, Villéger et al. 2008, Mouillot et al. 2011). Bats are a functionally diverse and important group, playing roles in insect control, pollination and seed dispersal, so changes to the functional diversity of bats may have effects on the overall ecosystem (Boyles et al. 2011, Kunz et al. 2011). How different agricultural land uses affect the functional diversity of bats is poorly understood, especially in the palaeotropics where bat assemblages are ecologically distinct from neotropical assemblages due to a different evolutionary history (Heller and Volleth 1995).

5.2.1 Trait filtering

Species richness is an important component of biodiversity, but quantifying impacts of different processes using richness as a metric can be limiting, as richness may not reveal important functional differences (Mouillot et al. 2013). Species richness may for example be high in areas of intermediate disturbance, but this disturbance may act as a filter, allowing a narrower range of trait values to persist (Hamer et al. 2003, Gray et al. 2007, Cardinale et al. 2012, Fauset et al. 2012, Mouillot et al. 2013, Edwards et al. 2013, 2014). Traditional biodiversity measures may therefore underestimate biodiversity loss and changes to ecosystem functioning in modified habitats (Cardinale et al. 2012, Mouillot et al. 2013). It is widely considered that specialist species are more vulnerable to disturbance than generalist species, as they are probably associated with specific niches.

These niches may be lost or degraded in agricultural landscapes, whereas generalist species may occupy several niches, and potentially the most common niches, so are less likely to be lost with the loss of one or two niches. To see whether or not trait filtering is occurring, I can quantify whether the species in a certain habitat are more or less specialized than expected by chance (Mouillot et al. 2013).

In bats, individual traits may be suited to particular agro-ecosystems or habitats. Traits such as size, wing loading, wing aspect ratio, echolocation call frequency and type and diet have been shown to affect the structuring of bat communities in modified habitats (Schnitzler and Kalko 2001, Law and Chidel 2002, Duchamp and Swihart 2008, Klingbeil and Willig 2009, Threlfall et al. 2011, Hanspach et al. 2012, Denzinger and Schnitzler 2013).

In bats, wing morphology is an important predictor of foraging habitat, foraging strategy, dispersal ability, home range size and even probability of extinction (Norberg and Rayner 1987, Arita and Fenton 1997, Jones et al. 2003). Bats with high aspect ratio (long, narrow) wings, and a high wing loading, are typically fast, energy efficient fliers able to fly long distances – they are typically better adapted to open spaces (Norberg and Rayner 1987, Altringham 2011). Greater wing loading makes flight more efficient by reducing drag across wings with a small surface area, but reduce the size of prey that can be carried (Norberg and Rayner 1987, Altringham 2011). Short wings enable easier take-offs from the ground and flight in cluttered space, and low aspect ratio allows slow flight without stalling (Altringham 2011). Bats with lower aspect ratio (short, broad) wings and lower wing loadings are manoeuvrable and able to take-off easily, and hence well adapted to forest and other cluttered habitats, but are slower and find it more costly to fly longer distances (Norberg and Rayner 1987, Altringham 2011). The wing morphology of an insectivorous or carnivorous bat will affect which prey it can capture.

Some bats show plasticity in their echolocation calls depending on the habitat, but echolocation calls typically vary little within species and can indicate the habitats where a bat is likely to be most successful (Fig 5.1). Higher frequencies give better detail in the immediate vicinity of the bat, more useful for species in cluttered spaces, whereas lower frequencies attenuate less with distance travelled so are better for exploiting more open habitats (Neuweiler 1984, Altringham 2011). Putting a lot of energy into the lower frequencies of an echolocation call, such as a quasi-constant frequency (QCF) tail in a frequency modulated (FM) call, can help bats to detect prey over longer distances (Altringham 2011). Using shorter, 'steeper' FM calls allows the bat to be ready to hear echoes returning quickly from close by in cluttered habitats and increases spatial resolution, and CF calls exploit Doppler shift to detect insect fluttering, picking out insect wings from background clutter (Altringham 2011). Bats can use harmonics to distinguish clutter echoes from target echoes, once again helping them to hunt in cluttered spaces (Bates et al. 2011).

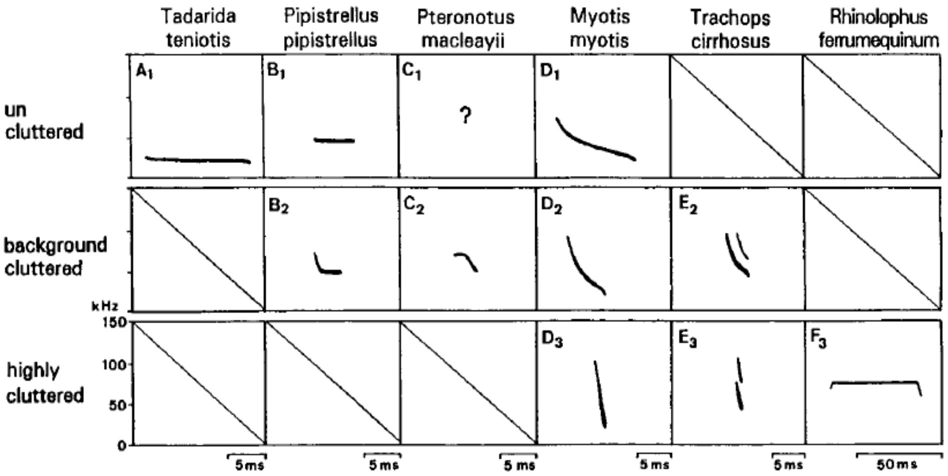

Figure 5.1: From Schnitzler and Kalko 2001. Echolocation call types of species exploiting different habitats. Calls with a strong constant frequency or quasi-constant frequency component are often used in uncluttered space. In background clutter the frequency modulated element of the call is more pronounced, and in high clutter calls are either shorter in duration and frequency modulated or high frequency and constant frequency. Harmonics are often used in more cluttered habitats, and calls are typically at higher frequencies.

It is unclear whether larger or smaller bats are better adapted to intensively cultivated agricultural habitats. Larger bats have higher wing loadings, making for more efficient long distance flight, and they typically use lower frequency echolocation calls which are better for exploiting open areas (Neuweiler 1984, Arita and Fenton 1997, Altringham 2011). However fruit bats are the largest bats in the palaeotropics and there may not be enough fruit for these species in most plantations. Insectivorous bats taking airborne prey may be more limited to smaller prey items, which may be too scarce in open areas to sustain larger bats (Fenton 1990). Smaller bats are also more agile and thus better at aerial hawking, the predominant hunting strategy in open spaces; most aerial hawking insectivore weigh under 30 g (Arita and Fenton 1997). Conversely, small, agile bats are also manoeuverable enough to hunt in cluttered habitats (Norberg and Rayner 1987, Arita and Fenton 1997, Altringham 2011).

5.2.2 Aims

In this chapter I aim to:

- Compare the functional diversity of coffee and tea plantations with that of forest fragments.
- Compare the functional diversity of rivers with and without riparian corridors.
- Compare observed functional diversity in the different habitats with that expected if communities were assembled randomly from the pool of species recorded in this study.
- Identify functional traits of bats that are associated with particular habitats in this landscape.
- Assess the relative utility of a trait space paradigm as opposed to functional guilds for identifying trends in this assemblage.

5.3 Methods

5.3.1 Functional space metrics defined

Many methods have been proposed for measuring functional diversity, but none have managed to simultaneously deal with multiple functional traits, take abundances into account, and maintain the relative interspecific functional distances which retain detail about each species’ differences from other species (Villéger et al. 2008). Villéger et al. (2008) propose multiple measures of functional diversity (functional richness (FRic), evenness (FEve) and divergence(FDiv)) using a multidimensional functional space, which in combination meet all the criteria set out by Mason et al. (2003) and Ricotta (2005). For example, FEve and FDiv but not FRic are unaffected by the number of species present; FRic and FDiv but not FEve are unaffected when a species is split in two species with the same trait values and total abundance; and FEve and FDiv but not FRic reflect the contribution of each species in proportion to its abundance (Villéger et al. 2008). I use these three criteria, plus functional specialisation, to assess the functional diversity of bats in the Valparai plateau (Villéger et al. 2010).

Functional diversity as defined by Villéger et al. is the distribution of species and their abundances in functional space. The functional diversity metrics FRic, FEve and FDiv describe how much of the functional space is filled and how the abundance of a community is distributed in functional space (Villéger et al. 2008). FSpe (functional specialisation) describes changes in the abundance of more functionally specialized species (Villéger et al. 2010, Mouillot et al. 2013).

To calculate these metrics, species are first plotted in functional space – in its simplest form by plotting a species' value for one trait on the X axis against its value for another trait on the Y axis. Functional richness describes the amount of functional space filled by the particular community, by linking all the most extreme species in functional space to build a hull (or polygon if working in two dimensions), and calculating the volume (or area) inside the hull. It is greatest when species have widely differing trait values (Villéger et al. 2008).

Functional evenness quantifies the regularity of species distribution in functional space, weighted by species abundance. It is based on a minimum spanning tree, which links all the points in the functional space with the minimum total length of tree. The regularity of species' distributions along this tree, and the regularity in abundance, gives the functional evenness.

Functional evenness is greatest when the functional distances between species and their abundances are all similar (Villéger et al. 2008).

Functional divergence describes the distribution of abundance within the volume/area of functional trait space that is occupied by species. It measures how species diverge in their distances (abundance weighted) from the non-abundance weighted centre of gravity (mean of all trait values) in functional space. Functional divergence is lower when abundant species are very close to the centre of gravity relative to rare species, and greater when abundant species are distant from the centre of gravity relative to rare species (Villéger et al. 2008).

Functional specialisation shows how generalist species (those close to the centre of functional space) and specialist species (further from the centre of functional space) vary in abundance. Functional specialisation is calculated using the positions of species relative to the centre of gravity calculated from the ‘regional pool’ or total pool of species from all habitats, while the functional diversity indices described only use the functional structure of each target community. Functional specialisation scores are greater when species far from the centre of gravity of the regional pool are high in abundance (Villéger et al. 2010).

5.3.2 Generating functional traits

Functional diversity traits are typically focussed on the morphological, physiological and behavioural traits that characterize the ecological role of a species (Petchey and Gaston 2006, Villéger et al. 2008, 2010). Based on the literature I chose to measure bat traits relating to size, echolocation call, diet and wing morphology, as these have been linked to functional characteristics of bats (Norberg and Rayner 1987, Schnitzler and Kalko 2001, Altringham 2011, Denzinger and Schnitzler 2013).

Traits were measured for all identified species, and for the rhinolophid species calling at 80 kHz thought to be *R. affinis*, based on that species’ echolocation call and distribution (since confirmed as *R. affinis*) (Korad et al. 2007). One morphospecies was not included as it was unidentified

(Table 4.4, Chapter Four). All measurements were taken from bats caught in this study other than for *R. affinis, M. pusillus* and *M. spasma*, which were taken from the literature, with *M. australis* measurements used for *M. pusillus* as these were considered one species until recently (Rhodes 2002, Jiang et al. 2007, Davies et al. 2013). *L. salimalii* was not included in this analysis as I did not have wing metrics for this species and only a single individual was seen.

Diet was established from the literature. Echolocation call type and frequency of maximum energy (FMAXE) were taken from my own measurements, as described in Chapter Two. Forearm length of bats (a strong correlate of overall body size) was measured in the field. Wing aspect ratio and relative wing loading were established from photographs taken in the field of bat wings spread against a gridded board of known cell size, and bat weights taken in the field were also used to calculate relative wing loading. All wing measurements were later taken from the photographs using ImageJ software (Abràmoff et al. 2004). Wing aspect ratio was calculated as wingspan^2/wing area, where wing area encompasses tail membrane and body between wings. Relative wing loading was calculated as ((body mass * gravity)/wing area)/body mass$^{0.333}$ (Table 5.2).

Table 5.1 Traits used to distinguish species in functional trait space.

Species	Diet	FMAXE (kHz)	Call type	Wing aspect ratio	F.A. (mm)	Relative wing loading
C. brachyotis	Fru	0	N	6.1	62	38.3
H. pomona	Ins	126	CF	5.2	41	32.4
H. tickelli	Ins	28	FM.QCF	6.9	55	40.9
M. spasma	Car	56	FMmult	5	56	33
M. horsfieldii	Ins	54	FM	6.7	39	35.8
M. montivagus	Ins	50	FM.QCF	6.6	45	38.1
M. fuliginosus	Ins	52	FM.QCF	7.1	47	34.1
M. pusillus	Ins	64	FM.QCF	6.8	41	30.5
P. ceylonicus	Ins	39	FM.QCF	7.3	39	45.3
R. leschenaultii	Fru	23	Clk	7	80	43.9
R. beddomei	Ins	43	CF	5.3	61	35.6
R. indorouxii	Ins	92	CF	5.8	51	33
R. lepidus	Ins	102	CF	6.1	41	31.8

S. heathii	Ins	41	FM.QCF	6.4	63	48.1
S. kuhlii	Ins	45	FM.QCF	6.1	50	44.5
Rhino80 (R. affinis)	Ins	80	CF	6.9	52	31

Fru= frugivore, Ins = insectivore, Car = insectivore and carnivore, N = no echolocation call, CF = call dominated by a constant frequency, FM.QCF = frequency modulated call terminating in a quasi-constant frequency sweep, FMMult = FM call always employing multiple harmonics, FM = frequency modulated call, Clk =echolocation call produced by clicking the tongue.

5.3.3 Creating the functional trait space

Because the functional traits in Table 5.1 were a mixture of categorical and continuous variables, I calculated a distance matrix using the Gower distance measure, before running a principal coordinates analysis (PCoA) to calculate a new trait matrix of transformed coordinates (Villéger et al. 2008). Two PCoA axes were used to ensure the maximum amount of data could be analysed, as you cannot calculate the FD statistics when you have fewer species than traits (Villéger et al. 2008).

5.3.4 Calculating functional diversity metrics

Functional richness, evenness, specialisation and divergence were calculated per site for acoustic and catching data combined, using the functions provided by Villéger et al. (2008) and Mouillot et al (2013). One site in tea could not be used as only two species were detected over two nights, so n=5 for all habitats other than tea where n=4. The functional diversity metrics were not calculated per night as this would have meant the loss of another tea site where the number of known species was low. For this analysis we were trying to maintain equal effort between sites so kept only the data from nights were transects and catching were done together.

I also calculated all functional diversity metrics with singletons per habitat removed. Species which occur very rarely in a habitat and may just be ‘passing through’ are unlikely to be making a substantial functional contribution. This will particularly affect the results of functional richness, which is not abundance weighted, but running the analyses without singletons allowed me to see if any particular species are driving trends in this relatively small assemblage.

5.3.5 Comparing the functional diversity of habitats

The same data were used to calculate functional diversity as were used to calculate the species level diversity metrics in Chapter Four. I combined the data from acoustic and catching methods for this chapter.

I used a generalized linear model with Poisson errors in the 'lme4' package in R to compare functional richness, specialisation and divergence between habitats (Bates et al. 2014). After running a Poisson GLM, over-dispersion was detected, and errors were corrected using a quasi-GLM model with the variance given by the mean multiplied by the dispersion parameter. I then ran pairwise comparisons using the false discovery rate multiplicity adjustment method in the 'lsmeans' package in R (Lenth 2014, R Core Team 2014).

I used a linear model in the 'lme4' package in R to compare the functional evenness between habitats (Bates et al. 2014). Pairwise comparisons were run as before (Lenth 2014, R Core Team 2014).

I re-ran all analyses after removing the species that appeared just once per habitat. All of these were analysed using generalized linear model with poisson errors in the 'lme4' package in R (Bates et al. 2014). After running a poisson GLM, over-dispersion was detected, and errors were corrected using a quasi-GLM model with the variance given by the mean multiplied by the dispersion parameter. Pairwise comparisons were run as before (Lenth 2014, R Core Team 2014).

5.3.6 Standardised effect size

In order to assess whether different habitats filtered traits, leaving more functionally similar species than would be expected by chance, I compared the standardised effect size (SES) of my four functional diversity metrics (FRic, FEve, FDiv and FSpe) across the five studied habitats. SES was calculated using the equation [(observed – mean expected)/standard deviation of expected]. The ‘expected’ functional diversity metrics were calculated from 1000 random communities generated from the overall species pool, with all species for which traits were measured included. To generate the random communities, an independent swap algorithm was used to maintain species richness and species abundance in the picante package of R (Kembel et al. 2010). One-sample t-tests with $\mu = 0$ were used to quantify whether the SES for each metric in each habitat was significantly different from zero.

5.3.7 Functional traits

Using the mean trait values calculated for each bat species (Table 5.1), I compared changes in the mean values of each trait across the assemblage in each habitat. Where traits were normal they were compared using an ANOVA followed by least squares mean pairwise comparisons with P values corrected by false discovery rate (Lenth 2014). Non-normal traits were compared between habitats using Kruskal-Wallis tests. Pairwise comparisons were performed using Wilcoxon signed ranks tests and corrected using false discovery rate, or where ranks were tied, I bootstrapped data using 1000 iterations and compared confidence intervals. Only bats for which all traits were available were used in these analyses, which excluded *L. salimalii* and one morphospecies.

5.3.8 Functional guilds

Species were grouped into the guilds described by Denzinger and Schnitzler (2013) based on diet, echolocation call and morphology. Guild richness was compared using a generalized linear model with poisson distribution, followed by a χ^2 test. Where the percentage of guilds per site was normally distributed they were compared using an ANOVA followed by least squares mean pairwise comparisons with P values corrected by false discovery rate (Lenth 2014). Non-normal data were compared between habitats using Kruskal-Wallis tests. Pairwise comparisons were performed using Wilcoxon signed ranks tests and corrected using false discovery rate. Only bats for which all traits were available were used in these analyses, which excluded *L. salimalii* and one morphospecies.

5.4 Results

5.4.1 PCoA on Species Traits

The axes of the Principle Coordinates Analysis captured 74% of the variance in the distance table (Figure 5.2).

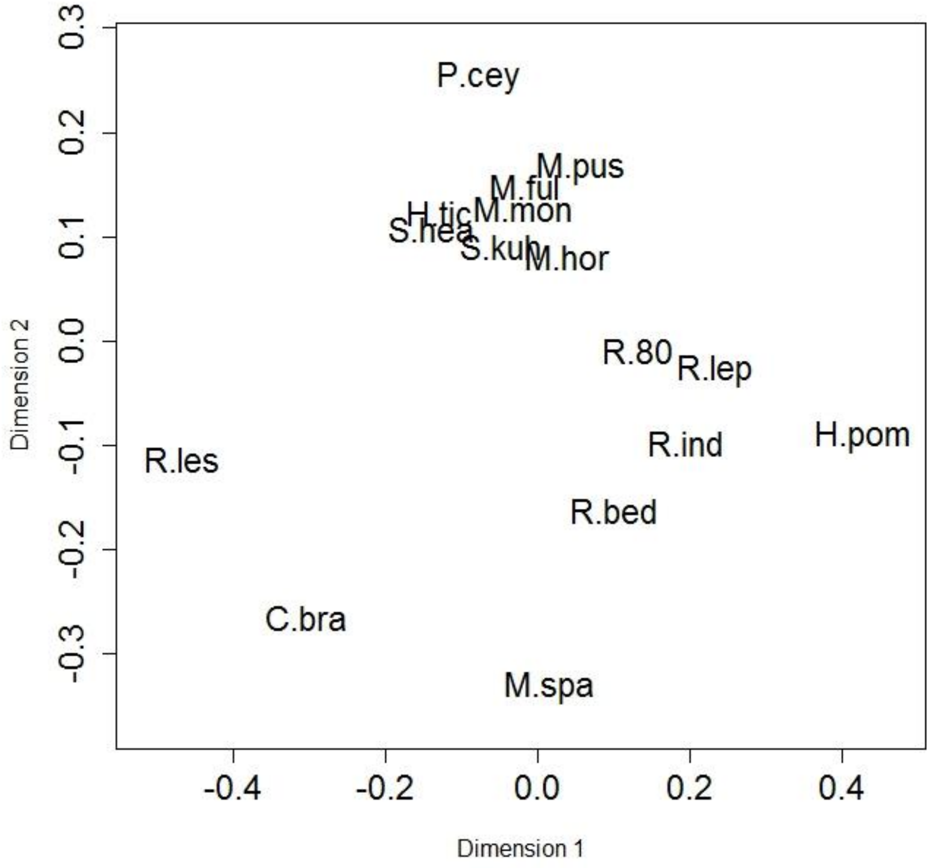

Figure 5.2: Plot of the principal coordinates analysis on the Gower distances between species. R.80 is thought to be *Rhinolophus affinis.*

5.4.2 Functional diversity metrics

I calculated the functional diversity metrics based on the data per habitat (Table 5.2), (Fig. 5.3) and per site (Appendix 2). Riparian corridors, coffee plantations and forest fragments showed greater bat functional richness, diversity and specialisation at the habitat scale than that tea plantations or tea riparian, but evenness was lower in coffee plantations than tea riparian (Table 5.2). Comparing the standardised effect size of each metric to the mean generated from random assembly of the regional pool, functional richness and specialisation were significantly greater than expected in forest fragments (Appendix 2, Fig 5.3). Functional specialisation was significantly lower than expected in tea and tea riparian, and functional divergence was significantly lower than expected in tea riparian (Appendix 2, Fig 5.3).

