Avian communities and ecoacoustics in a tropical human-modified landscape

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General Abstract

Large areas of the tropics have been cleared of forest and converted to agriculture. The consequent human-modified landscapes (HMLs) comprise a heterogenous mix of habitats; forest fragments and riparian strips are embedded in a matrix of cattle pasture, non-native timber plantations, and urban centres. These habitat changes can have dramatic consequences for wildlife, leading to range shifts and extirpations. In turn, this can influence the integrity of ecosystem services such as frugivory and seed dispersal. Understanding how habitat conversion affects natural ecosystems is critical to inform conservation interventions, but requires long-term biodiversity monitoring and detailed knowledge of species-level responses to HMLs.

The research presented in this thesis was conducted in the Emparador HML, in central Republic of Panama. In Chapter 2, we show that the regional avian community is shaped by extent of forest cover across the landscape, and to a lesser degree, extent of forest fragmentation and distance to core forest. Effects of forest cover and fragmentation were examined at local (10 ha) and landscape (500 ha) scales. Species-level responses to these factors varied widely; while abundance of many species increased with greater local-scale forest cover, greater landscape-scale forest cover was often associated with declines. Generalist species that readily persist in HMLs still responded positively to local-scale forest cover, suggesting that even smaller forest fragments in these landscapes are important for maintaining diverse avian assemblages. Critically, we found that species' responses were not associated with particular traits such as dietary composition or forest dependence, highlighting that species may often exhibit idiosyncratic responses to landscape structure.

Chapters 3 and 4 address the wider issue of long-term monitoring, and the potential for data collection over large spatiotemporal scales using remote audio recorders. Ecoacoustics, the study of environmental sound is a relatively new discipline, and as such there is still considerable uncertainty surrounding best-practice for collecting and processing recordings. One of the most straightforward means of utilising audio recordings for environmental monitoring is via acoustic indices. These are objective measures of sound based on features such as pitch and amplitude. To date, attempts to use these indices have been hindered by inconsistent or inappropriate methodologies. In Chapter 3, we determine how many recordings are required to comprehensively capture a soundscape, the acoustic

energy of a location. Furthermore, we demonstrate that there are habitat-specific patterns in acoustic indices values, suggesting that these indices reflect differences in vegetation structure and wildlife. We develop this further in Chapter 4, where we show that avian species richness and abundance are clearly linked to patterns in acoustic indices values. Critically, these patterns were coherent among habitat types emphasising their potential for monitoring. Acoustic indices sensitive to the frequencies occupied by bird song have the greatest potential for monitoring an avian community. The results from these two chapters suggest that acoustic indices can be effective tools for monitoring biodiversity, with values reflecting consistent differences across habitats, and among avian assemblages.

Audio recordings are a source of permanent, verifiable evidence that can be collected at much greater spatiotemporal scales than traditional biodiversity monitoring data. As the use of audio recorders grows, it is important to compare their efficacy with standard methods of data collection. In Chapter 5, we contrast data derived from audio recordings with that gathered using standard point count methods, and consider whether recorders are a feasible means of surveying antbirds (*Thamnophilidae*), a disturbance-sensitive avian taxon. Both approaches revealed species’ responses to landscape structure, with qualitatively similar patterns in response to forest cover and vegetation quality. We show that common species can be readily monitored using audio recorders, with greater levels of detectability compared with point counts. However, rarer species were more likely to be detected using point counts.

The work presented in this thesis helps to explain the patterns seen in avian responses to Neotropical HMLs. In particular we emphasise the importance of forest cover for maintaining bird assemblages in these landscapes. We demonstrate the utility of audio recorders for data collection, and highlight their potential for future biodiversity monitoring. In the face of human population growth, and ongoing habitat disturbance and agricultural intensification, conservation efforts are essential to avoid widespread species extinctions and ecosystem collapse. Interventions must take place in HMLs, to bolster ecosystem services, provide buffer zones for protected areas, and improve connectivity in the wider landscape.

Declaration of authorship

I, Tom Bradfer-Lawrence, declare that this thesis has been composed by myself and that it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extent of work carried out in collaboration with others.

Signed:____

Date:____

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Chapter 1. General introduction

1.1 Birds in the Neotropics

There are approximately 11,000 described bird species worldwide (Handbook of the Birds of the World & BirdLife International 2018), nearly 40% of which are found in the Neotropics. Neotropical avian diversity has arisen from a combination of extended isolation, geography and habitat stability (Fjeldså 2012; Fjeldså et al. 2012; Jetz et al. 2014; Leigh 1990; Oswald et al. 2016; Smith et al. 2014). This diversity can be highly concentrated, and just 100 hectares of Neotropical forest can support 250 bird species (Robinson et al. 2000; Terborgh et al. 1990; Thiollay 1994). The structural and climatic stability of lowland Neotropical forests means they support highly stable faunal communities (Didham & Lawton 1999; Janzen 1967). For example, at an undisturbed site in the Peruvian Amazon, fewer than 2% of bird species had significant changes in population size over an eight year study period (Brooks et al. 2005).

Forest habitat stability in the Neotropics has led to high levels of avian speciation and niche specialisation (Peres et al. 2010; Zimmer et al. 1997). Mutualistic and commensalistic associations among species are common; such as obligate membership of mixed-species foraging flocks (Camerlenghi et al. 2019; Martínez & Gomez 2013; Powell 1985), or affiliations with army ant (*Eciton burchellii*) swarms, where birds prey on arthropods flushed by the ants (Brumfield et al. 2007; Willis & Oniki 1978). Other taxa are dependent on birds' contributions to ecosystem services, including plant pollination (Nunes et al. 2016), seed dispersal (Bovo et al. 2018; Mello et al. 2015), and predation of invertebrate herbivores (Karp et al. 2013; Nyffeler et al. 2018; Van Bael et al. 2003). These diverse bird communities are an integral element of forest ecosystems, but their complex interdependencies render them vulnerable to anthropogenic disturbance.

1.2 Anthropogenic pressures in the Neotropics

Neotropical avian diversity is threatened by anthropogenically driven forest loss. Between 1990 and 2010, approximately 28,500 km^2 of forest was cleared each year in the Neotropics (Achard et al. 2014). These dramatic clearances were triggered by a combination of population growth, timber and mineral resource extraction, fires and expanding agriculture (Hansen et al. 2013; Potapov et al. 2017; Wright 2010). Of these factors, agriculture was the most important driver of forest clearance in Mesoamerica during the latter half of the 20th century (Kaimowitz 2008), and food production now accounts for over 40% of land use in the region (DeClerck et al. 2010). In consequence, much of the region's remaining lowland forest is heavily fragmented.

The human-modified landscapes (HMLs) that result from forest clearance are characterised by high levels of habitat heterogeneity. Any remaining forest fragments are embedded in a matrix of other habitats, including cattle pastures, croplands, timber plantations and urban settlements (Daily et al. 2001). Disturbance intensity can be highly variable in these landscapes. The least severe habitat alterations are associated with small-scale slash-and-burn agriculture, or shade-coffee plantations where a large proportion of the original forest canopy is retained (Petit & Petit 2003; Sekercioglu et al. 2019). Conversely, virtually all of the original vegetation cover is removed in intensive production systems with crop monocultures such as sugar cane or soy bean (DeClerck et al. 2010; Petit & Petit 2003).

Critically, HMLs are dynamic systems that continue to experience greater disturbance than the continuously forested landscapes they have replaced (Peres et al. 2010; Reid et al. 2019; Zahawi et al. 2015). These ongoing landscape impacts are highly variable in time and space (Peres et al. 2010). For example, if agricultural areas are left fallow then thick scrub will often regenerate in just a few years (Arroyo-Mora et al. 2005; Chazdon et al. 2011). In turn, clearance of such scrub is frequently achieved using bulldozers and fire (Chazdon et al. 2011), triggering another phase of rapid habitat alteration. More gradual changes in land cover occur during the maturation of timber plantations, or the development of secondary forest following land abandonment (DeWalt et al. 2003; Petit & Montagnini 2004).

1.3 Landscape factors that influence birds in HMLs

Habitat conversion and ongoing disturbance in HMLs can have dramatic consequences for bird communities. Five key habitat and landscape factors influence avian persistence in HMLs: habitat area, habitat quality, connectivity, matrix (non-habitat) quality, and landscape composition (Hodgson et al. 2011). These five influencing factors operate at a range of scales: the patch-scale (~10 ha), intermediate- or farm-scale (< 100 ha), and landscape-scale (~500 ha). At the patch-scale, habitat area and quality are key to species' persistence, whereas at the landscape-scale, connectivity, matrix quality and landscape composition become the critical factors (Doerr et al. 2011; Graham & Blake 2001, although see Hodgson et al. 2009, 2011).

1.3.1 Patch-scale effects

At the patch-scale (~10 ha), bird species diversity and abundance can be influenced by habitat area and quality. The effect of area follows island biogeography theory predictions (MacArthur & Wilson 1967); larger areas of habitat tend to support more species. For example, Graham & Blake (2001) found the abundances of two-thirds of forest-dependent bird species in Los Tuxtlas, Mexico were positively related to patch area. Similarly, larger forest fragments in Brazil had more terrestrial insectivorous bird species (Stouffer et al. 2011; Stratford & Stouffer 1999). Small patches are also likely to support fewer species because edge effects limit the area of core habitat (Banks-Leite et al. 2010). Patch edges have a more variable climate and greater rates of disturbance and predation (Cochrane 2001; Vetter et al. 2013), and such effects that may extend for 200 m or more into a forest patch (Canaday & Rivadeneyra 2001). In consequence, these edge habitats are often less suitable for forest-affiliated birds.

Patch quality is predominantly linked to vegetation structure, rather than land cover per se. Bird assemblage composition and presence of mixed-species feeding flocks have been linked to plant species richness, canopy cover and basal area in both shade-coffee and silvopasture habitats (Colorado Zuluaga & Rodewald 2015; Harvey et al. 2006; Karp et al. 2011; Komar 2006; McDermott et al. 2015; Philpott et al. 2008). However, larger and more speciose mixed-species flocks were not associated with greater structural complexity in secondary and mature forests (Colorado Zuluaga & Rodewald 2015), which suggests structure only influences species composition in simpler habitats (Tscharntke et al. 2012). Increased intensity of land management can simplify vegetation structure and composition and so reduce habitat quality, impacting on avian assemblages in HML patches (Petit & Petit 2003).

1.3.2 Intermediate-scale effects

At the scale of individual farms (i.e. between 10 and 100 ha - Harvey et al. 2004), habitat area and quality are still key factors determining bird persistence. Three traditional management practices that in Mesoamerican HMLs mean that these have a higher level of tree cover than equivalent landscapes elsewhere in the world (Zomer et al. 2009). Firstly, remnant trees are frequently left standing in pastures (Harvey & Haber 1998; Manning et al. 2006). Secondly, riparian strips are often retained due to concerns about erosion during heavy rains (Chazdon et al. 2011; Petit & Petit 2003). Thirdly, live fences are widely used as field boundaries and stock fencing (Estrada et al. 2000; Pulido-Santacruz & Renjifo 2011). The greater area of tree cover in Neotropical HMLs provides birds with more opportunities for foraging and nesting, boosting avian richness and abundance at the intermediate scale (Colorado Zuluaga & Rodewald 2015; Harvey & Haber 1998; Pulido-Santacruz & Renjifo 2011).

The higher tree cover found in Mesoamerican HMLs, particularly live fences and riparian strips, is also critical for the maintenance of connectivity among habitat patches. In Colombia, Pulido-Santacruz & Renjifo (2011) found that over 90% of avian movements in live fences were longitudinal, suggesting that birds were using them as corridors to move between habitat patches. Although live fences accounted for less than 2% of the total land area in the Rio Frio HML, Costa Rica, their presence was key to enhancing the structural connectivity of the landscape (Leon & Harvey 2006). This connectivity permits the flow of individuals and genes across a landscape, buffering populations and species in the face of disturbance (Eycott et al. 2012; Taylor et al. 1993; Vergara et al. 2013).

1.3.3 Landscape-scale effects

Factors at the intermediate scale contribute to the biodiversity value of the wider landscape, and it is this context which further mediates the value of a particular habitat patch for birds (Frishkoff & Karp 2019; Reid et al. 2014). This is encapsulated in countryside biogeography theory, which recognises some habitats in a matrix are more suitable for wildlife than others (Frishkoff et al. 2019; Reid et al. 2014). For example, a forest fragment surrounded by pasture is relatively more isolated than one surrounded by regenerating scrub (Daily et al. 2003; Mendenhall et al. 2014). This is because the scrub may provide supplementary resources and foraging opportunities, so allowing individuals to use areas beyond the immediate forest patch (Powell et al. 2013; Ruffell et al. 2017; Tscharntke et al. 2012; Wolfe et al. 2015a).

Matrix quality thus mediates the effects of patch area and isolation. Quantitative reviews suggest that the more similar the surrounding matrix is to a habitat patch, the more permeable the matrix, and thus the greater the wildlife benefit, echoing the importance of patch-scale structure to habitat quality (Eycott et al. 2012; Prevedello & Vieira 2010; Ruffell et al. 2017). Mesoamerican HMLs are typically composed of many small- to medium-sized landholdings, this heterogenous pattern of land ownership results in highly variable management intensity, even at small spatial scales (Harvey et al. 2004). Hence in these complex landscapes there are often areas of the matrix that offer refugia for wildlife (Chazdon et al. 2011; DeClerck et al. 2010; Karp et al. 2019). Indeed, Declerck et al. (2010) argue that Mesoamerican HMLs cannot be treated as landscapes composed of discreet habitat patches because low-intensity management creates a relatively benign matrix, and effective distance between patches may be low (Graham & Blake 2001). So although Neotropical HMLs are very different from original forest habitat, the high levels of tree cover, connectivity, and management heterogeneity mean that these landscapes support diverse bird assemblages (Frishkoff et al. 2014; Karp et al. 2011, 2019; Sekercioglu et al. 2007, 2019; Solar et al. 2015).

However, despite a reasonably comprehensive understanding of the factors influencing bird persistence at individual scales, difficulties emerge when integrating this evidence to consider the landscape in its entirety. Whilst the influences of habitat and landscape factors on bird assemblages can be assessed individually, they are all aspects of a single system and difficult to separate in the real world. Effects at one scale interact with those at another, working to relieve or compound the impacts of disturbance (Ewers & Didham 2006; Karp et al. 2019).

Landscape composition combines the effects of habitat area and quality, connectivity and matrix quality, but interactions between these different factors often complicates any synthesis (Andren 1994; Tscharntke et al. 2012). Previous research has shown that greater landscape heterogeneity supports more birds (Dietsch et al. 2007), and that there are increasing biodiversity losses across a disturbance gradient (Karp et al. 2011; Lawton et al. 1998; Schulze et al. 2004; Solar et al. 2015). There is also a broad acknowledgement of the importance of proximity to old-growth forest in determining the wildlife value of any individual HML site (Chazdon et al. 2011; Tscharntke et al. 2008). However, beyond such generalities, consensus regarding the relative importance of habitat area and quality, connectivity and matrix quality is often lacking. For example, whilst Prugh et al. (2008) and Doerr et al. (2011) contend that matrix quality outweighs the effects of patch area and connectivity, Hodgson et al. (2009, 2011) argue the reverse.

As yet, there have been few studies that integrate the impacts of habitat and landscape factors to understand how these influence species persistence in HMLs. Carrara et al. (2015) investigated the relative effects of landscape composition (forest cover and matrix composition), and landscape configuration (number of forest patches and edge density) on avian richness in forest patches at the 100 ha and 500 ha scales in southern Mexico. They found landscape composition, particularly at the 100 ha scale, to be the most important predictor for richness of forest specialists, while richness of non-forest bird species tended to increase with forest loss at both scales. More nuanced patterns were apparent in Costa Rica where Frishkoff & Karp (2019) reported that while forest species were sensitive to forest cover at both local (0.8 ha) and landscape (158 ha) scales, habitat generalists exhibited compensatory responses, with greatest abundances at sites with either high local or high landscape forest cover. These differing patterns probably arise because the importance of a particular factor (habitat area and quality, connectivity, and matrix quality) will vary according to landscape context.

1.4 Predicting avian responses to disturbance

In the Neotropics, the combination of forest habitat stability and narrow avian niche specialisation means that many birds are highly sensitive to habitat disturbance (Bregman et al. 2014; Rutt et al. 2019; Sekercioglu et al. 2007, 2019; Visco et al. 2015). Marked alterations in species assemblages and progressive loss of forest-associated bird species are typically associated with increasing intensity of land use (Moura et al. 2016, 2013; Petit & Petit 2003; Petit et al. 1999; Solar et al. 2015; Walter et al. 2017). Further impacts of land-use change include species invasions and loss of phylogenetic diversity (Frishkoff et al. 2014; Solar et al. 2015). Conservation interventions aimed at neutralising the effects of anthropogenic impacts requires detailed knowledge of species responses to disturbance.

Unfortunately, disturbance need not be dramatic or extensive in order to impact on avian communities. For example, some terrestrial insectivores are susceptible to changes in microhabitat structure such as leaf litter depth, extent of mid-storey vegetation or number of stems (Bhakti et al. 2018; Powell et al. 2015; Stratford & Stouffer 1999, 2015). Loss of commensal species such as army ants can also lead to extirpations (Harper 1989; Stouffer & Bierregaard 1995). Moreover, habitat disruption can be indirect; disturbance in one part of a landscape can influence bird communities in another by altering the local climate (Brawn et al. 2017; Khanna et al. 2017; Khanna & Medvigy 2014). Hence, there are multiple potential sources of disturbance that can influence bird assemblages, complicating our understanding of avian responses to HMLs.

Responses to disturbance are contingent on species-specific traits as well as landscape context, so that two species may respond to the same disturbance in different ways (Dietsch et al. 2007; Frishkoff et al. 2019; Frishkoff & Karp 2019; Moura et al. 2016; Vargas et al. 2012). However, certain habitat requirements and ecological and functional traits are particularly associated with greater disturbance sensitivity (Bregman et al. 2014; Newbold et al. 2013; Tobias & Pigot 2019). For example, medium-sized, non-flocking, canopy-dwelling omnivores tend to be relatively insensitive to habitat fragmentation (Bradfer-Lawrence et al. 2018; Lees & Peres 2008a; Stouffer et al. 2011). In contrast, raptors, large-bodied birds, and understorey insectivores have all been highlighted as particularly disturbance sensitive (Gray et al. 2007; Karr 1982; Moura et al. 2016; Powell et al. 2015; Sigel et al. 2010; Willis 1974). Determining which combinations of species traits and landscape factors are the most important drivers of avian community composition in HMLs is essential to understand the ecosystem processes in these landscapes, and to inform conservation efforts.

1.5 Conserving birds in Neotropical HMLs

Widespread anthropogenic alteration of landscapes drives major changes in both biodiversity and ecosystem functioning (Ceballos et al. 2015; Newbold et al. 2015; Pfeifer et al. 2017; Rosenberg et al. 2019; WWF 2018). Birds are a critical component of HML ecosystems, providing valuable services such as seed dispersal and herbivore predation that benefit humans (Karp et al. 2011; Nyffeler et al. 2018; Whelan et al. 2008, 2015). HMLs with low-intensity management may support bird communities that continue to provide these ecosystem services (Cardoso da Silva et al. 1996; Carlo & Morales 2016; Chapman et al. 2018; Walter et al. 2017). Indeed, species richness in Neotropical landscapes can increase with moderate levels of disturbance (Durães et al. 2013; Solar et al. 2015). However, while forest-affiliated bird species are often the most threatened by anthropogenic pressures, habitat generalists are also at risk in more intensively managed landscapes (Carvajal-Castro et al. 2019; Crooks et al. 2004; Hinsley et al. 2009). Loss of these generalist species will have knock-on effects on the wider HML system, and disrupt ecosystem services, so that conservation is essential (Van Bael et al. 2003).

The drivers of forest clearance are increasing rather than declining, so that management intensification and further deforestation are likely during the remainder of this century (Harvey et al. 2008; Laurance et al. 2014; Rudel et al. 2009). Land sparing, where areas are kept free of agriculture, is important for the preservation of global biodiversity, but protection will always be geographically limited (Laurance et al. 2014; Phalan et al. 2011). Given the rapid loss of tropical forest, and the inevitable limits to protected areas, effective biodiversity conservation has to take place in HMLs (Driscoll et al. 2013; Harvey et al. 2008; Vandermeer & Perfecto 2007). Indeed, biodiversity retention in agricultural landscapes is essential, as the efficacy of protected areas is contingent on well-maintained buffer zones in the surrounding landscape to connect protected areas and provide additional wildlife habitat (Chazdon et al. 2009; Norris 2008; Vandermeer & Perfecto 2007).

Maintaining and boosting connectivity across HMLs is key to ensuring species persistence (Newmark et al. 2017). Connectivity can be encouraged by protecting live fences and riparian strips, as these are frequently used by birds to travel between forest patches (Estrada et al. 2000; Gillies & St. Clair 2010; Leon & Harvey 2006; Pulido-Santacruz & Renjifo 2011). Even isolated trees in pasture can be important for maintaining avian dispersal (Cardoso da Silva et al. 1996; Luck & Daily 2003). In addition to ensuing existing forest fragments are connected, encouraging restoration and establishing new forest areas will help to increase the overall level of forest in a landscape (Calle & Holl 2019; Chazdon 2019), a critical factor for the persistence of many birds in HMLs (Brancalion et al. 2019; Karp et al. 2013, 2019; Walter et al. 2017).

Conservation and restoration efforts have to be integrated with human land uses (Chazdon 2019; Chazdon et al. 2009), however achieving this in complex HMLs is difficult. As discussed above, the combination of variable landscape contexts and species-specific responses to disturbance make it difficult to predict avian assemblage composition at a specific location. This hinders the design of effective conservation interventions, as no single approach will be suitable for all areas. Some crops, such as shade coffee, can be readily integrated with more natural vegetation cover, but this is not an option in more intensive agricultural systems such as pineapple production. Efficacy of interventions will also be dependent on broader HML context (Brancalion et al. 2019; Newmark et al. 2017); proximity to continuous forest or a large urban conurbation can have important consequences for wildlife populations. For example, the value of isolated trees for frugivores depends on the distance to extensive forest and intensity of land management in the matrix (Luck & Daily 2003). Given there will always be limited funding for conservation and restoration, and that landscape context will define the success of any intervention, identifying the best locations requires a rigorous, evidence-based decision making process.

1.6 Sources of evidence for conservation

Conservation interventions should be underpinned by scientific evidence in order to maximise their chances of success (Sutherland et al. 2004). When that evidence involves bird communities, data have generally been collected using point counts (Karp et al. 2019; Lees & Peres 2006; Mayhew et al. 2019; Reid et al. 2014; Rompre et al. 2009), mist nets (Banks-Leite et al. 2011; Karr 1982, 1990; Stouffer et al. 2011), or territory mapping (Camerlenghi et al. 2019; Robinson et al. 2000). These techniques allow collection of highly detailed datasets, and permit sophisticated analyses such as estimates of abundance, compositional changes and community dynamics (Martínez & Gomez 2013; Moura et al. 2013). However, there are drawbacks associated with these approaches, as they require expert surveyors and considerable time in the field (Burivalova et al. 2018; Hobson et al. 2002).

Recent technological developments, such as automated audio recorders and camera traps, offer a new and potentially cost-effective means of gathering data (Burivalova et al. 2019a). There are a variety of ways in which audio recordings might be used to survey and monitor biodiversity. The most straightforward analyses involve acoustic indices, which provide objective metrics based on acoustic features such as pitch and amplitude. Patterns in acoustic indices values have been associated with different habitat structures and changes animal populations (Jahn et al. 2017; Oliver et al. 2018; Rodriguez et al. 2014). More direct but time-consuming approaches involve determining species presences in recordings, permitting analyses of community composition (Pillay et al. 2019). The most complex methods assess bird vocalisations, in order to track behaviour patterns and infer abundance (Gibb et al. 2018; Metcalf et al. 2019; Pérez-Granados et al. 2019; Vold et al. 2017). Whichever type of analysis is chosen, audio recordings can be gathered over large spatial and temporal scales, and provide a permanent, unbiased record (Darras et al. 2018a; Deichmann et al. 2018; Sugai & Llusia 2019).

Crucially, output from analyses of recordings can be tied to landscape composition in similar ways to data gathered using point counts and mist nets (Gibb et al. 2018). Thus recorders are a potentially valuable tool in assessing the wildlife populations of HMLs, and could be a cost-effective source of evidence for conservation. However, to date, attempts to use recorders in these contexts have given mixed or contradictory results (Darras et al. 2018a; Fuller et al. 2015; Mammides et al. 2017). Before widespread adoption of this new technology, researchers and conservation practitioners need to be certain that analyses of recordings give consistent patterns.

1.7 Thesis aims and outline

As anthropogenic pressures increase, conservation interventions will likely be required to maintain avian communities and ecosystem services in HMLs. Effective conservation requires detailed understanding of how complex landscape compositions influence species' distributions and abundance. Critically, there is a need to determine how species-specific traits interact with landscape contexts. In addition to standard point count methods, recent developments in automated audio recorders provide the opportunity to gather data over wide spatiotemporal scales, potentially providing new insights for conservation planning. The overall aims of this thesis were to:

1. Assess the avian community of a Neotropical HML,
2. Determine whether there are predictable patterns between species traits and responses to HML composition,
3. Assess the potential of acoustic indices for surveying HMLs, determining (a) whether there are habitat-specific patterns among habitats, and (b) can acoustic indices be linked to avian species richness and abundance, and
4. Determine whether avian community information derived from audio recordings is equivalent to point counts.

1.8 Study region and data collection

The studies in this thesis were conducted in the Emparador HML in central Republic of Panama. The region is bordered by the Panama Canal to the north and east, and by the Interamericana highway to the south, and covers approximately 700 km^2 (Figure 1.1). There is a large area of forest bordering the canal, where the tree cover is protected to control soil erosion. To the south and west of this forest, the landscape is typical of many Mesoamerican HMLs, with a heterogenous matrix composed of forest fragments, riparian strips, regenerating scrub, timber plantations and cattle pasture. Based on aerial photographs, the region had already undergone substantial deforestation by the 1950s, although many field boundaries have persisted since that time. Urban areas are concentrated near the highway, but with further small settlements distributed throughout the landscape.

The avian community in this HML was assessed in two ways, using standard point count methodology and automated audio recorders. Point counts were conducted at 190 sites

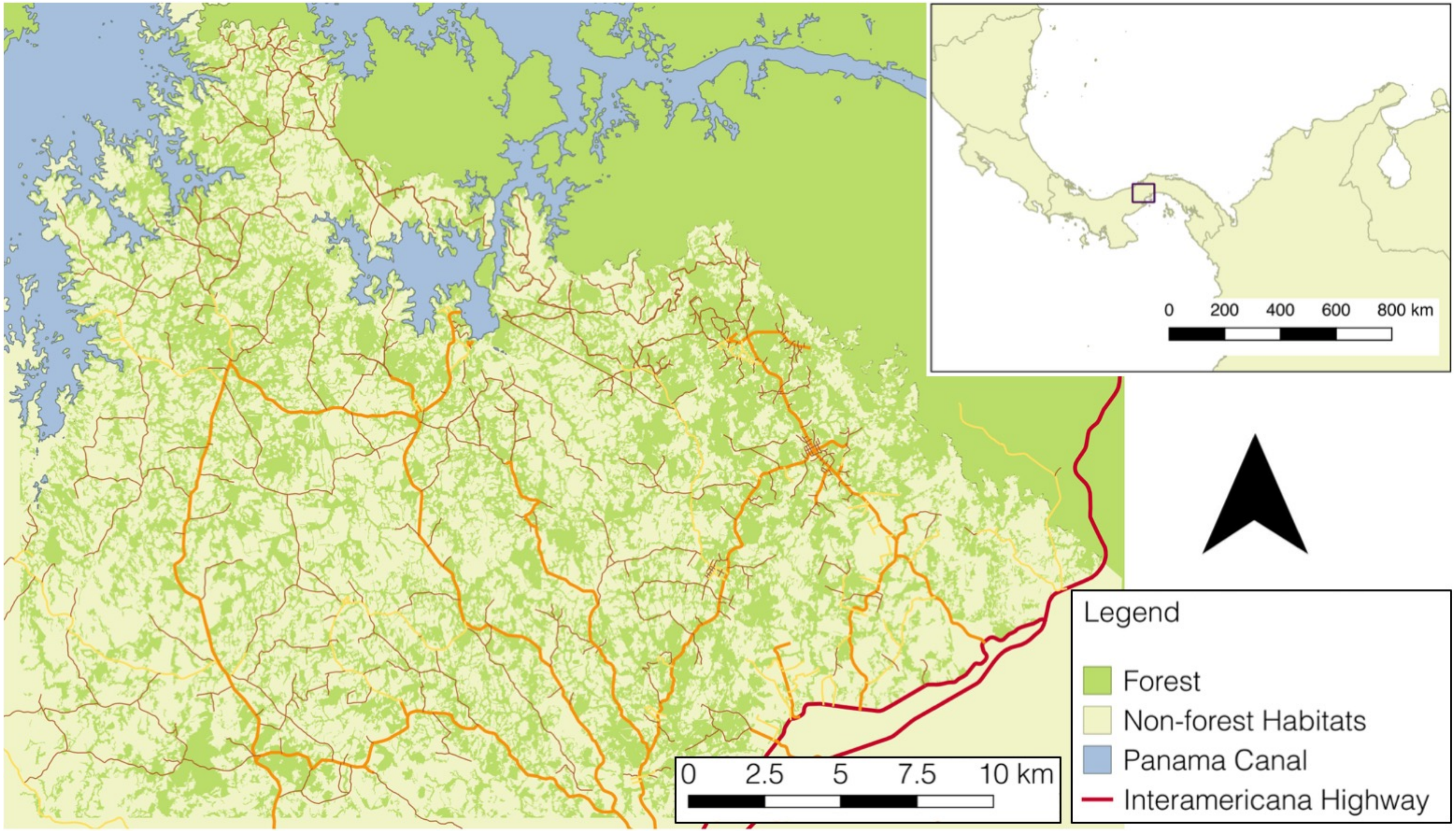


Figure 1.1 - The Emparador human-modified landscape, central Republic of Panama. Inset map shows the broader regional context with the study area identified by the box.

across the landscape, covering the main habitat types listed above. Each site was visited a total of eight times over the course of two seasons (dry and wet). During the 1520 point count surveys we recorded 36,598 individual birds. Automated audio recorders were deployed for one week at 148 sites. Forty-five of these sites were visited twice, once in each season. This gave a total of over 37,000 hours of audio recordings. At 60 core sites we collected both point count and audio recorder data. At these same core sites, we assessed woody vegetation in a 20 m x 20 m plot, recording canopy height, and number and circumference of stems for plants over 1.3 m in height.

1.9 Outline of chapters

Chapter 2. Can trait-based assemblages predict species-level responses to landscape structure in Neotropical human-modified landscapes?

Designing effective conservation actions to support bird populations in HMLs requires detailed knowledge of how well individual species respond to this structural complexity. However, tropical bird communities often contain a large proportion of rare species that are infrequently detected during field surveys, making it difficult to ascertain how landscape structure dictates persistence of individual species.

One potential resolution of this issue involves grouping species according to their functional traits and habitat preferences, and examining group-level responses to landscape structure. We divided species into eight functional groups according to dietary traits and habitat preferences. Using the point count data to build a Poisson-Binomial mixture model, we examined changes in avian abundances as a response to distance to core forest, and forest cover and extent of fragmentation at local (10 ha) and landscape (500 ha) scales. We sought to answer: (1) Are there consistent responses within functional groups to forest cover, fragmentation and distance to core forest? (2) Do functional groups have common species-level response patterns to HML structure? (3) Are there particular species that have the greatest difficulty persisting in HMLs, and do these species respond in the same way at the same spatial scales? and (4) Can specific traits be used to identify these sensitive species?