I had to drop one tea plantation site from the analysis where only two known species were present, and a minimum of three species per site were needed to run the statistics. Therefore the results are somewhat biased towards greater functional diversity and specialisation in tea than was actually recorded.

Table 5.2: Functional richness at the habitat level, calculated on the summed data for each habitat.

Combined data	Nbsp	FRic	FEve	FDiv	FSpe
Riparian corridors	13	0.231	0.500	0.781	0.222
Coffee	11	0.231	0.357	0.779	0.25
Forest fragments	11	0.224	0.669	0.855	0.274
Tea riparian	9	0.161	0.409	0.602	0.203
Tea	8	0.161	0.300	0.614	0.215

Nbsp = number of species, FRic = Functional richness, FEve = functional evenness, FDiv = functional divergence, FSpe = functional specialisation.

5.4.3 Functional diversity metrics without singletons

After removing any species that occurred just once per habitat, I calculated the overall functional diversity metrics based per habitat (Table 5.3, Fig. 5.4), and per site (Appendix 2). Except for functional richness in tea plantations which dropped considerably, results were unchanged when singletons were dropped for the analysis (Table 5.3). Comparing the standardised effect size of each metric to the mean generated from random assembly of the regional pool, the patterns were unchanged except that functional richness in tea was significantly lower than expected (Table 5.3, Fig 5.4).

Table 5.3: Functional richness at the habitat level, calculated on the summed data for each habitat with species occurring just once per habitat removed.

Combined data	Nbsp	FRic	FEve	FDiv	FSpe
Riparian corridors	10	0.192	0.337	0.774	0.213
Coffee	10	0.171	0.662	0.774	0.248
Forest fragments	10	0.224	0.639	0.864	0.280
Tea riparian	8	0.14	0.312	0.642	0.201
Tea	5	0.025	0.477	0.748	0.210

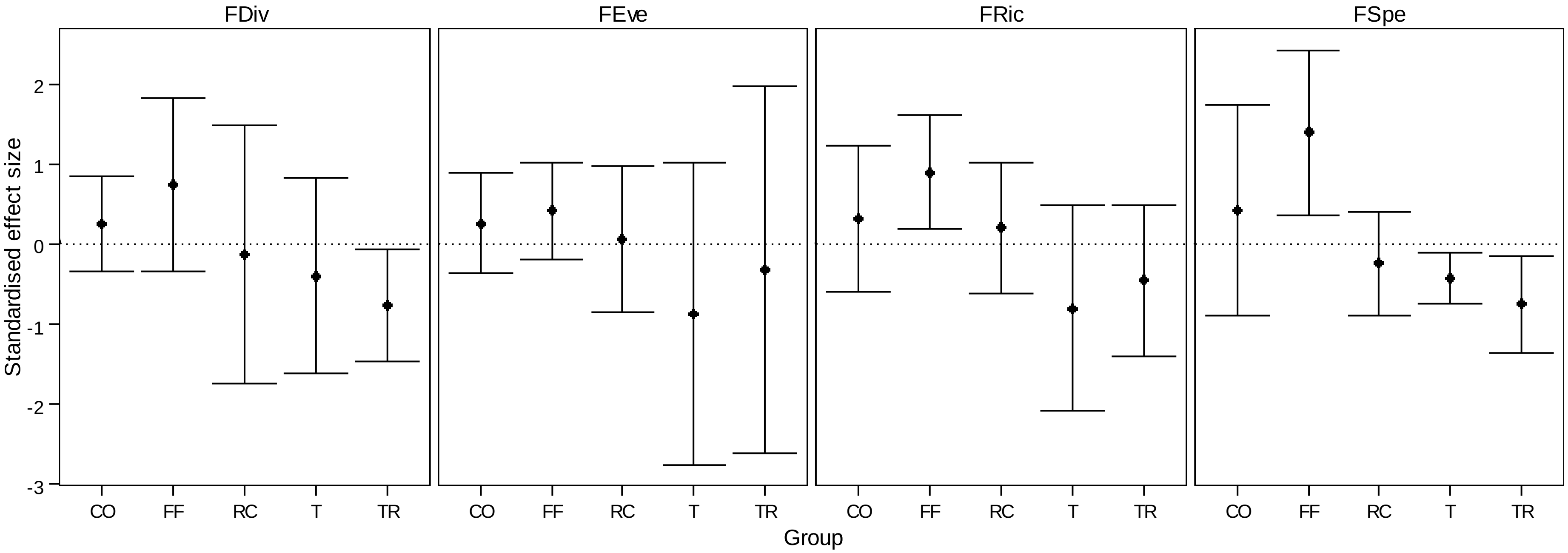

Figure 5.3: Mean standardised effect size of the functional metrics in the different habitats. Zero line represents mean score for 1000 randomized communities. Circles represent means and whiskers represent 95% confidence intervals, so habitats where the whiskers do not cross the dashed line are significantly different from expected. FDiv = Functional Divergence, EEve = Functional Evenness, FRic = Functional Richness, FSpe = Functional Specialisation. CO= coffee plantations, FF = forest fragments, RC = riparian corridors, T = tea plantations, TR = tea riparian.

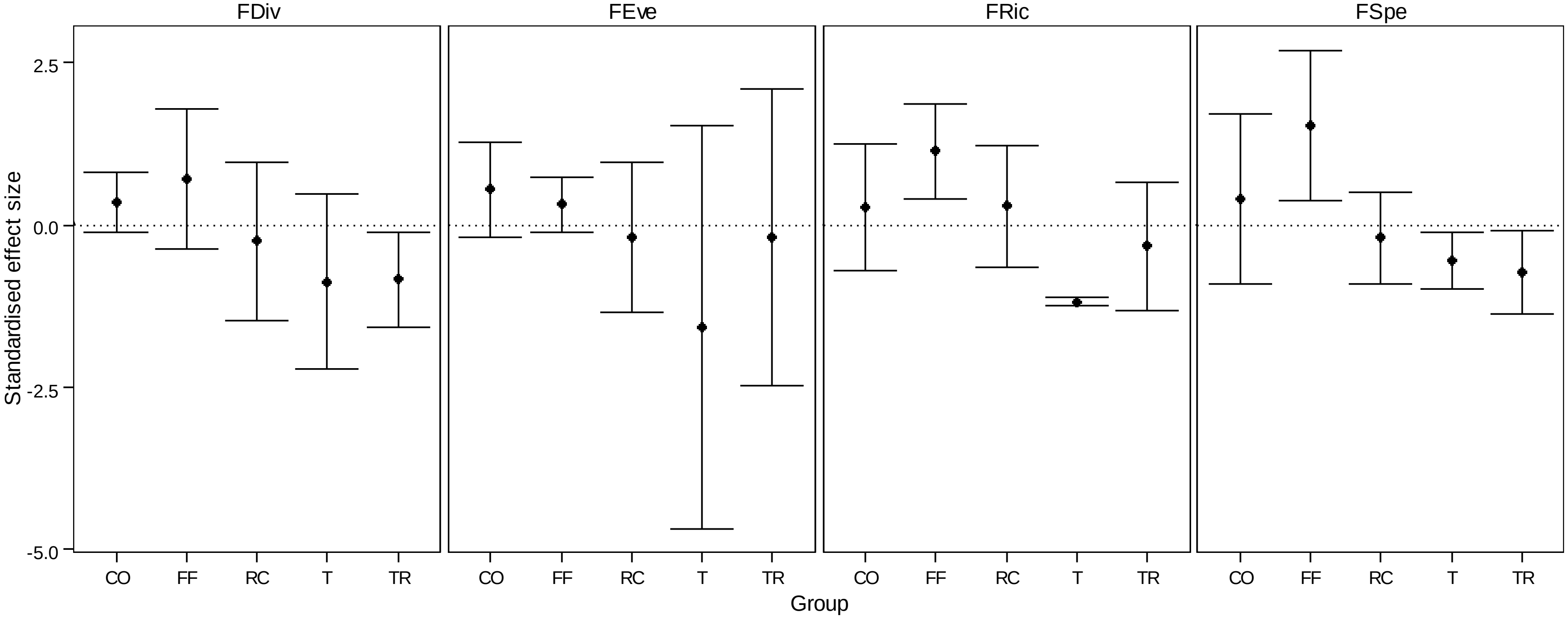

Figure 5.4: Mean standardised effect size of the functional metrics in the different habitats without singletons. Zero line represents mean score for 1000 randomized communities. Circles represent means and whiskers represent 95% confidence intervals, so habitats where the whiskers do not cross the dashed line are significantly different from expected. FDiv = Functional Divergence, EEve = Functional Evenness, FRic = Functional Richness, FSpe = Functional Specialisation. CO= coffee plantations, FF = forest fragments, RC = riparian corridors, T = tea plantations, TR = tea riparian.

5.4.4 Functional richness

There was a significant difference in bat functional richness between habitats (F=3.52, d.f. = 4, *P*=0.026), with forest fragments having significantly greater functional richness than tea plantations (Appendix 2, Figs 5.5, 5.6).

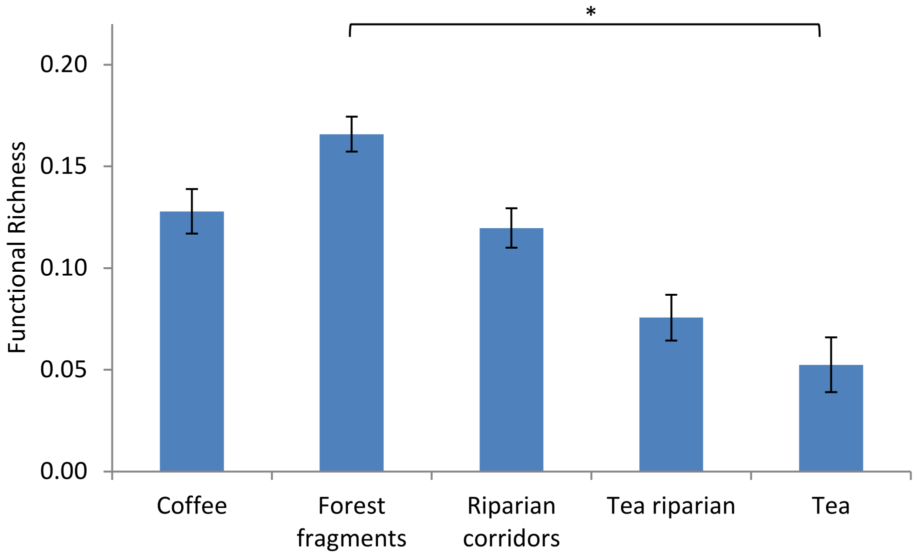

Figure 5.5: Mean per site functional richness with standard errors. *P* values after multiple comparisons correction: <0.05=*, <0.01=**, <0.001=***

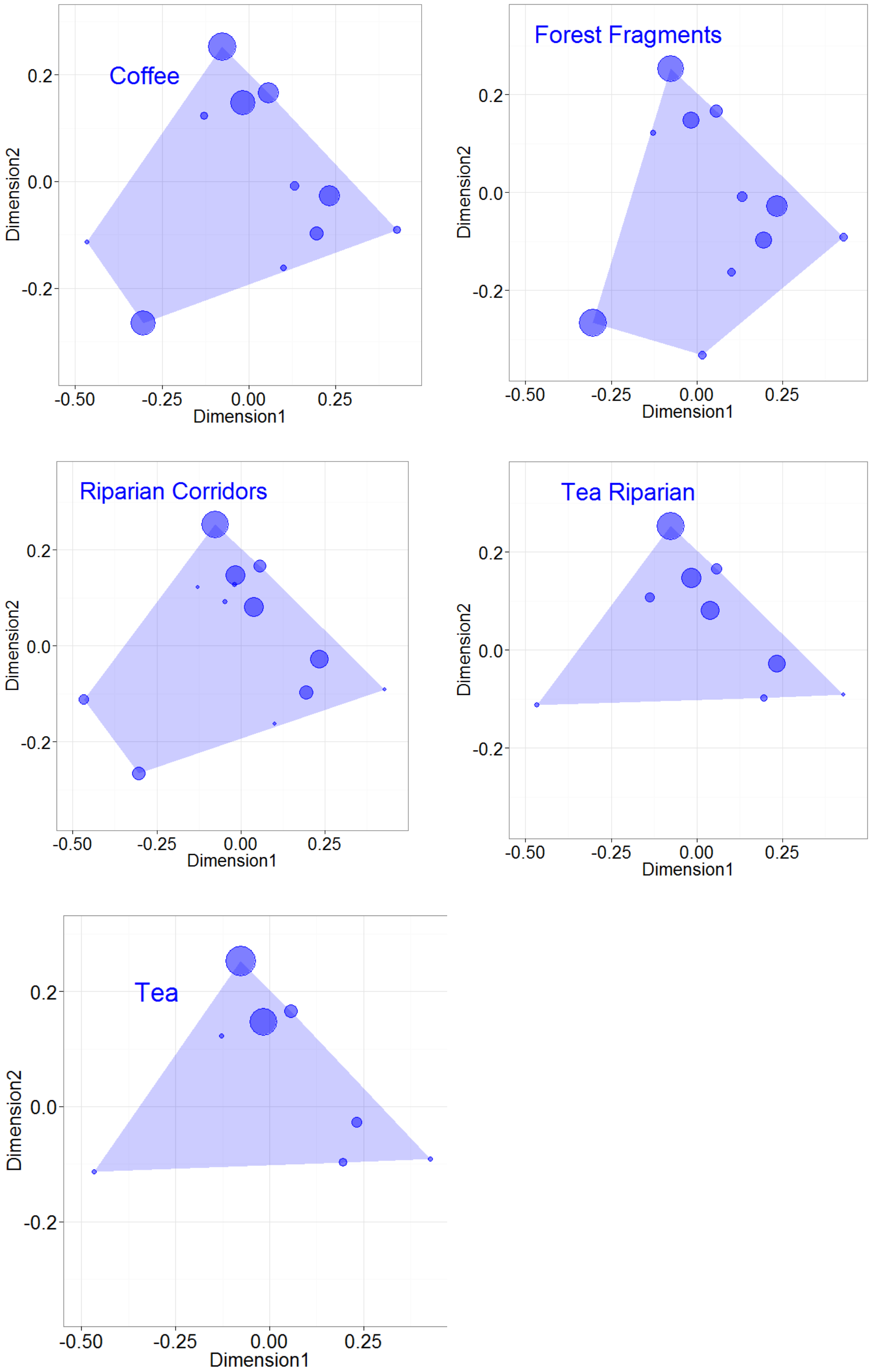

Figure 5.6: Plot of functional richness at the habitat level, based on all sites per habitat combined. Circles represent species, with larger circles indicating greater relative abundance of that species. The area of functional space filled by the polygon represents the functional richness of the community.

5.4.5 Functional evenness

There were no significant differences in bat functional evenness between habitats (Adjusted R^2 =0.0002, $F_{4,19}$=1.001, *P*=0.43; Appendix 2, Fig 5.7).

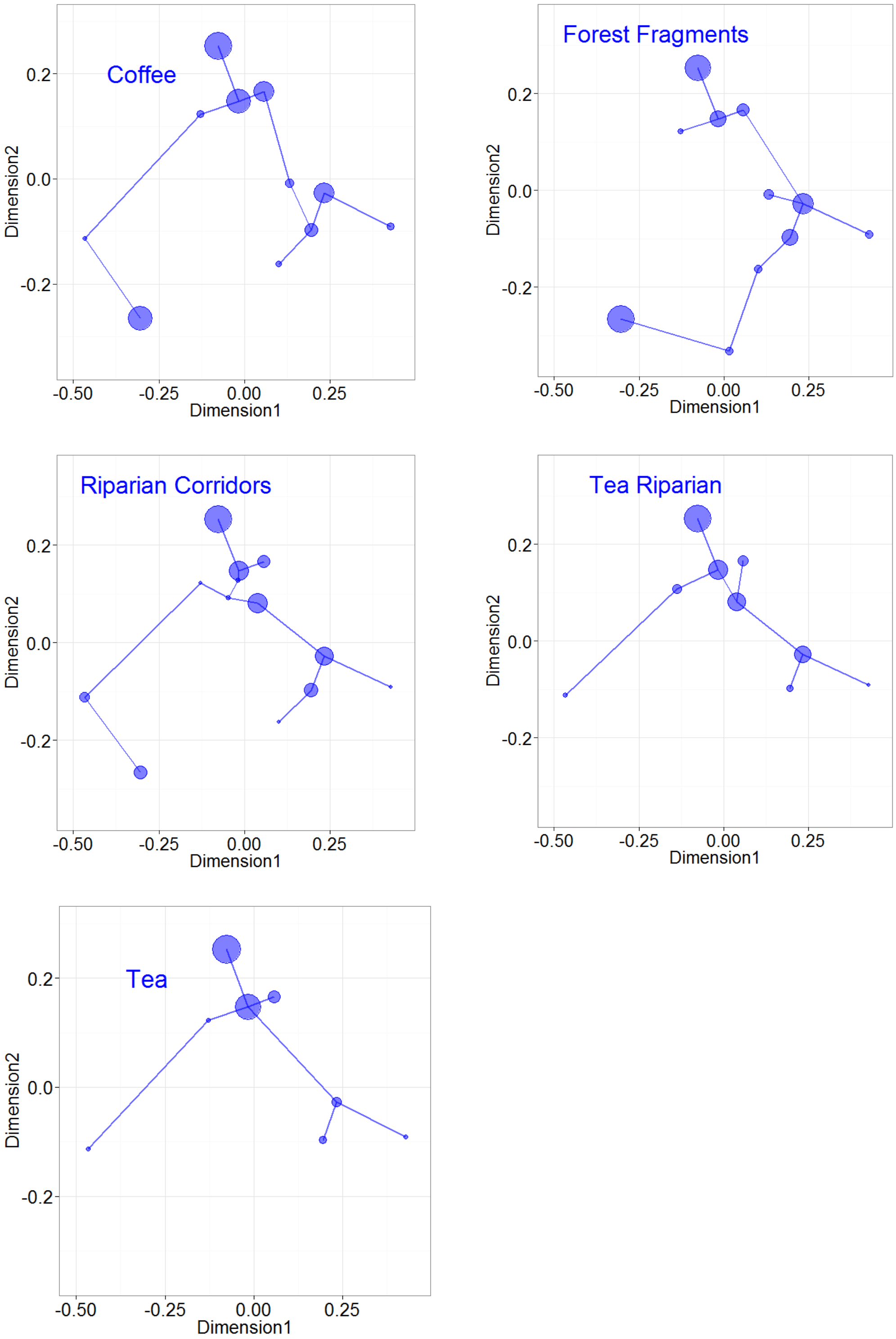

Figure 5.7: Plot of functional evenness at the habitat, based on all sites combined. The minimum spanning tree linking all species is shown Functional evenness is quantified by the regularity of species' distributions along this tree, and the regularity in their abundance.

5.4.5 Functional divergence

There were no significant differences in bat functional divergence between habitats (F=2.32, d.f.=4, *P*=0.094, Figure 5.8, Appendix 2). Forest fragments had borderline significantly greater functional divergence than tea riparian (Appendix 2, Figs 5.8. 5.9).

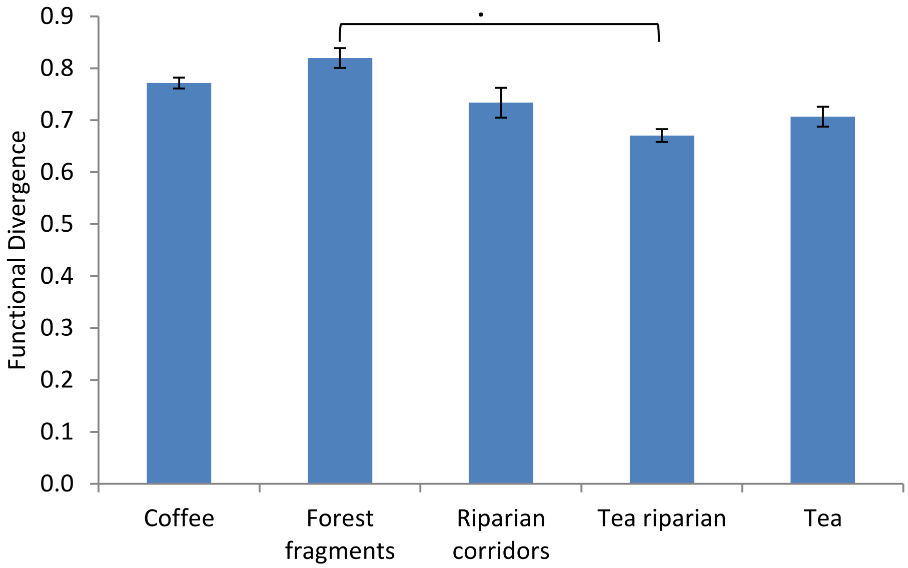

Figure 5.8: Mean per site functional divergence with error bars representing standard deviation. Dot represents *P* <0.055 after multiple comparisons correction.

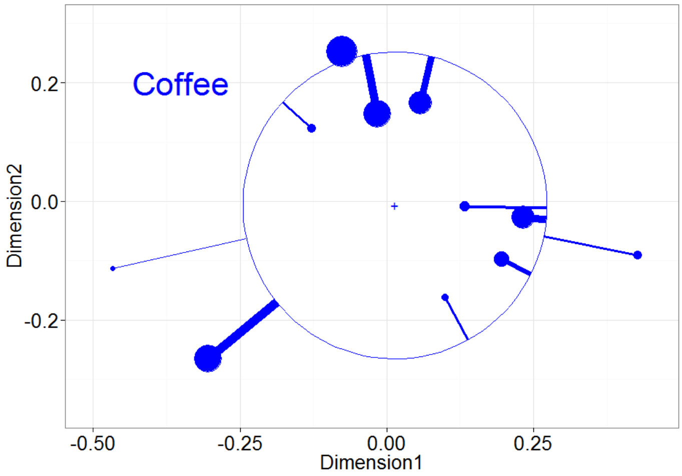

Figure 5.9a: Plot of functional divergence of bats in coffee plantations at the habitat level, based on all sites combined. The cross represents the centre of gravity of the community and the circle represents the mean distance of species from the centre of gravity. Lines represent divergence of each species from the mean, weighted by abundance.

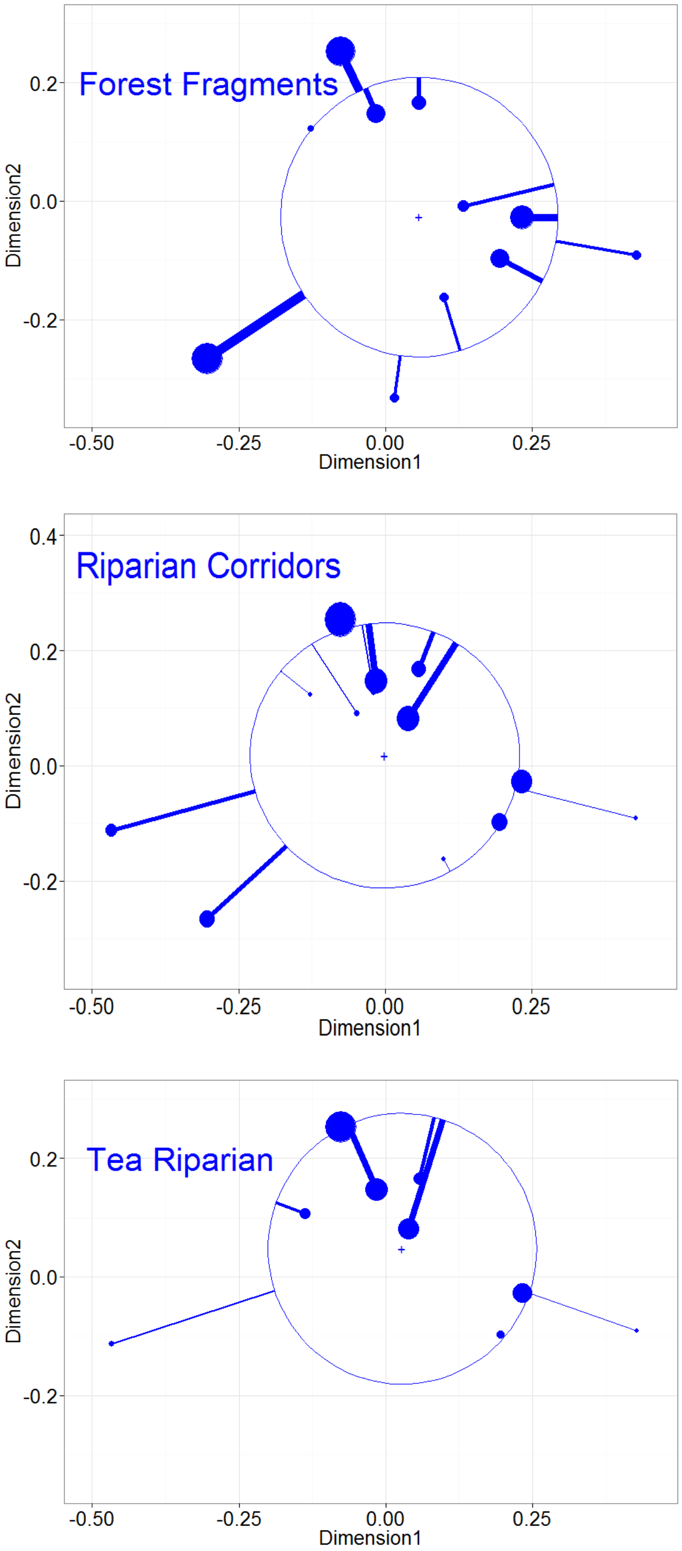

Figure 5.9b: Plot of functional divergence of bats iin forest fragments, riparian corridors and tea riparian at the habitat level, based on all sites combined. The cross represents the centre of gravity of the community and the circle represents the mean distance of species from the centre of gravity. Lines represent divergence of each species from the mean, weighted by abundance.

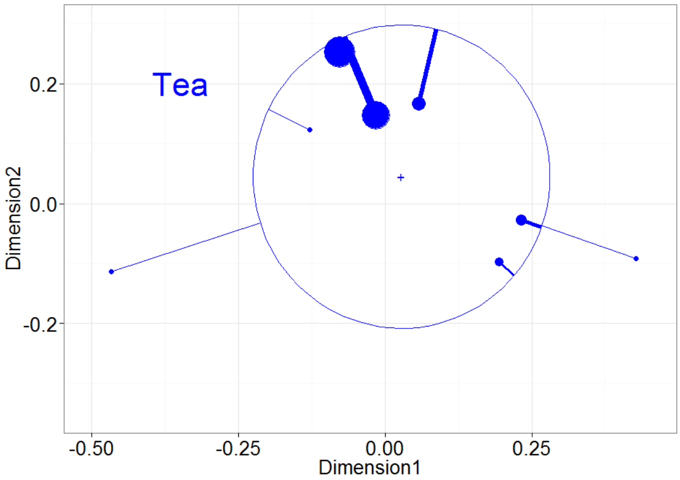

Figure 5.9c: Plot of functional divergence of bats in tea plantations at the habitat level, based on all sites combined. The cross represents the centre of gravity of the community and the circle represents the mean distance of species from the centre of gravity. Lines represent divergence of each species from the mean, weighted by abundance.

5.4.6 Functional specialisation

There was a significant difference in bat functional specialisation between habitats (F=7.28, d.f. = 4, *P*=0.0009). Forest fragments had significantly greater functional divergence than did riparian corridors, tea riparian and tea plantations, and coffee plantations had greater functional divergence than tea riparian (Appendix 2, Figs 5.10, 5.11).

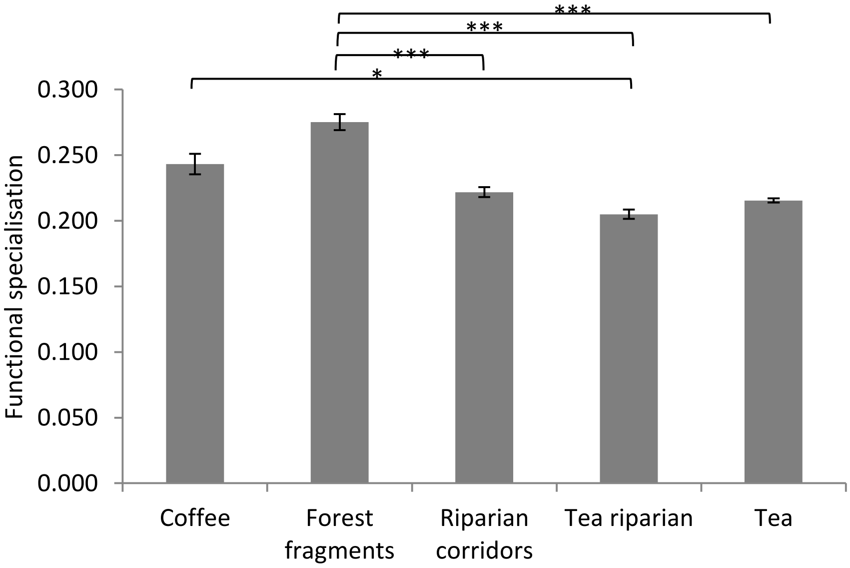

Figure 5.10: Mean per site functional specialisation with standard errors. *P* values after multiple comparisons correction: <0.05=*, <0.01=**, <0.001=***

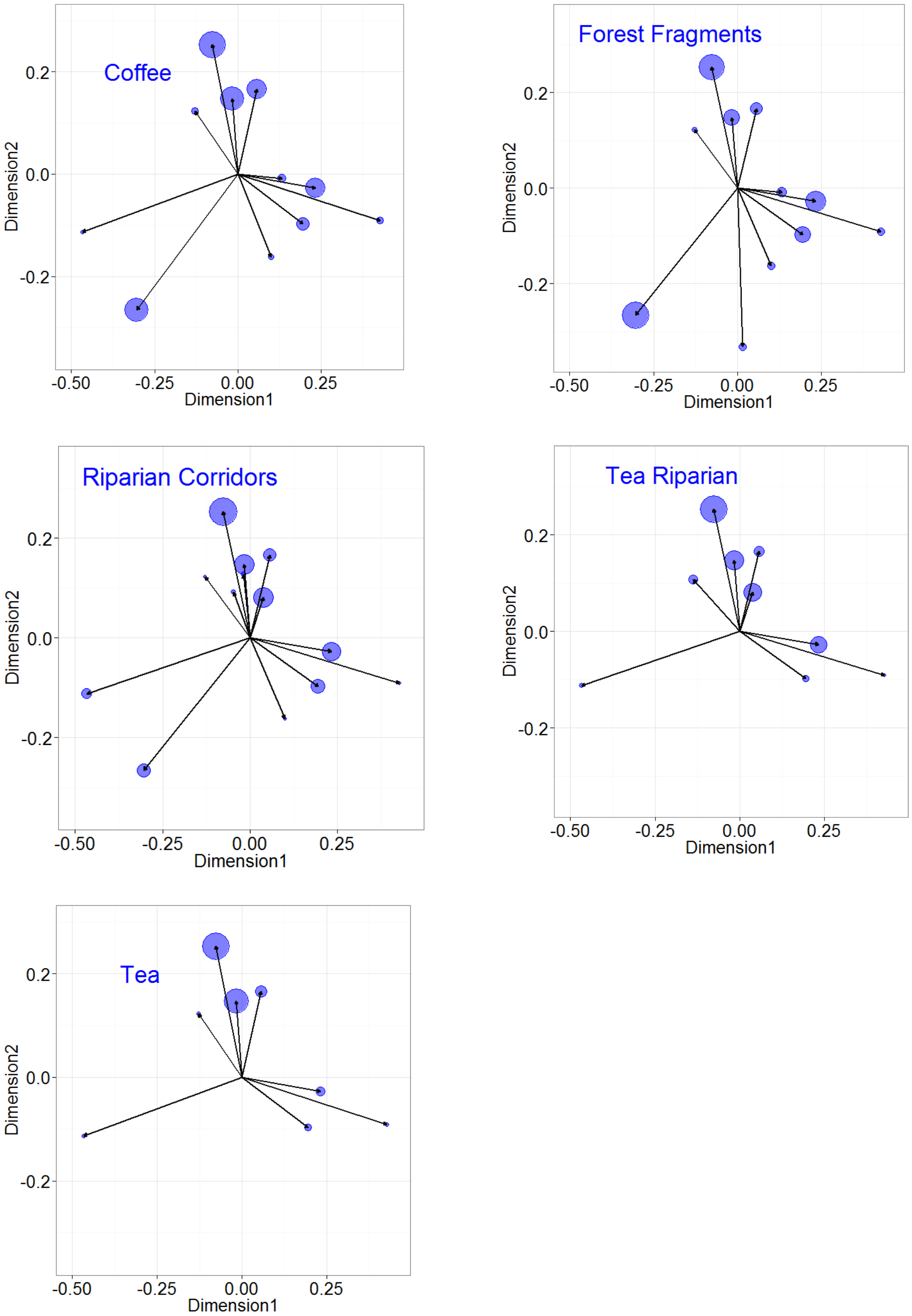

Figure 5.11: Plot of functional specialisation at the habitat level, based on all sites combined. The lines radiate from the mean of all species traits to each species.

5.4.7 Functional richness without singletons

When singletons were removed from each habitat, there was a significant difference in functional richness between habitats (F=8.78, d.f. = 4, p=0.0003). Forest fragments had significantly greater functional richness than tea riparian and tea plantations, and coffee plantations, riparian corridors and tea riparian all had significantly greater functional richness than tea plantations (Appendix 2, Fig 5.12).

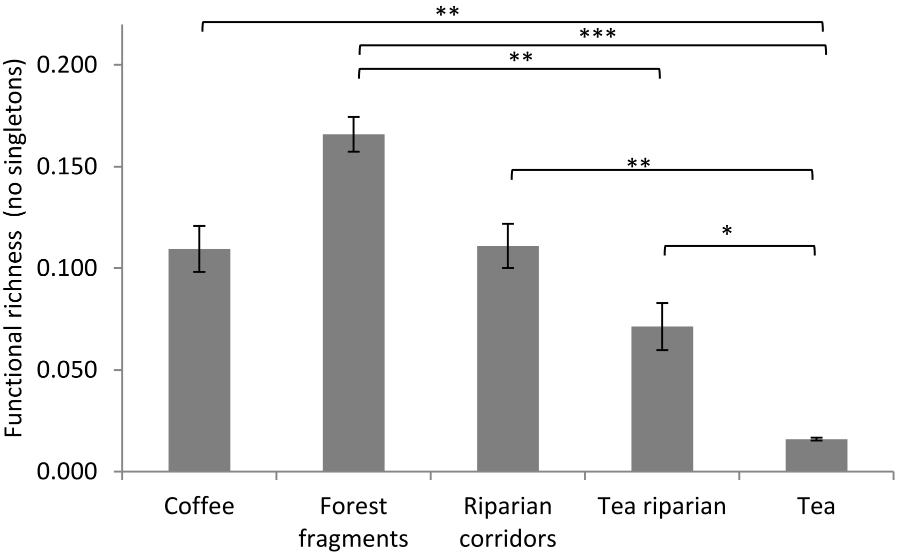

Figure 5.12: Mean per site functional richness after singletons have been removed, with standard errors. *P* values multiple comparisons correction: <0.05=*, <0.01=**, <0.001=***

5.4.8 Functional evenness without singletons

There were no significant differences in functional evenness between habitats after singletons were removed (F=1.8, d.f. =4, *P*=0.17) (Appendix 2).

5.4.9 Functional divergence without singletons

After singletons were removed from every habitat there were significant differences in functional divergence between habitats (F=4.02, d.f.=4, *P*=0.015). Coffee and forest fragments had significantly greater functional divergence than tea riparian and tea plantations (Appendix 2, Fig 5.13).

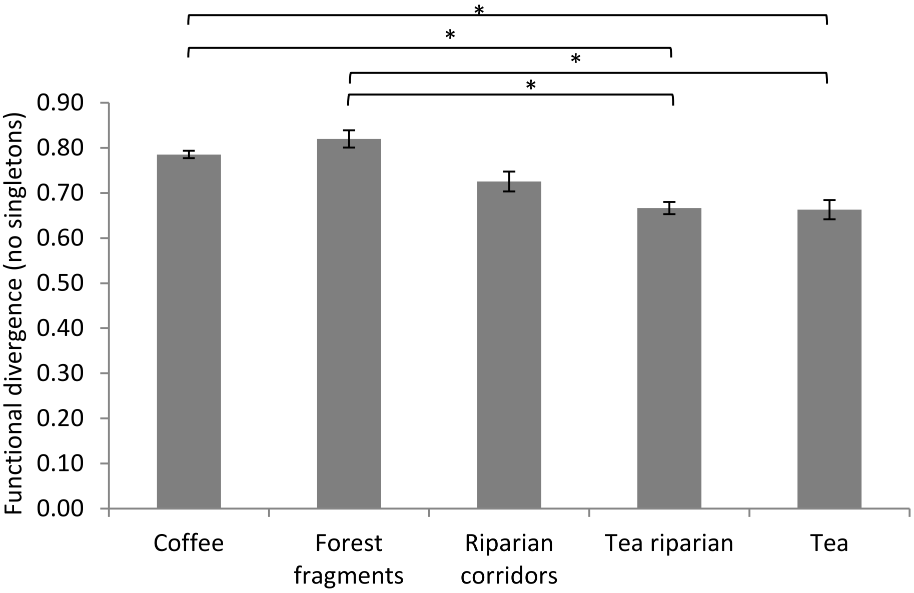

Figure 5.13: Mean per site functional divergence after singletons have been removed, with error bars representing standard deviation. *P* values after multiple comparisons correction: <0.05=*, <0.01=**, <0.001=***

5.4.10 Functional specialisation without singletons

After singletons were removed from every habitat, there were significant differences in functional specialisation between habitats (F=7. 51, d.f. = 4, *P*=0.0008). Forest fragments had significantly greater functional specialisation than all other habitats, and coffee plantations had greater functional specialisation than tea riparian (Appendix 2, Fig 5.14).