Chapter 3. Guidelines for the use of acoustic indices in environmental research.

Acoustic indices have great potential for biodiversity monitoring. However, reported patterns linking acoustic indices with habitats have been contradictory, possibly because there is no accepted best practice for the collection and analysis of audio recordings. We used 26,000 hours of recordings from 117 sites across a range of habitats, in order to investigate: (1) What duration of recordings is necessary to quantify the soundscape of a site using acoustic indices, and does this vary among habitat type or acoustic index? (2) Should recordings be continuous, or can they be limited to temporal sub-samples to minimise storage volumes and subsequent analysis? and, (3) Which acoustic indices best reflect temporal variation over the course of the day, and between seasons, and are there different patterns among habitats? We use the answers to these questions to propose: (1) guidelines for designing studies using audio recordings for the rapid assessment of multiple sites, and (2) a workflow for comparing recordings with seven of the most commonly used indices, permitting discrimination among habitat-specific soundscapes.

Chapter 4. Rapid assessment of avian species richness and abundance using acoustic indices.

The soundscape of a site, and hence acoustic indices values, is not only driven by habitat structure, but also its wildlife assemblage. Changes in acoustic indices values may therefore reflect changes in the species present at a site. However, thus far, evidence supporting this link has been equivocal; we argue that this is because of conceptual and methodological limitations in previous research.

The principal question we addressed was whether acoustic indices can be used as biodiversity monitoring tools? We used 84 hours of audio recordings covering 315 dawns from 43 sites, coupled with bird assemblage and vegetation data collected in the field. We hypothesised that greater avian species richness, avian abundance, and vegetation structural complexity would be reflected in acoustic indices values indicating greater soundscape complexity. We sought to confirm that biodiversity metrics are reflected in acoustic indices values, and to identify which indices are most useful for monitoring avian communities.

Chapter 5. Monitoring an avian taxon of conservation concern across landscape gradients using point counts and automated audio recorders.

There have been few tests of the efficacy of audio recordings to track changes in species occupancy across heterogenous landscapes, nor whether results derived from recordings collected in these contexts are comparable with those from standard assessment methods such as point counts. Here we evaluated the potential of automated audio recorders for surveying assemblages of a disturbance-sensitive Neotropical avian group, the antbirds (*Thamnophilidae*), across a range of habitat types.

We recorded antbird species using both audio recordings and point counts at 40 sites. We linked these occupancy data to measures of vegetation structure (number of stems), habitat integrity (Normalised Difference Vegetation Index) and landscape composition (forest cover and fragmentation). Using Bayesian hierarchical models that accounted for imperfect detectability, we asked: (1) Are the data from recorders sufficient to show variation in antbird species occupancy at sites with differing vegetative characteristics and landscape settings? and (2) Are antbird occupancy patterns derived from recorders equivalent to those from point count surveys?

Chapter 6. General discussion.

Considerable research attention has been devoted to understanding HML ecosystems over the last decade, and we show how our results compliment current knowledge. Specifically, we show how our findings aid comprehension of landscape influences on avian persistence, avian habitat use, and the maintenance of ecosystem services in HMLs. We discuss avenues for future research, highlighting aspects of HML systems that are most likely to be important for biodiversity conservation. The situation in Panama is contrasted with other Neotropical HMLs, considering both historic context and potential future trajectories. Finally we discuss the conservation and policy implications of our findings for maintaining avian biodiversity in Emparador and other Neotropical HMLs.

Chapter 2. Can trait-based assemblages predict species-level responses to landscape structure in Neotropical human-modified landscapes?

Research ideas conceived by Tom Bradfer-Lawrence. TBL and Nick Gardner collected the field data. TBL and Eben Broadbent constructed the land cover map. Daisy Dent, Stephen Willis and Nils Bunnefeld supervised the work. TBL led the writing of the text. All authors commented on a draft version of this chapter.

2.1 Abstract

Sustaining bird populations in human-modified tropical landscapes is essential for the long-term conservation of tropical forest species and maintenance of ecosystem services. Human-modified landscapes are composed of multiple habitat patches, including forest fragments, timber plantations, pasture and cropland. Vegetation structure and matrix composition often vary markedly across spatial scales. Designing effective conservation actions to support bird populations in these landscapes requires detailed knowledge of how individual species respond to this structural complexity. However, tropical bird communities often contain a large proportion of rare and sparsely distributed species that are infrequently detected during field surveys, and this makes it difficult to ascertain how landscape structure dictates persistence of individual species.

One potential solution to the issue of rare species is to group species according to their functional traits and habitat preferences, and examine group-level responses to landscape structure. To investigate this approach we undertook 1520 point counts across a human-modified landscape in the Republic of Panama. We divided species into eight functional groups according to dietary and morphological traits and habitat preferences. Using a Poisson-Binomial mixture model to account for imperfect detection, we examined changes in species' abundances as a response to forest cover and extent of fragmentation at local (10 ha) and landscape (500 ha) scales, and distance to core forest. Forest cover had a greater influence on species' abundances than fragmentation, and effects of both predictors were stronger at the landscape scale. Open habitat species tended to increase with greater distance to core forest, while few species exhibited declines, perhaps because the most sensitive forest-affiliated species have already been lost from the regional species pool. Critically, species' abundances varied significantly within functional group at both spatial scales in response to the landscape parameters, and there were no clear trait patterns that could be used *a-priori* to predict species responses. We demonstrate how these contrasting responses to landscape structure are reflected in species abundances for trait groups important for ecosystem functioning, namely frugivores and insectivores. Variable intra-group responses may be the result of spatial partitioning among functionally similar species. We conclude that coarse trait-based groupings are inappropriate for predicting responses to landscape structure, but suggest that key ecosystem processes may be maintained in low-intensity human-modified landscapes despite species turnover.

2.2 Introduction

Each year approximately 76,000 km^2 of tropical forest are cleared for agriculture, leaving forest fragments embedded in a heterogenous matrix of other habitats, such as cattle pasture and regenerating scrub (Achard et al. 2014; DeClerck et al. 2010; Wright 2010). The isolation of forest as fragments within human-modified landscapes (HMLs) triggers shifts in the abundance and composition of animal populations both locally and across the broader landscape (Bregman et al. 2014; Sekercioglu 2007; Solar et al. 2015; Stouffer et al. 2006). In turn, changes in wildlife populations potentially threaten ecosystem services such as seed dispersal and control of invertebrate herbivores (Bovo et al. 2018; Karp et al. 2011; Mello et al. 2015; Nyffeler et al. 2018; Sekercioglu 2012; Van Bael et al. 2003).

Conservation interventions may be required to preserve species and ecosystem services in HMLs, however the evidence needed to inform effective conservation actions is often lacking. Specifically, although we have a broad understanding of how habitat disturbance impacts animal populations, it can be difficult to predict the response of individual species, especially rare species (Banks-Leite et al. 2012; Moura et al. 2016). Species-specific responses are likely driven by a combination of functional and morphological traits, habitat preferences, and responses to landscape structure at a variety of spatial scales (Betts et al. 2014; Newbold et al. 2013). Given that many tropical species are rare, and HMLs are heterogeneous and complex, it is difficult to infer causal links between species responses, their traits, and HML structure (Lindell et al. 2004).

The influence of local and landscape habitat structure on avian persistence in tropical HMLs has received considerable research attention. Studies have examined landscape composition (e.g. proportion of remaining forest cover), configuration (e.g. extent of fragmentation), and synergistic interactions between the two (Carrara et al. 2015; Morante-Filho et al. 2018; Moura et al. 2013). At the local scale (~1 - 100 ha), patch area has a strong effect on species richness and assemblage composition, with smaller patches supporting fewer species (Graham & Blake 2001; Stouffer et al. 2011; Stratford & Stouffer 1999). This influence has been ascribed to edge effects, as edges have markedly different conditions to those of forest interiors, including an altered climate, potentially increased predation rates, and a greater frequency of anthropogenic disturbances such as fire (Cochrane 2001, 2003; Vetter et al. 2013). Such effects can stretch for 200 m or more into a forest patch (Canaday & Rivadeneyra 2001; Restrepo & Gomez 1998; Zurita et al 2012), and species sensitive to such disturbances are therefore restricted to the core area of any patch. Thus patches with a higher ratio of edge to area will support fewer forest species because the core area is smaller (Banks-Leite et al. 2010).

Local scale effects of area and edge on bird populations can be moderated by the composition of the surrounding matrix (Durães et al. 2013; Eycott et al. 2012; Prevedello & Vieira 2010; Stouffer et al. 2006; Wolfe et al. 2015a). Many forest-affiliated bird species are highly sensitive to both the proportion and configuration of remaining forest cover in the wider landscape (>100 ha; Banks-Leite et al. 2010; Blandón et al. 2016; Carrara et al. 2015; Karp et al. 2019; Rompre et al. 2009; Vidal et al. 2019). Critical thresholds of forest cover have been reported at the landscape scale; when forest cover drops below this threshold extirpations of forest-affiliated bird species increase markedly, leading to major shifts in community composition (Banks-Leite et al. 2014; Betts et al. 2007; Martensen et al. 2012; Swift & Hannon 2010). For example, in the Brazilian Atlantic Forest, Vidal et al (2019) found that below 40% forest cover, specialist frugivores were replaced by generalist omnivores, substantially altering community composition. This threshold is comparable with other Neotropical studies, which report thresholds of between 20 and 50% forest cover (Melo et al. 2018; Morante-Filho et al. 2018; Rompre et al. 2009).

Species turnover following changes in forest cover implies that bird species respond to HML structure in different ways. Studies frequently use a dichotomy of "forest specialist" versus "generalist" species to explain these responses, with specialists often declining with greater forest loss (Banks-Leite et al. 2014; Blandón et al. 2016; Kormann et al. 2018). However, such broad, post-hoc classifications inevitably obscure substantial inter-species variation in responses to forest loss and fragmentation (Betts et al. 2014; Monkkonen & Reunanen 1997; Pearman 2002; Swift & Hannon 2010; Valente & Betts 2019). Some forest-affiliated species are able to persist in HMLs while others decline. This complicates the design of conservation interventions for biodiversity and ecosystem services, and raises the question: how can we move beyond the broad specialist-generalist classification, but still discern common patterns in community responses to HML structure?

Avian responses to HML structure are likely dictated by their morphological and functional traits. For example, large-bodied frugivores often decline following forest loss while smaller-bodied insectivores increase (Newbold et al. 2013; Sekercioglu 2012). Behavioural traits have also been used to identify sensitive species, for example, ground foraging species are at greater risk of extinction from habitat disturbance than bark gleaning species (Tobias & Pigot 2019), and migratory species persist more readily in HMLs than sedentary species (Sekercioglu et al. 2019). So by grouping bird species using functional and morphological traits, it may be possible to identify group-level responses to landscape structure at a finer scale than just forest specialist or habitat generalist (Frishkoff & Karp 2019). This might reveal more informative patterns regarding species' responses to local and landscape habitat structure, and so inform conservation interventions (Pearman 2002). For example, wide-ranging omnivorous species can often persist in HMLs following habitat fragmentation (Graham 2001; Vidal et al. 2019), so presence at a specific location might be determined by local habitat structure. Conversely, forest-affiliated understorey insectivores often have low dispersal abilities and can be highly sensitive to fragmentation (Laurance 2004; Lees & Peres 2010; Moore et al. 2008; Woltmann et al. 2012), so their persistence might be dependent on broader, landscape-scale habitat structure (Pearman 2002).

Thus, grouping species by traits might offer greater insight into responses to HML structure, potentially improving the design of conservation interventions for threatened species (Pavlacky et al. 2015). In this study we examine the abundances of 250 bird species at 190 point count locations across a human-modified landscape in central Panama to assess whether *a-priori* defined trait-based species groups have common responses to habitat structure. Specifically, we consider;

1. Are there consistent responses within functional groups to distance to core forest, and to forest cover and fragmentation at local (10 ha) and landscape (500 ha) scales?
2. Do functional groups have common species-level response patterns to HML structure?
3. Are there particular species that have the greatest difficulty persisting in HMLs, and do these species respond in the same way at the same spatial scales? and,
4. Can specific traits be used to identify these sensitive species?

2.3 Methods

2.3.1 Study landscape

The Emparador landscape lies to the southwest of the Panama Canal in the Republic of Panama. The region has a tropical climate, with a dry season between mid-December and April, and rainfall concentrated during the remainder of the year, peaking in November (Windsor 1990). There is a pronounced rainfall gradient from south to north across the isthmus, ranging from 1969mm to 2334mm across the Emparador landscape (Pyke et al. 2001). A large area of continuous forest borders the canal, while the rest of the landscape comprises a heterogenous mix of cattle pasture, non-native timber plantations, small urban areas, forest fragments, riparian strips and regenerating scrub vegetation. The open areas of the HML underwent substantial deforestation before the 1950s, since when ongoing disturbance has been of much lower intensity, so that land use patterns are relatively fixed.

2.3.2 Point count data collection

Across the Emparador landscape, we established 190 point count locations, each of which was a minimum of 200m apart (Figure 2.1). Points were grouped in 18 transects, with one transect surveyed in a single morning (9 – 12 points each), and located in such a way as to cover a broad range of the matrix compositions present in the landscape (Figure 2.S1). Each point count was surveyed eight times in 2017, four times in each of wet and dry seasons, giving a total of 1520 counts. Revisits to transects were a mean of 25 +/- 3 days apart within season. During each survey, two experienced ornithologists (TBL and NG) conducted 10-minute, unlimited radius point counts. Counts began 30 minutes after nautical twilight and were completed within 4 hours of dawn. Number of detections declined slightly over each morning (see Figure 2.S2 and Table 2.S2), so to avoid potential order effects we varied the sequence of points visited during each survey, and accounted for time of count in the modelling (see below). Point counts were located in either forest, plantation, scrub or pasture, and there was higher detectability in pasture compared to the other habitat types (Figure 2.S3, this was also accounted for in the modelling (see below). We recorded all birds seen and heard, except vultures, hirundines and swifts; these three taxa are wide-ranging and largely aerial, thus their presence often does not reflect usage of the location being surveyed. We classified the habitat type in which the bird was located as being either forest, plantation, scrub, pasture, or aerial. We were highly conservative in our assessment of repeat detections to avoid double counting.

2.3.3 Trait-based clustering

Using R (ver 3.6.0; R Core Team 2018), we conducted hierarchical clustering with the package "cluster" (ver 2.1.0; Maechler et al. 2019). We divided all species recorded during the point count surveys into eight groups, based on functional and morphological traits and habitat preferences. Trait data comprised body size, dietary composition and foraging strata from Wilman et al. (2014), forest dependency rating from BirdLife International (2019), and PCA scores derived from a morphological trait dataset in Pigot et al (2020).

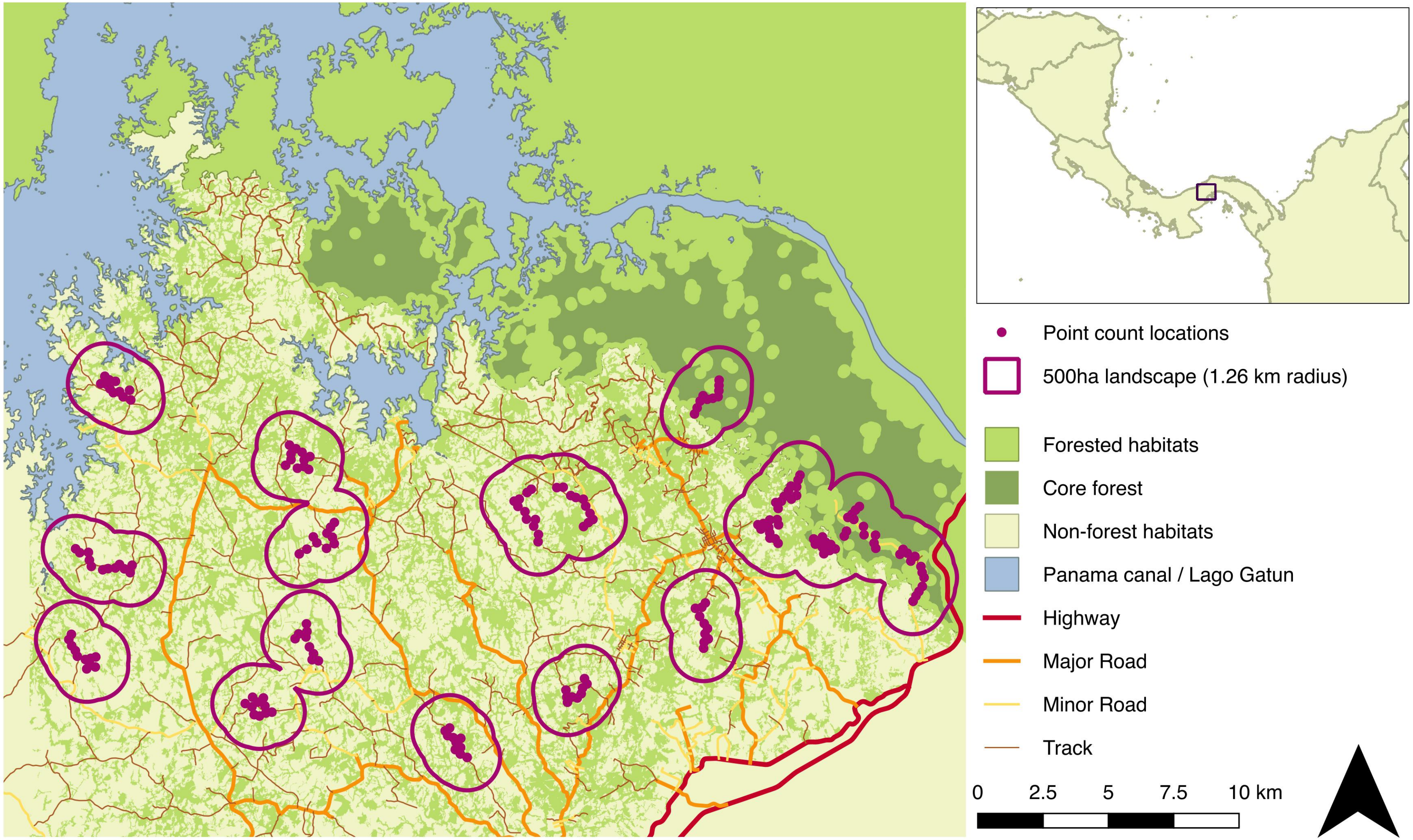


Figure 2.1 - Map of the Emparador landscape, Republic of Panama, showing core and peripheral forest habitats, and the 190 point count locations.

These trait data were augmented with each species' apparent habitat preference. This was the proportion of detections in each of the five habitat classes recorded during the point counts.

2.3.4 Landscape analysis

We generated a landcover map of the Emparador landscape from two satellite imagery sources. Cloud-free, 4-band multispectral imagery from PlanetLabs satellites were selected for both dry and wet seasons, from either 2016 or 2017. This was supplemented with three Sentinel 1 radar layers (ESA, 2019) collected in 2017; one each from the dry season (February), early wet season (July) and late wet season (October). These 11 layers were stacked and processed using eCognition segmentation software (ver 9.2, Trimble). The resulting polygons were then classified into six landcover types (forest, scrub, plantation, pasture, urban and water) using a random forest classifier (Breiman 2001; Carreiras et al. 2017). We ground-truthed a minimum of 200 points per landcover class in the field. We built the model using 70% of these data, and tuned it to find the best parameters with the "caret" R package (ver 6.0.84; Kuhn 2019). We used 10-fold cross-validation on the final version, and tested the classifier with the remaining 30% of ground-truthed points. Testing demonstrated the model to be 92.5% accurate.

From the landcover map we determined proportion of forest cover and forest edge density (as a measure of fragmentation) at each point count location in QGIS (ver 3.4). These were calculated at two radii: 180 m, and 1260 m, equating to approximately 10 ha, and 500 ha. The distances were chosen to minimise potential correlation between the different spatial scales. We also calculated the distance from each point count to the closest area of core forest, defined as forest over 200 m from any patch edge and at least 10 ha in size. Forest cover and fragmentation values at the 10 ha and 500 ha scales, and distance to core forest were used in the species abundance modelling (see below).

2.3.5 Abundance modelling

In a Bayesian framework we constructed a Poisson-Binomial mixture model to examine abundance of each species as a response to landscape parameters, while accounting for imperfect detection (Kery & Royle 2016; Yamaura et al. 2011). The count C of each species (i) at each site (j) during visit (k) came from a Binomial distribution:

$$C_{i,j,k} \sim \text{Binomial}(N_{i,j}, p_{i,j,k})$$

Where N is the true number of individuals of each species, and p is the detection probability, here modelled as;

$$\text{Logit}(p_{i,j,k}) = \alpha 0_{\text{habitat}} + \alpha 1 \text{ x time}_{j,k} + \alpha 2 \text{ x season}_{j,k}$$

With “habitat” identifying the main habitat surrounding the point count in a 50 m radius (forest, plantation, scrub or pasture), “time” indicating the time of point count as number of minutes since morning nautical twilight, and “season” (with four levels: early dry, late dry, early wet and late wet). True abundance, with data augmentation *phi* that accounts for never detected species (Kery & Royle 2016), came from a Poisson distribution:

$$N_{i,j} \sim \text{Poisson}(phi_{i,j}, lambda_{i,j})$$

We modelled abundance as a function of landscape structure, thus;

$$\log(\text{lambda}_{i,j}) = \beta 0_i + \beta 1_i \text{ x forest \_10ha}_j + \beta 2_i \text{ x forest \_500ha}_j + \\ \beta 3_i \text{ x fragmentation\_10ha}_j + \beta 4_i \text{ x fragmentation\_500ha}_j + \beta 5_i \text{ x distance}_j + \gamma_{\text{transect}j}$$

Where “forest” and “fragmentation” reflect those features at local (10 ha) and landscape (500 ha) scales, and “distance” indicates Euclidian distance to closest core forest patch. Numeric parameters were scaled and centred prior to analysis. We assumed that no immigration or emigration took place within season, and included random effects of season and transect to account for potential autocorrelation.

Modelling was conducted using JAGS (ver 4.3.0, Plummer 2017), via R software using the package “jagsUI” (ver 1.5.0; Kellner 2018). We used 100,000 iterations with the first 50,000 discarded as burn-in, with 8 chains and a thinning rate of 20 to give 4000 posterior samples. We confirmed convergence by checking trace plots and examining the Gelman-Rubin statistic (Gelman & Rubin 1992). To improve convergence we excluded species with fewer than 20 detections. In almost all cases model parameters converged successfully ($\hat{R}$ values < 1.1, Table 2.S3). Where convergence was not reached it resulted in wider Bayesian Credible Intervals (BCIs) for that parameter for the individual species, increasing the probability of a false negative but not a false positive.

2.3.6 Impacts of landscape structure on species abundances

Using the model output we simulated each trait groups' responses to forest cover and fragmentation at the 10 ha and 500 ha scales, and distance to core forest, demonstrating their changing abundance across the Emparador HML. To examine intra-group variation, we produced predicted distribution maps for example species from trait groups likely to be key for ecosystem processes. These illustrate how species with common traits might diverge in their responses to HML structure, and demonstrate how model output might be used in conservation planning.

Finally, we examined species-level responses to the landscape parameters at the two spatial scales. We assessed whether there are specific trait profiles that can be used to identify species sensitive to declines in forest cover and increases in fragmentation, and whether those species have similar responses at the same spatial scales.

2.4 Results

2.4.1 Trait-based species groups

Cluster analysis of the 250 species present in the study region yielded eight trait-based groups with distinct patterns in traits and habitat preferences (Figures 2.2 & 2.S4). Dietary composition was the predominant driver of group membership. Insectivores accounted for 124 species, of which 121 were placed in two groups, separated according to level of forest dependency (Birdlife International 2019). Species in the nectivore and frugivore groups were largely composed of medium and highly forest-dependent species (93% and 88% of groups respectively), and were detected most frequently in forest habitats (71% and 50% of detections respectively). Insectivores with low forest dependency were more strongly associated with pasture and scrub (33% and 35% of detections) than forest habitats (22% of detections; Figure 2.S5). Two groups were composed of omnivorous species, but one group had overwhelmingly frugivorous and insectivorous diets (42% each) and were associated with forest (60% of detections). The second omnivorous group of 28 species largely comprised vertivores and aquatic predators consuming vertebrate and invertebrate prey (48% and 40% respectively).

2.4.2 Species abundance models

We recorded 36,598 individual detections from 250 species. Of these, 163 species had more than 20 detections and were used in the abundance modelling (total detections = 36,189). Forest cover influenced abundance of many species at the 10 ha and 500 ha scales (Figure 2.3). At the local scale, there were consistent responses within some of the trait-based groups; frugivores, nectivores and forest-dependent insectivores increased in abundance with greater forest cover at 10 ha (increase in abundance between zero forest cover and complete forest cover for frugivores = 46%; nectivores = 10%; high forest dependent insectivores = 75%; Figure 2.4). At the landscape scale, group-level trends were less clear. Forty-four species still exhibited significant positive responses to increasing forest cover, but 72 other species, typically those associated with more disturbed or open habitats, had significant negative responses (Figure 2.3). Contrasting within-group responses to forest cover created U-shaped predicted abundance curves, with the highest values at the limits (Figure 2.4). These diverging patterns were most notable in frugivores, and high forest-dependent insectivores, with two to three times as many individuals predicted at extreme levels of forest cover compared to intermediate values.

Overall, more species were influenced by forest cover than fragmentation. Fifty-four percent of species showed significant responses to forest cover at 10 ha, and 64% at 500 ha, whereas only 17% of species has significant responses to fragmentation at 10 ha and 45% at 500 ha. Each trait-based group included some species that responded positively to increasing fragmentation at the 500ha scales (Figures 2.S5 and 2.S6), species that tended to be associated with more open habitats. Thirty-four percent of species were significantly influenced by distance to core forest.

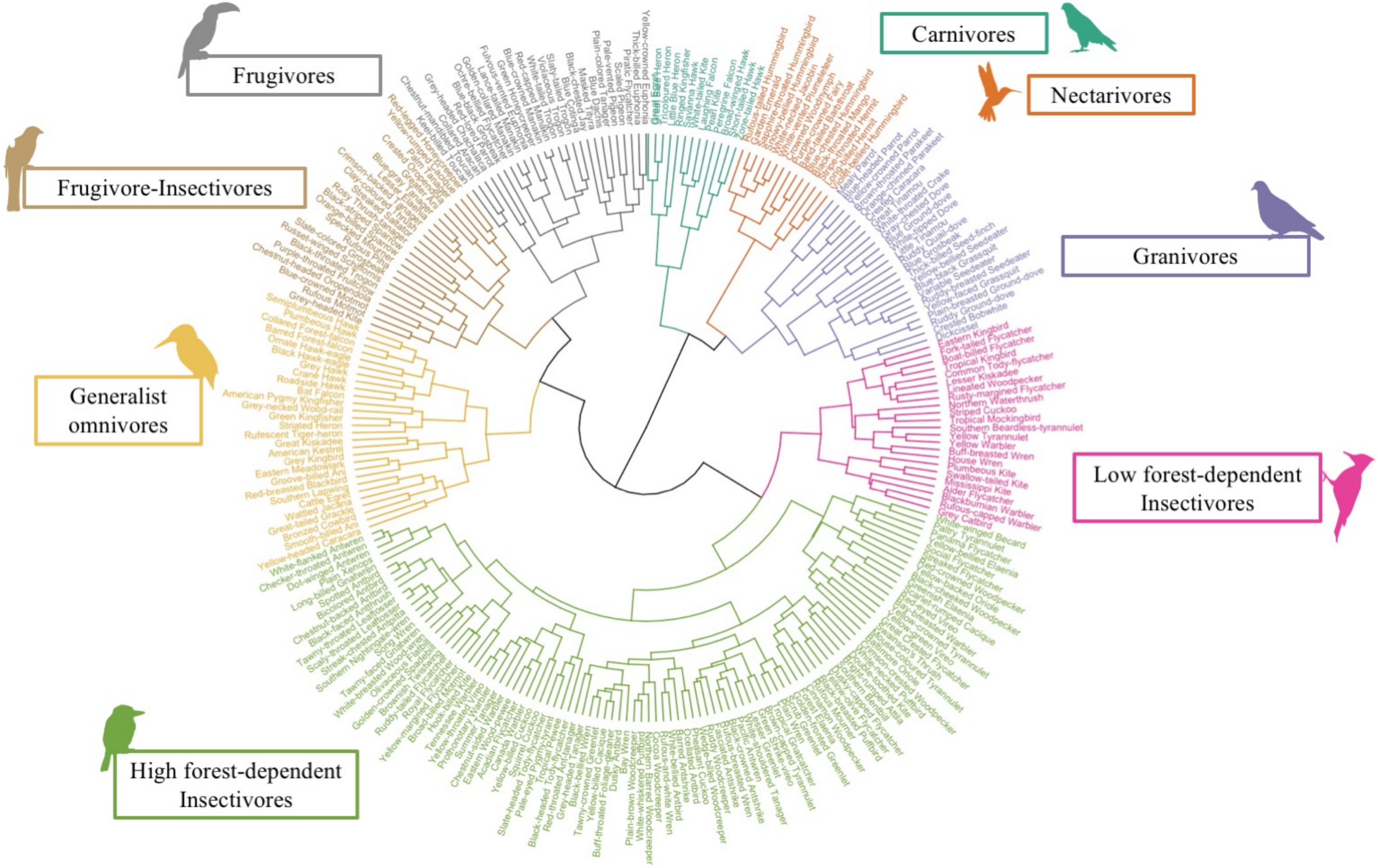


Figure 2.2 - The 250 species detected during point count surveys in this study, clustered into eight groups based on dietary traits and habitat preferences.

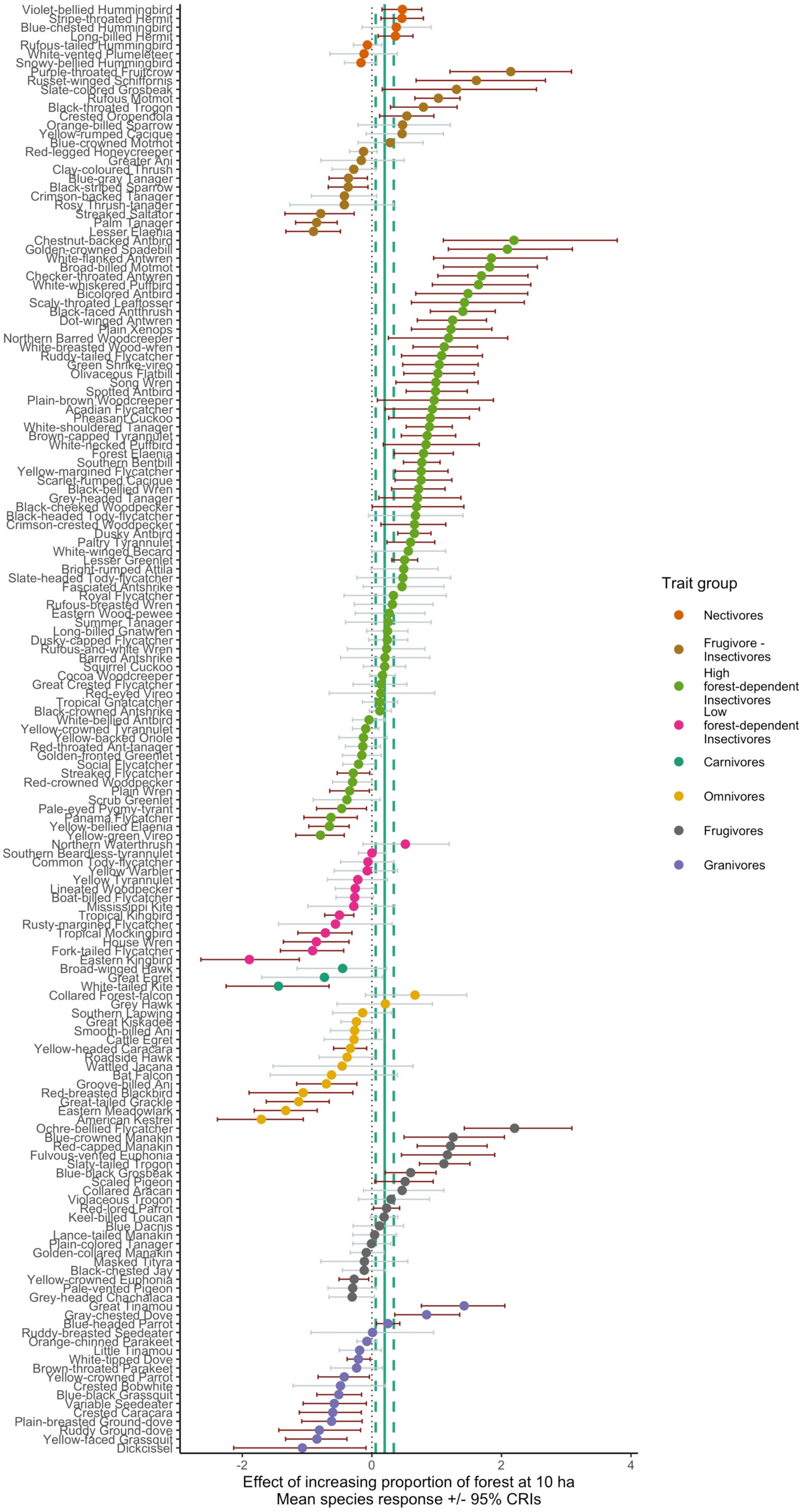


Figure 2.3a - Species responses to the proportion of forest cover at 10 ha, with species clustered by trait-based groups. Shaded bars denote species with 95% BCIs that do not include zero (implying a significant response). Overall community mean value and 95% BCIs shown by the vertical green lines.

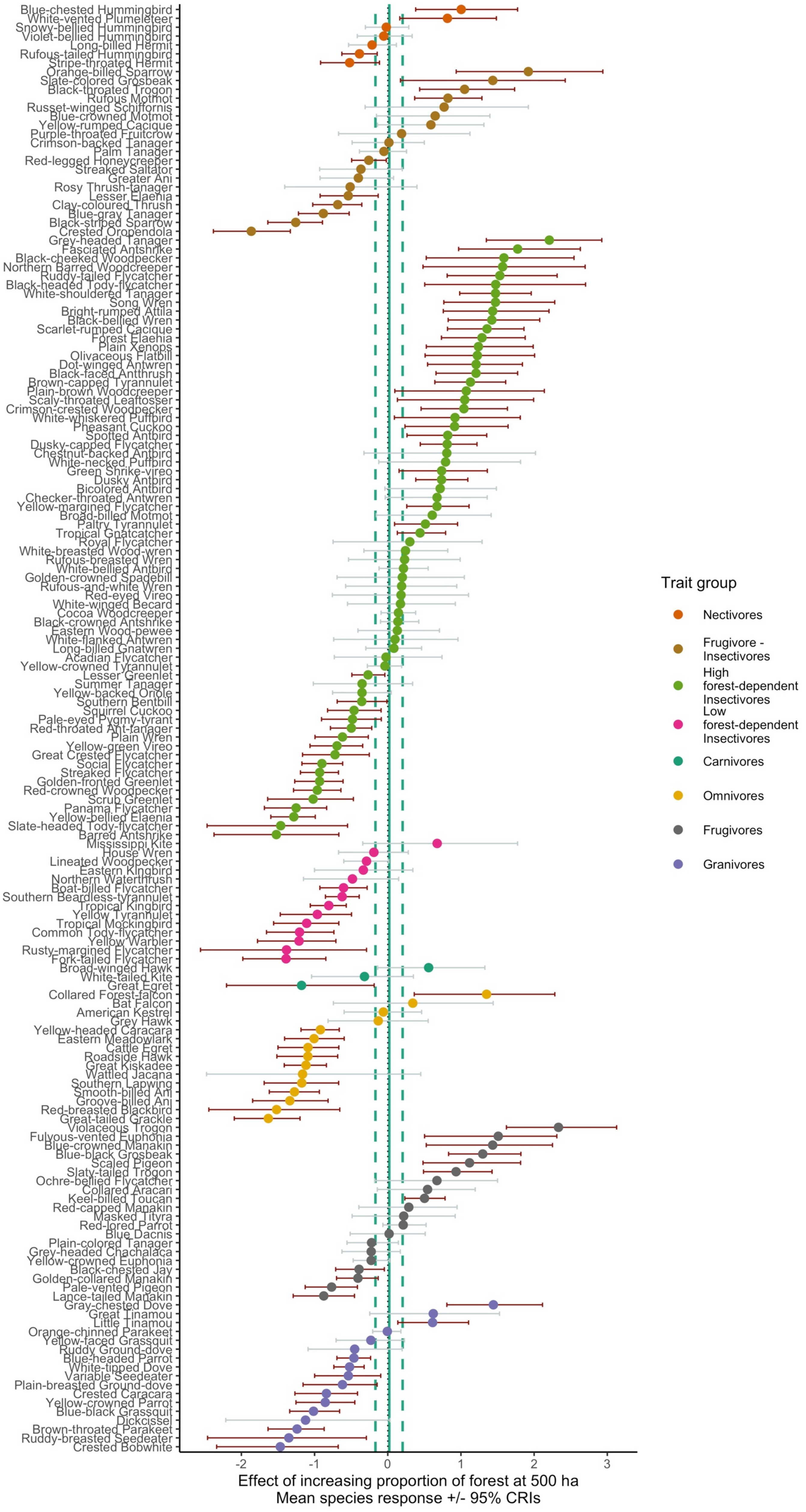


Figure 2.3b - Species responses to the proportion of forest cover at 500 ha, with species clustered by trait-based groups. Shaded bars denote species with 95% BCIs that do not include zero (implying a significant response). Overall community mean value and 95% BCIs shown by the vertical green lines.

2.4.3 Species responses to landscape structure

In total, 34% and 28% of species exhibited a significant positive response to increasing forest cover at the 10 ha and 500 ha scales respectively, while 20% and 36% had significant negative responses. Fragmentation had a limited effect at 10 ha; 17% significant positive responses, but only 2% of species had significant negative responses to increasing fragmentation. Similarly, at the 500 ha scale, 42% of species had significant positive responses to increasing fragmentation, while only 5% of species responded negatively. Twenty-seven percent of species had significant positive responses to increasing distance to forest, and only 7% were negative.

The predicted abundance maps (Figure 2.5) show contrasting responses to the Emparador landscape for six example species across the three trait groups that likely provide important contributions to ecosystem services: frugivores, frugivorous-insectivorous omnivores, and the high forest-dependent insectivores. Despite their similar traits and habitat preferences, each species pair exhibited differences in predicted abundance across the landscape. Abundance of both frugivorous manakin species responded positively to forest cover at 10 ha scale (Figure 2.3; 1.2 and 0.3), but exhibited contrasting responses at the 500ha scale (0.2 and -1.2). This is evident in the predicted distributions, with red-capped manakin (*Pipra mentalis*) restricted to larger areas of forest, while lance-tailed manakin (*Chiroxiphia lanceolata*) is predominantly found in areas with more fragmented habitats (Figures 2.5a & 2.5b). The omnivorous species showed diverging responses to forest at both scales, with Russet-winged Schiffornis (*Schiffornis stenorhyncha*) increasing with greater forest cover, while Clay-coloured Thrush (*Turdus grayi*) declined (Figures 2.5c & 2.5d). In the high forest-dependent insectivores all had greater predicted abundance in core forest, there was marked variation in persistence in the open landscape. Cocoa woodcreeper (*Xiphorhynchus sussarans*) was predicted throughout the HML, while Northern barred woodcreeper (*Dendrocolaptes sanctithomae*) was not (Figures 2.5e & 2.5f).

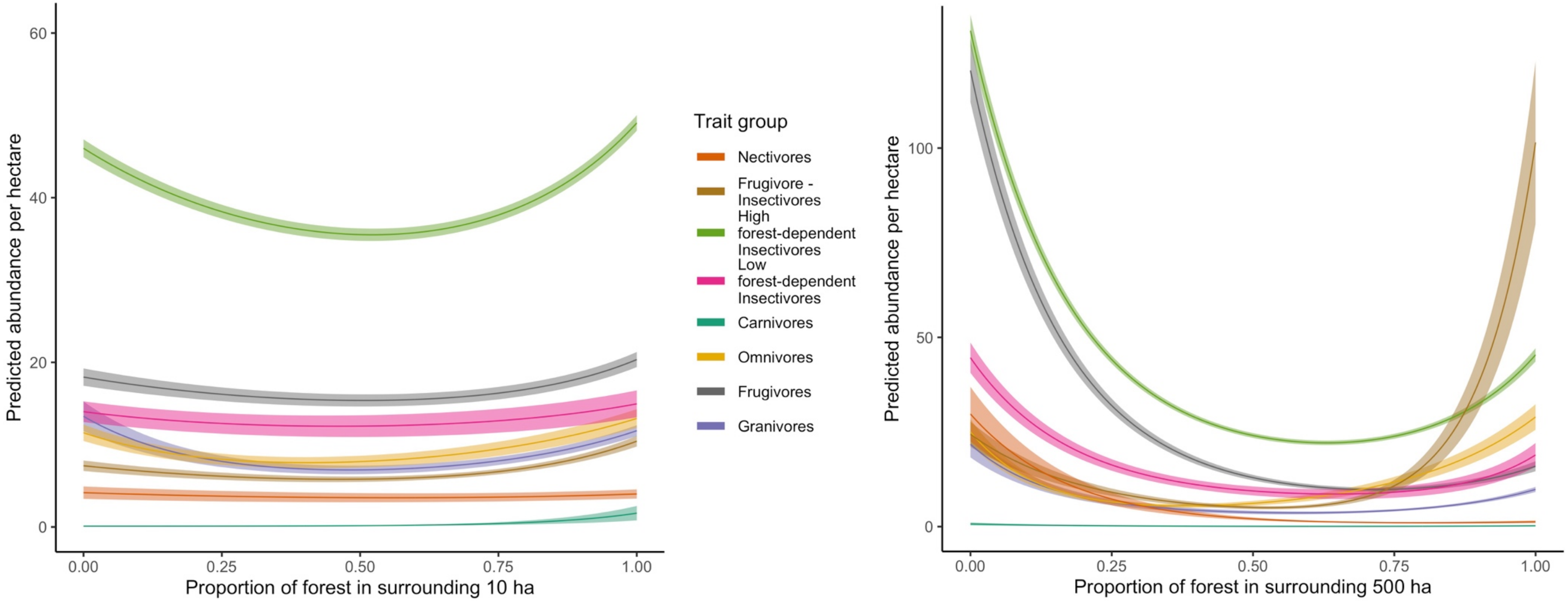


Figure 2.4a & b - Change in abundance of trait-based groups with increasing forest cover at 10 ha (left) and 500 ha (right) scales.

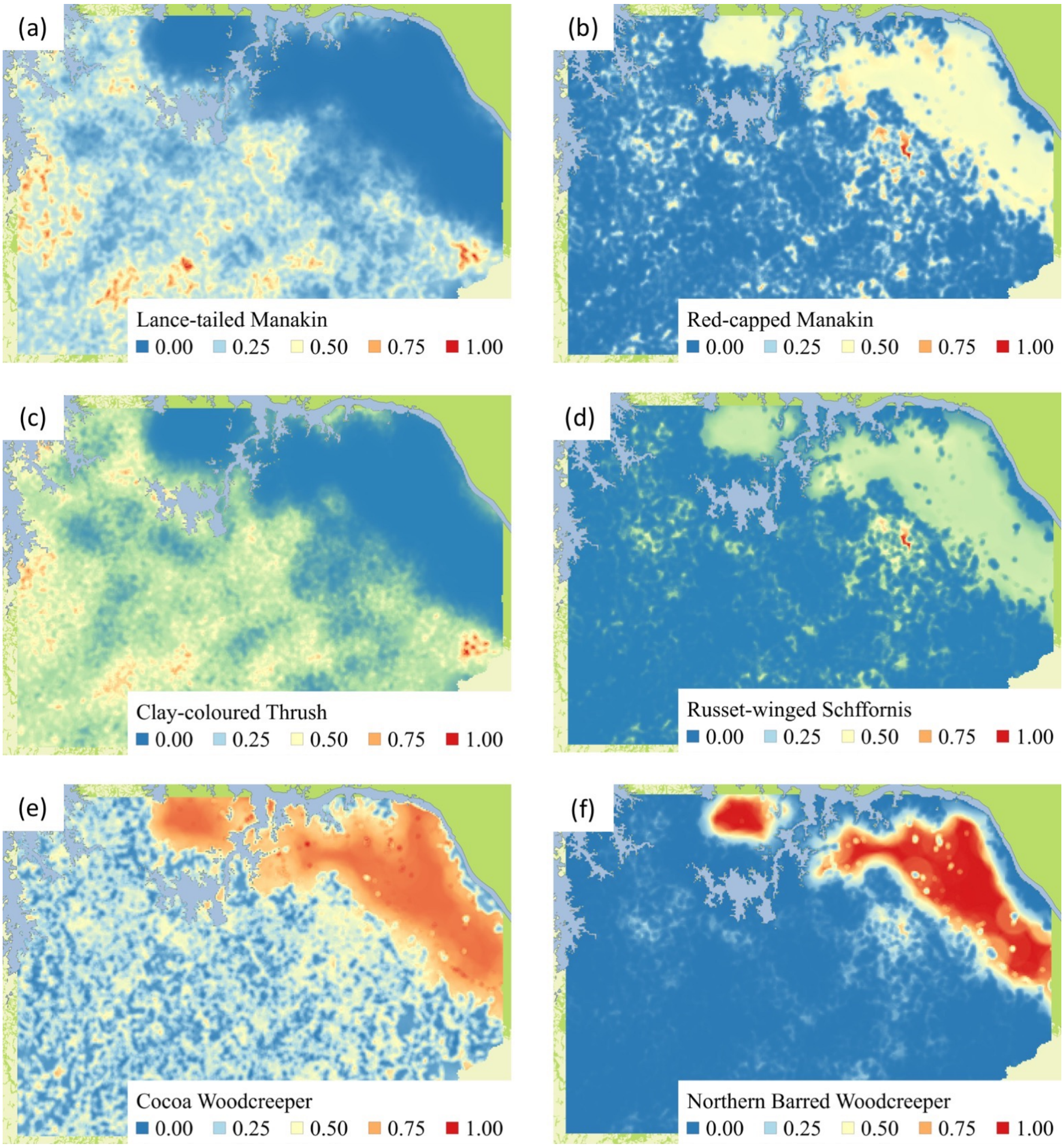


Figure 2.5 – Changes in example species relative abundances across the Emparador landscape as a response to changes in forest cover and forest edge density at 10 ha and 500 ha scales and distance to core forest, refer to Figure 2.1 for distribution of forest cover. Contrasting responses are apparent in most trait-groups. Example species shown here for frugivores (a) Lance-tailed Manakin and (b) Red-capped Manakin; frugivorous-insectivorous omnivores (c) Clay-coloured Thrush and (d) Russet-winged Schiffornis; and high-forest dependency insectivores: (e) Cocoa Woodcreeper and (f) Northern Barred Woodcreeper.

2.4.4 Trait patterns among species sensitive to forest loss

There were no clear trait patterns in dietary category, foraging strata or forest dependency among those species that declined with increasing forest loss and fragmentation. The only trend was a decline in detections of forest-affiliated species with lower forest cover (Figure 2.S7).

2.5 Discussion

2.5.1 Trait-based groups' responses to forest cover and fragmentation

At the overall community level, greater local-scale forest cover, and greater local- and landscape-scale fragmentation were all associated with higher abundance of individuals. Conversely, greater landscape-scale forest cover and distance to core forest had no effect on abundance at the community level, although there were strong species-level effects. We identified eight trait-based functional groups, of which seven had consistent patterns in habitat preferences, forest dependence, and dietary composition. However, membership of a particular functional group was a poor predictor of species-level responses to forest cover and fragmentation at both local and landscape scales. This may reflect a weakness in attempting to classify the community into discrete groups using coarse traits, as this disguises considerable variation in morphology and behaviour. For example, despite distinguishing between resident and migratory species in the clustering, this critical ecological feature did not appear to drive separation among functional groups.

In all trait groups there were individual species that exhibited diverging abundance patterns in responses to changes in forest cover. These responses were stronger, and intra-group differences more pronounced, at the landscape scale. This might be because many species such as insectivores and frugivores are functionally constrained, and reliant on forest at the local scale for foraging (Morante-Filho et al. 2018). Thus, differing ecological strategies of individual species become more apparent at the landscape scale. For example, although frugivorous manakins share very similar functional traits, there is marked intra-taxon variation in predicted abundance patterns with changing landscape structure (Figure 2.5). This intra-group variation was reflected in the strong U-shaped predicted abundance curves exhibited by three groups (frugivores, and both insectivore groups) with changing forest cover at the landscape scale. This indicates that some species are most abundant at high levels of forest cover, and some at low forest cover, irrespective of the groups' forest dependency rating (Birdlife International 2019). This suggests these three groups have the greatest range in ecological strategies, with individual species able to persist in markedly different landscape contexts. Such responses may be the result of spatial partitioning; species have evolved to avoid competition with functionally similar species (Ferger et al. 2016; Karr 1971).

Greater fragmentation led to increases in abundance for many species across all trait groups, particularly at the landscape scale. Intra-group divergence was much less marked compared to the effect of forest cover, with only five frugivore and insectivore species showing a significant decline in abundance with increased fragmentation. Higher levels of disturbance have been associated with greater species richness in multiple taxa in the tropics (Hill & Hamer 2004). This positive effect of fragmentation on species abundances may stem from the concomitantly increased landscape heterogeneity, which leads to a greater length of ecotone habitat and hence an increase in potential resources (Fahrig et al. 2011; Frishkoff et al. 2019; Morante-Filho et al. 2018).

Fragmentation can have dramatic negative effects on bird communities in previously undisturbed landscapes (Lees & Peres 2006; Stouffer et al. 2011). However, our study landscape is typical of many Mesoamerican HMLs, with long-term human presence and relatively stable land use patterns (Koch et al. 2019; Piperno 2011). Aerial photographs of the region from 1955 show that forest cover was already fragmented across much of the HML, and there are field boundaries that have remained consistent until the present day. Thus the most disturbance-sensitive bird species were likely extirpated from Emparador following this initial phase of deforestation. Despite repeated surveying throughout the HML, we did not record many of the forest-affiliated species found in the wider region (Robinson et al. 2000).

While repeated anthropogenic disturbance is still ongoing in HMLs such as Emparador (Barlow & Peres 2004; Reid et al. 2019; Zahawi et al. 2015), and further species losses may occur with increased intensification of land use (Sekercioglu et al. 2019), community dynamics are likely more moderate compared with the shifts occurring in South American HMLs. In parts of the Amazon for example, more rapid, broad-scale deforestation and fragmentation has dramatic consequences for previously undisturbed avian communities (Bregman et al. 2016; Hamer et al. 2015; Lees & Peres 2006).

Forest cover influenced the abundance of more species than fragmentation at both spatial scales, regardless of response direction. Both the relatively greater importance of forest cover and the positive effect of fragmentation on species abundances matches patterns in similar HMLs in Mexico and Australia (Carrara et al. 2015; Pavlacky et al. 2015). Such findings may arise because the species able to persist in Emparador and other long-established HMLs are likely to be the more adaptable component of the regional species pool. Alternatively, fragmentation may be less important than forest cover in Emparador because there is insufficient variability in the landscape to contain the full range of potential matrix compositions; at the 500 ha scale, fragmentation levels were similar across the landscape (Figure S1b). Although a stronger fragmentation gradient might reveal clearer influences, such gradients are uncommon in Mesoamerican HMLs. Central American HMLs are frequently composed of many small- to medium-sized landholdings (i.e. between 5 and 100 ha - Melo et al. 2018), and hence at larger spatial scales the landscape becomes homogenous. Indeed, Banks-Leite et al. (2010) argue that Mesoamerican HMLs cannot be treated as landscapes composed of discreet habitat patches because the low-intensity management creates a relatively benign matrix, with high levels of connectivity and low effective distances among patches (Ewers & Didham 2006).

2.5.2 Trait patterns of species that struggle to persist in HMLs

All functional trait groups included some species that struggled to persist in the open landscape, and there were no clear trait patterns to explain individual species' shifts in abundance as a response to HML structure. Closely related species with apparently similar traits can exhibit contrasting reactions to both habitat and landscape structure (Hamer et al. 2015; Sberze et al. 2010). Moreover, previous trait-based approaches have found that a single species can exhibit distinct responses at different locations (Boesing et al. 2018), and traits emphasised as important drivers of occupancy in one study are not necessarily highlighted as important in others, even within the same system (Hatfield et al. 2018).

Diverging patterns among functional groups may result from a failure to integrate species' responses to local and landscape habitat structures (Frishkoff et al. 2019). However, dividing species responses to HML structure into four categories, positive or negative, significant or not, may well have obscured any finer-scale patterns. More nuanced analysis of the continuous responses to HML structure might yet reveal certain traits to be important drivers of avian response. Alternatively, the longer-term shift in avian community composition, with extirpations of the most sensitive forest-affiliated species, may have altered trait space and hence obscure the importance of particular traits in driving responses to the landscape. We selected functional and ecological traits that might reasonably be expected to drive responses (Hatfield et al. 2018), although responses may be driven by different traits to the ones studied here (Bregman et al. 2016; Lees & Peres 2010). Clearer patterns might be revealed by using finer groupings that incorporated additional behavioural traits, such as foraging strategies, or that used the original continuous morphological data rather than categorical traits and PCA scores (Bregman et al. 2016; Tobias & Pigot 2019).

2.5.3 Conservation implications

Avian abundance increased with greater local-scale forest cover, even for HML-associated species, implying that forest fragments provide important resources such as foraging and roosting opportunities. Conservation efforts should prioritise and protect forest fragments that remain in HMLs. Even isolated trees in pastures can bolster wildlife populations, providing resources and facilitating movements (Gillies & St. Clair 2010; Manning et al. 2006). Establishing new forest patches, particularly in locations close to large areas of continuous forest, will help to further buffer HML bird communities and ecosystem services. While sensitive species are at greatest risk in the face of land use intensification, more robust species may still benefit from careful landscape-scale intervention, particularly when it is informed by the sort of detailed abundance mapping conducted here.

Many avian species can persist in Neotropical HMLs with low-intensity land management (Frishkoff et al. 2014; Karp et al. 2011, 2019; Sekercioglu et al. 2007, 2019). Highly sensitive, forest-associated species were likely extirpated from the Emparador HML during initial forest clearance, and the bird community is now dominated by more robust species capable of persisting in the fragmented matrix. Critically, disturbance-tolerant species may be the key providers that maintain ecosystem services in HMLs (Nyffeler et al. 2018). For example, Carlo & Morales (2016) demonstrate the importance of two avian habitat generalists for seed dispersal in the early stages of forest regeneration in Puerto Rico.

We suggest that more robust, generalist species may underlie the apparent range of habitat thresholds reported in the literature (Melo et al. 2018), as they can persist in a wider array of landscape structures (Morante-Filho et al. 2018). Although a single, broad-scale habitat threshold value can indicate when changes in avian community composition may occur in HML ecosystems (Swift & Hannon 2010), thresholds are less useful for identifying where conservation interventions need to take place. Prioritising locations for conservation action requires detailed analysis of landscape structure. Explaining inter-species differences in response to fine-scale landscape structure is the next step in improving the design of conservation interventions.

Here, we found that functional traits and habitat preferences were not necessarily an effective means of predicting how a species will respond to HML structure. Although conservation efforts often prioritise the most sensitive species in a community, bolstering network redundancy via conservation of less-sensitive species may actually be more achievable, and provide equally effective protection for ecosystem services. Our results clearly suggest that encouraging preservation of forest fragments in HMLs will benefit the majority of the avian community, not just those members traditionally associated with forested habitats.

2.6 Acknowledgements

Our thanks to the Autoridad de Canal de Panama and all the private landowners who granted access to their land for the bird surveys. Thanks to Autoridad Nacional del Ambiente for permission to conduct research in Panama (permits SE/A-134-16 and SE/A-67-18), and the Smithsonian Tropical Research Institute for logistical support. Luke Frishkoff and Thiago Silva both gave helpful advice regarding aspects of the analyses. TBL was funded by the Natural Environment Research Council UK, and the IAPETUS Doctoral Training Partnership.

2.7 Supplementary Information

Table 2.S1 – Species list with Latin binomial names, nomenclature follows HBW and Birdlife International (2019).

Common name	**Scientific name**
Great Tinamou	*Tinamus major*
Little Tinamou	*Crypturellus soui*
Grey-headed Chachalaca	*Ortalis cinereiceps*
Crested Bobwhite	*Colinus cristatus*
Scaled Pigeon	*Patagioenas speciosa*
Pale-vented Pigeon	*Patagioenas cayennensis*
Ruddy Quail-dove	*Geotrygon montana*
White-tipped Dove	*Leptotila verreauxi*
Gray-chested Dove	*Leptotila cassinii*
Plain-breasted Ground-dove	*Columbina minuta*
Ruddy Ground-dove	*Columbina talpacoti*
Blue Ground-dove	*Claravis pretiosa*
White-necked Jacobin	*Florisuga mellivora*
Band-tailed Barbthroat	*Threnetes ruckeri*
Stripe-throated Hermit	*Phaethornis striigularis*
Long-billed Hermit	*Phaethornis longirostris*
Purple-crowned Fairy	*Heliothryx barroti*
Black-throated Mango	*Anthracothorax nigricollis*
Garden Emerald	*Chlorostilbon assimilis*
White-vented Plumeleteer	*Chalybura buffonii*
Crowned Woodnymph	*Thalurania colombica*
Rufous-tailed Hummingbird	*Amazilia tzacatl*
Blue-chested Hummingbird	*Amazilia amabilis*
Snowy-bellied Hummingbird	*Amazilia edward*
Sapphire-throated Hummingbird	*Lepidopyga coeruleogularis*
Violet-bellied Hummingbird	*Juliamyia julie*
Greater Ani	*Crotophaga major*
Smooth-billed Ani	*Crotophaga ani*
Groove-billed Ani	*Crotophaga sulcirostris*
Striped Cuckoo	*Tapera naevia*
Pheasant Cuckoo	*Dromococcyx phasianellus*
Squirrel Cuckoo	*Piaya cayana*
Yellow-billed Cuckoo	*Coccyzus americanus*
White-throated Crake	*Laterallus albigularis*
Grey-necked Wood-rail	*Aramides cajaneus*

Rufescent Tiger-heron	*Tigrisoma lineatum*
Striated Heron	*Butorides striata*
Cattle Egret	*Bubulcus ibis*
Great Blue Heron	*Ardea herodias*
Great Egret	*Ardea alba*
Tricoloured Heron	*Egretta tricolor*
Little Blue Heron	*Egretta caerulea*
Southern Lapwing	*Vanellus chilensis*
Wattled Jacana	*Jacana jacana*
White-tailed Kite	*Elanus leucurus*
Pearl Kite	*Gampsonyx swainsonii*
Grey-headed Kite	*Leptodon cayanensis*
Hook-billed Kite	*Chondrohierax uncinatus*
Swallow-tailed Kite	*Elanoides forficatus*
Black Hawk-eagle	*Spizaetus tyrannus*
Ornate Hawk-eagle	*Spizaetus ornatus*
Double-toothed Kite	*Harpagus bidentatus*
Crane Hawk	*Geranospiza caerulescens*
Mississippi Kite	*Ictinia mississippiensis*
Plumbeous Kite	*Ictinia plumbea*
Roadside Hawk	*Rupornis magnirostris*
Plumbeous Hawk	*Cryptoleucopteryx plumbea*
Savanna Hawk	*Buteogallus meridionalis*
Semiplumbeous Hawk	*Leucopternis semiplumbeus*
Grey Hawk	*Buteo nitidus*
Broad-winged Hawk	*Buteo platypterus*
Short-tailed Hawk	*Buteo brachyurus*
Zone-tailed Hawk	*Buteo albonotatus*
Slaty-tailed Trogon	*Trogon massena*
White-tailed Trogon	*Trogon chionurus*
Violaceous Trogon	*Trogon violaceus*
Black-throated Trogon	*Trogon rufus*
Blue-crowned Motmot	*Momotus momota*
Rufous Motmot	*Baryphthengus martii*
Broad-billed Motmot	*Electron platyrhynchum*
Ringed Kingfisher	*Megaceryle torquata*
American Pygmy Kingfisher	*Chloroceryle aenea*
Green Kingfisher	*Chloroceryle americana*
White-necked Puffbird	*Notharchus hyperrhynchus*
Black-breasted Puffbird	*Notharchus pectoralis*
White-whiskered Puffbird	*Malacoptila panamensis*
Chestnut-mandibled Toucan	*Ramphastos ambiguus*

Keel-billed Toucan	*Ramphastos sulfuratus*
Collared Aracari	*Pteroglossus torquatus*
Crimson-crested Woodpecker	*Campephilus melanoleucos*
Cinnamon Woodpecker	*Celeus loricatus*
Lineated Woodpecker	*Hylatomus lineatus*
Black-cheeked Woodpecker	*Melanerpes pucherani*
Red-crowned Woodpecker	*Melanerpes rubricapillus*
Laughing Falcon	*Herpetotheres cachinnans*
Barred Forest-falcon	*Micrastur ruficollis*
Collared Forest-falcon	*Micrastur semitorquatus*
Crested Caracara	*Caracara cheriway*
Yellow-headed Caracara	*Milvago chimachima*
American Kestrel	*Falco sparverius*
Bat Falcon	*Falco rufigularis*
Peregrine Falcon	*Falco peregrinus*
Orange-chinned Parakeet	*Brotogeris jugularis*
Blue-headed Parrot	*Pionus menstruus*
Red-lored Parrot	*Amazona autumnalis*
Yellow-crowned Parrot	*Amazona ochrocephala*
Mealy Parrot	*Amazona farinosa*
Brown-throated Parakeet	*Eupsittula pertinax*
Dot-winged Antwren	*Microrhopias quixensis*
Checker-throated Antwren	*Epinecrophylla fulviventris*
Pacific Antwren	*Myrmotherula pacifica*
White-flanked Antwren	*Myrmotherula axillaris*
Fasciated Antshrike	*Cymbilaimus lineatus*
Barred Antshrike	*Thamnophilus doliatus*
Black-crowned Antshrike	*Thamnophilus atrinucha*
Dusky Antbird	*Cercomacroides tyrannina*
Ocellated Antbird	*Phaenostictus mcleannani*
Bicolored Antbird	*Gymnopithys bicolor*
Spotted Antbird	*Hylophylax naevioides*
Chestnut-backed Antbird	*Poliocrania exsul*
White-bellied Antbird	*Myrmeciza longipes*
Streak-chested Antpitta	*Hylopezus perspicillatus*
Black-faced Antthrush	*Formicarius analis*
Tawny-throated Leaftosser	*Sclerurus mexicanus*
Scaly-throated Leaftosser	*Sclerurus guatemalensis*
Ruddy Woodcreeper	*Dendrocincla homochroa*
Plain-brown Woodcreeper	*Dendrocincla fuliginosa*
Wedge-billed Woodcreeper	*Glyphorynchus spirurus*
Northern Barred Woodcreeper	*Dendrocolaptes sanctithomae*