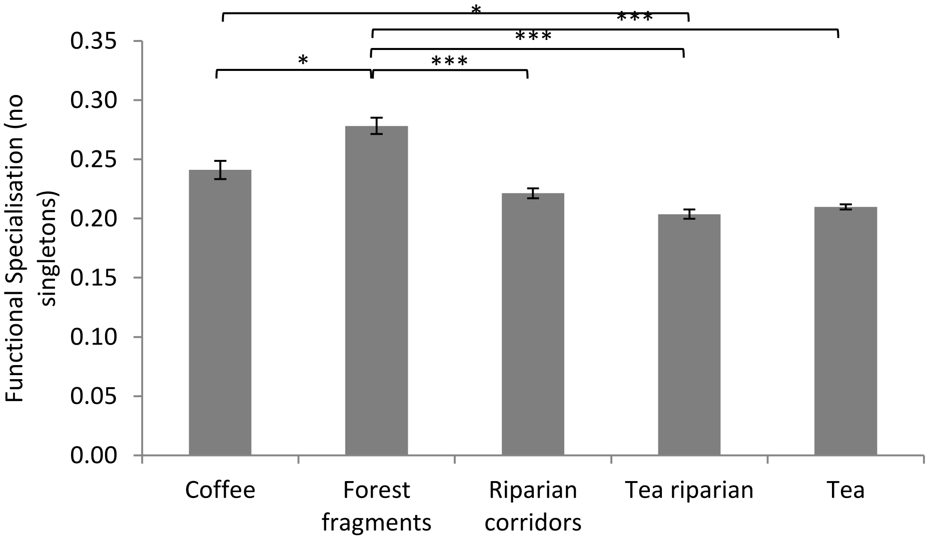

Figure 5.14: Mean per site functional specialisation after singletons have been removed, with error bars representing standard deviation. *P* values after multiple comparisons correction: <0.05=*, <0.01=**, <0.001=***

5.4.12 Functional traits

5.4.12.1 Diet

The percentage of insectivorous species did not change significantly between habitats after correction for multiple comparisons. Insectivore-carnivores were only seen in forest fragments. There were significant differences in the percentage of the assemblage represented by frugivores in different habitats (Kruskal-Wallis χ^2= 13.84, df = 4, *P* =0.007). The percentage of frugivores in tea plantations (mean = 0.909, 95% CI= (0.0, 1.818)) and tea riparian (mean= 1.6, 95% CI (0.0, 2.4)) were significantly lower than those in riparian corridors (mean= 10.899, 95% CI (3.54, 16.22)), coffee plantations (mean = 15.471, 95% CI (3.37, 27.60)) and forest fragments (mean = 27.3, 95% CI (14.60, 40.35)).

5.4.12.2 Call type

The percentage of bats emitting constant frequency calls did not vary significantly between habitats ($F_{4,20}$=2.661, *P*= 0.063). The percentage of bats using frequency modulated calls with a quasi-constant frequency tail (FM.QCF calls) varied significantly between habitats ($F_{4,20}$=11.36, *P*<0.0001; Fig 5.17, Table 5.3). Tea had a greater percentage of FM.QCF bats than all other habitats. Forest fragments had a lower percentage of FM.QCF bats than did coffee plantations, tea riparian, and tea plantations (Table 5.4). Bats making multiharmonic FM calls were only seen in forest. The percentage of bats using frequency modulated calls was significantly different between habitats (Kruskal-Wallis χ^2= 16.155, df = 4, *P* = 0.002). The percentage of bats making FM calls was higher in tea riparian (mean= 15.4, 95% CI (14.60, 40.35)) and riparian corridors (mean 15.191, 95% CI (4.39, 24.35)) than in all other habitats (all: mean = 0, 95% CI (0, 0)).

Table 5.4: Pairwise comparisons of percentage of bats using FM calls with a QCF tail between habitats, with *P* values corrected by false discovery rate (Q).

Contrast	Estimate	SE	df	T ratio	*P* value	Q value
Coffee-Forest fragments	18.578	7.771	20	2.391	0.027	0.045 *
Coffee-Riparian Corridors	5.937	7.771	20	0.764	0.454	0.4538
Coffee-Tea	-31.161	7.771	20	-4.010	0.001	0.002 **
Coffee-Tea Riparian	-7.873	7.771	20	-1.013	0.323	0.359
Forest fragments-Riparian Corridors	-12.641	7.771	20	-1.627	0.119	0.1493
Forest fragments-Tea	-49.739	7.771	20	-6.401	<.0001	<.0001 ***
Forest fragments- Tea Riparian	-26.451	7.771	20	-3.404	0.003	0.007 **
Riparian Corridors -Tea	-37.098	7.771	20	-4.774	0.000	0.0006 ***
Riparian Corridors - Tea Riparian	-13.810	7.771	20	-1.777	0.091	0.1296
Tea- Tea Riparian	23.288	7.771	20	2.997	0.007	0.014 *

5.4.12.3 Call frequency

Mean frequency of maximum energy (FMAXE) in the echolocation calls of the assemblage varied significantly with habitat type, being lowest in tea plantations and highest in forest fragments (Kruskal-Wallis χ^2= 15.253, df = 4, *P*= 0.004; Fig 5.16). Comparing each habitat with the ones with the closest mean values, then those once removed if the nearest neighbour was not significant, bats in tea had significantly lower FMAXEs than those in tea riparian (W = 5916.5, *P*= 0.046), and bats in tea riparian had significantly lower FMAXEs than those in forest fragments (W = 5832.5, *P* = 0.044).

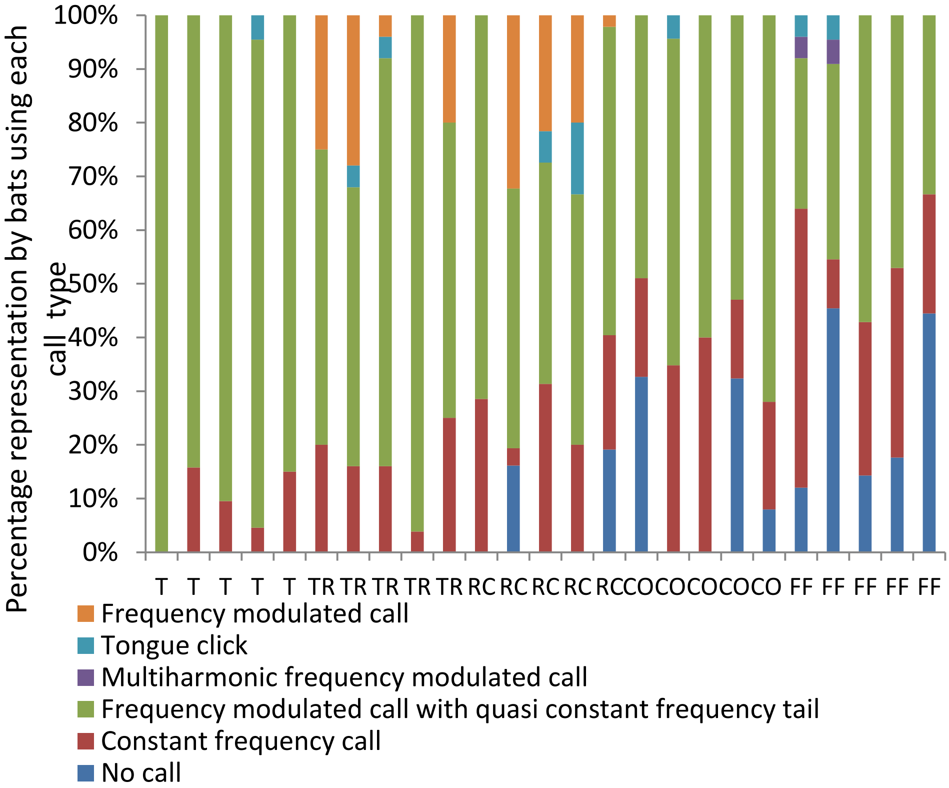

Figure 5.15: Percentages of bats with different call types in each habitat, based on summed data for all the sites per habitat. T= tea plantations, TR= tea riparian, RC= riparian corridors, CO= coffee, FF=forest fragments

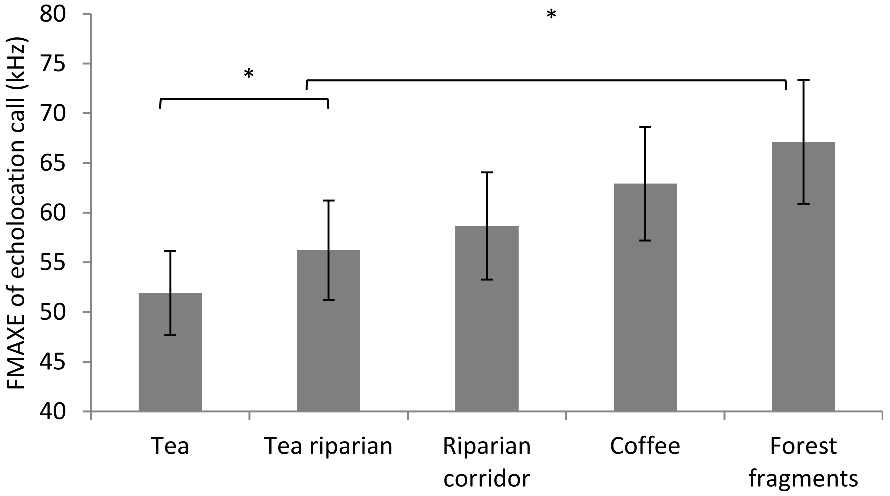

Figure 5.16: Mean frequency of maximum energy of the echolocation calls of the assemblages in each habitat, with error bars representing standard deviation. *P* values: <0.05=*, <0.01=**, <0.001=***

5.4.12.4 Wing aspect ratio

Mean wing aspect ratio (WAR) of the assemblage varied significantly with habitat type, being highest in tea plantations and lowest in forest fragments (Kruskal-Wallis χ^2= 47.783, df = 4, *P* <0.0001; Fig 5.17). Comparing each habitat with the ones with the closest mean values, then those once removed if the nearest neighbour was not significant, bats in tea riparian had a lower mean WAR than tea (W = 8379.5, *P* = 0.005), bats in riparian corridors had a lower mean WAR than tea riparian (W = 12490.5, *P* = 0.023), and bats in forest fragments had a lower mean WAR than riparian corridors (W = 5805, *P* = 0.002).

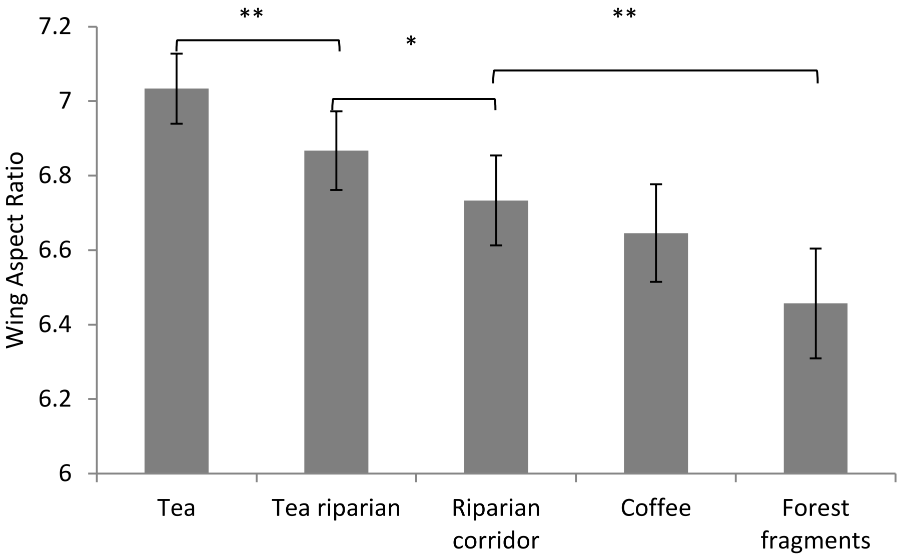

Figure 5.17: Mean wing aspect ratio of the assemblages in each habitat., with standard errors. *P* values: <0.05=*, <0.01=**, <0.001=***

5.4.12.5 Relative wing loading

Mean relative wing loading (RWL) of the assemblage varied significantly with habitat type, being highest in tea plantations and lowest in coffee plantations (Kruskal-Wallis χ^2= 11.273, df = 4, *P*= 0.024; Fig 5.18). Bats in tea and tea riparian had significantly greater relative wing loadings than those in coffee (tea: W = 5707.5, *P* = 0.015, fdr corrected Q value=0.058, tea riparian: W = 9968.5, *P* = 0.004, fdr corrected Q value = 0.03).

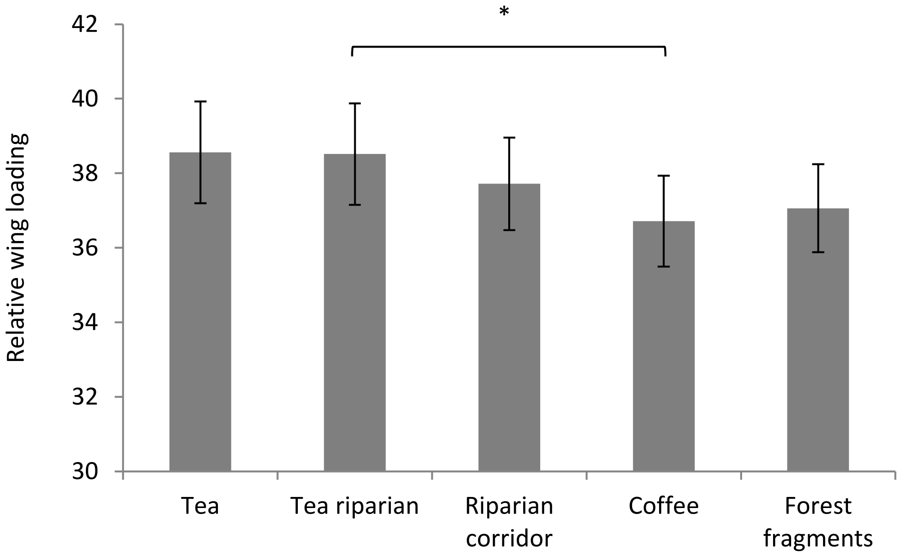

Figure 5.18: Mean relative wing loading of the assemblages in each habitat, with standard errors. *P* values after multiple comparisons corrections: <0.05=*, <0.01=**, <0.001=***

5.4.12.6 Forearm length

Mean forearm length (FA) of the assemblage varied significantly with habitat type, being lowest in tea riparian and highest in forest fragments (Kruskal-Wallis χ^2= 48.938, df = 4, *P* <0.0001; Fig 5.19). Bats in tea, (W = 8832.5, *P* <0.0001, fdr adjusted Q value = 0.0007), tea riparian (W = 16484, *P* <0.0001, fdr adjusted Q value < 0.0001) and riparian corridors (W = 17760.5, *P* =0.0004, fdr adjusted Q value = 0.0007) had significantly smaller forearm lengths than those in coffee plantations. Bats in tea riparian had significantly shorter forearms than those in riparian corridors (W = 16342, *P* = 0.032, fdr adjusted Q value = 0.046).

Bats in tea plantations (W = 5144.5, *P* <0.0001, fdr adjusted Q value = 0.0001), tea riparian (W = 9344, *P* <0.0001, fdr adjusted Q value < 0.0001), riparian corridors (W = 10220.5, *P* = 0.0001, fdr adjusted Q value = 0.0004) had smaller average forearm lengths than those in forest fragments.

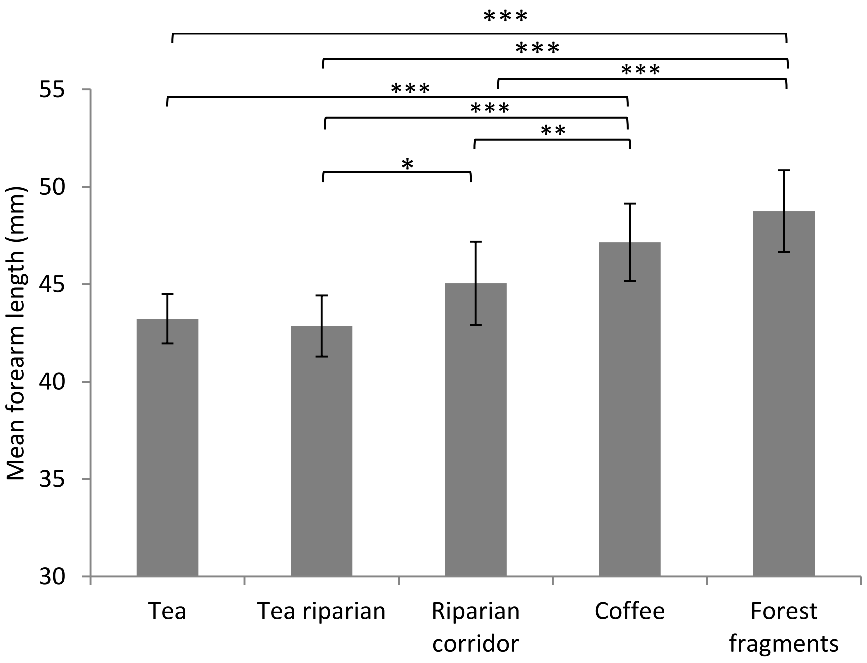

Figure 5.19: Mean relative forearm length of the assemblages in each habitat, with standard errors. P values after multiple comparisons **corrections: <0.05=*, <0.01=**, <0.001=*****

I reran the analysis excluding fruit bats, the largest bats in the assemblage, to focus on the responses of insectivorous and carnivorous bats. Mean forearm length (FA) of the insectivorous and carnivorous bats in the assemblage varied significantly with habitat type, being lowest in riparian corridors and highest in forest fragments (Kruskal-Wallis χ2= 19.184, df = 4, *P*=0.0007; Fig 5.20). Bat species in tea riparian and riparian corridors had smaller mean forearm lengths than those in coffee (tea riparian: W = 12066, *P*=0.0004, fdr corrected Q value = 0.0008; riparian corridors: W = 12575.5, *P*=0.003, fdr corrected Q value = 0.004) and those in forest (tea riparian: W = 6110, *P*=0.003, fdr corrected Q value = 0.004; riparian corridors: 6425.5, *P*= 0.009, fdr corrected Q value = 0.011).

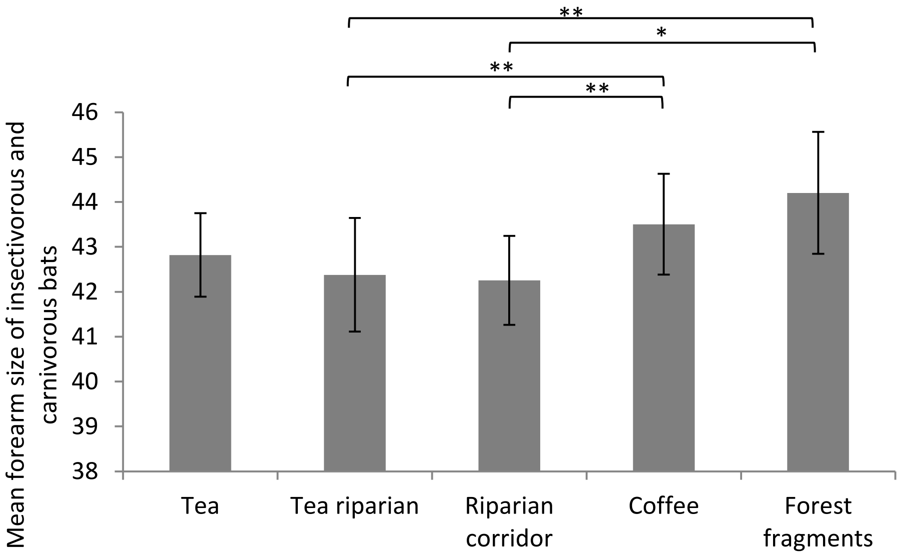

Figure 5.20: Mean relative forearm length of the insectivorous and carnivorous bats in the assemblages in each habitat. ***P* values after multiple comparisons corrections: <0.05=*, <0.01=**, <0.001=*****

5.4.13 Functional guilds

Mean guild richness did not vary between habitats (Deviance = 2.576, df = 4, *P*= 0.631), even when singletons between habitats were removed (Deviance=3.74. df=, *P*= 0.442).

Bats classed as 'open space aerial foragers' according to the criteria of Denzinger and Schnitzler (2013) (*H. tickelli*) did not change significantly in proportional representation between habitats (Kruskal-Wallis $\chi 2$= 4.511, df = 4, *P*=0.341; Fig 5.21). The percentage of 'narrow space flutter detecting foragers' (*H. pomona, R. indorouxii, R. lepidus, R. beddomei, R. affinis*) did not vary significantly between habitats ($F_{4,20}$=2.671, *P*=0.0621). There were too few data to compare 'narrow space passive gleaning foragers' (*M. spasma*), however this species was only seen in forest fragments.