Cocoa Woodcreeper	*Xiphorhynchus susurrans*
Plain Xenops	*Xenops minutus*
Buff-throated Foliage-gleaner	*Automolus ochrolaemus*
Golden-collared Manakin	*Manacus vitellinus*
Red-capped Manakin	*Ceratopipra mentalis*
Blue-crowned Manakin	*Lepidothrix coronata*
Lance-tailed Manakin	*Chiroxiphia lanceolata*
Purple-throated Fruitcrow	*Querula purpurata*
Rufous Piha	*Lipaugus unirufus*
Blue Cotinga	*Cotinga nattererii*
Royal Flycatcher	*Onychorhynchus coronatus*
Ruddy-tailed Flycatcher	*Terenotriccus erythrurus*
Masked Tityra	*Tityra semifasciata*
White-winged Becard	*Pachyramphus polychopterus*
Russet-winged Schiffornis	*Schiffornis turdina*
Speckled Mourner	*Laniocera rufescens*
Golden-crowned Spadebill	*Platyrinchus coronatus*
Ochre-bellied Flycatcher	*Mionectes oleagineus*
Brownish Twistwing	*Cnipodectes subbrunneus*
Olivaceous Flatbill	*Rhynchocyclus olivaceus*
Yellow-olive Flycatcher	*Tolmomyias sulphurescens*
Yellow-margined Flycatcher	*Tolmomyias assimilis*
Southern Bentbill	*Oncostoma olivaceum*
Pale-eyed Pygmy-tyrant	*Lophotriccus pileatus*
Slate-headed Tody-flycatcher	*Poecilotriccus sylvia*
Common Tody-flycatcher	*Todirostrum cinereum*
Black-headed Tody-flycatcher	*Todirostrum nigriceps*
Paltry Tyrannulet	*Zimmerius vilissimus*
Brown-capped Tyrannulet	*Ornithion brunneicapillus*
Southern Beardless-tyrannulet	*Camptostoma obsoletum*
Yellow-bellied Elaenia	*Elaenia flavogaster*
Lesser Elaenia	*Elaenia chiriquensis*
Yellow-crowned Tyrannulet	*Tyrannulus elatus*
Forest Elaenia	*Myiopagis gaimardii*
Greenish Elaenia	*Myiopagis viridicata*
Yellow Tyrannulet	*Capsiempis flaveola*
Mouse-coloured Tyrannulet	*Phaeomyias murina*
Bright-rumped Attila	*Attila spadiceus*
Piratic Flycatcher	*Legatus leucophaius*
Great Kiskadee	*Pitangus sulphuratus*
Lesser Kiskadee	*Philohydor lictor*
Boat-billed Flycatcher	*Megarynchus pitangua*

Streaked Flycatcher	*Myiodynastes maculatus*
Rusty-margined Flycatcher	*Myiozetetes cayanensis*
Social Flycatcher	*Myiozetetes similis*
Tropical Kingbird	*Tyrannus melancholicus*
Eastern Kingbird	*Tyrannus tyrannus*
Grey Kingbird	*Tyrannus dominicensis*
Fork-tailed Flycatcher	*Tyrannus savana*
Rufous Mourner	*Rhytipterna holerythra*
Dusky-capped Flycatcher	*Myiarchus tuberculifer*
Panama Flycatcher	*Myiarchus panamensis*
Great Crested Flycatcher	*Myiarchus crinitus*
Acadian Flycatcher	*Empidonax virescens*
Alder Flycatcher	*Empidonax alnorum*
Eastern Wood-pewee	*Contopus virens*
Tropical Pewee	*Contopus cinereus*
Scrub Greenlet	*Hylophilus flavipes*
Green Shrike-vireo	*Vireolanius pulchellus*
Tawny-crowned Greenlet	*Tunchiornis ochraceiceps*
Lesser Greenlet	*Pachysylvia decurtata*
Golden-fronted Greenlet	*Pachysylvia aurantiifrons*
Yellow-green Vireo	*Vireo flavoviridis*
Red-eyed Vireo	*Vireo olivaceus*
Yellow-throated Vireo	*Vireo flavifrons*
Black-chested Jay	*Cyanocorax affinis*
Tawny-faced Gnatwren	*Microbates cinereiventris*
Long-billed Gnatwren	*Ramphocaenus melanurus*
Tropical Gnatcatcher	*Polioptila plumbea*
Southern Nightingale-wren	*Microcerculus marginatus*
House Wren	*Troglodytes aedon*
Black-bellied Wren	*Pheugopedius fasciatoventris*
Rufous-breasted Wren	*Pheugopedius rutilus*
Rufous-and-white Wren	*Thryophilus rufalbus*
Buff-breasted Wren	*Cantorchilus leucotis*
Bay Wren	*Cantorchilus nigricapillus*
Plain Wren	*Cantorchilus modestus*
White-breasted Wood-wren	*Henicorhina leucosticta*
Song Wren	*Cyphorhinus phaeocephalus*
Grey Catbird	*Dumetella carolinensis*
Tropical Mockingbird	*Mimus gilvus*
Swainson's Thrush	*Catharus ustulatus*
Clay-coloured Thrush	*Turdus grayi*
Yellow-crowned Euphonia	*Euphonia luteicapilla*

Thick-billed Euphonia	*Euphonia laniirostris*
Fulvous-vented Euphonia	*Euphonia fulvicrissa*
Rosy Thrush-tanager	*Rhodinocichla rosea*
Black-striped Sparrow	*Arremonops conirostris*
Orange-billed Sparrow	*Arremon aurantiirostris*
Eastern Meadowlark	*Sturnella magna*
Red-breasted Blackbird	*Leistes militaris*
Yellow-billed Cacique	*Amblycercus holosericeus*
Chestnut-headed Oropendola	*Psarocolius wagleri*
Crested Oropendola	*Psarocolius decumanus*
Scarlet-rumped Cacique	*Cacicus uropygialis*
Yellow-rumped Cacique	*Cacicus cela*
Yellow-backed Oriole	*Icterus chrysater*
Baltimore Oriole	*Icterus galbula*
Bronzed Cowbird	*Molothrus aeneus*
Great-tailed Grackle	*Quiscalus mexicanus*
Northern Waterthrush	*Parkesia noveboracensis*
Prothonotary Warbler	*Protonotaria citrea*
Tennessee Warbler	*Leiothlypis peregrina*
Bay-breasted Warbler	*Setophaga castanea*
Blackburnian Warbler	*Setophaga fusca*
Yellow Warbler	*Setophaga petechia*
Chestnut-sided Warbler	*Setophaga pensylvanica*
Rufous-capped Warbler	*Basileuterus rufifrons*
Canada Warbler	*Cardellina canadensis*
Dickcissel	*Spiza americana*
Blue Grosbeak	*Passerina cyanea*
Blue-black Grosbeak	*Cyanoloxia cyanoides*
Red-throated Ant-tanager	*Habia fuscicauda*
Summer Tanager	*Piranga rubra*
Green Honeycreeper	*Chlorophanes spiza*
Red-legged Honeycreeper	*Cyanerpes cyaneus*
Blue Dacnis	*Dacnis cayana*
Streaked Saltator	*Saltator striatipectus*
Slate-colored Grosbeak	*Saltator grossus*
Yellow-faced Grassquit	*Tiaris olivaceus*
Blue-black Grassquit	*Volatinia jacarina*
Grey-headed Tanager	*Eucometis penicillata*
White-shouldered Tanager	*Islerothraupis luctuosa*
Crimson-backed Tanager	*Ramphocelus dimidiatus*
Variable Seedeater	*Sporophila corvina*
Yellow-bellied Seedeater	*Sporophila nigricollis*

Thick-billed Seed-finch	*Sporophila funerea*
Ruddy-breasted Seedeater	*Sporophila minuta*
Blue-gray Tanager	*Tangara episcopus*
Palm Tanager	*Tangara palmarum*
Plain-colored Tanager	*Tangara inornata*

2.S1 Proportion of forest and fragmentation across the landscape

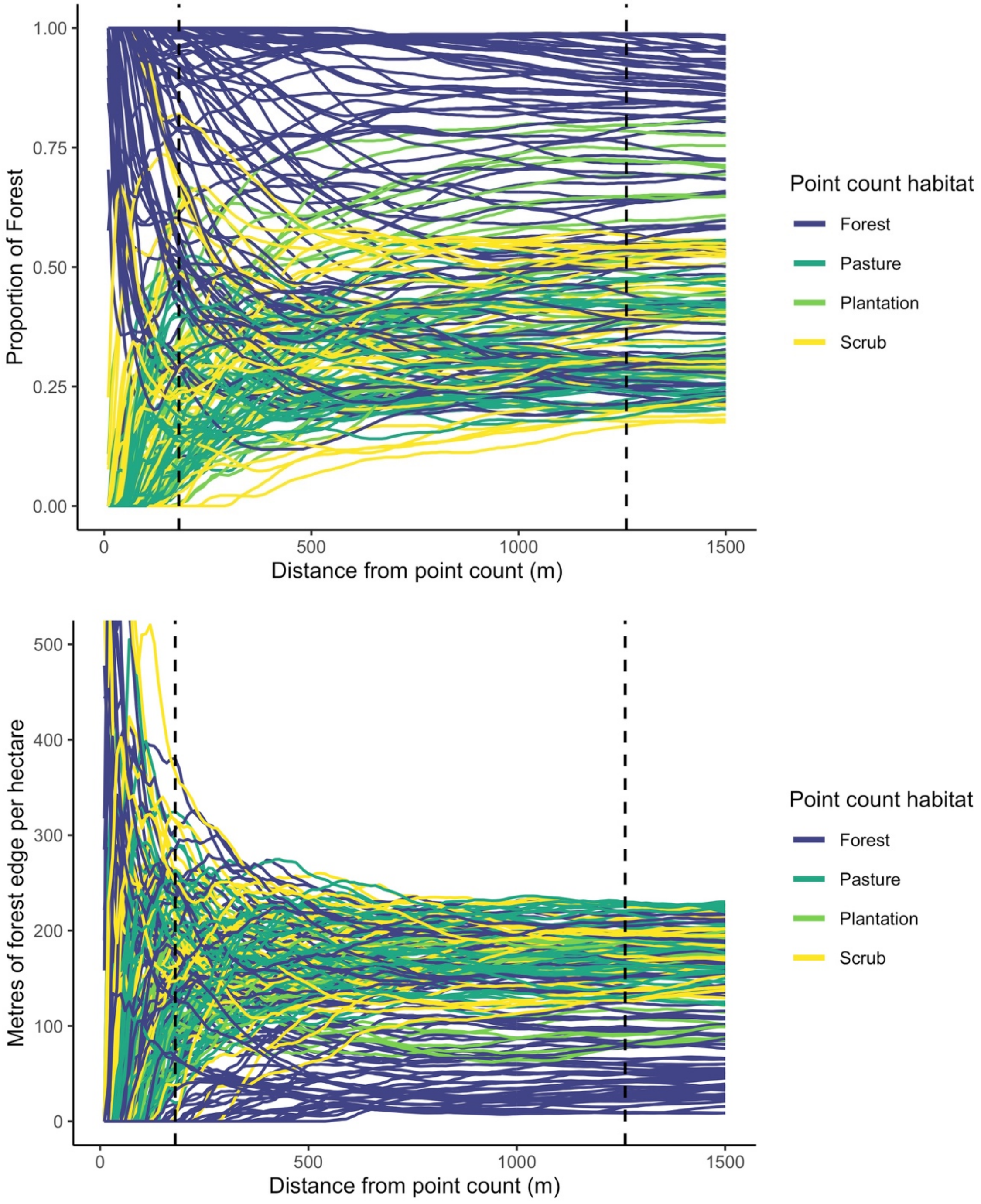


Figure 2.S1a & b - Proportion of forest and forest edge density with increasing distance from each point count. Vertical dotted lines indicate 180m and 1260m (i.e. 10 ha and 500 ha landscapes respectively). Y-axis of 2.S1b truncated at 500m to remove outliers.

2.S2 Differences in number of individual detections over a morning

To test whether number of detections during each point count varied over the course of a morning, we conducted a generalised linear mixed model (GLMM) with Poisson errors and a log link, with a random effect of transect to account for potential spatial autocorrelation. We used the lme4 package in R (ver. 1.1.21, Bates et al. 2015). Figure 2.S2 shows changes in the predicted mean number of detections per point count over each survey. The model shows that the highest number of detections were between the second and eighth point counts. By the twelfth point count there were significantly fewer detections, implying avian activity had declined by this point of the morning so that detectability was reduced (Table 2.S2). We therefore incorporated time of point count in the detection component of the modelling in the main text.

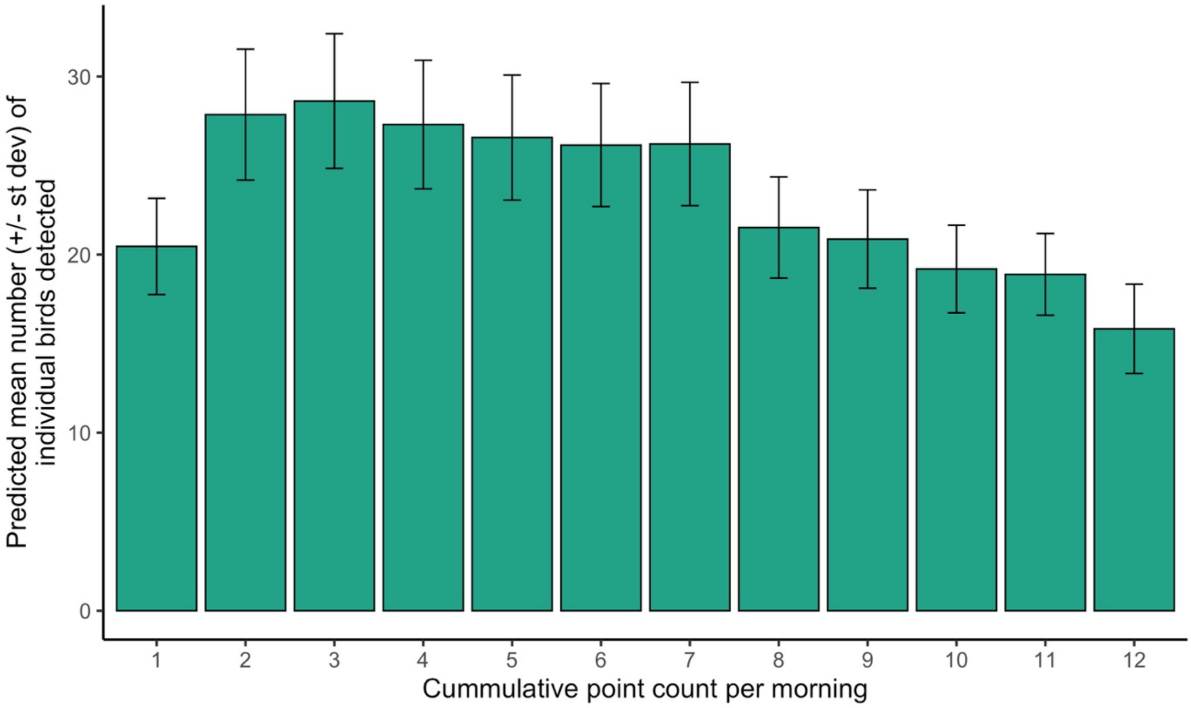


Figure 2.S2 - Decline in number of detections over the course of each survey morning.

2.S3 Detectability differences among habitat types.

To investigate potential differences in detectability among habitat types, we used the R package "Distance" (ver 0.9.8, Miller et al. 2019) to conduct distance sampling (Buckland et al. 2015; Marques et al. 2007). We truncated the data to 200 m and used multiple covariate distance sampling with a half-normal key function (Buckland et al. 2015). Probability of detection was greater in pasture than the other habitats, and slightly lower in forest (Figure 2.S3). To account for this variation, we included random intercepts for habitat type in the detectability stage of the modelling.

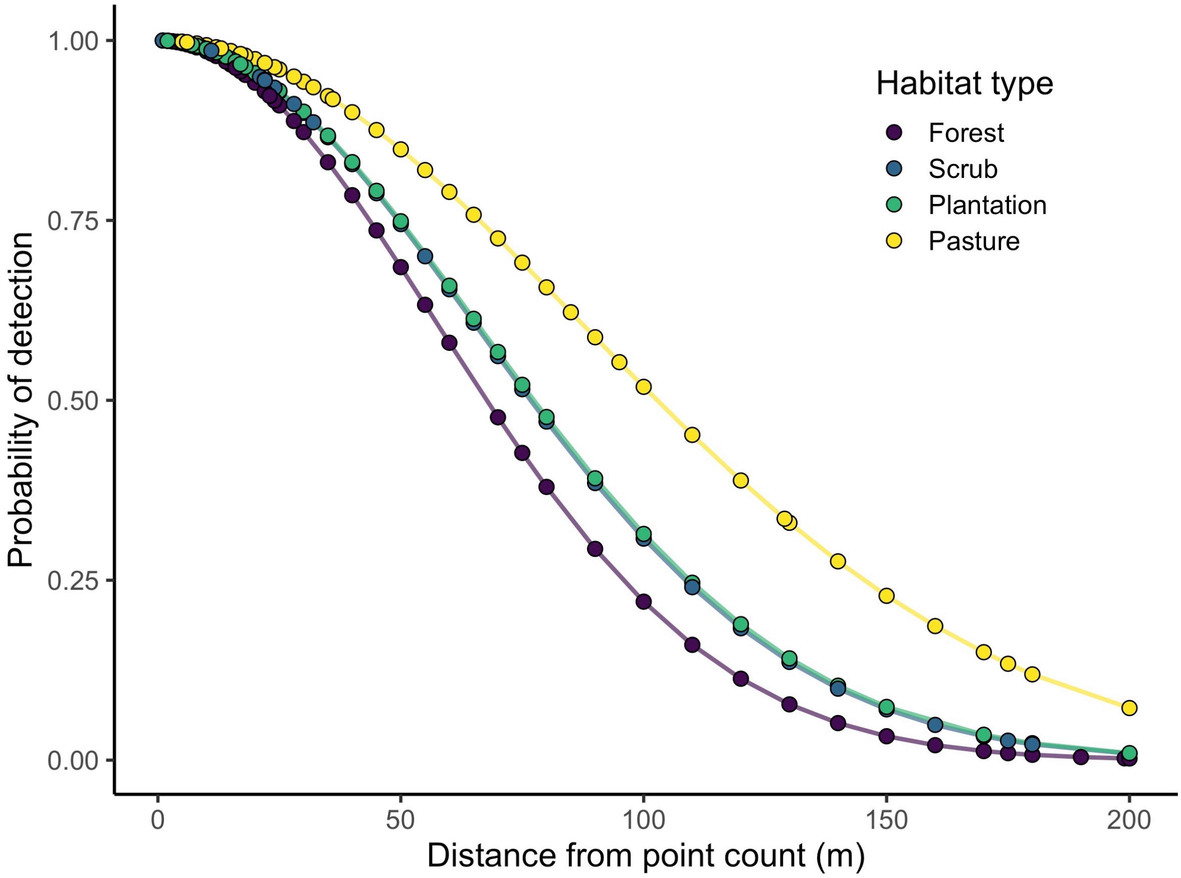
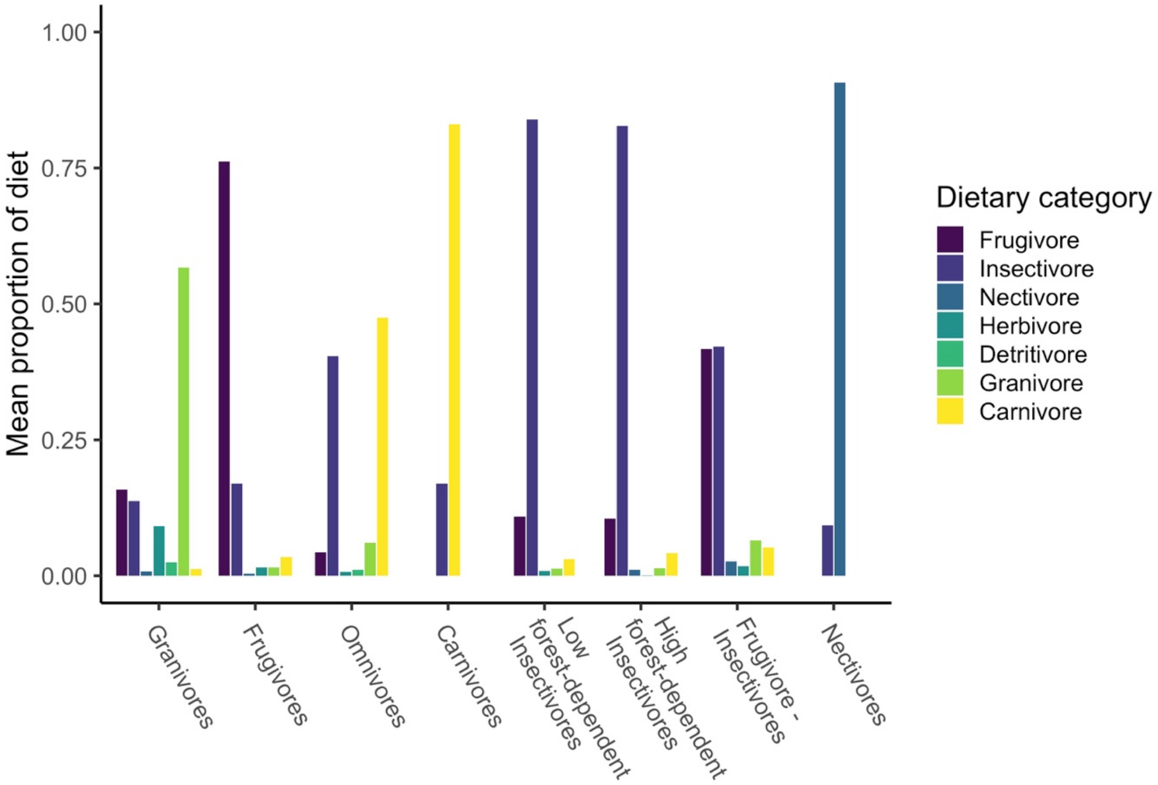
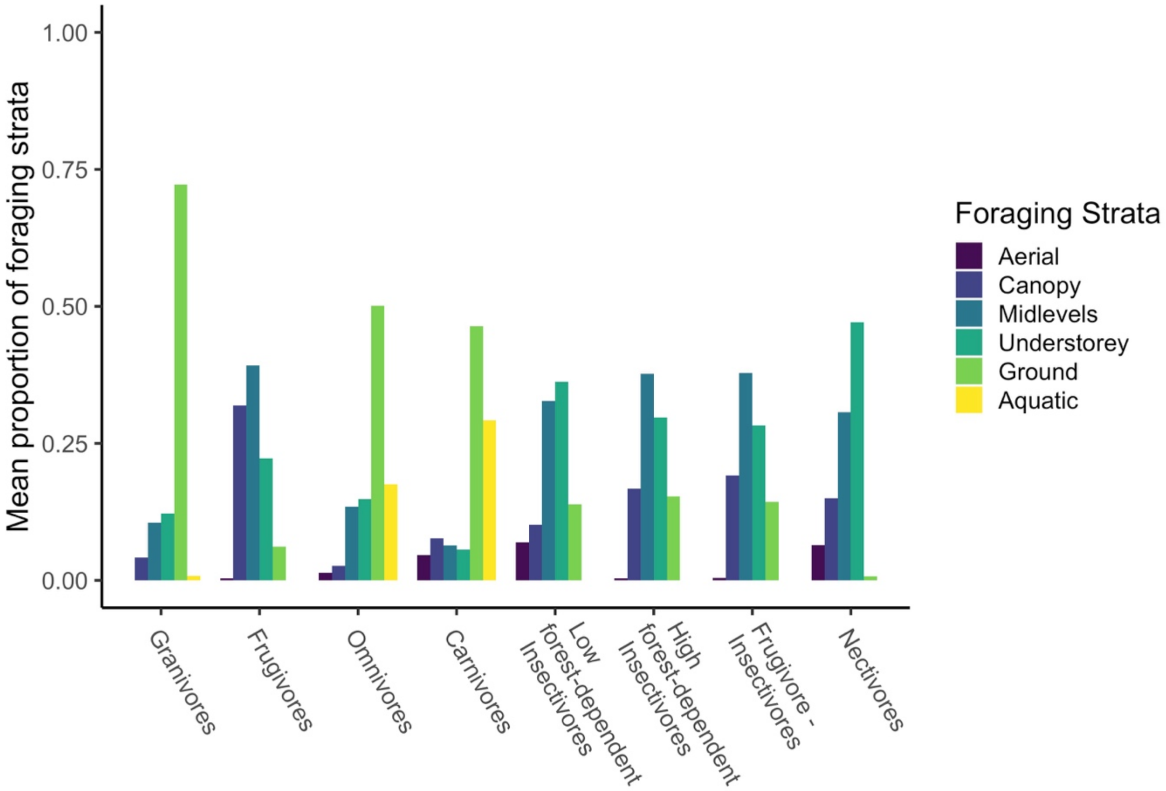
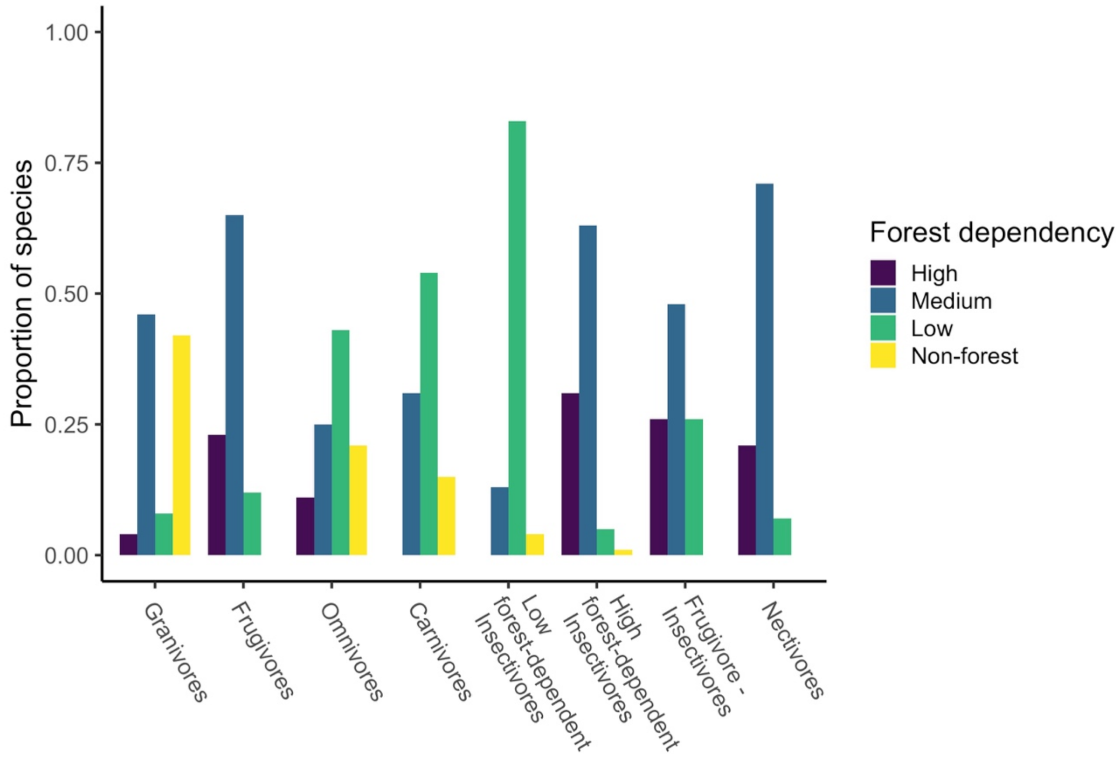


Figure 2.S3 - Probability of detection among habitats with increasing distance from point count.

2.S4 Trait patterns in functional groups







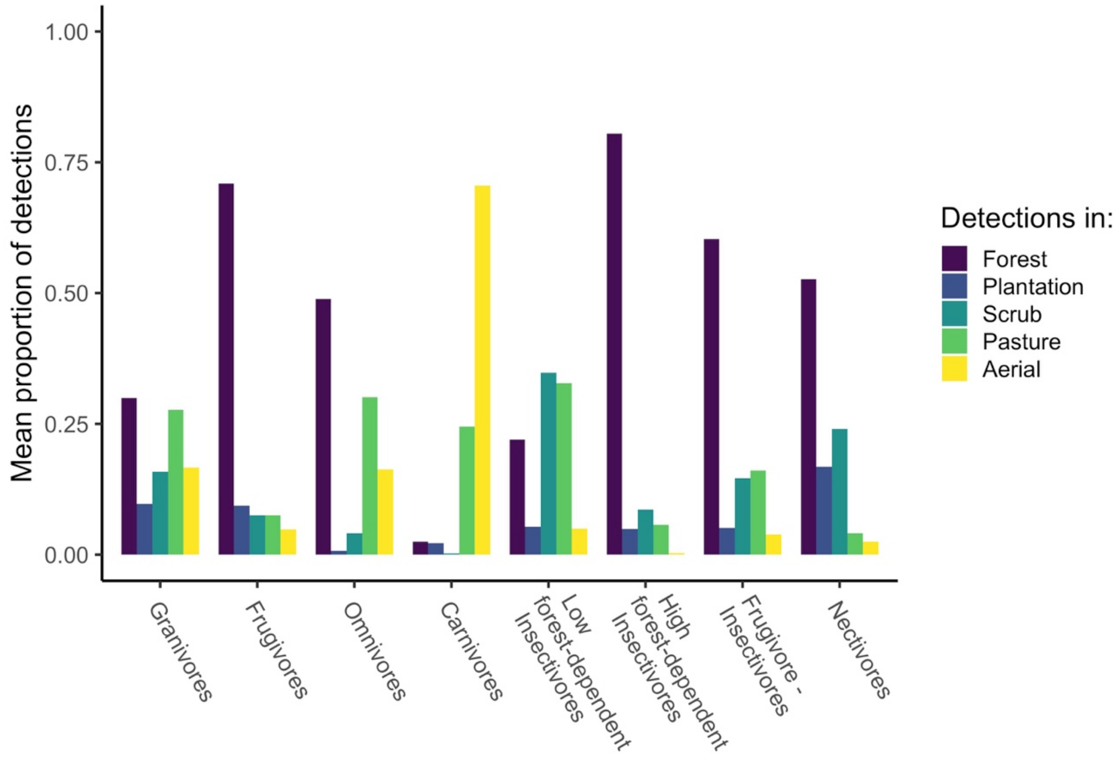


Figure 2.S4 - Species trait and habitat preference information for the eight species groups. Dietary and foraging strata data from Wilman et al (2014), forest dependency data from Birdlife International (2019), habitat preferences from this study.

2.S5 Species-level effects of fragmentation

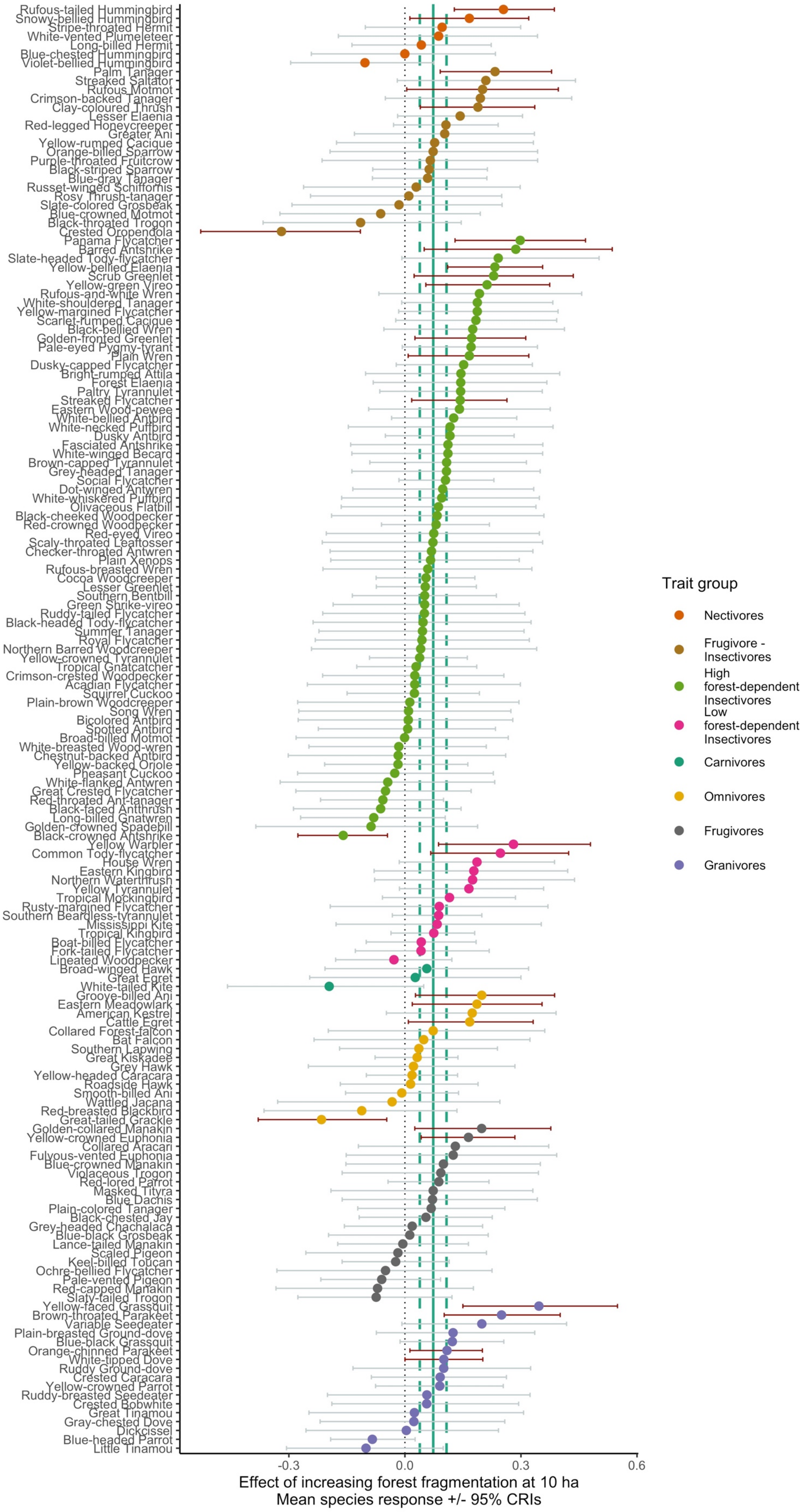


Figure 2.S5a - Species responses to forest fragmentation at 10 ha, with species clustered by trait-based groups. Shaded bars denote those species with 95% BCIs that do not include zero (implying a significant response). Community mean value and 95% BCIs shown by the vertical green lines.

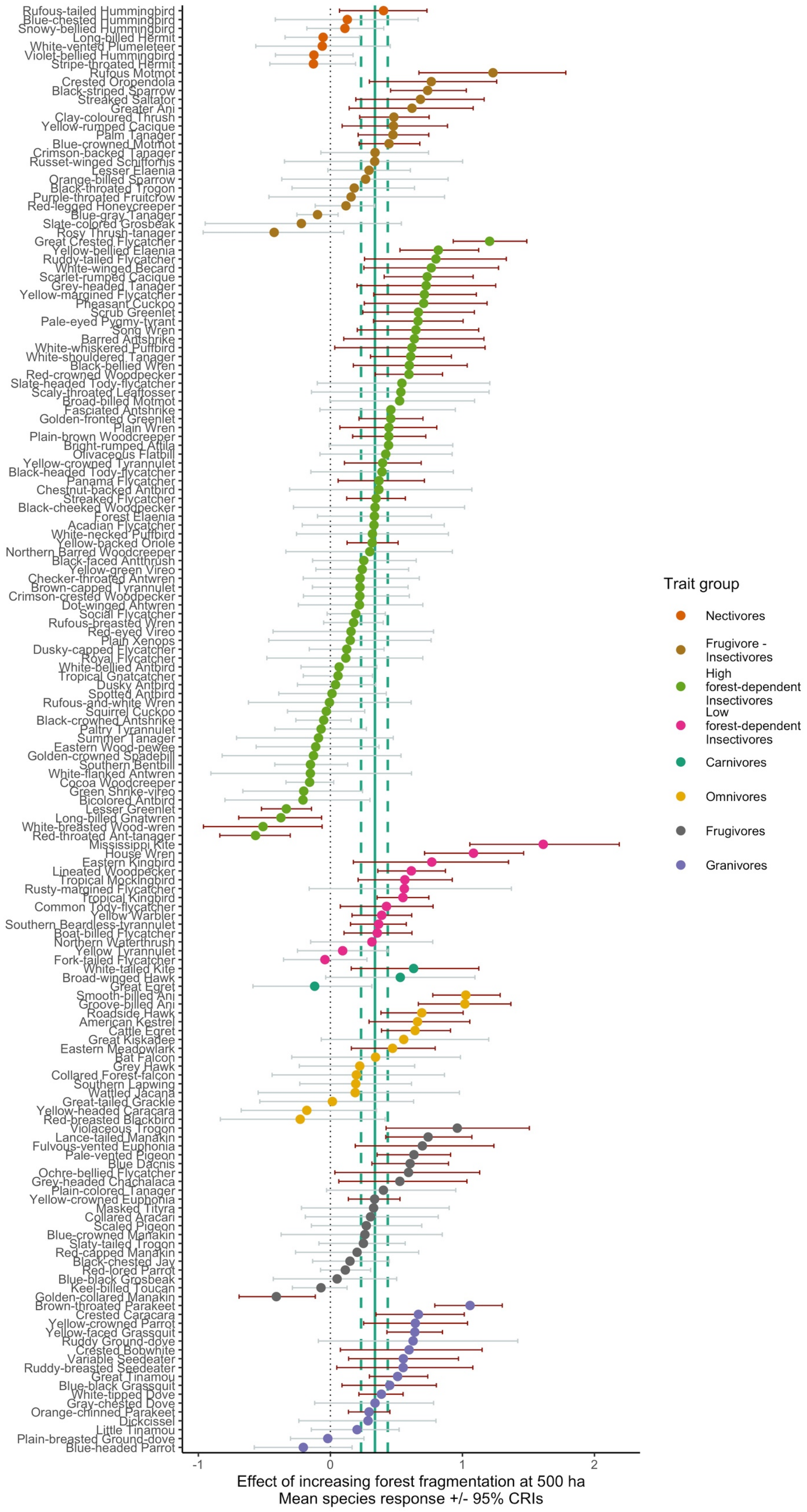


Figure 2.S5b - Species responses to forest fragmentation at 500 ha, with species clustered by trait-based groups. Shaded bars denote those species with 95% BCIs that do not include zero (implying a significant response). Community mean value and 95% BCIs shown by the vertical green lines.

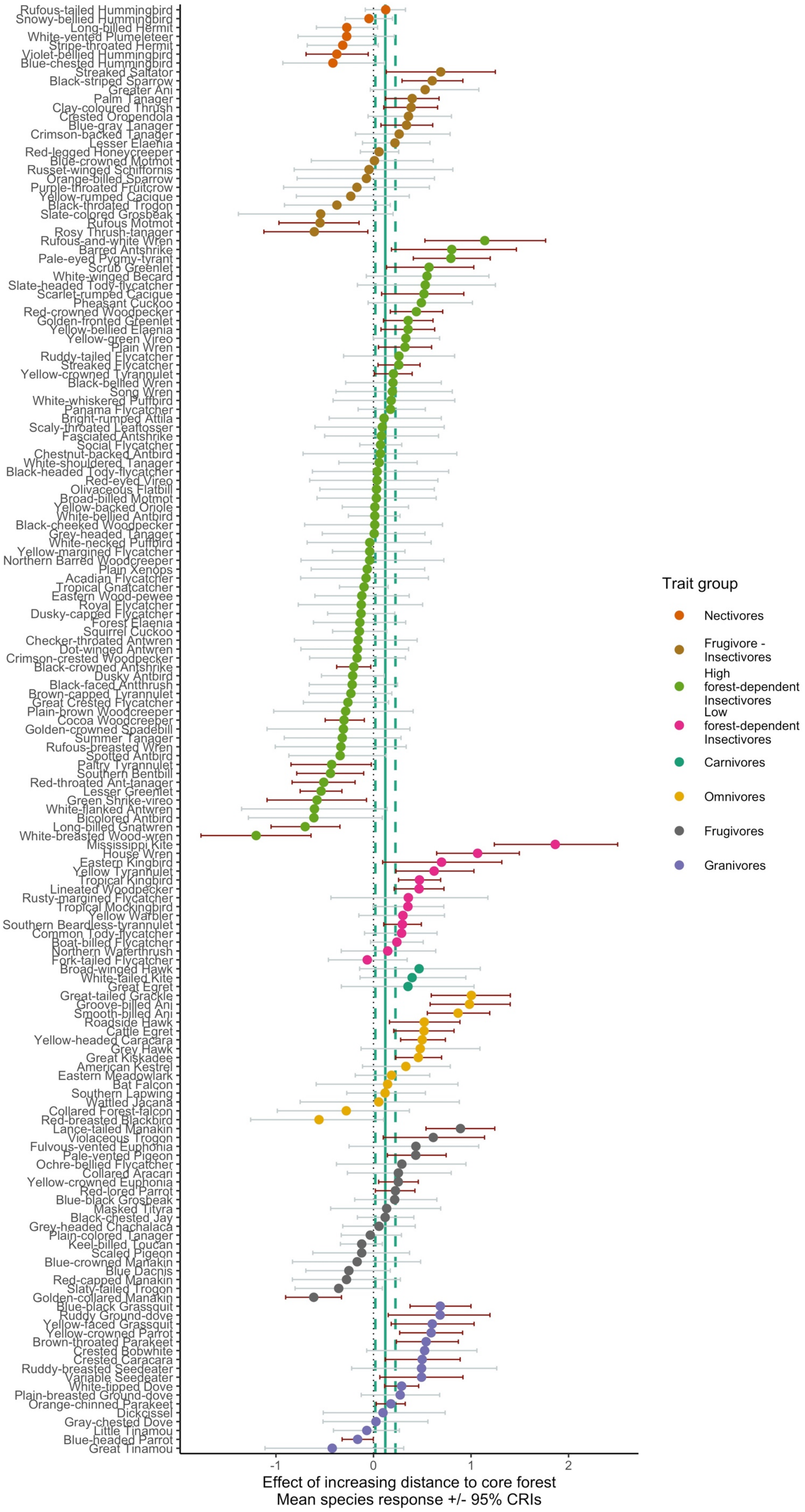


Figure 2.S5c - Species responses distance to core forest, with species clustered by trait-based groups. Shaded bars denote those species with 95% BCIs that do not include zero (implying a significant response). Community mean value and 95% BCIs shown by the vertical green lines.

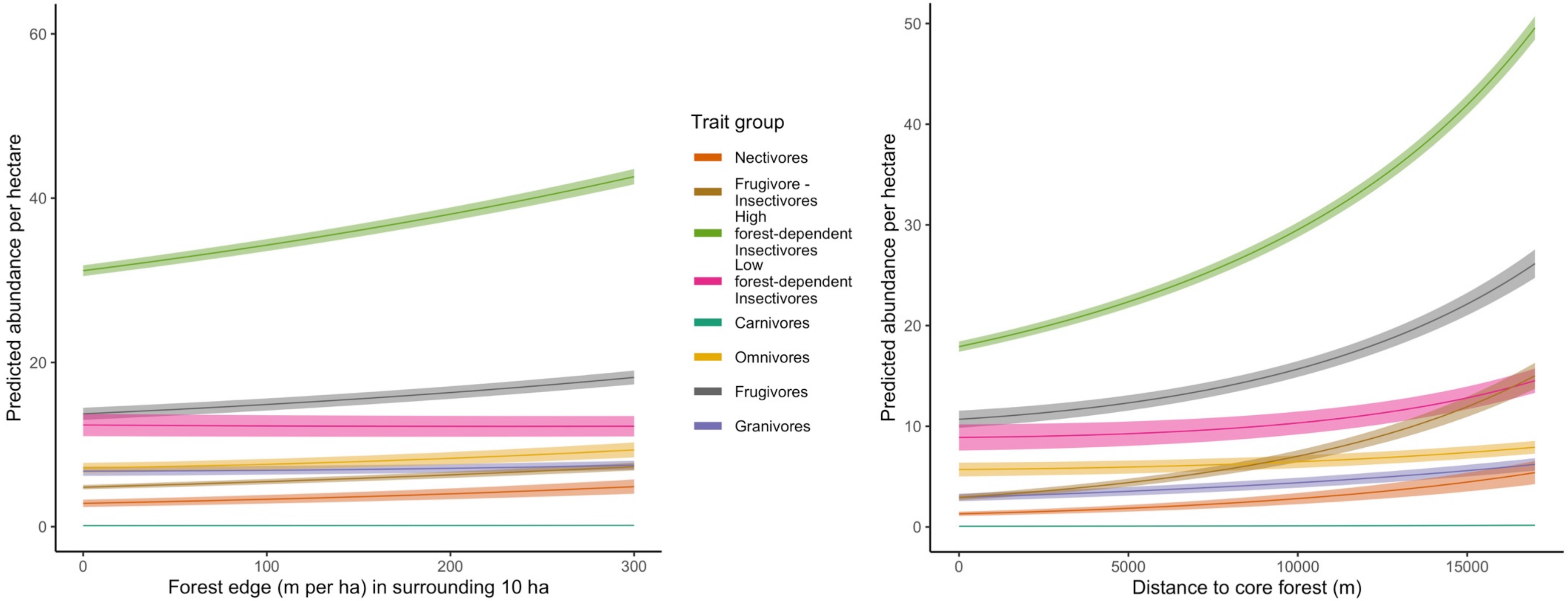
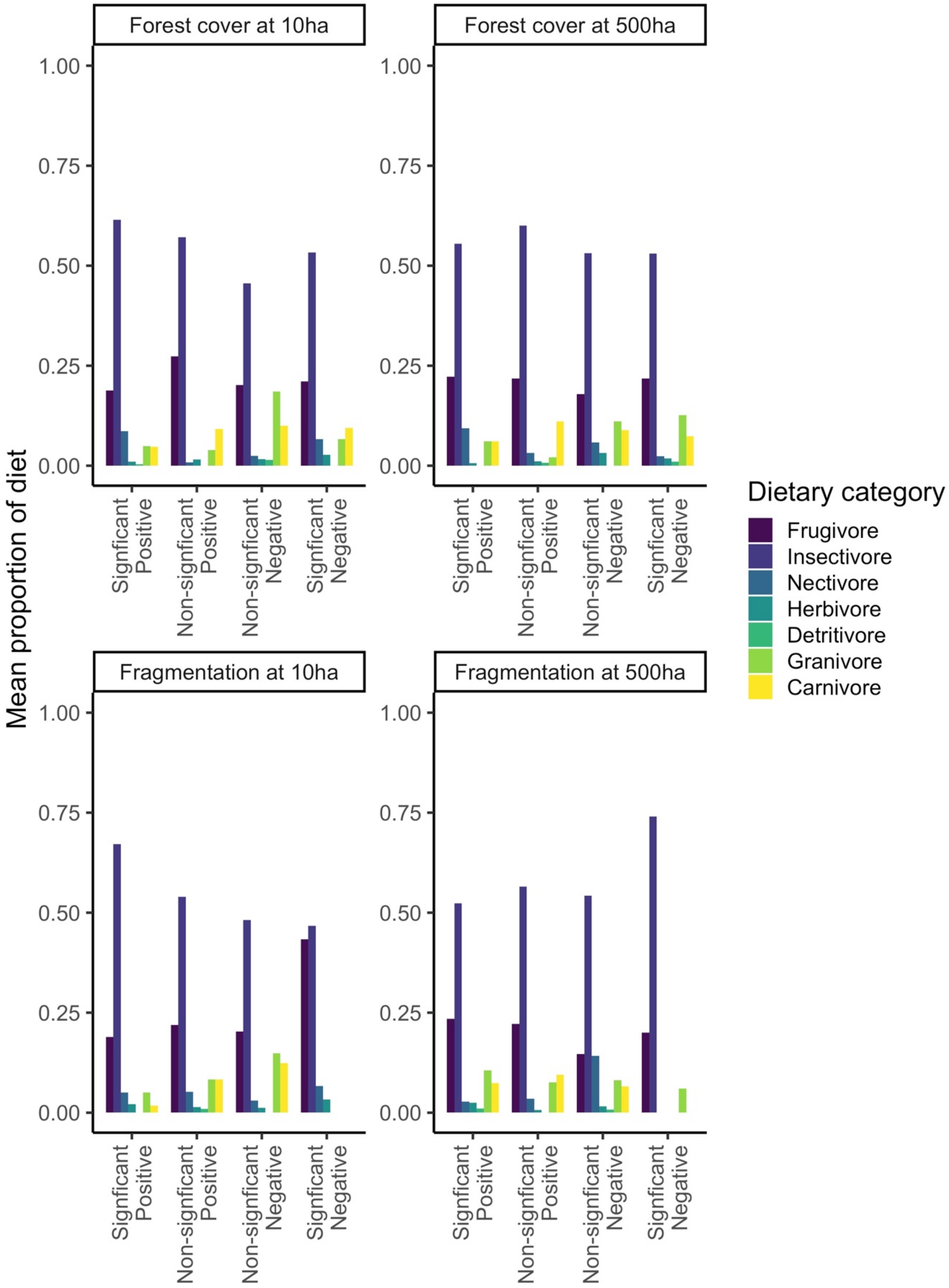
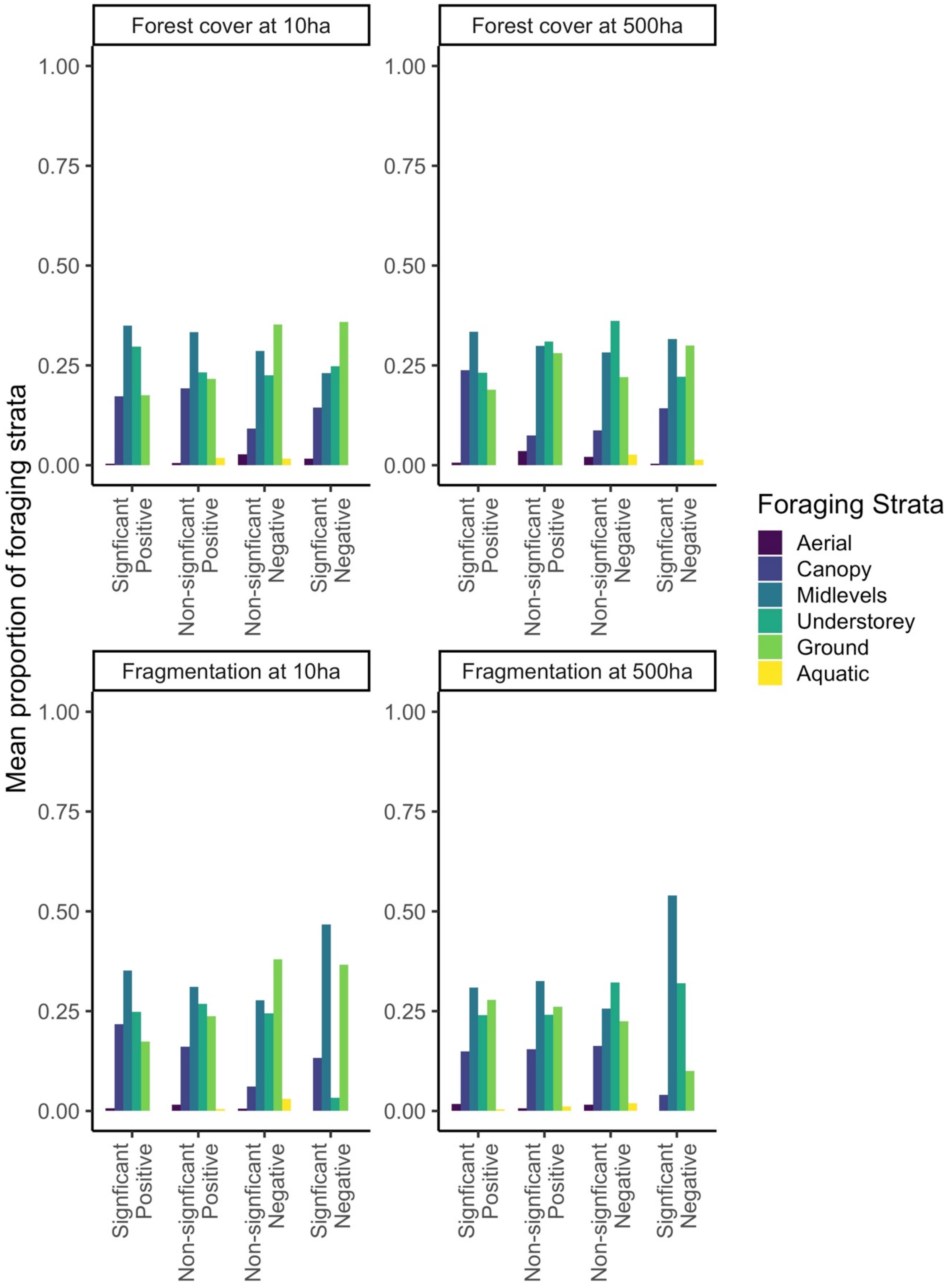
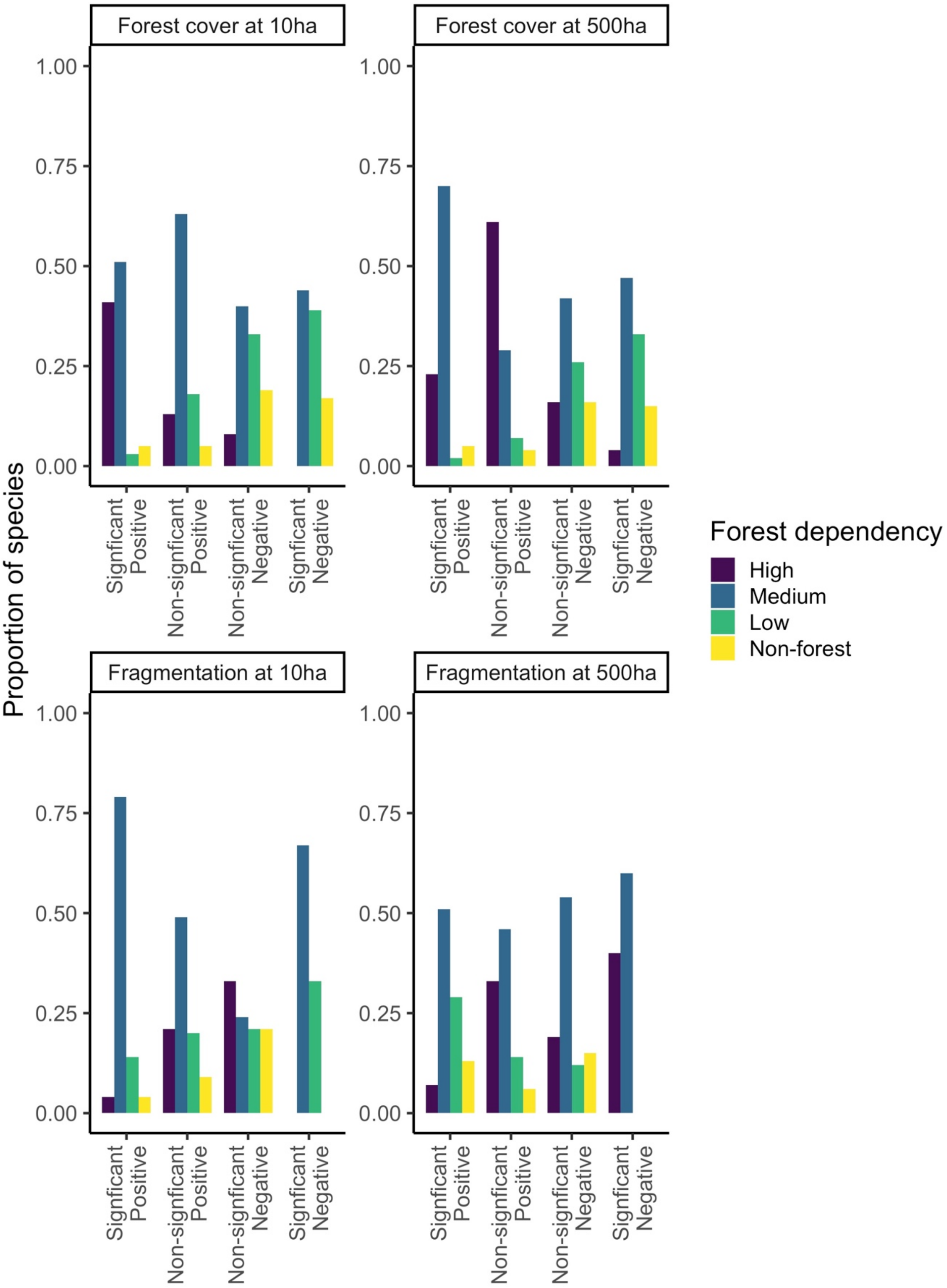


Figure 2.S6 - Change in abundance of trait-based groups with increasing fragmentation (as measured by forest edge density) at 10 ha (left) and with increasing distance to core forest (right).

2.S6 Trait patterns among species sensitive to forest loss




Forest cover at 10ha
Forest cover at 500ha
Fragmentation at 10ha
Fragmentation at 500ha
Mean proportion of foraging strata
1.00
0.75
0.50
0.25
0.00
Signficant Positive
Non-signficant Positive
Non-signficant Negative
Signficant Negative
Foraging Strata
Aerial
Canopy
Midlevels
Understorey
Ground
Aquatic


Forest cover at 10ha
Forest cover at 500ha
Fragmentation at 10ha
Fragmentation at 500ha
Proportion of species
1.00
0.75
0.50
0.25
0.00
Signficant Positive
Non-signficant Positive
Non-signficant Negative
Signficant Negative
Forest dependency
High
Medium
Low
Non-forest

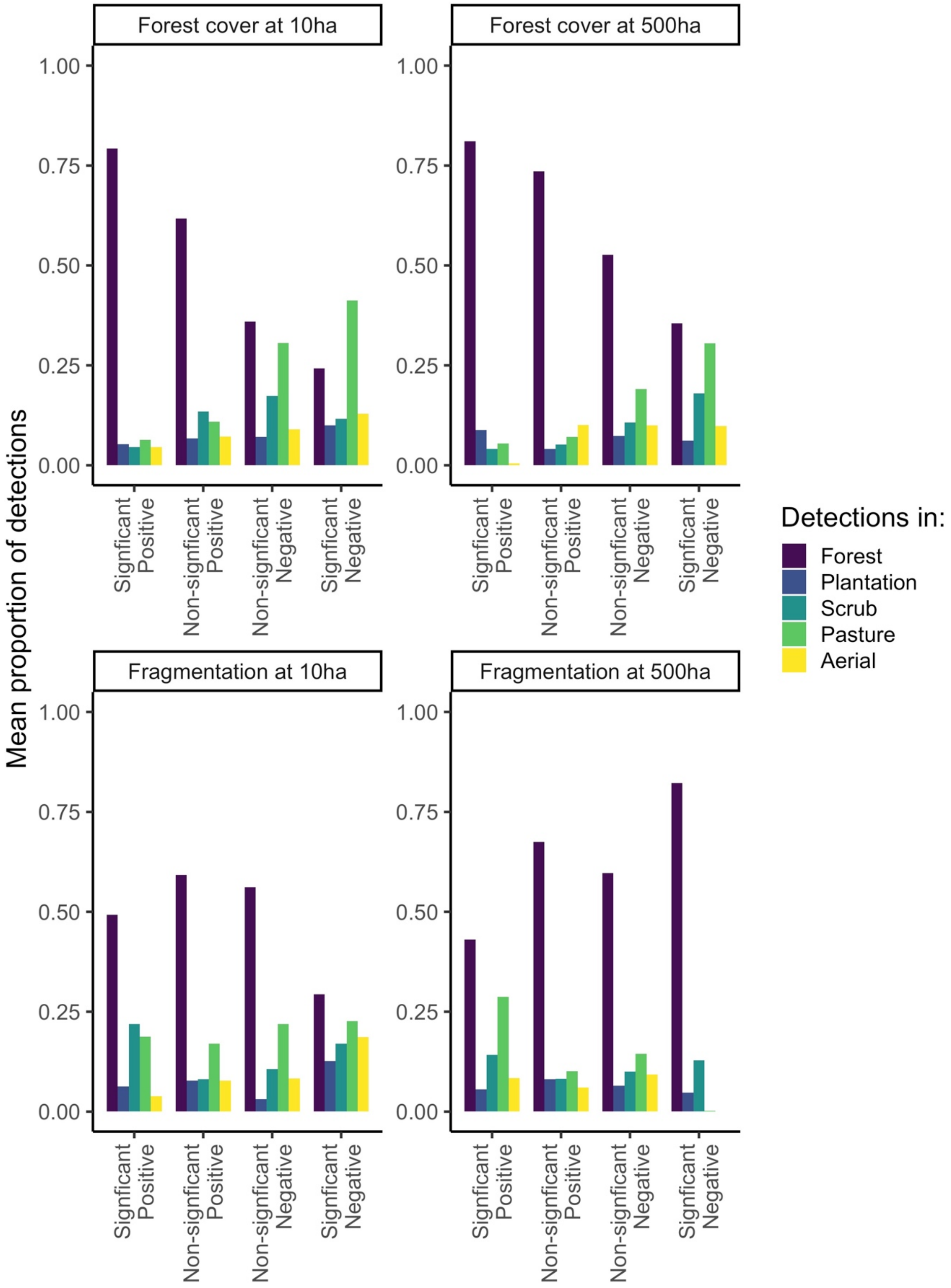


Figure 2.S7 - Functional traits and habitat preferences for four species groups, based on responses to levels of forest cover and fragmentation at 10 ha and 500 ha scales. Dietary and foraging strata data from Wilman et al (2014), forest dependency data from Birdlife International (2019), habitat preferences from this study.

2.S7 Model output tables

Table 2.S2 - GLMM to test whether number of detections during each point count varied over the course of a morning. Model output from a Generalised Linear Mixed Model (GLMM), with Poisson errors and a log link, with a random effect of transect to account for potential spatial autocorrelation..

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	3.01	0.036	82.924	< 0.0001
Point Count 2	0.31	0.024	12.73	< 0.0001
Point Count 3	0.34	0.024	13.924	< 0.0001
Point Count 4	0.29	0.024	11.838	< 0.0001
Point Count 5	0.26	0.025	10.664	< 0.0001
Point Count 6	0.25	0.025	9.974	< 0.0001
Point Count 7	0.25	0.025	10.065	< 0.0001
Point Count 8	0.05	0.026	1.968	0.049
Point Count 9	0.02	0.026	0.765	0.444
Point Count 10	-0.07	0.027	-2.675	0.007
Point Count 11	-0.02	0.033	-0.618	0.537
Point Count 12	-0.21	0.056	-3.716	0.0002

Table 2.S3 – Hierarchical model output showing species-level mean and 95% BCIs of the posterior distribution for each parameter, with $\hat{R}$ and Effective Sample Size values. This table is large and so only available electronically. It is stored in DataSTORRE, the University of Stirling's online data repository, available at http://hdl.handle.net/11667/141.