Tea had a greater percentage of 'Edge space aerial foragers' (*P. ceylonicus, M. pusillus, M. fuliginosus, S. heathii, S. kuhlii*) than all other habitats, and tea riparian had a greater percentage than did forest fragments ($F_{4,20}$=10.89, *P*<0.0001; Table 5.5).

Table 5.5: Pairwise comparisons of percentage of 'edge space aerial foragers' between habitats, with *P* values corrected by false discovery rate (Q). Pink indicates significance as given by Q value.

Contrast ESAF	Estimate	SE	df	T ratio	*P* value	Q value
Coffee-Forest fragments	17.274	8.104	20	2.132	0.046	0.076
Coffee-Riparian Corridors	4.044	8.104	20	0.499	0.623	0.623
Coffee-Tea	-33.199	8.104	20	-4.097	0.001	0.002 **
Coffee-Tea Riparian	-10.820	8.104	20	-1.335	0.197	0.219
Forest fragments-Riparian Corridors	-13.229	8.104	20	-1.632	0.118	0.148
Forest fragments-Tea	-50.473	8.104	20	-6.228	<.0001	<.001 ***
Forest fragments- Tea Riparian	-28.094	8.104	20	-3.467	0.002	0.006 **
Riparian Corridors -Tea	-37.244	8.104	20	-4.596	0.000	<.001 ***
Riparian Corridors - Tea Riparian	-14.864	8.104	20	-1.834	0.082	0.117
Tea- Tea Riparian	22.379	8.104	20	2.762	0.012	0.0241 *

The percentage of 'edge space trawling foragers' (*M. montivagus, M. horsfieldii*) varied significantly between habitats (Kruskal-Wallis χ2= 16.155, df = 4, *P*=0.003; Fig 5.21). The percentage of 'edge space trawling foragers' was higher in tea riparian (mean= 15.4, 95% CI (14.60, 40.35)) and riparian corridors (mean 16.069, 95% CI (5.61, 25.53)) than in all other habitats (all: mean = 0, 95% CI (0, 0)).

There were significant differences in the percentage of the assemblage represented by 'narrow space passive active gleaning foragers' (*C. brachyotis, R. leschenaultii*) in different habitats – the results are the same as those for 'frugivores' in '5.4.12.1 Diet'.

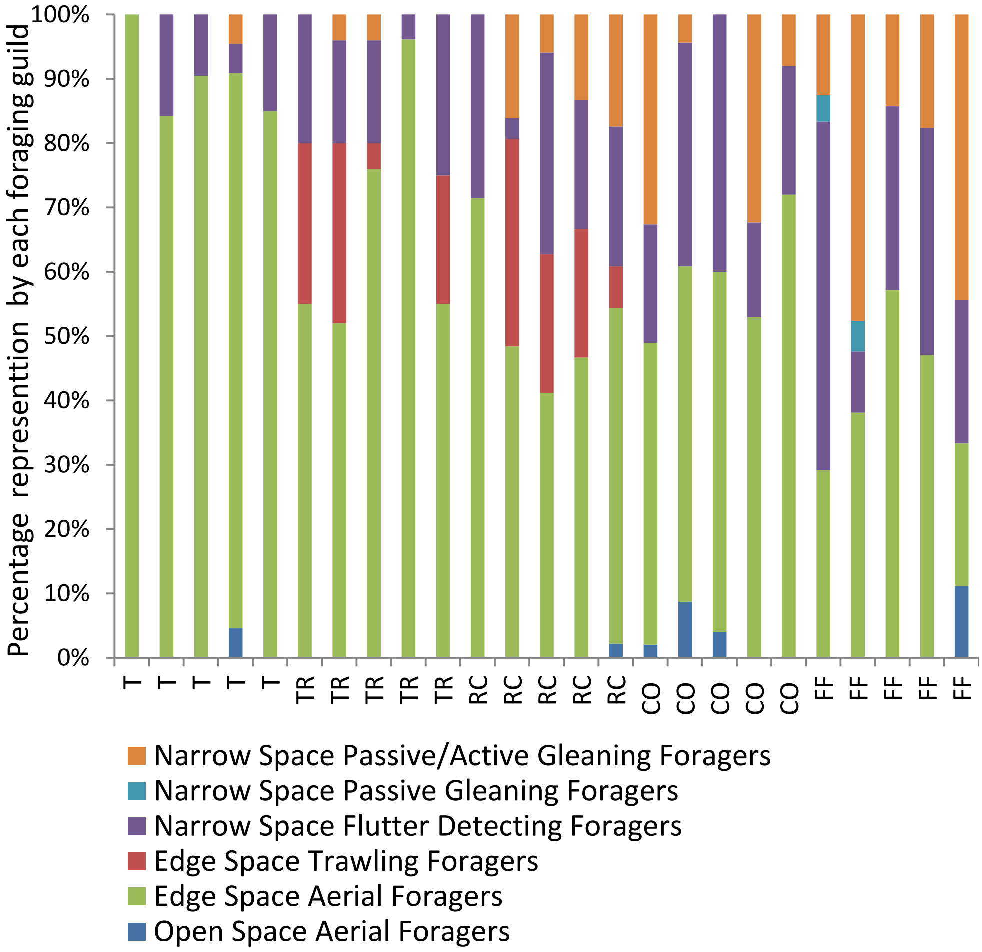

Figure 5.21: Percentages of different guilds in each habitat, based on summed data for all the sites per habitat.

5.5 Discussion

It is clear from this study that tea plantations contain a functionally reduced and filtered bat assemblage compared to forest fragments, with fewer functional specialists. Bat assemblages in tea plantations were filtered by wing morphology, size, diet and echolocation call from forest fragments, but bat assemblages in coffee plantations were functionally very similar to those in forest fragments. Bats in rivers without riparian corridors showed trait filtering when compared to rivers with riparian corridors. Coffee plantations and riparian corridors had functional diversity scores that did not differ from that expected by a process of random assembly, indicating that trait filtering is weak in these habitats. Forest fragments showed greater functional specialisation and richness than expected. It is likely that we have not sampled all the species present in the wider landscape, as the Valparai plateau is adjacent to several protected areas of primary rainforest. It will be interesting to see whether these results stay the same once species from the intact forest are added to the pool.

5.5.1 Functional diversity of coffee and tea plantations

Trait filtering has occurred in tea plantations, as indicated by the low functional specialisation in tea compared to other habitats and that expected by random community assembly. The decline in both functional richness and specialisation from forest fragments to tea plantations indicates that specialist species had been lost, but new disturbance-tolerant species were not gained. This means several functional niches have been lost Looking at the different traits measured, most traits showed altered values in tea plantations from forest fragments.

The loss of frugivores in tea plantations when compared to forest fragments and coffee plantations is presumably due to the lack of chiropterophilous flowers and fruits in tea plantations. *Megaderma spasma*, which is an insectivore-carnivore, was seen in forest fragments but not tea plantations. *M. spasma* is a typically forest-adapted species, slow but manoeuvrable, hunting partly by vision/passive listening and echolocating quietly (Norberg and Fenton 1988, Fenton 1990). This species gleans its prey from tree trunks, branches, leaves or the forest floor and consumes large insects as well as vertebrates (Davison and Zubaid 1992, French 1997). Energy costs of traveling longer distances to feed might make it difficult for this species to hunt in open tea plantations, and there may be fewer prey.

Bats in tea had low FMAXE, mostly used FM.QCF calls, had high WAR and high RWL; all features characteristic of fast, efficient flying bats that detect a wide range of prey across large distances in open environments (Norberg and Rayner 1987, Schnitzler and Kalko 2001, Altringham 2011, Denzinger and Schnitzler 2013). Bat species in tea plantations were also smaller than those in coffee plantations and forest fragments, which was mostly but not completely driven by the absence of larger frugivorous bats. Larger insectivorous bats may, on average, eat larger insects, which might not be present in tea plantations.

Functional richness in tea was significantly lower than expected from the process of random assembly only after singletons were removed, indicating that functional richness in tea was mostly driven by scarce species that would add little to the functioning of the ecosystem. The other functional diversity metrics changed less when singletons were removed, as expected due to the abundance weighting built into those metrics.

Coffee plantations were not significantly functionally poorer than forest fragments, but when singletons were removed coffee plantations showed reduced functional specialisation compared to forest fragments. More bat species in coffee plantations used FM.QCF calls than were seen in forest fragments. Coffee plantations have a more open understory than forest fragments, and these calls are likely to be more useful in this habitat than in the denser forest fragments. From a functional viewpoint, shade coffee plantations are a reasonable replacement for forest fragments for bats, and could play an important role in buffer zones of national parks.

Forest fragments scored higher than expected on functional richness and specialisation, indicating that this habitat contained a greater diversity of functional traits and more species with specialist traits than would be expected by chance. This may be because in sampling across an agricultural landscape, the few specialist species are concentrated in forest fragments.

5.5.2 Functional diversity of rivers with and without riparian corridors.

Traditional measures of biodiversity such as species richness did not show significant differences between rivers with and without riparian corridors, possibly due to insufficient sampling, but functional trait analysis revealed differences between the two habitats. Rivers without riparian corridors scored lower than expected on functional divergence and specialisation, indicating that trait filtering is occurring. In rivers without riparian corridors, bat species had on average higher wing aspect ratios and were smaller than those on rivers with riparian corridors, indicating that they were more open-adapted species than those seen along riparian corridors. There were also significantly more frugivores along rivers with riparian corridors, probably due to the absence of fruit in areas without mature native trees in this landscape.

5.5.3 Importance of functional traits in assemblage structuring

All traits studied showed significant changes in different habitats. Diet varied between habitats, but only changes in the percentage of frugivores could be distinguished statistically. Other studies have also found dietary guild specific responses to habitat change (Klingbeil and Willig 2009, Avila-Cabadilla et al. 2009, 2012). In this study I had little detailed information on the dietary habits of many species, so our understanding could be improved with a better knowledge of food preferences.

Echolocation call type and frequency varied between assemblages in different habitats. Other studies also found higher frequency calls, and steep FM calls, were more associated with forested habitat (Threlfall et al. 2011, Hanspach et al. 2012).

Wing aspect ratio was one of the strongest factors in determining assemblage composition in this study, increasing as habitats became more open. A much weaker but still significant effect was seen in relative wing loading, with average relative wing loadings increasing in more open habitats. Jones et al. (2003) found that low aspect ratio wings independently predicted extinction risk in non-pteropodid bats. Duchamp and Swihart (2008) and Hanspach et al. (2012) found wing loading to be slightly more important than wing aspect ratio for structuring communities, and Threlfall et al. (2011) found aspect ratio to be more important.

Mean forearm length was about as important as wing aspect ratio in determining assemblage composition in different habitats, with open spaces having smaller bats on average than more complex environments. This was driven greatly by frugivorous bats, two of the largest species in the assemblage. Even after frugivores were removed from the analysis, however, significant differences in body size were seen between habitats, with smaller average forearm length of bats still seen in more open areas.

Some studies on temperate or subtropical insectivorous bat communities found larger bat species more often in open areas, and smaller bat species in more forested environments (Threlfall et al. 2011, Hanspach et al. 2012). Ford et al. (2005) expected a North American assemblage to follow this pattern but no obvious pattern emerged. The relationship between body size and disturbance tolerance may be different depending on the genera present in the regional species pool, and merits further investigation.

All the traits present had some explanatory power in describing the structuring of the assemblages, and their relative importance can be assessed to some degree by their test statistics. As I did not measure habitat variables I could not perform an RLQ analysis, which would more accurately quantify the relative filtering of different traits in modified habitats. This could form the basis of further work.

5.5.4 Functional guilds and functional diversity

Mean per site guild richness did not vary significantly between habitats – but functional richness based on trait space did vary significantly, with forest fragments being functionally richer than tea plantations. When singletons were removed, guild richness still did not vary significantly, but functional richness was lower in tea plantations than in all other habitats, and lower than expected from a process of random assembly. Functional richness was distinctly more sensitive at detecting functional differences in this study than guild richness.

The percentage of the assemblage comprised of guilds such as ‘narrow space flutter detector foragers’ and ‘narrow space passive gleaning foragers’ did not vary significantly between habitats, but when they were plotted in trait space these species had an impact on scores of functional diversity and specialisation. Forest fragments had significantly greater functional specialisation than tea plantations, tea riparian and riparian corridors, while coffee plantations had greater functional specialisation than tea riparian. Functional specialisation is influenced by many specialised trait combinations so may be more sensitive at detecting changes in less common specialist species, where low numbers and non-normally distributed data may make inter-habitat comparisons difficult using guilds.

Many bat species are flexible in behaviour and foraging habitat and do not necessarily behave according to the expectations of their guild. *H. tickelli* fitted the description of Denzinger et al (2013) as an ‘open space aerial forager’ due to its low frequency echolocation call. This species was however more abundant (although non-significantly) in coffee plantations and forest fragments than in tea plantations. The predominant species in tea - a very open habitat - were classified as ‘edge space aerial foragers’ and ‘narrow space flutter detecting foragers’.

Plotting the species by trait in functional space I saw that *Rhinolophus lepidus* and *Rhinolophus indorouxii* –the two ‘narrow space flutter detecting foragers’ found in tea – were plotted closer to the ‘edge space aerial foragers’ than were *Rhinolophus* *beddomei* and *Hipposideros pomona*, which were rare or absent in open habitats. This may explain why *R. lepidus* and *R. indorouxii* were seen in tea where other 'narrow space flutter detecting foragers' were not.

Functional diversity captures more information about each species when presented as a continuum in trait space rather than as a set of categories. This is because functional guild analyses assume all species within each group are highly similar, although this assumption is rarely explicitly tested (Tilman 2001). Several other authors also report bats to behave in a manner not expected by a species in the guild it was assigned to (Arlettaz 1999, Ford et al. 2005, Luck et al. 2013) or behaving in a manner different to that expected from its morphological traits (Saunders and Barclay 1992).

The input traits for our study could benefit from some additions, such as behavioural traits about foraging habitats that might separate riparian species thought to trawl/gaff from other vespertilionid bats, or detailed dietary analyses. However this information is currently not sufficiently detailed for all species in this assemblage, and the functional diversity and specialisation metrics have found some meaningful trends. Comparing the values for each trait across habitats was an informative approach, which could benefit from being combined with environmental variables in an RLQ analysis. Looking at the values for each trait was more informative than comparing guilds.

5.5.5 Summary

Bat assemblages in coffee plantations show similar functional diversity and slightly lower functional specialisation relative to assemblages in forest fragments. However, bats in tea plantations showed a reduction in functional diversity and specialisation and had experienced trait filtering. Trait filtering was also apparent in riparian areas without corridors when compared to those with corridors.

As habitats became more open there was an increase in the number of bat species that were smaller, called at lower frequencies, had higher relative wing loadings and aspect ratios. Assemblages in more open areas contained fewer frugivores and were more dominated by FM.QCF bats.

Functional guild analyses were less sensitive than trait space based metrics, especially to changes in less common species.

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Chapter Six: General Discussion

6.1 Abstract

We report the presence of seventeen species from five families in the agricultural landscape of the Valparai plateau in the southern Western Ghats of India. Among these were a new location record for the endangered *Latidens salimalii,* and a new location record for *Barbastella leucomelas darjelingensis*, previously thought to be restricted to temperate regions of North India and Central Asia. We also report two species not predicted to live in this area by the IUCN range maps (*Hesperoptenus tickelli* and *Miniopterus pusillus*), and report a possible cryptic species in *R. lepidus*.

We built a GIS map for the area under study and generated habitat suitability models for ten species. The smaller scales from 100 – 500 m were generally the strongest predictors of the spatial distribution of foraging bats, probably due to their high mobility which allows them to find even small, isolated foraging habitat patches. The variables which best predicted the presence of bats were habitats containing native trees (positive response), tea plantations (negative response), habitat richness (positive response) and distance from water's edge (negative response).

We compared species richness, abundance and composition data from sampling bats using mist nets with using ultrasonic bat detectors on acoustic transects. Acoustic transects detected more species at greater abundances than did mist nets, highlighting the need for more acoustic monitoring of bats in tropical regions. According to the results of catching and acoustic work combined, coffee plantations did not differ significantly from forest fragments in bat species richness and abundance, but did differ in species composition. Tea plantations had lower species richness than coffee plantations or forest fragments and many species declined in abundance in tea, although two species increased in abundance in this habitat.

Functional richness and specialisation of bats in forest fragments were significantly greater than expected from a process of random assembly, and functional specialisation in tea was significantly poorer than expected, indicating that trait based filtering was occurring in tea plantations. The bat species in tea plantations were on

average smaller, with lower frequency echolocation calls, higher relative wing loadings and higher wing aspect ratios than bat species in coffee plantations and forest fragments, with more species using frequency modulated calls with a quasi-constant frequency tail. These are traits typical of fast, efficient flyers hunting across large distances in open environments (Norberg and Rayner 1987, Schnitzler and Kalko 2001, Altringham 2011, Denzinger and Schnitzler 2013). There were less frugivorous bats in tea plantations than in coffee plantations and forest fragments, probably due to the lack of fruit in this habitat.

Traditional biodiversity metrics did not detect significant differences in bat assemblages between rivers with and without riparian corridors. However functional diversity analyses showed that while rivers with riparian corridors did not differ from the regional species pool, rivers without riparian corridors had lower than expected functional specialisation and functional divergence than expected. Rivers without riparian corridors had fewer frugivores than rivers with riparian corridors, and had bat species with on average higher wing aspect ratios than on rivers with riparian corridors. Higher wing aspect ratios suggest that these species are more open-adapted, fast hunters.

Trait space based functional metrics appear to be more sensitive at picking up trends than categorical measures such as guild richness. They also have the benefits of working equally well with non-normally distributed data and not obscuring intra-guild differences.

6.2 Bat species present in the Valparai plateau

In the agricultural landscape we found eighteen species of five families and twelve genera, and recorded a potential morphospecies. This is a comparable number to the twenty species caught in a recent survey in the protected wet evergreen forests of Kudremukh National Park in the Western Ghats of Karnataka (Raghuram et al. 2014; Table 6.1), indicating that per site bat diversity may be lower in India than in South East Asia where 40 or more species are often seen per site (Heller and Volleth 1995, Struebig et al. 2008).

The discovery of *Barbastella leucomelas darjelingensis* in this region extends the range of this species – indeed, bats of this genus have not previously been reported from tropical assemblages. Finding *Latidens salimalii* may provide new opportunities for the conservation of this endangered species. *H. tickelli* and *M. pusillus* were not predicted to live in this area based on IUCN range maps, but have both been seen in south India so it is not surprising to find them in this landscape (Korad et al. 2007, Bumrungsri et al. 2008, Csorba et al. 2008c). Ten species that the IUCN predicted to be present in the Valparai area were not recorded: *Pteropus giganteus*, *Hipposideros ater, H. fulvus*, *H. speoris, Megaderma lyra, Harpiocephalus harpia lasyurus, Pipistrellus coromandra* and *P. tenuis* (Bates 1997, Csorba et al. 2008a, 2008b, 2008d, 2008e, Francis et al. 2008,

Table 6.1: Comparison of species seen in Valparai and in Kudremukh National Park.