Chapter 3. Guidelines for the use of acoustic indices in environmental research

This chapter has been published as:

Tom Bradfer-Lawrence, Nick Gardner, Lynsey Bunnefeld, Nils Bunnefeld, Stephen G. Willis, Daisy H. Dent (2019). Guidelines for the use of acoustic indices in environmental research. Methods in Ecology and Evolution, 10, 1796 – 1807

TBL, LB, NB, SW and DD conceived the study; TBL and NG collected the data; TBL, NB and DD designed the analysis; TBL led the writing of the text. All authors contributed critically to draft versions prior to publication. Two anonymous reviewers commented on an earlier draft version during the revision process.

3.1 Abstract

1. Ecoacoustics, the study of environmental sound, is a growing field with great potential for biodiversity monitoring. Audio recordings could provide a rapid, cost-effective monitoring tool offering novel insights into ecosystem dynamics. More than 60 acoustic indices have been developed to date, each reflecting distinct attributes of the soundscape, (i.e. the total acoustic energy at a given location, including noise produced by animals, machinery, wind and rain). However, reported patterns in acoustic indices have been contradictory, possibly because there is no accepted best practice for the collection and analysis of audio recordings.

2. Here, we propose: (1) guidelines for designing studies using audio recordings for the rapid assessment of multiple sites, and (2) a workflow for comparing recordings with seven of the most commonly used indices, permitting discrimination among habitat-specific soundscapes. We collected and analysed over 26,000 hours of recordings from 117 sites across a range of habitats in a human-modified tropical landscape in central Panama; an order of magnitude more recordings than used in previously published studies.

3. We demonstrate that: (1) Standard error variance of indices stabilises within 120 hours of recordings from a single location. (2) Continuous recording should be used rather than sub-sample recording on a schedule; sub-sampling is a common practice but delays capture of site variability and maximising total duration of recording should be prioritised. (3) Use of multiple indices to describe soundscape patterns reveals distinct diel and seasonal soundscape patterns among habitats.

4. We advocate collecting at least 120 hours of continuous recordings per site, and using a range of acoustic indices to categorise the soundscape, including the Acoustic Complexity Index, Acoustic Evenness Index, Acoustic Entropy Index and the Normalised Difference Soundscape Index. Differences among habitat types can be captured if multiple indices are used, and magnitude of variance is often more important than mean values. The workflow we provide will enable successful use of ecoacoustic techniques for environmental monitoring.

3.2 Introduction

Ecoacoustics, the study of environmental sound, is a rapidly evolving field (Sueur et al. 2014). Recent developments in automated sound collection and processing offer enormous potential for rapid and cost-effective monitoring of biodiversity, an essential task in the face of global land-use change (Burivalova et al. 2019a; Laiolo 2010; Ribeiro et al. 2017). By identifying temporal shifts in soundscapes, this monitoring can be used to assess how species are affected by anthropogenic disturbance (Burivalova et al. 2019a). However, the relative novelty of this field and the pace of innovation mean there are currently no accepted standards regarding the quantity of data (i.e. the length of recordings) or sampling intensity necessary for characterising the soundscape of a given habitat. Similarly, guidance on how such data can be used for effective, yet simple, biodiversity monitoring is lacking (Priyadarshani et al. 2018).

Thousands of hours of sound recordings have been collected from a multitude of habitats around the world, but methods for translating these data into a rapid monitoring process are not keeping pace (Gibb et al. 2018; Priyadarshani et al. 2018). Data on faunal presence can be extracted from audio recordings using either manual or automated methods. However, both manual and automated approaches are time-consuming, necessitate expert knowledge and, in the case of automated recognisers, are still subject to high error rates (Furnas & Callas 2015; Sevilla & Glotin 2017). Rather than focus on individual species, alternative approaches are required that summarise the huge quantities of sound recordings now available. To this end, over 60 indices have been developed to rapidly classify soundscapes based on their acoustic properties, providing metrics for habitat assessment and monitoring (Buxton et al. 2018; Sueur et al. 2014).

The soundscape is comprised of the total acoustic energy at a given location, incorporating biophony (noise produced by animals), anthrophony (noise produced by humans and machines), and geophony (noise from natural processes such as wind and rain) (Pijanowski et al. 2011). Each acoustic index reflects different characteristics of the soundscape, such as pitch, saturation, and amplitude. Often these involve contrasting short time steps or frequency bands within a recording. For example, the widely used Acoustic Complexity Index (ACI) contrasts the amplitude difference between one short time step (e.g. 0.03 secs) and the next, within a narrow frequency band (e.g. 62 Hz). The ACI is sensitive to the inherent irregularity of biophony, particularly from bird song, while it is relatively impervious to persistent sound of a constant intensity. Audio indices such as ACI reduce the enormous complexity of the soundscape to a single number, greatly simplifying extraction of information from recordings.

Acoustic indices are now used in a range of ecological research. Recently, a promising method using false colour spectrograms constructed with acoustic indices has been developed as a means of detecting particular species or taxon choruses (Towsey et al. 2014a; Towsey et al. 2018). However, research focus has generally concentrated on investigating overall soundscape patterns. For example, Rodriguez et al. (2014) used acoustic indices to describe clear diel cycles in tropical forest soundscapes, and differences between the canopy and understory strata. Seasonal shifts in soundscapes have been examined in both temperate and tropical habitats (Farina et al. 2011; Pieretti et al. 2015; Rankin & Axel 2017). There are also clear distinctions in the soundscapes of different habitat types (Bormpoudakis et al. 2013; Depraetere et al. 2012; Villanueva-Rivera et al. 2011), with habitat disturbance or conversion reflected in changes in the soundscape, likely triggered by shifts in faunal assemblages (Burivalova et al. 2018; Deichmann et al. 2017; Tucker et al. 2014) From these studies it is clear that ecoacoustics has enormous potential for environmental research.

Despite the promising results described above, studies have reported contradictory patterns, even when using the same acoustic indices. For example, some have found higher biophony and lower soundscape variability to be associated with lower levels of disturbance (Fuller et al. 2015; Machado et al. 2017), while others have found no differences among habitat types (Mammides et al. 2017; Ng et al. 2018). These disagreements may have arisen because to date there has been no consistency in data collection, and little agreement on the best indices for soundscape assessment. Although guidelines on the use of ecoacoustics for biodiversity monitoring have been published, these focus on assessing faunal presence rather than soundscape analysis (Browning et al. 2017; Llusia et al. 2011). Thus, inconsistent methodologies may underlie the inconsistent patterns.

Ecoacoustic studies have used a wide range of recording schedules (e.g. from continuous to <1 minute per hour) and data volumes (e.g. from >200 hours to <5 minutes per site; see supporting information). Inter-soundscape comparisons are common, without consideration of whether intra-soundscape variation has been accurately captured. While geophony is a key constituent of natural soundscapes, recordings with “high” levels of geophony are often removed from analyses, without a common definition of what “high” might be. Moreover, studies often present just one or two indices, with little justification for their selection. We argue that these inconsistencies are limiting the efficacy of acoustic indices in biodiversity monitoring. Given each index reflects different spatio-temporal features (Eldridge et al. 2016), considering several indices in concert may give a much better representation of the soundscape rather than any one individual index. Here, we use seven commonly employed acoustic indices derived from recordings collected across a human-modified landscape in central Panama to ask:

1. What duration of recordings is necessary to quantify the soundscape of a site, and does this vary among habitat type or index?
2. Should recordings be continuous, or can they be limited to temporal sub-samples to minimise storage volumes and subsequent analysis?
3. Which indices best reflect temporal variation over the course of the day, and between seasons, and are there different patterns among habitats?

3.3 Materials and Methods

3.3.1 Study Landscape

Acoustic data were collected in the Emparador landscape, located in the central region of the Republic of Panama, to the west of the Panama Canal (Figure 3.1). The landscape covers approximately 700 km^2 and is highly heterogeneous, with tracts of extensive continuous forest, agricultural pasture, remnant forest fragments, non-native tree plantations, regenerating scrub and small urban centres. The landscape is bordered by the Panama Canal to the north and east, and the Interamericana highway to the south. The human population is distributed throughout the landscape, with sizeable areas of new urban development close to the Interamericana Highway. Rainfall varies from 2334mm in the north to 1969mm in the south (Pyke et al. 2001). There is a pronounced dry season between late December and late April when the mean daytime temperature is 31°C. The remainder of the year is wet, with a mean daytime temperature of 28°C (Robinson et al. 2004).

3.3.2 Data Collection

One hundred and seventeen deployment sites (hereafter "sites") were selected for this study, with 14-24 sites in each of the six main habitats present in the Emparador landscape: continuous forest, fragmented forest, riparian forest, scrub, teak plantation and pasture (Figure 3.1). A detailed description of the six habitats, their typical features, and numbers of sites in each habitat is provided in Table 3.S1. Sites were positioned in patches of uniform habitat of at least one hectare, and were separated by a minimum distance of 500m from sites in other habitat types, and 1000m from those in the same habitat.

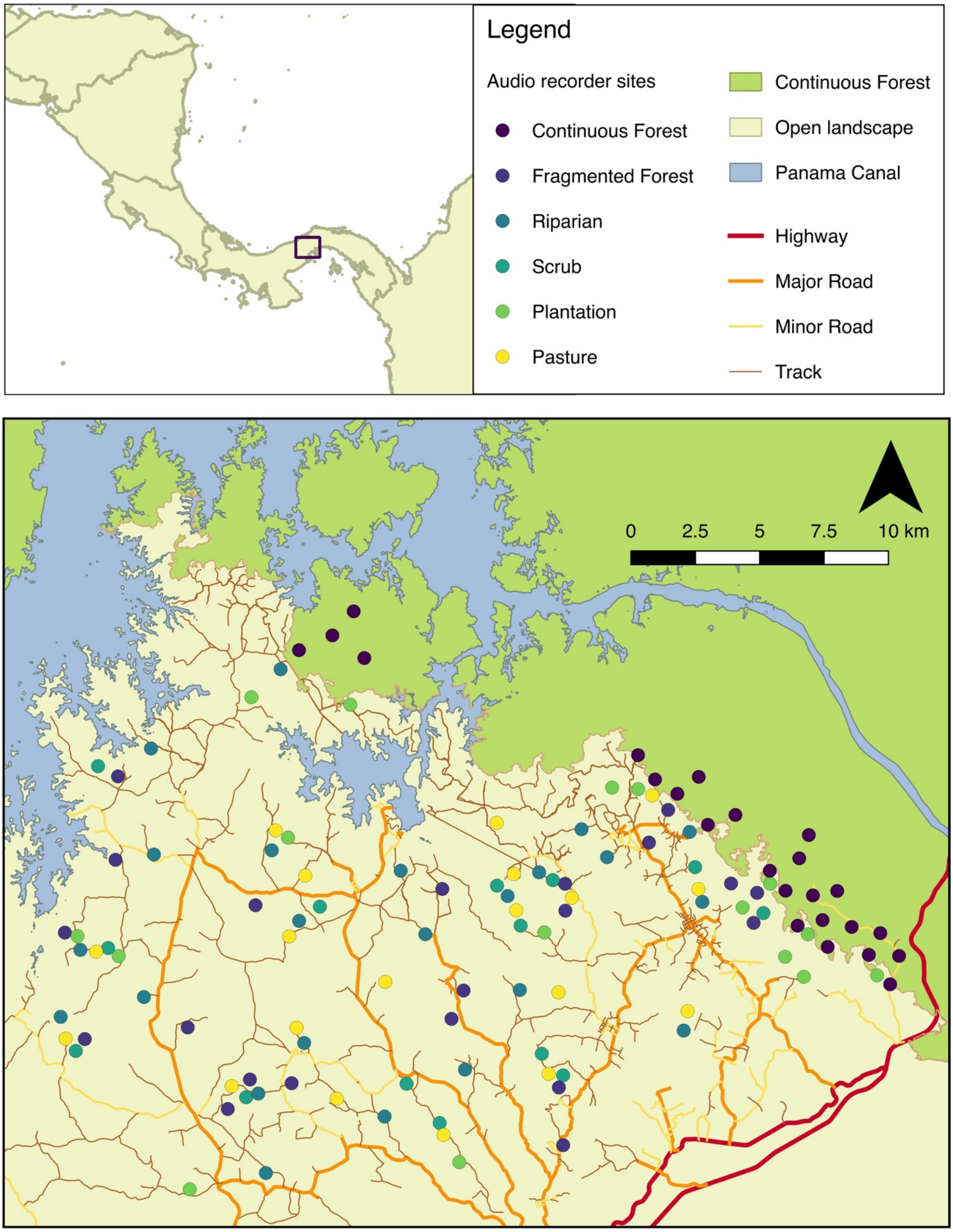


Figure 3.1 - Map of the study region in central Republic of Panama showing the 117 sites where audio recordings were collected.

Audio recordings were collected between January and September 2017. Recorders were deployed for one week at each site. There were a total of 154 deployments, 90 in the dry season and 64 in the wet season. Eighty sites were only visited once during the study, the remaining 37 sites had two separate deployments of a week each, one in the dry season and one in the wet season, to facilitate study of intra-site seasonal patterns (mean 160 days +/- 26 between deployments). After each deployment, recorders were rotated between habitat types to minimise any bias that might arise from hardware variability. Sound recordings were collected using Solo recorders with omnidirectional microphones positioned between 1 and 2m above the ground (Whytock & Christie 2017). Most recordings were collected with Primo EM172 microphones (Primo, Singapore), however logistical issues necessitated switching to Snowflake microphones (Blue, USA) during the wet season in some cases. Testing suggested no systematic disparity in recordings collected with the different microphone models (see supporting information), so we did not distinguish between the two sets of recordings in the main analyses. Solo recorders collect audio continuously, but for ease of analysis recordings are automatically divided into 10-minute files. A sampling rate of 32,000 Hz was used as a balance between capturing the majority of the human-audible soundscape against storage volume requirements.

Pre-processing was limited to a 500 Hz low-stop filter prior to analyses to reduce microphone self-noise (Pieretti et al. 2015). This will have removed some genuine sources of low-frequency noise, but microphone self-noise may bias indices values. Several studies have screened recordings to exclude those with high levels of geophony (Depraetere et al. 2012; Gasc et al. 2013; Pieretti et al. 2015), or anthrophony (Bormpoudakis et al. 2013), as some indices can be strongly influenced by these elements. However, we consider these to be key components of the soundscape, so no recordings were excluded.

3.3.3 Data Analyses

3.3.3.1 Calculation of Acoustic Indices

157,476 10-minute files were included in this study, equivalent to three years of continuous audio. Index calculation and all analyses were conducted with the software R (ver 3.5.1; R Core Team 2018). We calculated soundscape indices values for each 10-minute recording, although for one section of the analysis, values were calculated for individual minutes (see below). Using the packages *seewave* (ver 2.1.0; Sueur et al. 2008a) and *soundecology* (ver 1.3.3; Villanueva-Rivera & Pijanowski 2018), the following seven indices were calculated using the default values of each function: Acoustic Complexity Index (ACI), Acoustic Diversity Index (ADI), Acoustic Evenness (AEve), Bioacoustic Index (Bio), Acoustic Entropy (H), Median of the amplitude envelope (M), and the Normalised Difference Soundscape Index (NSDI). A description of each index and the patterns they reflect is in Table 3.1, with additional details in Table 3.S2 and example sonograms in Figure 3.S1. We selected these indices as they are the most frequently used in ecoacoustic research and have been compared in other multi-index studies (Fuller et al. 2015; Machado et al. 2017; Mammides et al. 2017; Ng et al. 2018 but see Buxton et al. 2016; Buxton et al. 2018a). Selected indices also had to meet the following criteria: simple to calculate (i.e. existing functions in R packages), their values reflect soundscape patterns with links to ecological dynamics, and they are supported by peer-reviewed publication.

Table 3.1 - Summary of the acoustic indices used in this study, the general soundscape patterns they reflect, and examples from this study. Further information including how the indices are calculated is detailed in Table S2.

Index and reference	Soundscape patterns	Patterns in this study
Acoustic Complexity Index (ACI) (Pieretti et al. 2011)	Based on difference in amplitude between one time sample and the next within a frequency band, relative to the total amplitude within that band. Designed to quantify the inherent irregularity in biophony, while being relatively impervious to persistent sound of a constant intensity.	High values indicate storms, intermittent rain drops falling from vegetation, stridulating insects, or high levels of bird activity. Lowest values came from recordings with consistent cicada noise that fills the whole spectrogram.
Acoustic Diversity Index (ADI)	Increases with greater evenness across frequency bands. An even signal (either noisy across all	Highest values were from recordings with high levels of geophony or anthrophony (wind, helicopters or

(Villanueva-Rivera et al. 2011)	frequency bands or completely silent) will give a high value, while a pure tone (i.e. all energy in one frequency band) will be closer to 0.	trucks) blanketing the spectrogram with noise, or from very quiet recordings with little variation among frequency bands. Lowest values reflect dominance by a narrow frequency band, usually by nocturnal insect noise.
Acoustic Evenness (AEve) (Villanueva-Rivera et al. 2011)	Higher values indicating greater unevenness among frequency bands, i.e. most of the sound intensity appears in a restricted range of frequencies. Acoustically rich habitats may produce low values because there is little variation in intensity among frequency bands in saturated soundscapes.	Reverse of ADI patterns. High values identify recordings with dominance by a narrow frequency band of insect noise. Low values are associated with windy recordings with many occupied frequency bands, or near silent recordings with no acoustic activity.
Bioacoustic Index (Bio) (Boelman et al. 2007)	A function of both amplitude and number of occupied frequency bands between 2 - 11 kHz. Value is relative to the quietest 1 kHz frequency band; higher values indicate greater disparity between loudest and quietest bands.	Highest values produced by blanket cicada noise, with high amplitude and minimal variation among frequency bands. Low values arise when there is no sound between 2 and 11 kHz, although there is sometimes insect biophony outside these bounds.
Acoustic entropy (H) (Sueur et al. 2008b)	Increases with greater evenness of amplitude among frequency bands and/or time steps. Returns a value between 1 (an even signal, either noisy across frequency bands or completely silent) and 0 (a pure	Highest values from near-silent recordings, with no wind, and only faint bird calls. Lowest values produced when insect noise dominated a single frequency band.

	tone with all energy in one frequency band).	
Median of the amplitude envelope (M) (Depraetere et al. 2012)	Reflects the amplitude of a recording. Louder recordings will give higher values, reflecting noisier soundscapes.	Highest values associated with high levels of geophony, particularly storms. Low levels of M produced by very quiet recordings, little biophony or geophony.
Normalised Difference Soundscape Index (NDSI) (Kasten et al. 2012)	Relies on a theoretical frequency split between anthrophony (1 - 2 kHz) and biophony (2 - 11 kHz). The ratio of the two components give values of -1 to +1, with +1 indicating no anthrophony in the soundscape.	High values reflect high levels of insect biophony, with minimal noise in the 1 - 2 kHz range. Low values arise when insect biophony dominates the 1 - 2 kHz band.

3.3.3.2 Minimum quantity of recordings and recording schedules

To determine the minimum number of recordings required to describe a site's soundscape, we randomly assigned the 10-minute recordings from each site into groups of six to create “pseudo-hours”. Randomisation of the entire recording set from each site removed any diel effects, permitting focus on overall soundscape variability. We calculated mean index value and standard error for each pseudo-hour. Mean value was determined from the six recordings within each pseudo-hour, but standard errors were cumulative over time, i.e. error was estimated using all pseudo-hours up to and including the latest to simulate successively longer deployments. For example, standard error for the fourth hour was calculated using the indices values from the first four pseudo-hours, for the fifth hour standard error was calculated with the first five pseudo-hours and so on, (Figure 3.S2). As simulated deployments became longer, the inclusion of more data led to a decline in standard errors. Standard errors stabilised when natural variability rather than data paucity was determining the index variance. Reduction in this variance over time was modelled using nonlinear regression, to quantify the effect of increasing deployment lengths. For this analysis we treated all deployments as separate, even though some were revisits to the same site. A global model with index as a random effect would not converge, and so each index was modelled separately using the same distribution. We selected the Weibull distribution as it is both relatively simple and versatile, with a range of potential shapes from exponential to humped (Bolker 2008). We explored potential habitat and seasonal differences in variance reduction but found no support for separate models, implying similar patterns across all habitats and seasons.

Recording on a temporal schedule, rather than continuously, is common practice in acoustic monitoring to improve battery performance and reduce data storage (Pieretti et al. 2015). To examine the effect of scheduled recording, we divided recordings into single minutes and calculated acoustic indices for each. We then simulated a range of schedules used in previous acoustic indices studies: continuous, one minute in every two, one in five, one in 10, one in 30 and one in 60 minutes. All schedules were treated as if they came from a one-week deployment, so resulting datasets spanned the same length of time but those from sparser schedules contained fewer data. Cumulative standard errors were calculated for each schedule as described above. Reduction in variance of standard error as a percentage of the maximum was modelled over deployment length using nonlinear regression. Again, a global model with schedule as a random effect would not converge and so separate models with a Weibull distribution were used for each schedule.

3.3.4 Indices for characterising temporal and spatial patterns

Acoustic indices from the 10-minute recordings were used to generate mean and standard deviation values per hour for each habitat in dry and wet seasons (Pieretti et al. 2015). To test for diel patterns, each hour was classed as either day (06:00 – 17:00) or night (18:00 – 05:00). Finer scale temporal trends were explored using the mean value per 10-minute recording within habitat and season.

Temporal and spatial soundscape patterns among habitats were explored in four ways. First, we performed non-metric multidimensional scaling (NMDS) to investigate habitat-specific diel and seasonal patterns, using the mean and standard deviation of acoustic indices values per hour. We used two axes and the Horn-Morisita dissimilarity index (Horn 1966), and checked the output met minimum stress requirements (Kruskal 1964). Second, the ordination was extended with permutational multivariate analysis of variance (PERMANOVA) to quantitatively test the effect of diel phase, season and habitat type on mean hourly indices values (Anderson 2001). These two analyses were conducted with the package *vegan* (ver 2.5.2; Oksanen et al. 2018). Third, to illustrate finer-scale temporal patterns over 24 hours, we considered trends in mean index value from each 10-minute recording block. This was undertaken for each habitat for both dry and wet seasons, and curves were fitted to these patterns with Generalised Additive Models (GAMs), using the package *mgcv* (ver 1.8.26; Wood 2004).

Finally, to determine which indices were most important in separating habitat-specific soundscapes, we undertook a random forest (RF) classification (Breiman 2001) using the *randomForest* package (ver 4.6.14; Liaw & Wiener 2002). We built a RF using mean hourly indices values and standard deviations, plus the factors “dry” or “wet” season, diel phase “day” or “night”. 75% of the data were used for forest construction and the remaining 25% reserved for testing.

3.4 Results

3.4.1 Minimum quantity of recordings and recording schedules

Standard errors rapidly shrank with increasing deployment time; all indices showed a common pattern of exponential decline as standard errors converging on the mean (Figure 3.2). These patterns were consistent for all indices, across all sites and habitats, and between seasons, as evidenced by fitting the same Weibull distribution to all datasets (Table 3.S3). After 120 hours of recordings, variance stabilised to 8.9 - 12.1 %.

Similar patterns of exponential decline in standard errors were evident when exploring the importance of scheduling (Figure 3.3). Sparser schedules were associated with greater variability, a pattern consistent across all indices. Extrapolation of the one-minute-in-10 model suggested that more than 26 weeks of recording would be required to reduce index variance to a similar level achieved with seven days of continuous recordings (one-in-10 = 2.1% after 4368 hours, continuous = 1.56% after 168 hours). Convergence was a product of total recording length irrespective of the schedule used.

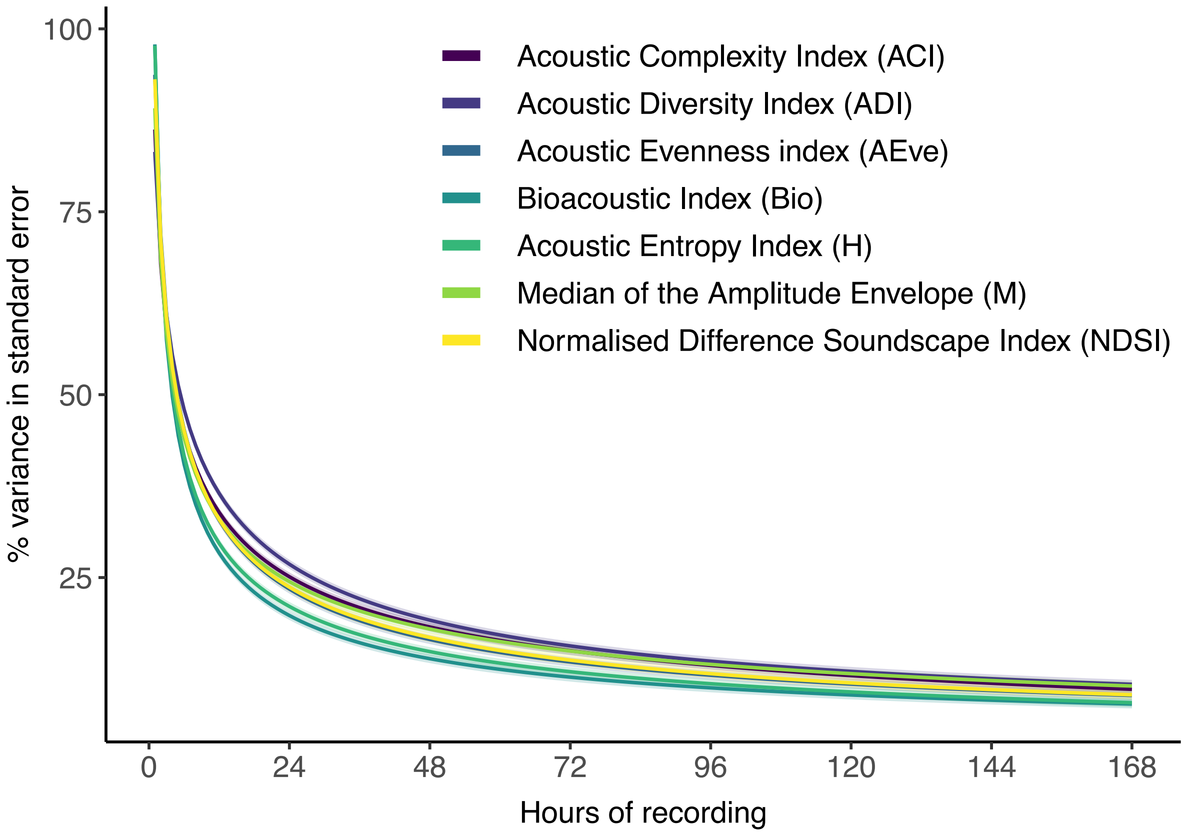


Figure 3.2 - Reduction in variance of standard errors for seven acoustic indices, from a total of 154 recordings sets. Curves for each index show predicted values from nonlinear regression models with a Weibull distribution +/- 1 standard deviation. Standard deviations are very small and do not show on this figure

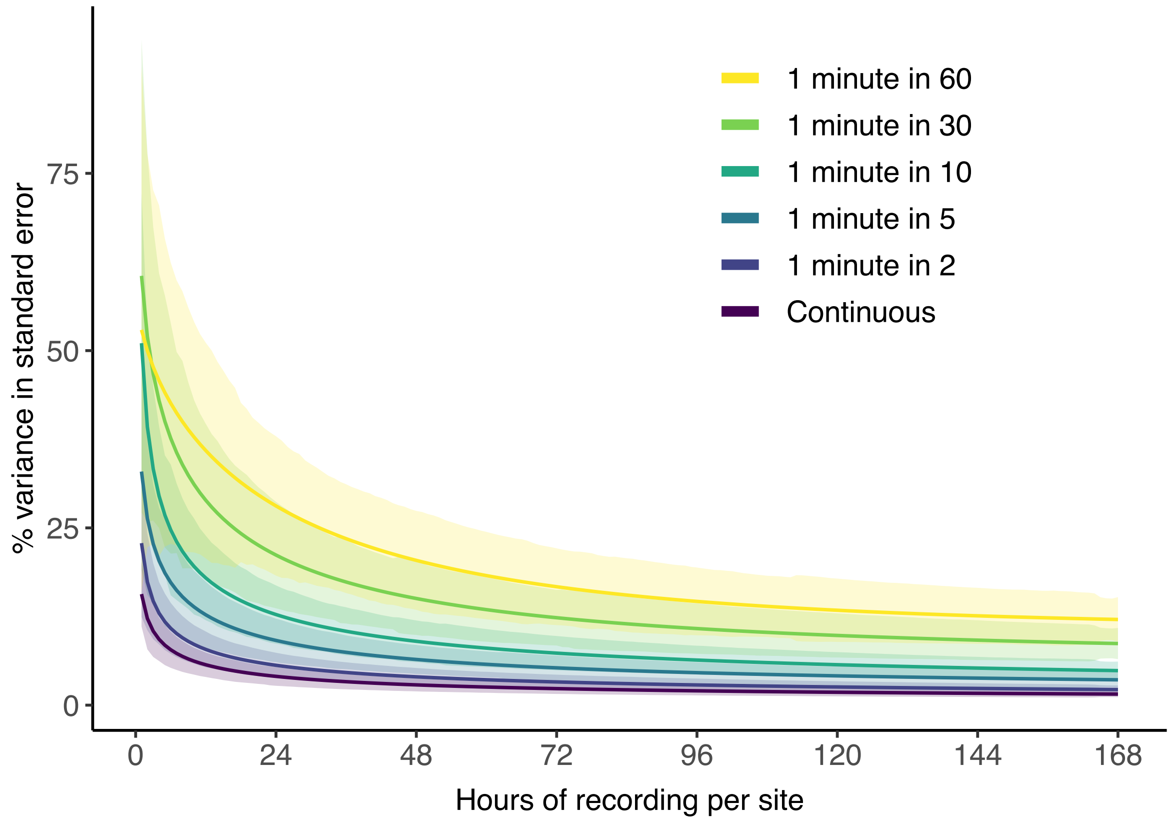


Figure 3.3 - Effect of collecting audio recordings on a schedule. Reduction in variance of standard errors for six temporal recording schedules with increasing lengths of recording. Total dataset includes seven acoustic indices from 154 recording sets. Curves show predicted values from nonlinear regression models with a Weibull distribution +/- 1 standard deviation.

3.4.2 Indices for characterising spatial and temporal patterns

The NMDS ordination showed clear patterns (Figure 4); dry and wet season recordings separated along axis 1 suggesting distinct soundscapes at different times of the year, while axis 2 illustrated a clear division between day and night soundscapes. The effect of habitat was less clear, with no obvious pattern in habitat type driving separation among the points. These results were reflected in the PERMANOVA; diel phase, season, habitat type and the diel phase-season interaction were all significant (Table S5).