Genus	Valparai, Tamil Nadu	Kudremukh National Park, Karnataka
Pteropodidae	*Rousettus leschenaultii*	*Rousettus leschenaultii*
	Cynopterus brachyotis	*Cynopterus brachyotis*
	Latidens salimalii	*Cynopterus sphinx*
		Pteropus giganteus
Vespertilionidae	*Myotis horsfieldii*	*Myotis horsfieldii*
	Hesperoptenus tickelli	*Hesperoptenus tickelli*
	Scotophilus kuhlii	*Scotophilus kuhlii*
	Pipistrellus ceylonicus	*Pipistrellus ceylonicus*
	Scotophilus heathii	*Pipistrellus affinis*
	Barbastella leucomelas darjelingensis	*Pipistrellus tenuis*
	Miniopterus fuliginosus	*Pipistrellus coromandra*
	Miniopterus pusillus	*Harpiocephalus harpia*
	Myotis montivagus	*Murina cyclotis*
	One morphospecies	*Tylonycteris pachypus*
Rhinolophidae	*Rhinolophus lepidus*	*Rhinolophus lepidus*
	Rhinolophus beddomei	*Rhinolophus beddomei*
	Rhinolophus indorouxii	*Rhinolophus rouxii*
	Rhinolophus affinis?	
Hipposideridae	*Hipposideros pomona*	*Hipposideros galeritus*
Megadermatidae	*Megaderma spasma*	*Megaderma spasma*
		Megaderma lyra

Molur et al. 2008a, 2008b, Srinivasulu and Molur 2008). Several of these were seen in a recent survey in Kudremukh National Park at 13 °N in the Western Ghats, some 500 km to the north of Valparai (Raghuram et al. 2014; Table 6.1). This paper was not discussed in my echolocation call library paper as it was not then published. The location in which they were seen was at a lower altitude (max. 880 m) and higher latitude than Valparai, and the site is separated from Valparai by the Palakkad Gap, a low elevation break in the Western Ghats. We recorded the same families in Valparai as were seen in Kudremukh National Park, north of the Palakkad Gap, and families were similarly represented in terms of species numbers. About half the assemblage - nine species (Table 6.1) were seen in both sites.

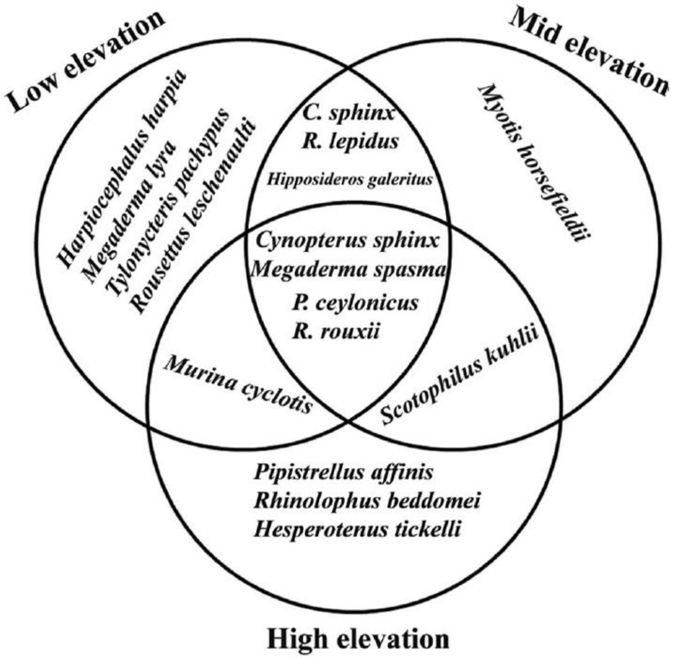

Figure 6.1: Species seen at low elevation (86-108 m), mid elevation (409-512 m) and high elevation (860-880 m) sites in Kudremukh National Park, Karnataka.

The differences in assemblage composition between the sites may be due to altitudinal differences (Fig 6.1), or may be due to the inability of some of these species to cross the Palakkad Gap. It is also possible that some species remain undetected, for example some of the species from Kudremukh may be present in the intact forests surrounding Valparai but not in the agricultural landscape itself.

Most of the species recorded in Kudremukh echolocated at similar frequencies to those reported in this thesis from Valparai. The CF component of *Rhinolophus beddomei* echolocation calls were slightly lower at 38.5-38.7 kHz in Kudremukh compared to 41.7-43.3 kHz in Valparai. *Rhinolphus lepidus* echolocated at a lower frequency at Kudremukh, with the CF component at 95 kHz (93.2-96.8) in Kudremukh, compared to a mean of 102.3 kHz (97-106.3) in Valparai. This difference in call frequency may indicate that *R. lepidus* is in fact different cryptic species or subspecies in the two locations. As seen in the *R. rouxii* species complex, genetically distinct species with slightly different morphometric measurements and very different echolocation calls can be found in neighbouring states in India (Chattopadhyay et al. 2010, 2012) – indeed different species from the *R. rouxii* complex were seen in Kudremukh and Valparai. Further genetic and morphological data are needed to explore this hypothesis.

6.3 Acoustic recording versus bat capture

Most studies of bats in the tropics rely entirely on data from bats caught in mist nets, and/or harp traps, despite research indicating that acoustic methods may record more species and be more representative of bat assemblages (Fenton 1990, O'Farrell and Gannon 1999, Gannon et al. 2003, MacSwiney et al. 2008). The use of acoustic methods has been hampered by the lack of call libraries in the tropics.

While not all of the species from Valparai were distinguishable based on echolocation call, and some do not echolocate, the majority of species could be effectively sampled with acoustic detectors. Our work showed that while combining the results of catching and acoustic data is the optimum strategy, acoustic transects alone should be used in preference to catching alone. The mean number of bat species per habitat as detected by catching ranged from 0.2-1.7 per habitat per night as assessed by catching, 4-6.4 species where acoustic detectors were used, and 4.2-7.4 species where both methods were combined. Rarefied species richness could not be calculated for bats detected by catching, as there were too many zeroes in the dataset. The species composition of bat assemblages as measured by catching alone were not significantly different between different habitats, but most habitats could be distinguished on the basis of species composition based on the results of acoustic transects alone. We encourage more use of acoustic methods to study bats in tropical areas.

6.4 Habitat suitability modelling in tropical bats

Fine scale habitat suitability models were built for ten species. While some studies considered that the mobility of bats means fine scale factors are not likely to be good predictors of occurrence (Milne et al. 2006), others have shown that in fact their mobility allows many bat species to exploit small, isolated habitat resources, and bat presence is best predicted at scales of 20 m - 500 m (Ober et al. 2008, Pinto and Keitt 2008, Meyer and Kalko 2008, Lookingbill et al. 2010, Fabianek et al. 2011, Razgour et al. 2011, Akasaka et al. 2012, Bellamy et al. 2013, Hahn et al. 2014). In our models, all the variables in the best performing model for each species were either non-scalar variables or between 100 and 500 m in scale.

The most important variables in predicting species occurrence were percentage cover of tea plantations and distance to water (negative responses), and native tree cover and habitat richness (positive responses), which were all seen in the final model for two or more species. Percentage native tree cover (encompassing forest fragments and modified habitat such as overgrown eucalyptus plantations and shaded coffee plantations) was a better predictor for all species than forest fragment cover, indicating that shade plantations and secondary regrowth can be important for maintaining bat diversity and habitat connectivity. However, eucalyptus plantations had fewer species than even tea plantations. 11.5% of this landscape is covered in forest fragments, 11% by coffee and less than 1% by cardamom, which combined means just under 25% of the agricultural landscape has good potential for all ten species modelled. Landscape composition (habitat type) and configuration (e.g. distance and density variables) together were used in predicting the occurrence of almost all species.

In this study the best performing models had only one to three variables. The AUC scores of models for the more generalist species were between 0.6 and 0.7; these species have weaker associations with any particular environmental variables as they can exploit many habitats, so patterns of occurrence are harder to predict. The more specialist species achieved higher test AUC scores of 0.88-0.92, with their occurrence very well predicted.

According to these models, *M. spasma* and *R. beddomei* are restricted to forest fragments and agroforestry plantations while *M. horsfieldii* is restricted to riparian areas. All three species have very low niche breadths, and relatively low niche overlap with other species. All other species were more disturbance tolerant and had weaker associations with particular habitats, although some were still relatively uncommon.

Forest fragment size was not in the final model for any species, but all the species for which maximum forest patch size had any predictive power showed a positive response to increased forest fragment size. The relatively high level of connectivity between forest fragments and agroforestry plantations in this landscape may facilitate the use of small forest fragments. Similarly bat species richness did not vary with forest fragment size, meaning that reforestation efforts of the Nature Conservation Foundation in this area are very valuable for bats even when conducted over just a few hectares.

Combining the data for all species to make species richness maps, waterways and areas with native trees were predicted to have the greatest richness, with the south-west corner that is dominated by tea showing the lowest richness. The species richness maps could be used in a predictive manner to model impacts potential future land use changes.

6.5 Bats and plantations

Species richness and abundance were lower in tea plantations than in coffee plantations, and species composition was significantly different in tea plantations from that in coffee plantations and forest fragments. Functional richness and specialisation were lower in tea plantations than in forest fragments – specialist species were lost, but new disturbance tolerant species were not gained. Bats in tea were characterised by lower FMAXE, FM.QCF calls, higher WAR and higher RWL than bats in forest fragments; indicating that the species remaining in this habitat were fast, efficient fliers that are able to detect prey at long distance in open spaces (Norberg and Rayner 1987, Schnitzler and Kalko 2001, Altringham 2011, Denzinger and Schnitzler 2013). Bat species in tea plantations were on average smaller than those in forest fragments, which was partly driven by the absence of frugivores and partly by the presence of smaller insectivorous species. No carnivorous bats were seen in this habitat.

Two bat species – *P. ceylonicus* and *M. fuliginosus* –showed slight negative responses to the percentage tea at the 100 m scale, but actually showed greater abundance in tea plantations than in forest fragments (both) or coffee plantations (*P. ceylonicus*). The reasons for this disparity are not entirely clear. It may be that while not seen at more locations in tea plantations than in other habitats, they are recorded more frequently per location, perhaps due to the openness of the plantation facilitating acoustic detection, perhaps due to increased abundance, or perhaps due to high levels of movement by the bats to hunt for prey.

Coffee plantations did not differ significantly from forest fragments in species richness or abundance. Coffee plantations did however differ from forest fragments in species composition, with one species significantly scarcer, and two significantly more common in coffee plantations. Coffee plantations did not differ significantly from forest fragments in functional diversity, but when singletons were removed showed reduced functional specialisation. The trait values in coffee plantations did not differ significantly from forest fragments other than that more bat species in coffee plantations used FM.QCF calls than in forest fragments.

Bats have not previously been studied in tea plantations, and we see that these plantations do contain several bat species but in filtered assemblages. Coffee plantations are functionally similar to forest fragments but do differ in species composition. They are not a replacement for forest, but could be a good land use to buffer protected areas from edge effects (Woodroffe and Ginsberg 1998, Hansen and Defries 2007, Laurance et al. 2012).

6.6 Bats and riparian areas

Many authors have noted the importance of riparian areas, and riparian vegetation, for bats, providing drinking water, abundant insect food and plant resources along open flyways (Lloyd et al. 2006, Avila-Cabadilla et al. 2012, Hagen and Sabo 2012, 2014). In this study riparian areas in tea differed little from non-riparian areas in tea, other than in acquiring one water adapted species. There were no significant differences in species richness, abundance or composition between riparian areas with or without corridors, which may be due to insufficient per site sampling, but there were significant differences between the habitats on a functional level.

While rivers with riparian corridors did not differ in any functional metrics from the scores expected by random community assembly, rivers without riparian corridors scored lower than expected on functional divergence and specialisation, indicating that trait filtering has occurred. Rivers with riparian corridors had more frugivorous bats and bats with lower wing aspect ratios than rivers without riparian corridors. There was no effect of corridor size or width on species richness in this study, meaning that any replanting of riparian areas with native trees would have a positive effect on bat functional diversity.

6.7 Landscape level bat conservation in the Valparai plateau

The relative emphasis given to development projects and environmental protection is an ongoing controversy in the Western Ghats, especially since the UNESCO World Heritage listing. In 2011, the Western Ghats Ecology Expert Panel report which recommended a cessation of the most damaging development activities in 60,000 km^2 of the most ecologically sensitive parts of the Western Ghats was rejected by the Ministry of Environment and Forests as too unfriendly to industry (Gadgil et al. 2011). The less environmentally stringent High-Level Working Group Report was adopted instead (Kasturirangan et al. 2013).

However at a local level, several landowners in the Valparai plateau have proven responsive to environmental concerns, leaving existing forest fragments on their land and permitting the planting of new forest fragments on land not currently under production. Based on the principles outlined by Fischer et al (2006) for conservation in land adjacent to protected areas, I suggest measures to improve the landscape for bats and hopefully for other taxa as well. Replanting forest patches has been an ongoing project for the Nature Conservation Foundation for many years, and the value of even small forest fragments for bats has been shown in this thesis.

1) Existing forest fragments should be protected, replanted where degraded and extended where possible.
2) New forest fragments – however small – should be planted where possible.

3) Riparian planting represents an excellent opportunity to connect the landscape for bats as many riparian banksides are unplanted. Even thin riparian corridors have value for bats.
4) Coffee and cardamom plantations under native shade trees should be retained wherever possible, and planted in preference tea plantations if the opportunity arises.

6.8 Further work

Having been granted permits to work in the Anamalai Tiger Reserve until December 2014, I will be returning to Valparai at the start of November 2014 to gather capture and acoustic data from the primary forest reserve. These data will provide a baseline for bat diversity in undisturbed areas to compare with the bat diversity in forest fragments, coffee and tea plantations. I will gather data both in riparian and in non-riparian areas of forest, and compare diversity in riparian primary forest areas with the diversity in riparian corridors and rivers without bankside vegetation.

If possible I will finish the analysis of the data from overnight detectors left at each site in order to improve the power of the analyses to detect differences in bat species richness, abundance and composition between habitats. In order to identify the morphospecies that has not yet been caught, I will use high level nets where the habitat structure permits the use of this equipment.

It would be interesting to look at the diversity of species at different altitudes in this forest reserve. The highest altitudes – over about 1800 m – are shola grasslands, and then the forest type varies as the mountains drop to the plains which are about 300 m asl. This wide variation in elevation is likely to affect the composition of bat assemblages.

I have a collection of genetic and faecal samples at the National Centre for Biological Sciences (NCBS), Bangalore from a variety of bat species which I hope can be useful to future students. Future Masters students could use these, for example to identify whether or not *R. lepidus* contains sub-species or cryptic species in South India, and to analyse faecal samples for dietary analysis.

6.9 Public engagement

Throughout my PhD I have considered it very important to undertake public engagement work. Bats are generally ignored at best and feared and hated at worst because of their associations with the night, witchcraft and disease. I am currently working on a booklet with photographs and descriptions of mammals in the Anamalai Hills with Divya Mudappa and K.H. Amithabachan of the Nature Conservation Foundation, to be published in Tamil, Malayali and English and stocked at the Visitor Centre in Valparai. In October 2012 I wrote the content for four posters that were displayed at the 'Western Ghats: Hidden Treasures' exhibition in Bangalore to educate the public about lesser known species from the Western Ghats biodiversity hotspot. In May-June 2012 I wrote a mini-series in the School version of The Hindu, one of the major Indian national papers, to educate children on the biology and conservation of bats. In May 2012 I gave talks to school students at the Beula Matriculation School, Valparai, Tamil Nadu, and to sixth-form students on a field course in Valparai from the Krishnamurti foundation school in Bangalore, India about the importance of bats in ecosystems.

On my return to India I hope to continue and expand this public engagement work. I will be writing reports for the landowners and forest department, where I will emphasize the important roles bats play in ecosystems. I aim to present my results in person to as many landowners as possible as well, in order to give them a chance to ask further questions. I hope to be able to coordinate more talks on bats in English-medium schools, and to combine this with surveys on attitudes of children towards bats. I am discussing the possibility of meeting with the founders of Youth for Conservation, a conservation education non-profit based in Tamil Nadu, to work together to include more information on bats into their current conservation education curriculum. I am also in discussion with the newly founded Bat Conservation India Trust to see where I can assist with their work. I have been invited to be a research associate of the Indian Bat Conservation Research Unit (IBCRU), and in this capacity I aim to work with others at IBCRU to conduct training workshops on techniques for studying bats for undergraduate and master's level students in South India.

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Appendix 1

Table A1.1: Pairwise comparisons of species richness using least squares means, with P values corrected by false discovery rate. 0.05=*, 0.01=**, 0.001=***. Darker greys signify greater significance (based on Q values).

Comparison	Estimate	SE	Z ratio	Uncorrected *P* value	Q value after fdr
Coffee, Acoustic - Forest Fragment, Acoustic	0.194	0.255	0.761	0.447	0.649
Coffee, Acoustic - Riparian Corridor, Acoustic	-0.057	0.239	-0.239	0.811	0.854
Coffee, Acoustic - Tea, Acoustic	0.391	0.270	1.448	0.148	0.332
Coffee, Acoustic - Tea Riparian, Acoustic	0.231	0.258	0.894	0.371	0.602
Coffee, Acoustic - Coffee, Both	-0.137	0.235	-0.585	0.559	0.696
Coffee, Acoustic - Coffee, Catching	1.917	0.479	4.002	<0.0001 ***	0.002 **
Forest Fragment, Acoustic - Riparian Corridor, Acoustic	-0.251	0.252	-0.997	0.319	0.573
Forest Fragment, Acoustic - Tea, Acoustic	0.197	0.281	0.699	0.485	0.653
Forest Fragment, Acoustic - Tea Riparian, Acoustic	0.036	0.270	0.135	0.893	0.893
Forest Fragment, Acoustic - Forest Fragment, Both	-0.279	0.250	-1.113	0.266	0.513
Forest Fragment, Acoustic - Forest Fragment, Catching	0.934	0.356	2.626	0.009 **	0.039 *
Riparian Corridor, Acoustic - Tea, Acoustic	0.448	0.267	1.678	0.093	0.262
Riparian Corridor, Acoustic - Tea Riparian, Acoustic	0.288	0.255	1.130	0.259	0.513
Riparian Corridor, Acoustic - Riparian Corridor, Both	-0.130	0.228	-0.569	0.569	0.696
Riparian Corridor, Acoustic - Riparian Corridor, Catching	1.099	0.333	3.296	0.001 **	0.006 **
Tea, Acoustic - Tea Riparian, Acoustic	-0.160	0.284	-0.565	0.572	0.696
Tea, Acoustic - Tea, Both	-0.083	0.289	-0.289	0.773	0.854
Tea, Acoustic - Tea, Catching	2.442	0.737	3.313	<0.001 ***	0.006 **
Tea Riparian, Acoustic - Tea Riparian, Both	-0.138	0.263	-0.525	0.600	0.710
Tea Riparian, Acoustic - Tea Riparian, Catching	1.216	0.403	3.022	0.003 **	0.013 *
Coffee, Both - Forest Fragment, Both	0.053	0.229	0.229	0.819	0.854
Coffee, Both - Riparian Corridor, Both	-0.050	0.224	-0.224	0.823	0.854

Coffee, Both - Tea, Both	0.445	0.256	1.736	0.083	0.248
Coffee, Both - Tea Riparian, Both	0.230	0.241	0.954	0.340	0.589
Coffee, Both - Coffee, Catching	2.054	0.475	4.324	<0.0001 ***	0.002 **
Forest Fragment, Both - Riparian Corridor, Both	-0.103	0.227	-0.453	0.651	0.751
Forest Fragment, Both - Tea, Both	0.392	0.259	1.514	0.130	0.325
Forest Fragment, Both - Tea Riparian, Both	0.177	0.243	0.727	0.468	0.653
Forest Fragment, Both - Forest Fragment, Catching	1.213	0.343	3.532	<0.001 ***	0.005 **
Riparian Corridor, Both - Tea, Both	0.495	0.254	1.950	0.051 .	0.178
Riparian Corridor, Both - Tea Riparian, Both	0.280	0.238	1.175	0.240	0.513
Riparian Corridor, Both - Riparian Corridor, Catching	1.229	0.328	3.744	<0.001 ***	0.003 **
Tea, Both - Tea Riparian, Both	-0.215	0.269	-0.800	0.424	0.635
Tea, Both - Tea, Catching	2.526	0.735	3.437	<0.001 ***	0.005 **
Tea Riparian, Both - Tea Riparian, Catching	1.355	0.397	3.416	<0.001 ***	0.005 **
Coffee, Catching - Forest Fragment, Catching	-0.788	0.539	-1.462	0.144	0.332
Coffee, Catching - Riparian Corridor, Catching	-0.875	0.532	-1.645	0.100	0.265
Coffee, Catching - Tea, Catching	0.916	0.837	1.095	0.274	0.513
Coffee, Catching - Tea Riparian, Catching	-0.470	0.570	-0.824	0.410	0.635
Forest Fragment, Catching - Riparian Corridor, Catching	-0.087	0.417	-0.208	0.835	0.854
Forest Fragment, Catching - Tea, Catching	1.705	0.769	2.218	0.027 *	0.100
Forest Fragment, Catching - Tea Riparian, Catching	0.318	0.465	0.685	0.493	0.653
Riparian Corridor, Catching - Tea, Catching	1.792	0.764	2.346	0.019 *	0.078
Riparian Corridor, Catching - Tea Riparian, Catching	0.405	0.456	0.888	0.374	0.602
Tea, Catching - Tea Riparian, Catching	-1.386	0.791	-1.754	0.080	0.248

Table A1.2: Pairwise comparisons of estimated species richness using least squares means, with P values corrected by false discovery rate. 0.05=*, 0.01=**, 0.001=***. Darker pinks signify greater significance (based on Q values).

Comparison	Estimate	SE	df	t ratio	Uncorrected *P* value	Q value after fdr
Coffee – Forest	-1.8	1.554	20	-1	0.260	0.434

fragment						
Coffee – Riparian corridor	-0.700	1.554	20	-0.451	0.657	0.657
Coffee - Tea	2.250	1.554	20	1.448	0.163	0.404
Coffee - Tea riparian	1.350	1.554	20	0.869	0.395	0.565
Forest fragment – Riparian corridor	1.100	1.554	20	0.708	0.487	0.609
Forest fragment - Tea	4.050	1.554	20	2.607	0.017 *	0.169
Forest fragment - Tea riparian	3.150	1.554	20	2.027	0.056	0.240
Riparian corridor - Tea	2.950	1.554	20	1.899	0.072	0.240
Riparian corridor – Tea riparian	2.050	1.554	20	1.319	0.202	0.404
Tea – Tea riparian	-0.900	1.554	20	-0.579	0.569	0.632

TableA1. 3: Pairwise comparisons of abundance estimates, with *P* values corrected by false discovery rate. 0.05=*, 0.01=, 0.001=***. Darker greys signify greater significance (based on Q values).**

Comparison	Estimate	SE	Z ratio	Uncorrected *P* value	Q value after fdr
Coffee, Acoustic - Forest Fragment, Acoustic	0.771	0.284	2.711	0.007 **	0.023 *
Coffee, Acoustic - Riparian Corridor, Acoustic	-0.146	0.218	-0.667	0.505	0.614
Coffee, Acoustic - Tea, Acoustic	0.216	0.239	0.901	0.367	0.507
Coffee, Acoustic - Tea Riparian, Acoustic	-0.051	0.223	-0.228	0.820	0.858
Coffee, Acoustic - Coffee, Both	-0.202	0.216	-0.937	0.349	0.506
Coffee, Acoustic - Coffee, Catching	1.432	0.364	3.933	<0.001 ***	0.001 ***
Forest Fragment, Acoustic - Riparian Corridor, Acoustic	-0.916	0.278	-3.295	0.001 ***	0.006 **
Forest Fragment, Acoustic - Tea, Acoustic	-0.555	0.295	-1.882	0.060	0.128
Forest Fragment, Acoustic - Tea Riparian, Acoustic	-0.822	0.282	-2.913	0.004 **	0.014 *
Forest Fragment, Acoustic - Forest Fragment, Both	-0.373	0.305	-1.220	0.223	0.372
Forest Fragment, Acoustic - Forest Fragment, Catching	0.795	0.421	1.886	0.059	0.128
Riparian Corridor, Acoustic - Tea, Acoustic	0.361	0.232	1.557	0.119	0.215
Riparian Corridor, Acoustic - Tea Riparian, Acoustic	0.095	0.215	0.440	0.660	0.743
Riparian Corridor, Acoustic - Riparian Corridor, Both	-0.209	0.200	-1.044	0.297	0.460

Riparian Corridor, Acoustic - Riparian Corridor, Catching	1.460	0.342	4.264	<0.0001 ***	0.001 ***
Tea, Acoustic - Tea Riparian, Acoustic	-0.267	0.237	-1.127	0.260	0.418
Tea, Acoustic - Tea, Both	-0.018	0.251	-0.073	0.942	0.942
Tea, Acoustic - Tea, Catching	3.989	1.321	3.020	0.003 **	0.011 *
Tea Riparian, Acoustic - Tea Riparian, Both	-0.126	0.214	-0.591	0.554	0.656
Tea Riparian, Acoustic - Tea Riparian, Catching	2.004	0.452	4.431	<0.0001 ***	0.001 ***
Coffee, Both - Forest Fragment, Both	0.600	0.243	2.472	0.014 *	0.041 *
Coffee, Both - Riparian Corridor, Both	-0.152	0.197	-0.774	0.439	0.573
Coffee, Both - Tea, Both	0.399	0.228	1.751	0.080	0.164
Coffee, Both - Tea Riparian, Both	0.025	0.206	0.120	0.904	0.925
Coffee, Both - Coffee, Catching	1.634	0.358	4.569	<0.0001 ***	0.001 ***
Forest Fragment, Both - Riparian Corridor, Both	-0.752	0.237	-3.180	0.002 **	0.008 **
Forest Fragment, Both - Tea, Both	-0.201	0.263	-0.763	0.446	0.573
Forest Fragment, Both - Tea Riparian, Both	-0.575	0.244	-2.359	0.018 **	0.051.
Forest Fragment, Both - Forest Fragment, Catching	1.168	0.400	2.915	0.004 **	0.014 *
Riparian Corridor, Both - Tea, Both	0.552	0.222	2.491	0.013 *	0.041 *
Riparian Corridor, Both - Tea Riparian, Both	0.177	0.198	0.893	0.372	0.507
Riparian Corridor, Both - Riparian Corridor, Catching	1.669	0.336	4.963	<0.0001 ***	0.001 ***
Tea, Both - Tea Riparian, Both	-0.375	0.229	-1.635	0.102	0.192
Tea, Both - Tea, Catching	4.007	1.320	3.035	0.002 **	0.011 *
Tea Riparian, Both - Tea Riparian, Catching	2.131	0.449	4.745	<0.0001 ***	0.001 ***
Coffee, Catching - Forest Fragment, Catching	0.134	0.479	0.279	0.780	0.850
Coffee, Catching - Riparian Corridor, Catching	-0.118	0.450	-0.262	0.793	0.850
Coffee, Catching - Tea, Catching	2.773	1.349	2.055	0.040 *	0.100
Coffee, Catching - Tea Riparian, Catching	0.521	0.536	0.973	0.331	0.496
Forest Fragment, Catching - Riparian Corridor, Catching	-0.251	0.466	-0.539	0.590	0.681
Forest Fragment, Catching - Tea,	2.639	1.355	1.948	0.051.	0.122

Catching					
Forest Fragment, Catching - Tea Riparian, Catching	0.388	0.550	0.705	0.481	0.601
Riparian Corridor, Catching - Tea, Catching	2.890	1.345	2.150	0.032 *	0.084
Riparian Corridor, Catching - Tea Riparian, Catching	0.639	0.525	1.218	0.223	0.372
Tea, Catching - Tea Riparian, Catching	-2.251	1.376	-1.636	0.102	0.192

Table A1.4: Pairwise comparisons of diversity, with, with P values corrected by false discovery rate. 0.05=*, 0.01=**, 0.001=***. Greys indicate significance level

Comparison (Both methods =B, catching =C, transects=T)	Estimate	SE	Z ratio	Uncorrected *P* value	Q value after fdr
Coffee, Acoustic - Forest Fragment, Acoustic	0.120	0.734	0.163	0.871	0.997
Coffee, Acoustic - Riparian Corridor, Acoustic	0.003	0.746	0.004	0.997	0.997
Coffee, Acoustic - Tea, Acoustic	0.547	0.702	0.779	0.436	0.997
Coffee, Acoustic - Tea Riparian, Acoustic	0.339	0.715	0.473	0.636	0.997
Coffee, Acoustic - Coffee, Both	-0.117	0.760	-0.154	0.878	0.997
Coffee, Acoustic - Coffee, Catching	3.205	0.822	3.898	<0.0001 ***	<0.0001 ***
Forest Fragment, Acoustic - Riparian Corridor, Acoustic	-0.117	0.734	-0.159	0.874	0.997
Forest Fragment, Acoustic - Tea, Acoustic	0.427	0.688	0.620	0.535	0.997
Forest Fragment, Acoustic - Tea Riparian, Acoustic	0.219	0.702	0.312	0.755	0.997
Forest Fragment, Acoustic - Forest Fragment, Both	-0.174	0.740	-0.235	0.814	0.997
Forest Fragment, Acoustic - Forest Fragment, Catching	2.120	0.696	3.046	0.002 **	0.018 *
Riparian Corridor, Acoustic - Tea, Acoustic	0.544	0.701	0.776	0.438	0.997
Riparian Corridor, Acoustic - Tea Riparian, Acoustic	0.336	0.715	0.470	0.639	0.997
Riparian Corridor, Acoustic - Riparian Corridor, Both	-0.109	0.758	-0.144	0.886	0.997
Riparian Corridor, Acoustic - Riparian Corridor, Catching	2.088	0.700	2.985	0.003 **	0.023 *
Tea, Acoustic - Tea Riparian, Acoustic	-0.208	0.669	-0.311	0.756	0.997
Tea, Acoustic - Tea, Both	-0.042	0.656	-0.064	0.949	0.997

Tea, Acoustic - Tea, Catching	19.353	1398.184	0.014	0.989	0.997
Tea Riparian, Acoustic - Tea Riparian, Both	-0.123	0.693	-0.177	0.860	0.997
Tea Riparian, Acoustic - Tea Riparian, Catching	0.901	0.646	1.394	0.163	0.66
Coffee, Both - Forest Fragment, Both	0.063	0.766	0.082	0.935	0.997
Coffee, Both - Riparian Corridor, Both	0.011	0.772	0.014	0.989	0.997
Coffee, Both - Tea, Both	0.622	0.718	0.866	0.387	0.997
Coffee, Both - Tea Riparian, Both	0.333	0.739	0.451	0.652	0.997
Coffee, Both - Coffee, Catching	3.322	0.834	3.981	<0.0001 ***	<0.0001 ***
Forest Fragment, Both - Riparian Corridor, Both	-0.052	0.764	-0.068	0.946	0.997
Forest Fragment, Both - Tea, Both	0.559	0.710	0.787	0.432	0.997
Forest Fragment, Both - Tea Riparian, Both	0.270	0.731	0.369	0.712	0.997
Forest Fragment, Both - Forest Fragment, Catching	2.294	0.715	3.207	0.001 ***	0.015 *
Riparian Corridor, Both - Tea, Both	0.611	0.717	0.852	0.394	0.997
Riparian Corridor, Both - Tea Riparian, Both	0.322	0.738	0.437	0.662	0.997
Riparian Corridor, Both - Riparian Corridor, Catching	2.197	0.713	3.082	0.002 **	0.018 *
Tea, Both - Tea Riparian, Both	-0.289	0.682	-0.424	0.672	0.997
Tea, Both - Tea, Catching	19.395	1398.184	0.014	0.989	0.997
Tea Riparian, Both - Tea Riparian, Catching	1.023	0.657	1.557	0.119	0.595
Coffee, Catching - Forest Fragment, Catching	-0.965	0.788	-1.224	0.221	0.765
Coffee, Catching - Riparian Corridor, Catching	-1.114	0.780	-1.427	0.154	0.66
Coffee, Catching - Tea, Catching	16.695	1398.184	0.012	0.991	0.997
Coffee, Catching - Tea Riparian, Catching	-1.966	0.763	-2.577	0.01 **	0.0643
Forest Fragment, Catching - Riparian Corridor, Catching	-0.149	0.660	-0.225	0.822	0.997
Forest Fragment, Catching - Tea, Catching	17.660	1398.184	0.013	0.990	0.997
Forest Fragment, Catching - Tea Riparian, Catching	-1.001	0.639	-1.566	0.117	0.595
Riparian Corridor, Catching - Tea, Catching	17.809	1398.184	0.013	0.990	0.997
Riparian Corridor, Catching -	-0.852	0.629	-1.354	0.176	0.66

Tea Riparian, Catching					
Tea, Catching - Tea Riparian, Catching	-18.661	1398.184	-0.013	0.989	0.997

Appendix 2

Table A2.1: Functional diversity at the site level, calculated on the summed data for each site. Expected values based on 1000 random iterations are included, as well as the observed values and standardised effect size (SES). The results of T tests comparing the observed to expected values are given.

Habitat	Metric	Expected mean ± standard deviation	Observed values ± standard deviation	SES mean± standard deviation	T Value	*P* value
Coffee	FRic	0.106±0.067	0.128±0.049	0.326±0.662	0.995	0.380
Forest fragment	FRic	0.106±0.067	0.166±0.038	0.897±0.520	3.514	0.025 *
Riparian corridor	FRic	0.106±0.067	0.120±0.043	0.204±0.588	0.702	0.526
Tea	FRic	0.106±0.067	0.052±0.054	-0.805±0.708	-1.993	0.141
Tea riparian	FRic	0.106±0.067	0.076±0.050	-0.458±0.684	-1.348	0.252
Coffee	FEve	0.597±0.123	0.629±0.060	0.258±0.480	1.185	0.369
Forest fragment	FEve	0.597±0.123	0.648±0.059	0.413±0.474	1.907	0.185
Riparian corridor	FEve	0.597±0.123	0.606±0.088	0.068±0.686	0.229	0.700
Tea	FEve	0.597±0.123	0.494±0.143	-0.863±1.067	-1.443	0.256
Tea riparian	FEve	0.597±0.123	0.559±0.222	-0.322±1.680	-0.382	0.725
Coffee	FDiv	0.746±0.101	0.772±0.047	0.258±0.446	1.221	0.332
Forest fragment	FDiv	0.746±0.101	0.820±0.086	0.744±0.798	1.916	0.135
Riparian corridor	FDiv	0.746±0.101	0.734±0.128	-0.127±1.177	-0.210	0.830
Tea	FDiv	0.746±0.101	0.707±0.076	0.683	-1.029	0.394
Tea riparian	FDiv	0.746±0.101	0.670±0.056	-0.769±0.541	-3.008	0.044 *
Coffee	FSpe	0.230±0.033	0.243±0.035	0.414±0.959	0.870	0.436
Forest fragment	FSpe	0.230±0.033	0.275±0.027	1.390±0.779	3.710	0.021 *
Riparian corridor	FSpe	0.230±0.033	0.222±0.017	-0.236±0.473	-1.017	0.377
Tea	FSpe	0.230±0.033	0.215±0.007	-0.430±0.184	-4.345	0.024 *
Tea riparian	FSpe	0.230±0.033	0.205±0.016	-0.749±0.447	-3.463	0.026 *

NB: The number of sites is 5 for all habitats other than Tea, where one site had too few species (N=2) to run the analysis.

Table A2.2: Functional richness at the transect level, calculated on the summed data for each transect with species occurring just once per habitat removed. Expected values based on 1000 random iterations are included, as well as the observed values and standardised effect size (SES). The results of T tests comparing the observed to expected values are given.

Group	Metric	Expected mean ± standard deviation	Observed values ± standard deviation	SES mean± standard deviation	T value	*P* value
Coffee	FRic	0.092±0.065	0.110±0.050	0.267±0.702	0.767	0.489
Forest fragments	FRic	0.092±0.065	0.166±0.038	1.139±0.536	4.325	0.013 *
Riparian corridors	FRic	0.092±0.065	0.111±0.049	0.290±0.679	0.860	0.442
Tea	FRic	0.092±0.065	0.016±0.003	-1.181±0.113	-55.313	<0.0001 ***
Tea riparian	FRic	0.092±0.065	0.071±0.052	-0.324±0.718	-0.906	0.419
Coffee	FEve	0.599±0.132	0.670±0.076	0.544±0.555	2.098	0.135
Forest fragments	FEve	0.599±0.132	0.640±0.044	0.313±0.343	2.120	0.182
Riparian corridors	FEve	0.599±0.132	0.575±0.120	-0.190±0.859	-0.437	0.667
Tea	FEve	0.599±0.132	0.397±0.253	-1.563±1.739	-1.594	0.213
Tea riparian	FEve	0.599±0.132	0.575±0.237	-0.192±1.667	-0.225	0.816
Coffee	FDiv	0.750±0.101	0.785±0.037	0.351±0.347	2.161	0.127
Forest fragments	FDiv	0.750±0.101	0.820±0.086	0.700±0.792	1.815	0.151
Riparian corridors	FDiv	0.750±0.101	0.725±0.098	-0.253±0.902	-0.560	0.615
Tea	FDiv	0.750±0.101	0.663±0.084	-0.879±0.764	-2.060	0.136
Tea riparian	FDiv	0.750±0.101	0.666±0.059	-0.844±0.567	-3.147	0.038 *
Coffee	FSpe	0.228±0.033	0.241±0.035	0.407±0.951	0.864	0.439
Forest fragments	FSpe	0.228±0.033	0.278±0.031	1.532±0.871	3.664	0.022 *
Riparian corridors	FSpe	0.228±0.033	0.221±0.019	-0.190±0.515	-0.755	0.501
Tea	FSpe	0.228±0.033	0.210±0.009	-0.540±0.252	-3.959	0.030 *
Tea riparian	FSpe	0.228±0.033	0.204±0.017	-0.726±0.482	-3.108	0.037 *

* The number of sites is 5 for all habitats other than Tea, where one site had too few species (N=2) to run the analysis.

Table A2.3: Pairwise comparisons of functional richness between habitats, with p values corrected by false discovery rate (Q values). Greys indicates significance according to Q value.

Comparison	Estimate FRic	SE	Z ratio	P value	Q value
C-FF	-0.260	0.263	-0.991	0.322	0.402
C-RC	0.066	0.284	0.232	0.816	0.816
C-T	0.891	0.397	2.243	0.025	0.083
C-TR	0.525	0.324	1.622	0.105	0.210
FF-RC	0.326	0.268	1.219	0.223	0.319
FF-T	1.151	0.386	2.984	0.003	0.029 *
FF-TR	0.786	0.310	2.536	0.011	0.056
RC-T	0.825	0.400	2.060	0.039	0.099
RC-TR	0.459	0.328	1.401	0.161	0.269
T-TR	-0.366	0.430	-0.851	0.395	0.439

Table A2.4: Pairwise comparisons of functional evenness between habitats, with p values corrected by false discovery rate (Q values).

Comparison	Estimate FEve	SE	T ratio	P value	Q value
C - FF	-0.029	0.137	-0.228	0.8221	0.8221
C - RC	0.037	0.140	0.279	0.783	0.8221
C - T	0.241	0.158	1.554	0.137	0.6831
C - TR	0.118	0.143	0.853	0.404	0.7711
FF - RC	0.066	0.139	0.507	0.618	0.7724
FF - T	0.271	0.157	1.769	0.093	0.6831
FF - TR	0.147	0.142	1.081	0.293	0.7326
RC - T	0.204	0.159	1.291	0.212	0.7072
RC - TR	0.081	0.144	0.574	0.573	0.7724
T - TR	-0.124	0.161	-0.75	0.463	0.7711

TableA2. 5: Pairwise comparisons of functional divergence between habitats, with p values corrected by false discovery rate (Q values). Green indicates where results were significant before but not after multiple comparisons correction.

Comparison	Estimate FDiv	SE	Z ratio	P value	Q value
C - FF	-0.060	0.069	-0.872	0.383	0.547
C - RC	0.050	0.071	0.710	0.478	0.556
C - T	0.088	0.076	1.150	0.250	0.417
C - TR	0.141	0.073	1.934	0.053	0.177
FF - RC	0.111	0.070	1.581	0.114	0.285
FF - T	0.148	0.075	1.965	0.049	0.177
FF - TR	0.201	0.072	2.802	0.005	0.051 .
RC - T	0.037	0.077	0.484	0.628	0.628
RC - TR	0.090	0.074	1.226	0.220	0.417
T - TR	0.053	0.079	0.673	0.501	0.556

Table A2.6: Pairwise comparisons of functional specialisation between habitats, with p values corrected by false discovery rate. (Q values). Greys indicates significance according to Q value.