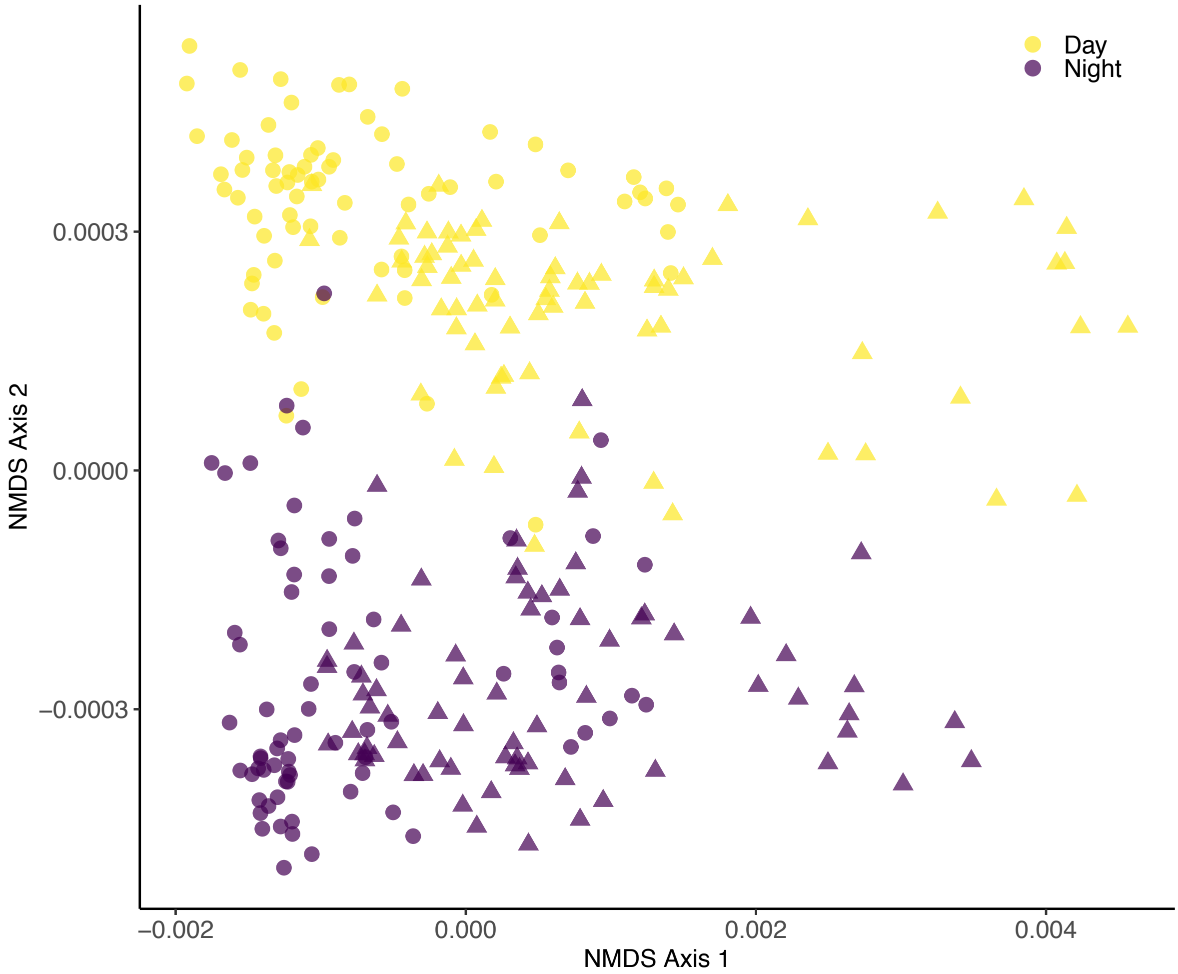


Figure 3.4 - Ordination plot showing the strong diel and seasonal divisions between soundscapes. Ordination was performed using non-metric multidimensional scaling (NMDS) with the Horn-Morisita dissimilarity index (Horn 1966). Stress value 0.002. Each point represents the soundscape of a habitat during one hour. This soundscape is composed of the mean hourly values and standard deviations for each of the seven acoustic indices. Circles show dry season soundscapes, triangles wet season soundscapes.

Six of the seven indices exhibited distinct patterns over the 24 hour period (Figure 3.5, Table 3.S6), often with marked shifts between the day and night soundscapes as implied by the NMDS ordination and PERMANOVA. Curves from the GAM fitted to 10-minute mean index values showed ADI and H values were high across all habitats during the day, but 6% and 9% lower at night respectively. Conversely, the AEve, Bio, M and NSDI values were lower during the day but 50 – 200% higher at night. Habitat-specific diel patterns were also apparent; the rise to daytime H values in pasture was an hour behind the other habitats, a lag mirrored in the Bio and NDSI indices values. AEve and Bio values in both fragmented forest and scrub were higher at night and lower during the day compared with other habitats. Diel patterns in ACI were not apparent, but values in pasture were more variable with a standard deviation of 17, compared to <10 for other habitats. Seasonal differences in diel patterns of all habitats were also evident. The switch from diurnal to nocturnal values in the ADI, AEve and Bio indices was much more gradual in the wet season, beginning around 90 minutes earlier than in the dry season across all habitats. In the wet season, diel variation was reduced in the AEve index (standard deviation 50% lower) but magnified in NDSI (standard deviation 50% higher).

The RF classifier built with mean hourly values per habitat was able to readily separate the data into the six habitat classes (Figure 3.6). When applied to the testing dataset, the RF was 84.7% accurate in assigning soundscapes to the correct habitat type. Both mean and standard deviation of ACI were more important than any other variables for distinguishing among habitat types (with removal accounting for a proportional drop in accuracy of 0.17 and 0.08 respectively). Mean AEve values, and the mean and standard deviations of H and NDSI were also important. Season and diel phase were of least importance.

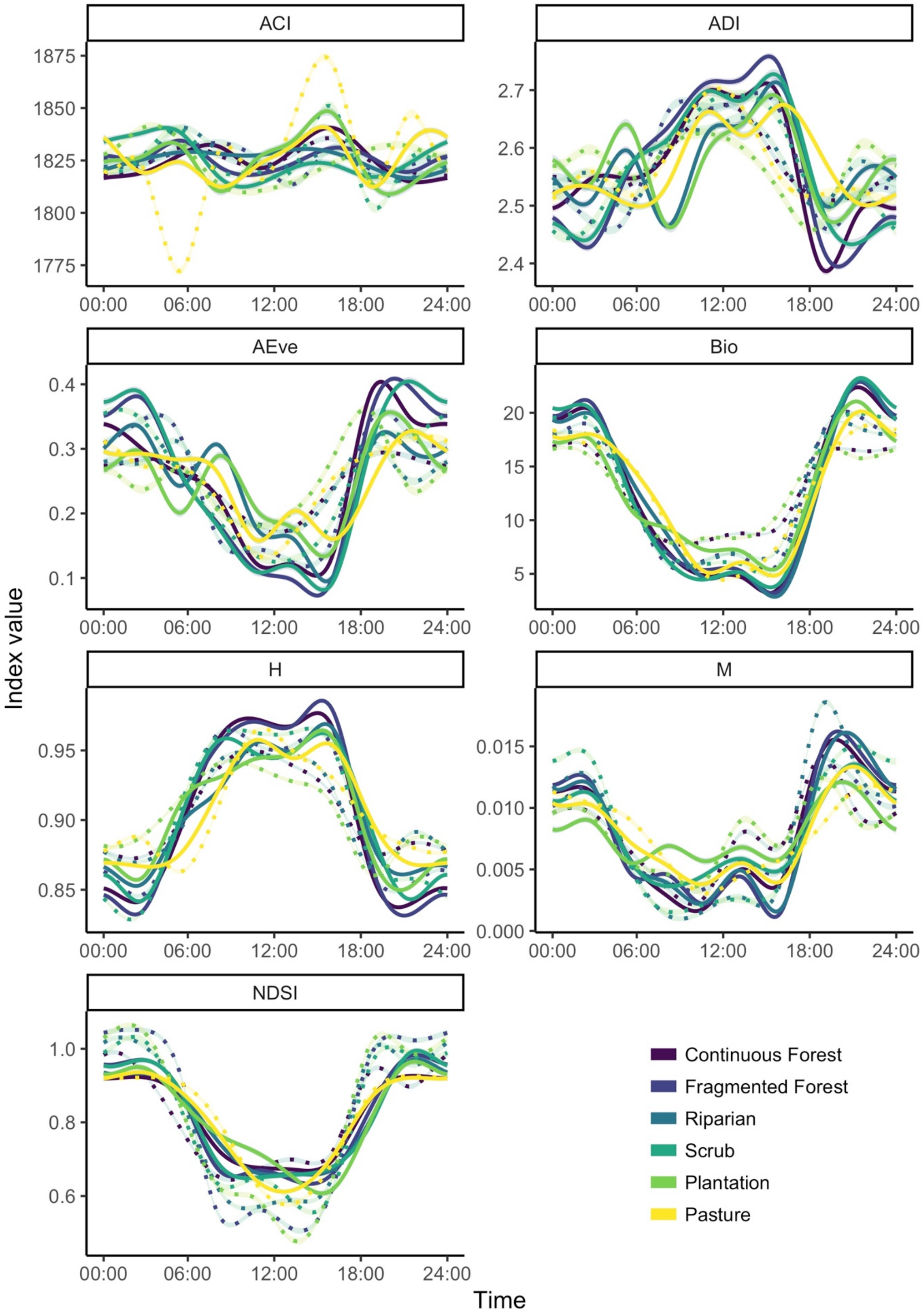


Figure 3.5 - Diel patterns in mean acoustic indices, with predicted values and standard errors from GAM output for each habitat. Solid line shows dry season values, dashed line wet season. Values calculated for each 10-minute recording window over 24 hours, from 154 recording sets.

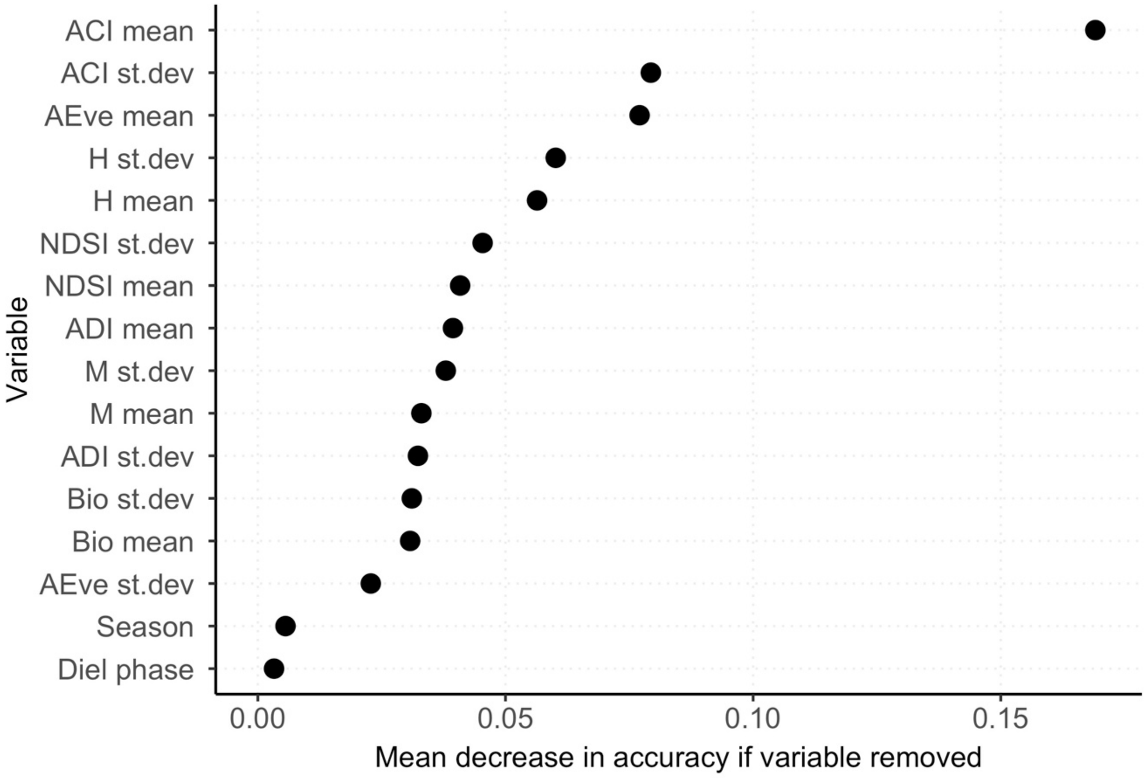


Figure 3.6 - Variables ranked by importance for classifying habitat type in a random forest model, showing proportional decline in predictive accuracy if a predictor is removed. Random forest constructed with the hourly mean and standard deviation values of seven acoustic indices, season (wet or dry), and diel phase (day or night). Internally estimated error rate was 20.8%, while testing with an independent dataset showed the classifier to be 84.7% accurate.

3.5 Discussion

3.5.1 Minimum quantity of recordings and recording schedules

We found a consistent pattern in variance reduction across all indices, habitats and seasons. Index variability was reduced to a mean of 10.9% of its maximum after 120 recording hours. We selected this cut-off as a balance between deployment length and capturing the majority of site variability. Beyond 120 hours variance decreased so slowly with increasing sampling duration that it was not worth the increased input of time and resources. Convergence of indices values was a product of the total amount of recordings used rather than the length of the deployment or recording schedule. Thereafter continued variability was likely due to inherent soundscape features of the site rather than insufficient length of recording.

Previous acoustic studies have used a median of 24 hours (range 0.1 – 1436 hours) of recordings per site in terrestrial systems (see supporting information); at which point variance in index standard error will still be high. Our analysis suggests that studies using <120 recording hours may not have fully described the soundscapes, limiting the power of their conclusions. Similar analyses with recordings from other terrestrial landscapes would be required to determine if this rate of variance reduction is typical. Tropical soundscapes are often more complex than those of temperate systems, therefore convergence might be achieved more rapidly in simpler environments. However, all habitats in this study shared common convergence patterns despite considerable variation in vegetation structure and faunal communities, so the time required for other locations may prove similar.

To our knowledge there is only one other study of temporal sampling, which advocated a one-minute-in-5 schedule as retaining the majority of information found in continuous recordings (Pieretti et al 2015). Our results from simulated datasets suggest that sparser sampling schedules (even 1-in-5) delays capture of inherent soundscape variability; and that continuous recordings are more effective for reliably capturing a soundscape. Sparse sampling schedules also require longer deployment times, so that site patterns might be complicated by seasonal shifts. Where monitoring seeks to describe patterns over longer temporal scales, it might be difficult to distinguish between short-term stochasticity and longer-term variability such as seasonal changes.

3.5.2 Indices for characterising temporal and spatial patterns in soundscapes

We found clear diel, seasonal and habitat-specific patterns among the soundscapes. Diel patterns were particularly pronounced, with all soundscapes showing a consistent distinction between day and night. Such findings are intuitive; almost every habitat in the world has discreet diurnal and nocturnal faunal assemblages. The diel division is evidenced by the common trends shown in most of the indices, regardless of habitat type, and reinforced by the clear division along axis 2 of the NMDS and the significant effect in the PERMANOVA.

Diel patterns in the soundscape were particularly marked with the AEve, Bio, H and NDSI indices. Overall, the indices imply that nocturnal soundscapes were more uneven; with fewer occupied frequency bands (ADI, AEve), a greater disparity between loudest and quietest bands (Bio, H) and lower levels of anthrophony (NDSI). This is consistent with insect and anuran communities dominating a limited range of frequencies (Villanueva-Rivera et al. 2011). Conversely, diurnal soundscapes were typically more even. Greater levels of anthrophony and more variable biophony lead to an increase in the number of occupied frequency bands (ADI, AEve, NDSI), and with a more even amplitude (Bio, H). The only index without a clear diel pattern was ACI, perhaps because it effectively filters out consistent sounds such as insect choruses that are likely to underlie the diel differences in the other indices.

The division of soundscapes into distinct diel phases has been widely reported. Equivalent patterns in NDSI values have been found previously, presumably because there is generally more anthrophony during daylight hours (Fuller et al. 2015). However, for some indices, specific patterns appear strongly dependent on region. Studies of Australian woodland sites report a diel split with the reverse of our results; high ADI and H values at night, and high Bio during the day (Fuller et al. 2015; Gage et al. 2017). This would be consistent with insects in nocturnal soundscapes in Australia occupying a broader range of frequency bands than in Panama. Trends in ACI are also inconsistent: either no clear pattern (this study; Fuller et al. 2015), or marked diel differences arising from nocturnal insect biophony (Pieretti et al. 2015). Villanueva-Rivera et al. (2011) showed that most of their temperate sites had distinct diel patterns in ADI, with strong peaks corresponding to dawn and dusk choruses, a pattern not evident in our recordings. These patterns may reflect genuine differences among soundscapes but, as noted earlier, such contradictory results may arise from the variable amounts of recordings analysed in these studies (Table 3.S7).

Soundscapes differed between seasons, with different diel patterns. Seasonal variation might be driven by changes in vegetation structure, or follow behavioural shifts in faunal communities, such as the onset of territorial birdsong (Buxton et al. 2016; Rankin & Axel 2017). In our recordings the most important seasonal influence was the frequency of storms, which had a notable impact on wet season soundscapes. Wet season diel variation was weaker in Bio and H index values, but stronger in NDSI, suggesting a smaller disparity between loudest and quietest frequency bands. Furthermore, the diel switch in ADI, AEve , Bio and H indices values was more gradual in the wet season, implying a less abrupt transition to nocturnal dominance of a reduced range of frequencies. Storm geophony likely underpinned this reduced diel shift, as storm events are less temporally restricted than biophony.

While temporal influences drove overall patterns, the RF implied consistent finer-scale differences among habitat soundscapes. Mean ACI and standard deviation were the most important variables for distinguishing among habitats, matching previous findings of habitat-specific patterns in ACI values (Fuller et al 2015; Pieretti et al 2015). The influence of geophony on ACI values likely permitted effective discrimination between open habitats (scrub and pasture), and habitats with trees. The low vegetation characteristic of pasture and scrub make these habitats exposed to wind and the associated sound. Conversely, rainstorms in forested habitats have a much greater influence on the soundscape, as water continues to drip from vegetation long after the rain has ceased.

We did not include urban sites in this study, and distinct patterns in acoustic indices have been found in urban habitats (Fairbrass et al. 2017; Joo et al. 2011). It would be interesting to ascertain how an acoustically rich anthrophony is reflected in acoustic indices values and whether urban sites might exhibit the same patterns in variance reduction and the effects of temporal subsampling reported here. Although our seven indices describe a range of soundscape features they are only a fraction of those available; other less commonly used indices may well contain additional important information. Further testing would be required to determine whether variance reduction in other acoustic indices follows similar patterns to those we report for the seven in this study.

3.5.3 Recommendations for acoustic monitoring

Recent reviews have highlighted the critical need for standardised protocols in ecoacoustic data collection and processing (Gibb et al 2018; Priyadarshani et al. 2018). We provide the following workflow to guide future ecoacoustic studies;

1. *Collect 120 hours of audio recordings per site*. This balances deployment length and capture of soundscape variability, although the time required to improve precision might vary in other biomes or ecosystems. Repeated short deployments during distinct seasons may be as suitable as a single long deployment.

2. *Avoid temporal sub-sampling*. Recording on a schedule only delays the capture of soundscape variability; sparse sampling schedules will require longer deployment times.

3. *Use multiple indices to describe soundscape patterns*. No single acoustic index can describe the entire soundscape; capturing inter-habitat differences requires multiple indices, as there are often competing explanations for a particular index value. For example, low Bio values could indicate either an impoverished soundscape with little noise or an acoustically rich environment; if the soundscape also has low H and high AEve values it would support the latter interpretation. The seven indices used in this study will not necessarily suit all situations and systems, and identifying the most appropriate indices to use will depend on study aims. Using a suite of indices will offer complimentary impressions of different aspects of the soundscape. Selection should be based on a solid understanding of the soundscape patterns underlying index values, and hence the ecological patterns they may reflect.

4. *Use mean values and standard deviations rather than raw values*. This draws out patterns that might otherwise be obscured by short-term variability. The magnitude of variability provides additional information, and in many cases standard deviations of indices were more important than mean values for distinguishing among the habitats.

5. *Consider more than just a single portion of the day*. Diel patterns are important for extracting differences between habitat types. Dry season values for Bio and NDSI were near uniform among habitats between 12:00 and 17:00, but differed widely outside these hours. Conversely, the greatest variation in ACI and AEve values was during afternoon.

Traditional approaches to biodiversity assessment are time-consuming, expensive and often limited to a small geographic area. Automated recording and analysis of soundscapes can be conducted at far greater spatial and temporal scales, potentially at lower costs. Soundscape analysis has been used as a tool for rapid biodiversity assessment; acoustic indices have been linked with measures of bird species richness, compositional shifts in bird communities, and songbird phenology (Buxton et al. 2016; Fuller et al. 2015; Lellouch et al. 2014; Towsey et al. 2014b). Increased forest disturbance has been associated with lower acoustic diversity in Tanzania (Sueur et al. 2008b), and lower acoustic saturation in Papua New Guinea (Burivalova et al. 2018). Yet it is unclear whether such results are representative of more general relationships between soundscapes and habitat integrity (Burivalova et al. 2019a; Gibb et al. 2018; Merchant et al. 2015). There are inconsistent patterns in the literature, which have led some to question the efficacy of acoustic indices for biodiversity monitoring (Browning et al. 2017; Eldridge et al. 2016; Servick 2014). We argue that variations in collection and processing methodologies probably underlie some of these uncertainties. Further research is needed to elucidate the complementarity of standard biodiversity monitoring methods and ecoacoustics, but a key aspect of integrating these approaches will be consistency in both data collection and analysis.

3.6 Acknowledgements

We thank two anonymous reviewers for their helpful and constructive comments. Our thanks to the Smithsonian Tropical Research Institute, the Autoridad de Canal de Panama, and all of the private landowners who granted permission to deploy recorders on their land. We thank the Autoridad Nacional del Ambiente for providing research permits to work in the Republic of Panama (permits SE/A-134-16 and SE/A-67-18). Robbie Whytock and James Christie offered helpful advice and support regarding the Solo audio recorders. Scott Jackson provided invaluable IT resources and support during indices calculations. TBL was funded by the Natural Environment Research Council UK, and the IAPETUS Doctoral Training Partnership.

3.7 Supplementary Information

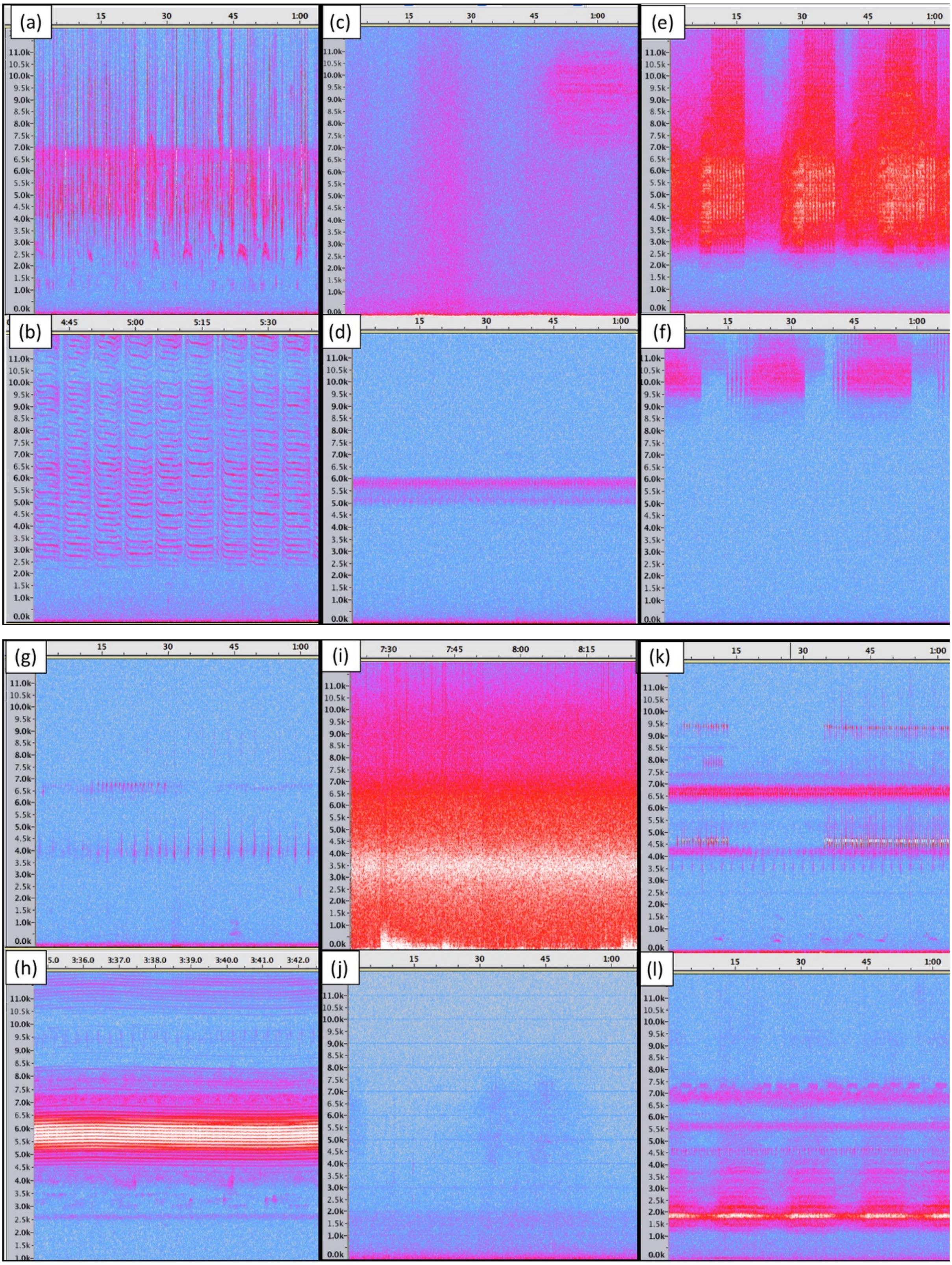
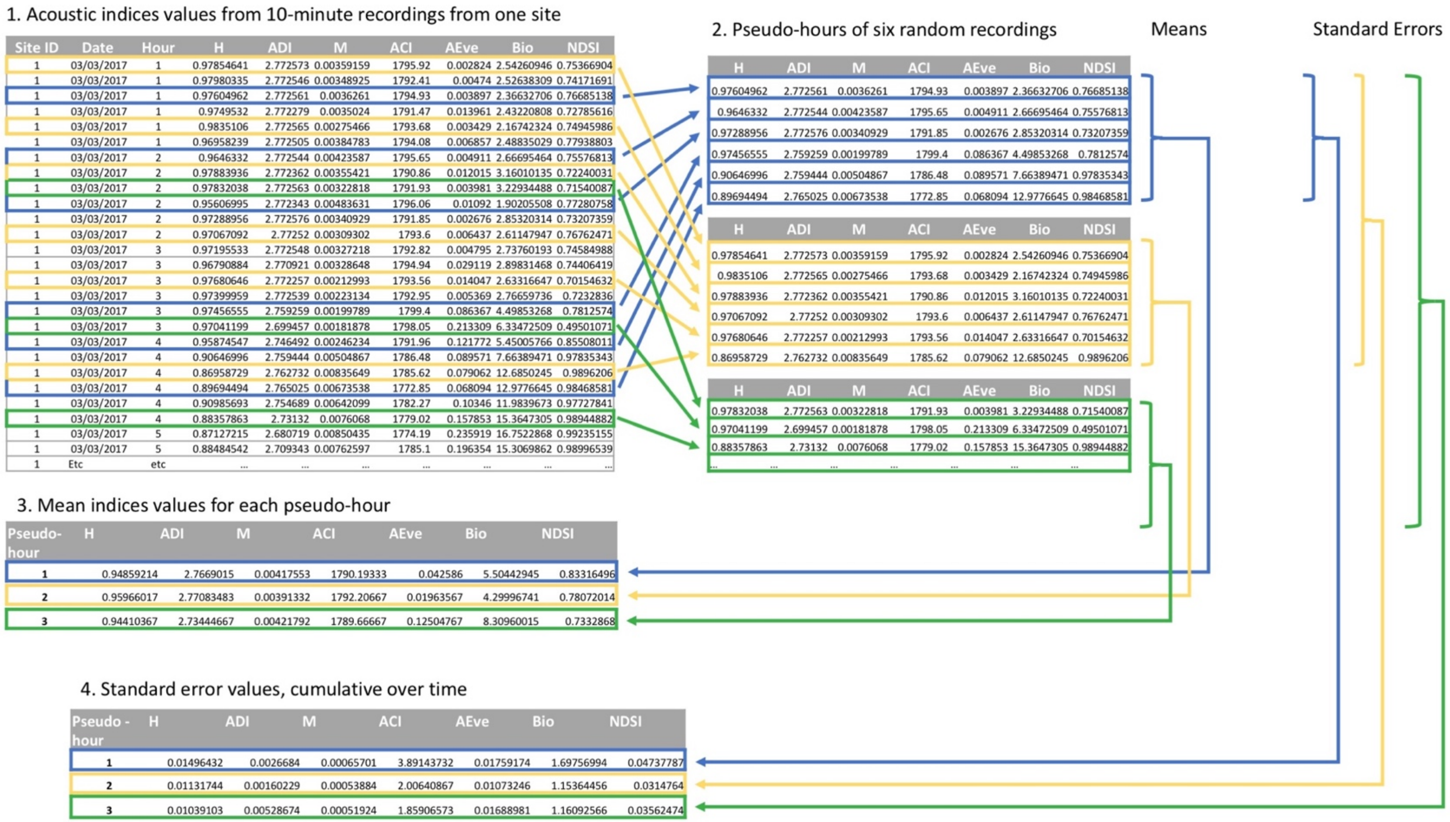


Figure 3.S1 - Example spectrograms showing the different features reflected by the acoustic indices, with time on the x-axis, and frequency on the y-axis. Full descriptions of the indices

are in Table 3.S2. ACI; (a) high value from a mixed species bird flock characterised by rapid temporal changes, (b) low value from persistent cicada noise. ADI; (c) high value caused by wind, (d) low value from a recording dominated by insect noise in a single frequency band. AEve patterns are the reverse of ADI, (c) is low value, and (d) is high. Bio; (e) high value from loud insect chorus filling the 2 – 11 kHz range, and (f) low value with little noise in that range. H; (g) high value where several species of birds and insects are calling and but acoustic energy is low and evenly distributed between frequency bands, and (h) low value when energy is focussed in a single band from an insect. M; (i) high value during a rainstorm, and (j) low value during a recording with little acoustic energy. NDSI; (k) high when energy is mostly in the 2 - 11 kHz range, and (l) low value when the 1 – 2 kHz frequency band dominates.



1. Acoustic indices values from 10-minute recordings from one site

Site ID	Date	Hour	H	ADI	M	ACI	AEve	Bio	NDSI
1	03/03/2017	1	0.97854641	2.772573	0.00359159	1795.92	0.002824	2.54260946	0.75366904
1	03/03/2017	1	0.97980335	2.772546	0.00348925	1792.41	0.00474	2.52638309	0.74171691
1	03/03/2017	1	0.97604962	2.772561	0.0036261	1794.93	0.003897	2.36632706	0.76685138
1	03/03/2017	1	0.9749532	2.772279	0.0035024	1791.47	0.013961	2.43220808	0.72785616
1	03/03/2017	1	0.9835106	2.772565	0.00275466	1793.68	0.003429	2.16742324	0.74945986
1	03/03/2017	1	0.96958239	2.772505	0.00384783	1794.08	0.006857	2.48835029	0.77938803
1	03/03/2017	2	0.9646332	2.772544	0.00423587	1795.65	0.004911	2.66695464	0.75576813
1	03/03/2017	2	0.97883936	2.772362	0.00355421	1790.86	0.012015	3.16010135	0.72240031
1	03/03/2017	2	0.97832038	2.772563	0.00322818	1791.93	0.003981	3.22934488	0.71540087
1	03/03/2017	2	0.95606995	2.772343	0.00483631	1796.06	0.01092	1.90205508	0.77280758
1	03/03/2017	2	0.97288956	2.772576	0.00340929	1791.85	0.002676	2.85320314	0.73207359
1	03/03/2017	2	0.97067092	2.77252	0.00309302	1793.6	0.006437	2.61147947	0.76762471
1	03/03/2017	3	0.97195533	2.772548	0.00327218	1792.82	0.004795	2.73760193	0.74584988
1	03/03/2017	3	0.96790884	2.770921	0.00328648	1794.94	0.029119	2.89831468	0.74406419
1	03/03/2017	3	0.97680646	2.772257	0.00212993	1793.56	0.014047	2.63316647	0.70154632
1	03/03/2017	3	0.97399959	2.772539	0.00223134	1792.95	0.005369	2.76659736	0.7232836
1	03/03/2017	3	0.97456555	2.759259	0.00199789	1799.4	0.086367	4.49853268	0.7812574
1	03/03/2017	3	0.97041199	2.699457	0.00181878	1798.05	0.213309	6.33472509	0.49501071
1	03/03/2017	4	0.95874547	2.746492	0.00246234	1791.96	0.121772	5.45005766	0.85508011
1	03/03/2017	4	0.90646996	2.759444	0.00504867	1786.48	0.089571	7.66389471	0.97835343
1	03/03/2017	4	0.86958729	2.762732	0.00835649	1785.62	0.079062	12.6850245	0.9896206
1	03/03/2017	4	0.89694494	2.765025	0.00673538	1772.85	0.068094	12.9776645	0.98468581
1	03/03/2017	4	0.90985693	2.754689	0.00642099	1782.27	0.10346	11.9839673	0.97727841
1	03/03/2017	4	0.88357863	2.73132	0.0076068	1779.02	0.157853	15.3647305	0.98944882
1	03/03/2017	5	0.87127215	2.680719	0.00850435	1774.19	0.235919	16.7522868	0.99235155
1	03/03/2017	5	0.88484542	2.709343	0.00762597	1785.1	0.196354	15.3069862	0.98996539
1	Etc	etc	...	...	...	...	...	...	...