Comparison FSpe	Estimate	SE	Z ratio	P value	Q value
C - FF	-0.124	0.058	-2.122	0.034	0.068
C - RC	0.092	0.062	1.492	0.136	0.194
C - T	0.121	0.066	1.833	0.067	0.111
C - TR	0.171	0.063	2.718	0.007	0.016 *
FF - RC	0.216	0.060	3.605	0.000	<0.001 ***
FF - T	0.245	0.064	3.801	0.000	<0.001 ***
FF - TR	0.295	0.061	4.818	<.0001	<0.001 ***
RC - T	0.029	0.067	0.433	0.665	0.665
RC - TR	0.079	0.064	1.231	0.219	0.273
T - TR	0.050	0.068	0.728	0.467	0.518

TableA2. 7: Pairwise comparisons of functional richness between habitats after singletons were removed, with p values corrected by false discovery rate (Q values). Pink indicates significance according to Q value.

Comparison	Estimate FRic WOS	SE	Z ratio	P value	Q value
C - FF	-0.415	0.241	-1.721	0.085	0.135
C - RC	-0.013	0.264	-0.051	0.960	0.960
C - T	1.926	0.579	3.326	0.001	0.003 **
C - TR	0.429	0.298	1.440	0.150	0.167
FF - RC	0.402	0.240	1.672	0.095	0.135
FF - T	2.341	0.569	4.116	<.0001	0.0004 ***
FF - TR	0.844	0.277	3.043	0.002	0.006 **
RC - T	1.939	0.579	3.351	0.001	0.003 **
RC - TR	0.442	0.297	1.489	0.137	0.167
T - TR	-1.497	0.595	-2.515	0.012	0.024 *

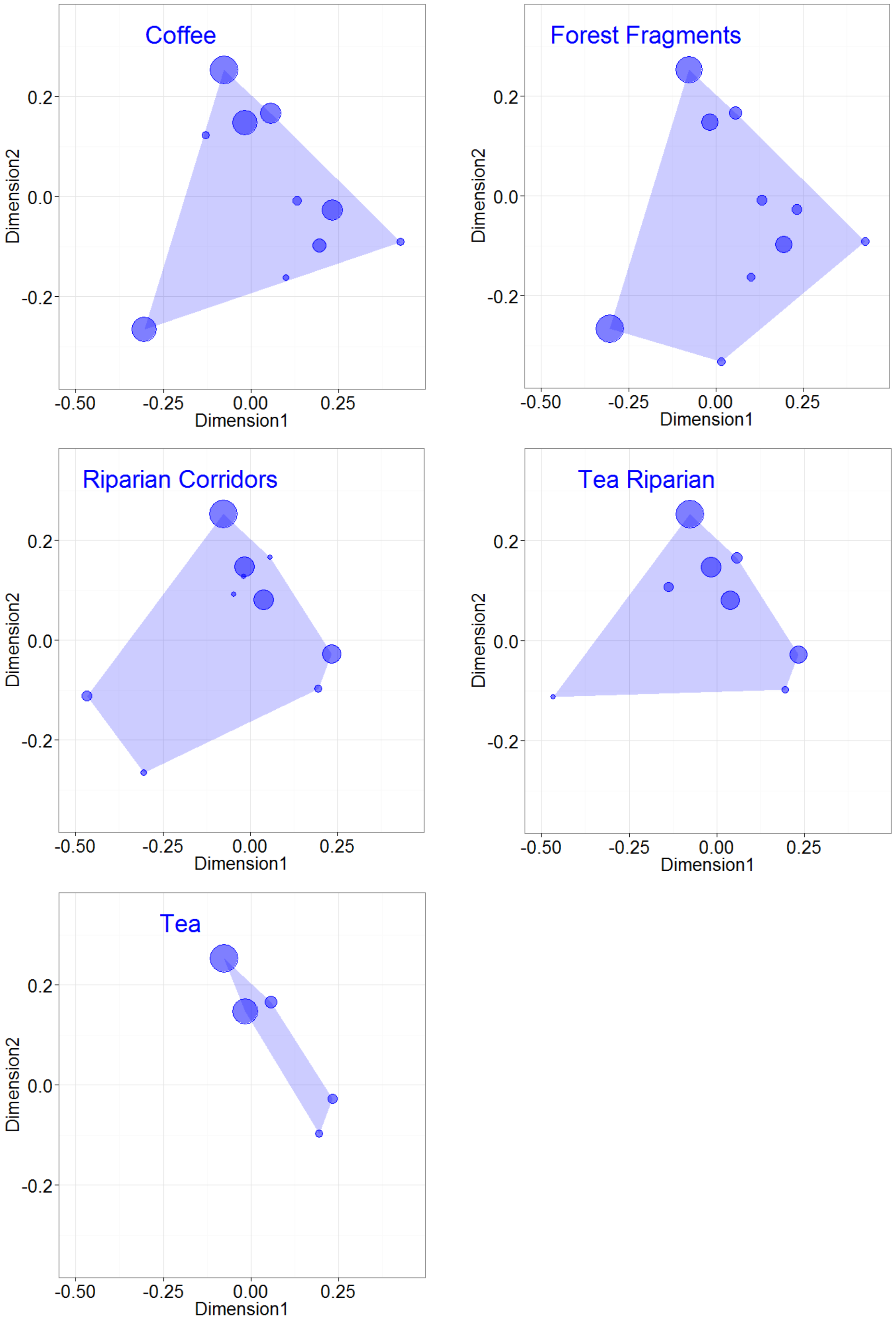

Figure A2.1: Plot of functional richness at the habitat level, based on all sites combined with singletons per habitat removed. Circles represent species, with larger circles indicating greater relative abundance of that species. The area of functional space filled by the polygon represents the functional richness of the community.

TableA2. 8: Pairwise comparisons of functional evenness between habitats after singletons were removed, with p values corrected by false discovery rate. (Q values). Pink indicates significance according to Q value. Green indicates where results were significant before but not after multiple comparisons correction.

Comparison	Estimate	SE	Z ratio	P value	Q value
C - FF	0.030	0.103	0.290	0.772	0.8574
C - RC	0.095	0.103	0.921	0.357	0.5949
C - T	0.273	0.109	2.493	0.013	0.1267
C - TR	0.095	0.103	0.925	0.355	0.5949
FF - RC	0.065	0.103	0.631	0.528	0.6601
FF - T	0.243	0.109	2.220	0.027	0.1323
FF - TR	0.065	0.103	0.634	0.526	0.6601
RC - T	0.178	0.109	1.625	0.104	0.2622
RC - TR	0.000	0.103	0.003	0.997	0.9974
T - TR	-0.177	0.109	-1.622	0.105	0.2622

Table A2.9: Pairwise comparisons of functional divergence between habitats after singletons were removed, with p values corrected by false discovery rate (Q values). Pink indicates significance according to Q value. Green indicates where results were significant before but not after multiple comparisons correction.

Comparison	Estimate	SE	Z ratio	P value	Q value
C - FF	-0.043	0.063	-0.689	0.491	0.546
C - RC	0.080	0.065	1.231	0.218	0.273
C - T	0.169	0.071	2.397	0.017	0.041 *
C - TR	0.164	0.066	2.480	0.013	0.041 *
FF - RC	0.123	0.064	1.918	0.055	0.110
FF - T	0.212	0.070	3.035	0.002	0.012 *
FF - TR	0.207	0.065	3.163	0.002	0.012 *
RC - T	0.090	0.072	1.248	0.212	0.273
RC - TR	0.084	0.067	1.252	0.211	0.273
T - TR	-0.005	0.073	-0.071	0.943	0.943

Table A2.10: Pairwise comparisons of functional specialisation between habitats after singletons were removed, with p values corrected by false discovery rate(Q values). Pink indicates significance according to Q value. Green indicates where results were significant before but not after multiple comparisons correction.

Comparison	Estimate	SE	Z ratio	P value	Q value
C - FF	-0.143	0.062	-2.316	0.021	0.041 *
C - RC	0.085	0.065	1.304	0.192	0.275
C - T	0.139	0.071	1.966	0.049	0.082
C - TR	0.168	0.067	2.519	0.012	0.03 *
FF - RC	0.228	0.063	3.610	0.000	<0.001 ***
FF - T	0.282	0.069	4.107	<0.0001	<0.001 ***
FF - TR	0.311	0.065	4.809	<0.0001	<0.001 ***
RC - T	0.054	0.072	0.745	0.456	0.507
RC - TR	0.083	0.068	1.219	0.223	0.279
T - TR	0.030	0.073	0.404	0.686	0.686

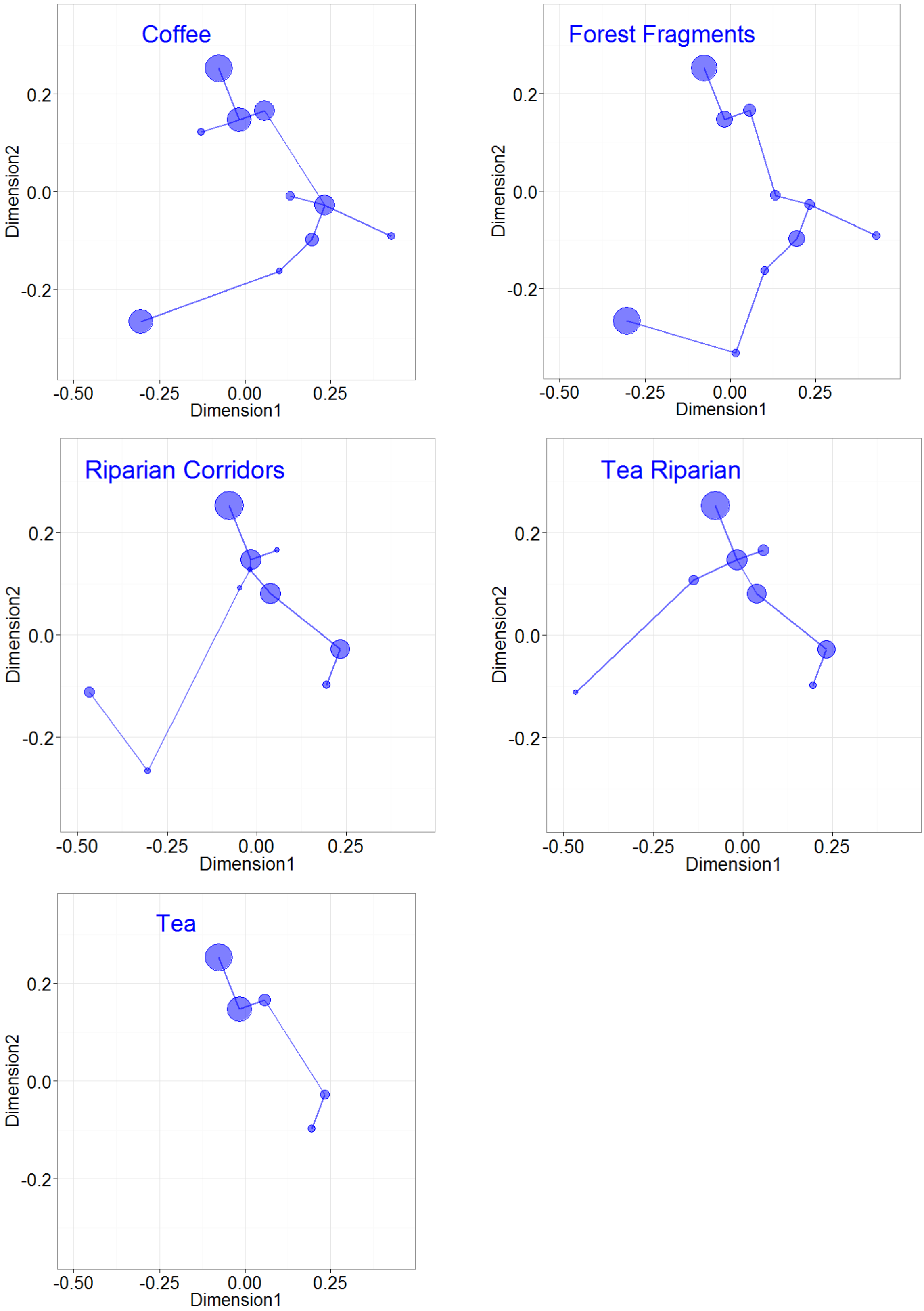

Figure A2.2: Plot of functional evenness at the habitat level, based on all sites combined once singletons were removed. The minimum spanning tree linking all species is shown Functional evenness is quantified by the regularity of species' distributions along this tree, and the regularity in their abundance.

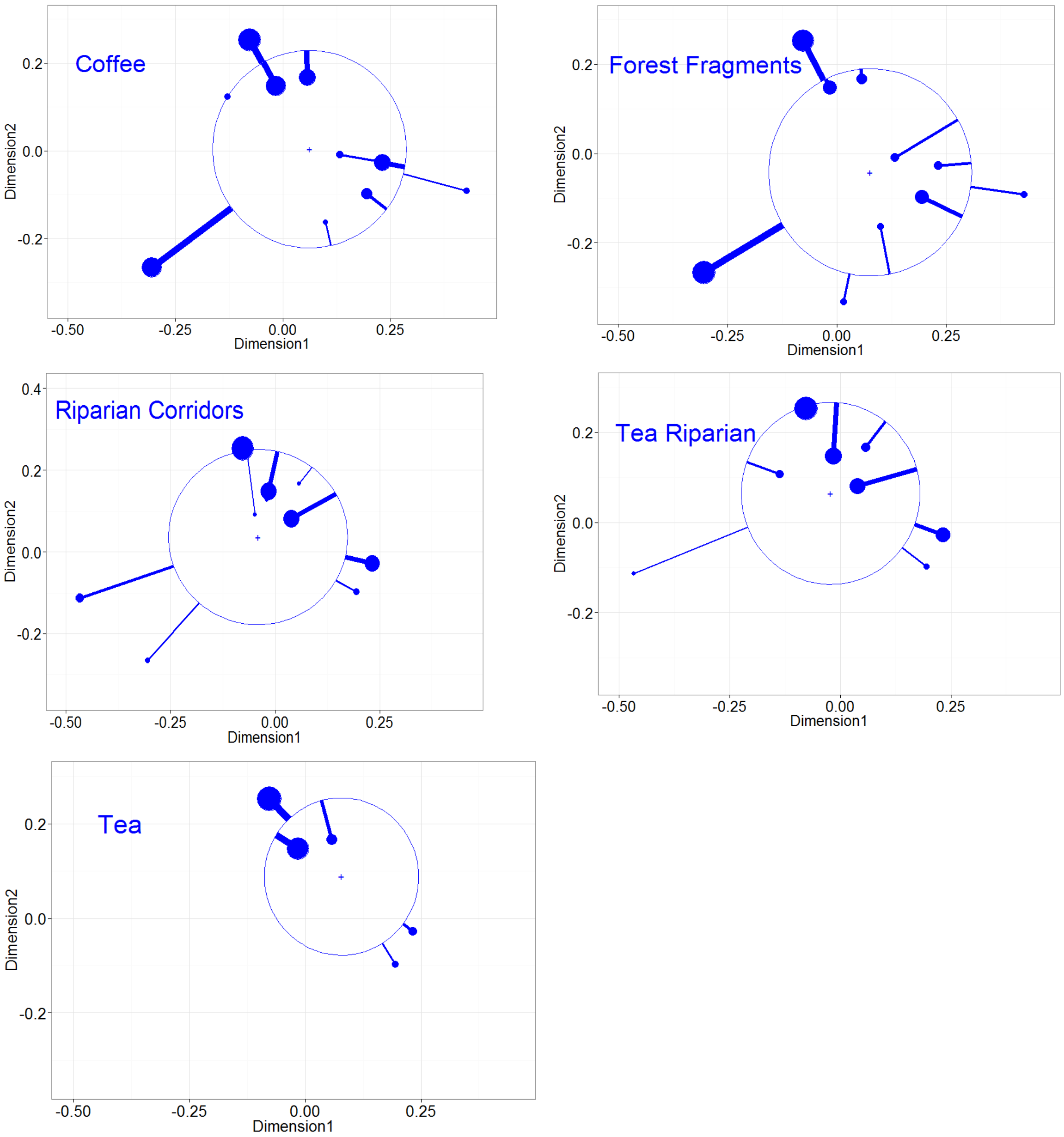

Figure A2.3: Plot of functional divergence at the habitat level for tea plantations, based on all tea plantation sites combined once singletons were removed.

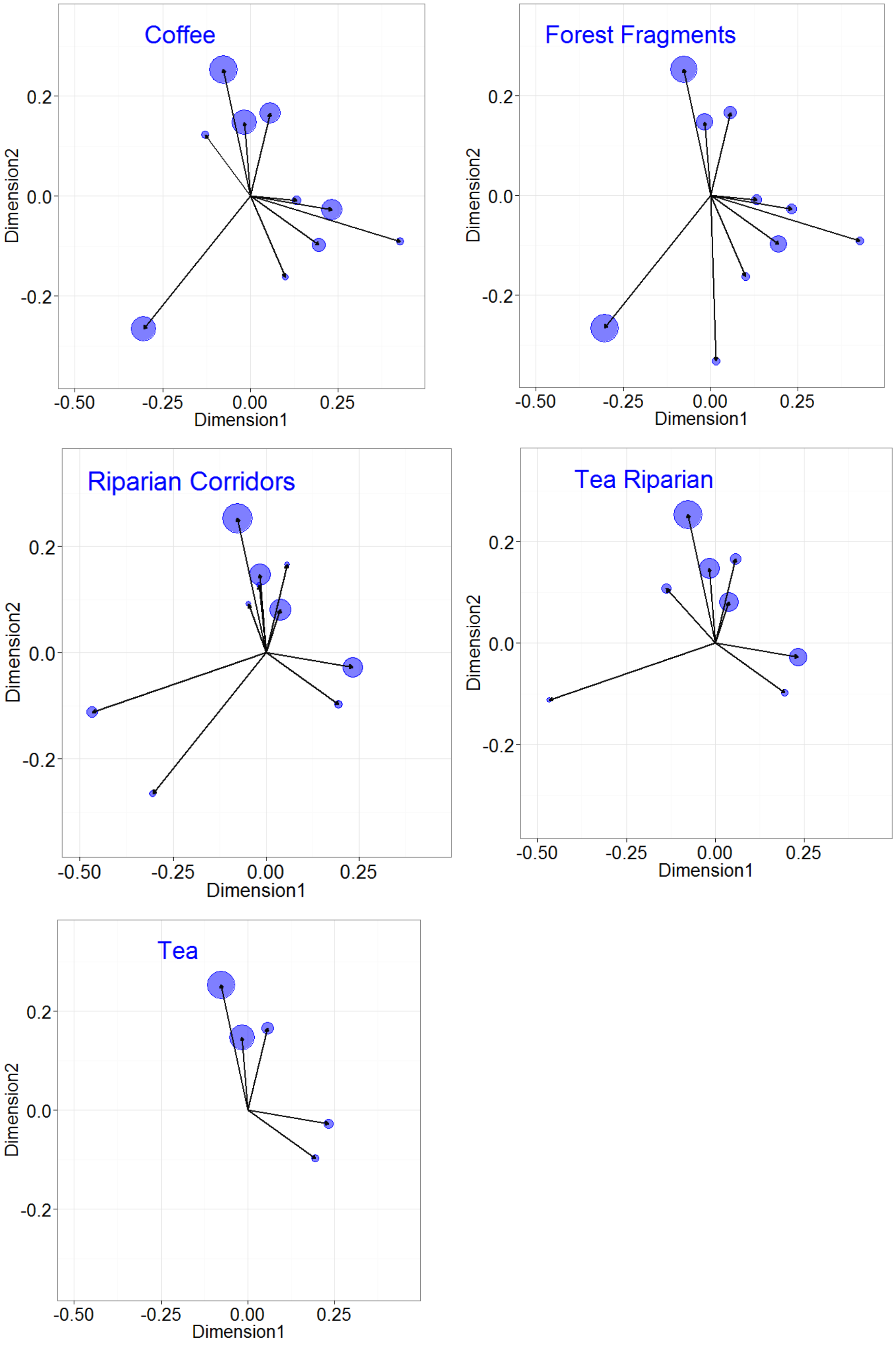

Figure A2.4: Plot of functional specialisation at the habitat level, based on all sites combined. The lines radiate from the centre of the community to each species.