2. Pseudo-hours of six random recordings

H	ADI	M	ACI	AEve	Bio	NDSI
0.97604962	2.772561	0.0036261	1794.93	0.003897	2.36632706	0.76685138
0.9646332	2.772544	0.00423587	1795.65	0.004911	2.66695464	0.75576813
0.97288956	2.772576	0.00340929	1791.85	0.002676	2.85320314	0.73207359
0.97456555	2.759259	0.00199789	1799.4	0.086367	4.49853268	0.7812574
0.90646996	2.759444	0.00504867	1786.48	0.089571	7.66389471	0.97835343
0.89694494	2.765025	0.00673538	1772.85	0.068094	12.9776645	0.98468581

H	ADI	M	ACI	AEve	Bio	NDSI
0.97854641	2.772573	0.00359159	1795.92	0.002824	2.54260946	0.75366904
0.9835106	2.772565	0.00275466	1793.68	0.003429	2.16742324	0.74945986
0.97883936	2.772362	0.00355421	1790.86	0.012015	3.16010135	0.72240031
0.97067092	2.77252	0.00309302	1793.6	0.006437	2.61147947	0.76762471
0.97680646	2.772257	0.00212993	1793.56	0.014047	2.63316647	0.70154632
0.86958729	2.762732	0.00835649	1785.62	0.079062	12.6850245	0.9896206

H	ADI	M	ACI	AEve	Bio	NDSI
0.97832038	2.772563	0.00322818	1791.93	0.003981	3.22934488	0.71540087
0.97041199	2.699457	0.00181878	1798.05	0.213309	6.33472509	0.49501071
0.88357863	2.73132	0.0076068	1779.02	0.157853	15.3647305	0.98944882
...	...	...	...	...	...	...

3. Mean indices values for each pseudo-hour

Pseudo-hour	H	ADI	M	ACI	AEve	Bio	NDSI
1	0.94859214	2.7669015	0.00417553	1790.19333	0.042586	5.50442945	0.83316496
2	0.95966017	2.77083483	0.00391332	1792.20667	0.01963567	4.29996741	0.78072014
3	0.94410367	2.73444667	0.00421792	1789.66667	0.12504767	8.30960015	0.7332868

4. Standard error values, cumulative over time

Pseudo - hour	H	ADI	M	ACI	AEve	Bio	NDSI
1	0.01496432	0.0026684	0.00065701	3.89143732	0.01759174	1.69756994	0.04737787
2	0.01131744	0.00160229	0.00053884	2.00640867	0.01073246	1.15364456	0.0314764
3	0.01039103	0.00528674	0.00051924	1.85906573	0.01688981	1.16092566	0.03562474

Figure 3.S2 - Demonstration of the calculations for the pseudo-hour means and standard errors used in determining the minimum quantity of recordings required to capture the soundscape of a site. Each 10-minute recording from a site (1) was randomly assigned to a group of six to form a "pseudo-hour" (2). Mean value was determined from the six recordings within each pseudo-hour (3), but standard errors were cumulative over time, i.e. error was estimated using all pseudo-hours up to and including the latest to simulate successively longer deployments

(4). Thus in the example shown here, the standard errors for the first pseudo-hour were calculated with the first six recordings, for the second pseudo-hour with the first 12 recordings, for the third pseudo-hour with first 18 recordings, and so on.

Table 3.S1 - Summary of the habitat types used in this study and their characteristic features.

Habitat and number of sites	Description
Continuous forest 24 sites	An area of lowland tropical moist forest bordering the Panama Canal, the forest extends to approximately 15,000 ha (above the threshold considered continuous in earlier studies: Cordeiro & Howe 2003; Lees & Peres 2006). This forest is structurally complex, with many large trees and a canopy height ranging from 25 – 35 m. For further details of forests in the region see Pyke et al. (2001). There are a few small areas of old-growth forest, but most of the habitat is considered to be mature secondary forest (~ 150 years old; Pyke et al. 2001; Robinson et al. 2004). There is ongoing, low-level disturbance in the form of poaching and occasional small scale-fires (Robinson et al. 2004; Wright et al. 2000). A quarry in the south, with associated infrastructure and vehicle traffic, is a considerable source of anthrophony in some of the soundscapes.
Fragmented forest 21 sites	Remnant fragments of forest now isolated in a non-forest matrix. These are more heavily disturbed areas; although canopy height can be the same as that of continuous forest, large trees have often been removed and there is a preponderance of vegetation typical of secondary forests (DeWalt et al. 2003). These sites experience poaching, timber extraction, and have a greater risk of fires than continuous forest (Robinson et al. 2004).
Riparian forest	The high rainfall in the region means that land managers are concerned about erosion, and so even in intensively managed land holdings, riparian vegetation is frequently retained (Chazdon et al. 2011). Riparian

23 sites	areas are generally narrow, often less than 50m wide. Given their linear nature, riparian forests have a very high edge-to-area ratio and as such experience a different climate to more compact forest fragments with a similar area. In addition to the disturbances present in forest fragments, riparian areas are also under pressure from incursions by livestock, and water extraction for livestock or irrigation (Harvey & Haber 1998).
Scrub 14 sites	Following land abandonment, natural vegetation recovers rapidly in this region's climate (Arroyo-Mora et al. 2005; Chazdon et al. 2011). This early successional habitat represents an important stage in the recovery from cleared land to secondary forest. For this study, a vegetation height of between 1 – 5m was used as the definition for scrub, which corresponds to less than a decade of vegetation regrowth (Guariguata & Ostertag 2001). However there are frequently isolated taller trees present in scrub as well, either left from the previous land use, or rapidly growing *Cercropia* sp. which have established since land abandonment.
Teak plantation 16 sites	Teak is a Asian tree species, widely planted for timber across the world. Sites are typified by a highly regular tree structure and canopy height of between 12 and 18 m. Understorey vegetation is often cleared on an annual basis to reduce competition with the timber crop (Wolfe et al. 2015b). These management practices lead to a simplified habitat structure and highly restricted flora. Teak is deciduous, thus there are strong seasonal differences in vegetation structure.
Pasture 19 sites	Cattle ranching is a widely practiced in the region, and large areas are given over to pasture. Boundaries are generally demarcated by live fences, whereby trees are closely planted and barbed wire strung between them to act as barriers (Chazdon et al. 2011). These can range from only a few metres in height up to full trees, and in consequence represent an important feature for much of the fauna in this habitat. Stocking densities tend to be

	low but any scrubby regrowth is cleared manually or by fire on a near-annual basis, so that the pasture is maintained as grass.
Other habitats	The six habitat types described above represent the main land uses in the region. Other habitats present but not considered in this study are urban areas, small-scale arable agriculture, and pineapple plantations.

Table 3.S2 - Summary of the acoustic indices used in this study, the general soundscape patterns they reflect, and examples from this study. For an introduction to the basic terms and concepts used in acoustic analysis see Villanueva-Rivera et al. (2011), and further descriptions of the indices see Eldridge et al. (2016). All the indices in this study were calculated using the R packages seewave (Sueur et al. 2008a) or soundecology (Villanueva-Rivera & Pijanowski 2018). Prior to analysis, recordings are processed with a Fourier transform to give the power of the signal.

Index and reference	R package and function	Soundscape patterns	Patterns in this study
Acoustic Complexity Index (ACI)	soundecology: “acoustic_complexity” *	Determines the difference in amplitude between one time sample and the next within a frequency band, relative to the total amplitude within that band. The concept underlying this index is that biophony is often of variable intensity, whilst that of anthrophony is	High values indicate storms, intermittent rain drops falling from vegetation, stridulating insects, or high levels of bird activity.

(Pieretti et al. 2011)		commonly constant. ACI was designed to quantify this inherent irregularity in biophony, particularly from bird song. The index is relatively impervious to persistent sound of a constant intensity. The original intention was to filter out airplane engine noise from temperate recordings (Pieretti et al. 2011). However, it is also likely to omit the constant insect noise characteristic of tropical habitats. In acoustically rich habitats, this might actually lead to low values in ACI, because intensity does not vary greatly over time even if the source of sound does. ACI value is cumulative and so will increase with the length of recording; to ensure comparability best practice is to report the value per minute*.	Lowest values came from recordings with consistent cicada noise that fills the whole spectrogram.
Acoustic Diversity Index (ADI)	soundecology: "acoustic_diversity"	ADI will increase with greater evenness across frequency bands. An even signal will give a high value (could be noisy across frequency bands or completely silent) and a pure tone (i.e. all energy in one frequency band) will be closer to 0.	Highest values were from recordings with either high levels of geophony and anthrophony (wind, helicopter and truck engines) which blanketed the spectrogram with noise, or from very

(Villanueva-Rivera et al. 2011)		The maximum ADI value is the log of the number of frequency bins used, so here ranges from 0 to +2.77.	quiet recordings with little variation among frequency bands. Lowest values reflect dominance by a narrow frequency band, usually by insect noise at night.
Acoustic Evenness (AEve – sometimes referred to as AE or AEI, but we prefer AEve to distinguish from H/AEI) (Villanueva-Rivera et al. 2011)	soundecology: “acoustic_evenness”	Returns values in a range of 0 to 1. Higher values indicating greater unevenness among frequency bands, i.e. most of the sound intensity appears in a restricted range of frequencies. Acoustically rich habitats may produce low AEve values because the soundscape is saturated, meaning that intensity does not vary greatly between the frequency bands.	Converse of the patterns in ADI. High values identify recordings with dominance by a narrow frequency band of insect noise. Low values are associated with windy recordings when many frequency bands are occupied, or near silent recordings with no activity.

Bioacoustic Index (Bio) (Boelman et al. 2007)	soundecology: “bioacoustic_index”	This index restricts recordings to between 2 – 11 kHz, the range in which the majority of birds sing. The value is a function of both sound level (dB) and the number of frequency bands used. However the value is relative to the quietest frequency band. Therefore, recordings with even activity throughout the 2 – 11 kHz range (e.g. during rain storms) may produce low Bio values, while higher values indicate greater disparity between loudest and quietest frequency bands.	The very highest values are produced by recordings with blanket cicada noises, with high amplitude and minimal variation among frequency bands. Low values arise when there is no sound between 2 and 11 kHz, although there is sometimes insect biophony outside these bounds.
Acoustic entropy (Total entropy of the time wave) (H) (Also known as AEI – Acoustic Entropy Index)	seewave: “H”	Related to the classic Shannon’s Index, were a number of categories each have a relative proportion associated with them. Here the categories are either frequency bands (Hf) or time samples (Ht), and the relative amplitude is the “proportion” in each category. Hf and Ht are multiplied to give the index, returns a value between 0 and 1. H increases with greater evenness of amplitude among frequency bands, (or with an increasing number of bands). An even signal will be closer to 1 (could be noisy across frequency bands or completely silent) and a pure	Highest values came from near-silent recordings, with no wind, and only faint bird calls. Lowest values came from recordings where insect noise dominated a single frequency band.

(Sueur et al. 2008a)		tone (i.e. all energy in one frequency band) will be closer to 0.	
Median of the amplitude envelope (M) (Depraetere et al. 2012)	seewave: “M”	Louder recordings will give higher values, and so reflect noisier soundscapes.	Highest values associated with high levels of geophony, particularly storms. Low levels of M were associated with very quiet recordings, with few faunal vocalisations or geophony.
Normalised Difference Soundscape Index (NDSI) (Kasten et al. 2012)	soundecology: “ndsi” **	Designed to estimate the level of anthropogenic disturbance in the soundscape. This index gives the ratio between anthrophony and biophony. This relies on the theoretical frequency split between the two facets of the soundscape. In some habitats, anthrophony is restricted to the 1 – 2 kHz range, while most biophony appears in the 2 – 8 kHz range. However, NDSI is sensitive to low frequency biophony. NDSI values range from -1 to +1, with +1 indicating no anthrophony in the soundscape.	High value recordings reflect high levels of insect biophony, with minimal noise in the 1 – 2 kHz range. Low values arise when insect biophony dominates the 1 – 2 kHz band.

		Following (Fuller et al. 2015), the upper biophony range was extended from 8 kHz to 11 kHz, to incorporate higher frequency sounds typical of tropical habitats (Sueur et al. 2014).	

* ACI can also be calculated using the *seewave* package (function "ACI"). However, the two packages produce different values and outputs can only be made to agree by altering the default parameters (Villaneuva-Rivera 2015). ACI value is cumulative and so will increase with the length of recording. Villanueva-Rivera & Pijanowski (2018) recommend reporting the ACI value per minute to provide readily comparable values between recording sets, and it is more straightforward to calculate a value per minute with output from the *soundecology* version of this index. Thus our preference is for the *soundecology* approach.

** NDSI can be calculated using the *seewave* function "NDSI". Outputs are not identical from the *seewave* and *soundecology* packages, probably because of the way in which the amplitude values are calculated. Moreover, "NDSI" (*seewave*) may have incorrectly implemented the original formulation as it uses 2000 – 8999 Hz instead of 2 – 8 kHz. In addition, when analysing stereo recordings, *seewave* only returns a single averaged value across channels rather than a separate value for each channel as in *soundecology*. In both "ndsi" and "NDSI" the amplitude values for biophony are summed across all 1 kHz frequency bands, whereas in Kasten et al. (2012) the index is described as using the largest 1kHz biophony band. Summing the biophony bands reduces apparent differences among recordings, so that only those with particularly dominant anthrophony have low NDSI values.

Chapter 4. Rapid assessment of avian species richness and abundance using acoustic indices

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TBL, NB, SW and DD conceived the study; TBL and NG collected the data; TBL and NB designed the analysis; TBL led the writing of the text. All authors contributed critically to draft versions prior to submission. Two anonymous reviewers commented on an earlier draft version during the revision process.

4.1 Abstract

Accelerating global shifts in climate and land use change are altering natural habitats and species assemblages, making management interventions crucial to halt the biodiversity crisis. Management decisions must be informed by accurate biodiversity assessments. However, such assessments are often time consuming, expensive, and require specialist knowledge. Monitoring environmental sound may offer a novel method for rapid biodiversity assessment. Changes in species assemblages at a given location are reflected in the site's acoustic energy, termed the soundscape. Soundscapes can be readily described using acoustic indices; metrics based on objective features such as pitch and amplitude. Changes in acoustic indices values may therefore reflect changes in species assemblages, alerting land managers to shifts in wildlife populations. However, thus far, evidence supporting the use of acoustic indices in biodiversity monitoring has been equivocal. Here, we test the practical application of acoustic indices for biodiversity monitoring while solving methodological issues and providing conceptual clarity.

Using 84 hours of audio recordings covering 315 dawns from 43 sites, coupled with bird assemblage and vegetation data collected in the field, we demonstrate strong relationships between acoustic indices and avian species richness and abundance. In contrast with many previous studies, we found that sites with high bird species-richness and abundance had less even soundscapes (i.e. acoustic energy was less evenly distributed among frequencies) compared with sites with low species richness and abundance. Crucially, these patterns were coherent across multiple acoustic indices, and across habitat types, emphasising their utility for monitoring. Acoustic indices sensitive to the frequencies at which birds sing are most useful for monitoring avian communities; the Acoustic Evenness Index, Biophony Index, and the biophony component of the Normalised Difference Soundscape Index exhibited the strongest relationship with species richness. Land managers can use acoustic indices for biodiversity monitoring, complementing other, more established, assessment methods.

4.2 Introduction

Biodiversity assessment is an increasingly urgent task in the face of global environmental change (Pereria et al 2013). Ecoacoustics, the study of environmental sound, may offer a more rapid and economical means of terrestrial biodiversity appraisal than traditional approaches (Burivalova et al. 2019a). Cheap, open-source audio recorders that can be deployed in the field for weeks or months at a time have made it relatively straightforward to collect tens of thousands of hours of sound recordings (Sueur & Farina 2015; Bradfer-Lawrence et al. 2019). Acoustic indices can be calculated from audio recordings, rather than manually categorising species composition, which is prohibitively time-consuming (Pijanowski et al. 2011). Acoustic indices are derived from features of the recordings such as amplitude and frequency, with individual indices typically describing different characteristics of the soundscape (Sueur et al. 2014). The soundscape is comprised of the acoustic energy at a given location and has three components: biophony, sounds produced by animals; anthrophony, sounds produced by humans or machinery; and geophony, sounds from natural processes such as wind or rain (Pijanowski et al 2011).

Any changes to a habitat and its fauna are likely to be mirrored in the local soundscape (Krause & Farina 2016; Burivalova et al. 2018; Gómez et al. 2018; Bradfer-Lawrence et al. 2019; Furumo & Aide 2019). In turn, these will be echoed in changing acoustic indices values reflecting differences in biophony and geophony. If acoustic indices values change in consistent and predictable ways as a response to shifting vegetation structure and species assemblages, indices could be used as proxies for tracking such alterations and hence represent an economical means of monitoring biodiversity change across both space and time at large scales (Bradfer-Lawrence et al. 2019; Laiolo 2010; Ribeiro et al. 2017).

To illustrate how acoustic patterns can reflect biodiversity, Figure 4.1 shows three sonograms of tropical dawn recordings with contrasting soundscapes. Patterns in acoustic energy vary in two ways: among frequencies and over time. One recording was collected in regenerating scrub habitat with low avian species richness (Figure 4.1a). There are few calling birds and low acoustic energy, and hence minimal variation across frequencies or time. In contrast, Figure 4.1b shows a recording from a large area of forest with a more complex vegetation structure and high avian species richness, features that are echoed in a highly uneven soundscape typified by rapid temporal irregularity and variation in acoustic energy among frequencies. Here, the dawn chorus contains numerous individuals of many species vocalising simultaneously between 1 and 10 kHz, but with few sounds outside this range. Figure 4.1c shows a recording collected during a rainstorm, a soundscape with high levels of acoustic energy and high temporal variation, but with the same minimal variation among frequency bands found in the scrub recording. Acoustic indices will reflect these differences, with a distinct combination of values for each soundscape, and values for the forest recording (Figure 4.1b) indicating a soundscape with an uneven distribution of energy among frequency bands compared to the other two recordings.

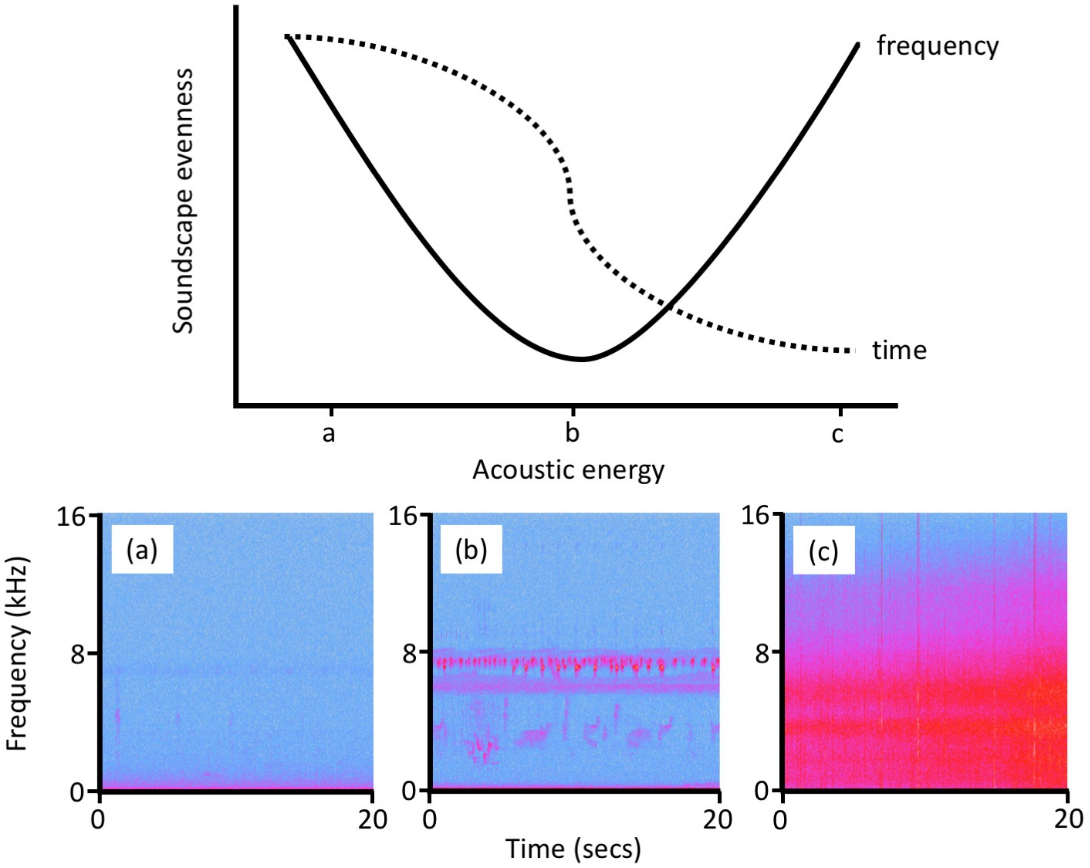


Figure 4.1 - Soundscape changes with increasing acoustic energy. At top, a hypothetical graph showing changes in soundscape evenness for frequency (solid line) and time (dotted line), and below, example sonograms from three recordings collected in central Panama in March 2017 at around 06:30 am. Panel (a) shows a sonogram from a scrub recording, with only two bird calls and low levels of insect noise. There are low levels of acoustic energy and the soundscape is very even, with little temporal or frequency variation. Panel (b) shows a sonogram from a forest recording, bird calls dominate frequencies between 1 and 6 kHz, and insects between 6 and 8 kHz. Above 9 kHz there are few sounds, so that acoustic energy is unevenly distributed among frequency bands, reflecting the complex faunal communities present in this habitat. Panel (c) shows a sonogram from a rainstorm, there are high levels of acoustic energy and high temporal variation in the soundscape but little differentiation among frequency bands. Thus soundscapes with low or high amounts of acoustic energy (points a and c) may be different temporally, but generally have low variation among frequencies. At intermediate levels of energy (point b), there is considerable temporal and frequency variation in the sonogram, so that the soundscape is uneven. Each recording will

have a unique combination of indices values, reflecting soundscape variation. Excerpts of these and other example recordings are available in the supplementary information.

Realising the potential of acoustic indices for monitoring biodiversity change relies on significant and coherent relationships between acoustic indices and widely used biodiversity metrics such as species richness. However, there are currently disagreements as to the strength and direction of such relationships. For example, the Acoustic Complexity Index (ACI) has been correlated positively with both avian species richness (Hilje et al. 2017) and peaks in avian vocalisations (Farina et al. 2011; Pieretti et al. 2011; Fuller et al. 2015; Gage et al. 2017). In contrast, other studies have found no relationship between ACI and avian species richness (Fuller et al. 2015; Buxton et al. 2016, 2018a, 2018b). Similarly, while a strong positive correlation between the Biophony index (Bio) and avian abundance has been found by some (Boelman et al. 2007; Fuller et al. 2015), others report the reverse (Gage et al. 2017). Some of these disagreements may have arisen from a failure to consider the influence of vegetation. Vegetation might influence acoustic indices values directly, by affecting sound transmission (Darras et al. 2016), or indirectly by shaping the animal populations present in an area (Burivalova et al. 2018). Vegetation effects on the soundscape can be strong; simplified vegetation structure is associated with lower soundscape saturation and lower Bio values indicating greater evenness among frequencies (Rankin & Axel 2017; Burivalova et al. 2019b, 2018).

The inconsistent patterns between species metrics and acoustic indices raise questions regarding the efficacy of indices for biodiversity assessment (Servick 2014; Merchant et al. 2015; Eldridge et al. 2016; Browning et al. 2017; Gibb et al. 2018). This is likely limiting uptake of these new technologies by land managers. We suggest there are several conceptual and methodological issues that underlie the reported inconsistencies, and these may be obscuring relationships between soundscapes, landscapes and biodiversity. Key amongst these limitations is the use of acoustic indices without a solid *a priori* understanding of the likely relationships between indices values and biodiversity. Apparent relationships have been reported because they were statistically significant, without the trends necessarily making ecological sense or inter-index patterns being complimentary. For example, some studies suggest that greater avian species richness is associated with higher evenness among frequencies (Fuller et al. 2015; Mammides et al. 2017), but this is unlikely unless all frequencies are occupied equally (Figure 4.1, and Eldridge et al 2018).

Conceptual weaknesses have been compounded by inconsistent or inappropriate methodologies. For example, while the bird assemblage contributes to the overall soundscape, there is likely to be considerable short-term variation. Calls are irregular within and among bird species, and affected by the animal's distance from the microphone, by habitat structure, and by other sources of biophony and geophony (Lellouch et al 2014). With so much soundscape variability a direct relationship between bird assemblages and acoustic indices is unlikely, hence attempts to link acoustic indices with concurrent avian counts have met with limited success (Lellouch et al. 2014; Mammides et al. 2017; Buxton et al. 2018b; Eldridge et al. 2018; Jorge et al. 2018; Zhao et al. 2019). Clearer trends might be apparent if acoustic indices were treated as site metrics more akin to net primary productivity. Furthermore, analysis techniques have frequently been limited to linear regressions or non-parametric statistics (Boelman et al. 2007; Tucker et al. 2014; Duarte et al. 2015; Mammides et al. 2017). Yet index values are often highly skewed, exhibiting non-normal error distributions, thus a more nuanced approach to analyses is probably required (Fairbrass et al 2017).

The principal question we address is: can acoustic indices be used as effective biodiversity monitoring tools, reflecting species richness and abundance? We hypothesise that greater avian species richness, avian abundance, and vegetation structural complexity will be reflected in acoustic indices values indicating greater soundscape complexity. We designed our study to avoid many of the issues that have limited earlier studies, treating indices as site characteristics and employing advanced analytical techniques. We consider a suite of well-established acoustic indices from week-long recordings collected from 43 sites with a range of vegetation types and varied avifaunas, and couple these recordings with over 126 hours of avian point count observations from the same sites.

4.3 Materials and Methods

This study was conducted in the Emparador landscape in the Republic of Panama. This human-modified landscape lies to the south and west of the Panama Canal, covering 700 km^2. Whilst there are still extensive tracts of forest, large areas have been converted to a matrix of cattle pasture and teak plantation, with remnant forest fragments and riparian forest. The climate is strongly seasonal, with very low rainfall between mid-December and mid-April, while the wet season generally peaks in October and November (Windsor 1990).

4.3.1 Data collection and preparation

Data were collected in 2017 from 43 sites representing the six main habitats present in the Emparador landscape; continuous forest, fragmented forest, riparian forest, teak plantations, regenerating scrub and cattle pasture (Figure 4.2). Sites were of uniform habitat, a minimum of 1 hectare in size, and at least 500 m from sites in other habitats and 1000 m from sites of the same habitat. Habitats followed a hypothesised gradient of decreasing structural complexity from continuous forest to cattle pasture.

4.3.2 Audio recordings

Audio recordings were collected using open-source “Solo” recorders with omnidirectional microphones (Whytock & Christie 2017). We opted for a sampling rate of 32,000 Hz as a balance between capturing the majority of human-audible sound and the memory capacity of the recorders (Bradfer-Lawrence et al 2019). Collection was limited to the dry season (early February to early May), when bird song makes a relatively greater contribution to the soundscape. Recorders were deployed for approximately one week at each site (range 6 – 11 days), deployment length was determined by how long the recorder battery retained power. This gave a total of 315 deployment days, from which we extracted data for the minute of sunrise and the following 15 minutes for each morning (sunrise times from timeanddate.com). This corresponded to the period with the greatest level of birdsong, and gave a total of 5040 minutes of analysis (between 96 and 176 minutes of recording per site). We did not screen recordings for high levels of geophony (wind and rain). Pre-processing was limited to a 500 Hz low-stop filter to reduce microphone self-noise. This filter likely removed some genuine environmental sound, but the self-noise represented a potential source of bias in the indices that needed to be controlled for (see supplementary information and Figure S1).

For each minute of recording we calculated the following acoustic indices; Acoustic Complexity Index (ACI), Acoustic Diversity Index (ADI), Acoustic Evenness Index (AEve), Bioacoustic Index (Bio), Acoustic Entropy Index (H), Amplitude (M), Normalised Difference Soundscape Index (NDSI), and the latter’s two constituents reflecting anthrophony and biophony (given the potential for diverging patterns in the two elements of NDSI, they were considered separately). Details of index calculation and the general patterns they reflect can be found in Table 4.S1. Over 60 acoustic indices have been proposed (Buxton et al 2018a), but we focussed on these nine indices because they are the most commonly used in the acoustic indices literature, and they capture a range of soundscape characteristics. All indices were calculated in R, using the packages ‘seewave’ (ver 2.1.0; Sueur et al. 2008a) and ‘soundecology’ (ver 1.3.3; Villanueva-Rivera & Pijanowski 2018). The default values of each R function were used, with the exception of NDSI which was modified to match the original formulation of Kasten et al (2012). In the original form, this index contrasts the power spectral density of the 1 kHz anthrophony bin (i.e. 1 – 2 kHz), against the power spectral density of the *largest* 1 kHz biophony bin (i.e. in the range 2 – 11 kHz). However, both the ‘seewave::NDSI’ and ‘soundecology::ndsi’ functions use an alternative method where the all biophony bins are summed prior to the contrast with the anthrophony. This tends to obscure differences among recordings, for a full discussion see supplementary information and Figure 4.S2).

4.3.3 Bird Assemblages

Bird assemblages at each site were assessed in the field using 10-min, unlimited radius point counts (Bibby et al. 2000). We conducted four visits to each of the 43 sites, giving a total of 172 counts. Counts were undertaken between 30 minutes after morning nautical twilight and 4 hours post-dawn. Revisits to sites were a minimum of 12 days apart. All counts were undertaken by TBL and NG. Double counting of individuals during surveys was highly unlikely given the minimum distance between sites. We recorded all birds seen or heard with the exception of vultures, hirundines and swifts; these three taxa are predominantly aerial in behaviour, so their presence may not reflect usage of the habitat being surveyed. We did not modify our counts based on detectability; hence, our data reflect relative site features rather than absolute measures of bird abundance (Anderson 2009). For each site we calculated mean bird species richness and mean number of individuals detected based upon sightings and vocalisations. We used the latter as our proxy for avian abundance. These two metrics were used as predictors in the modelling (see below).

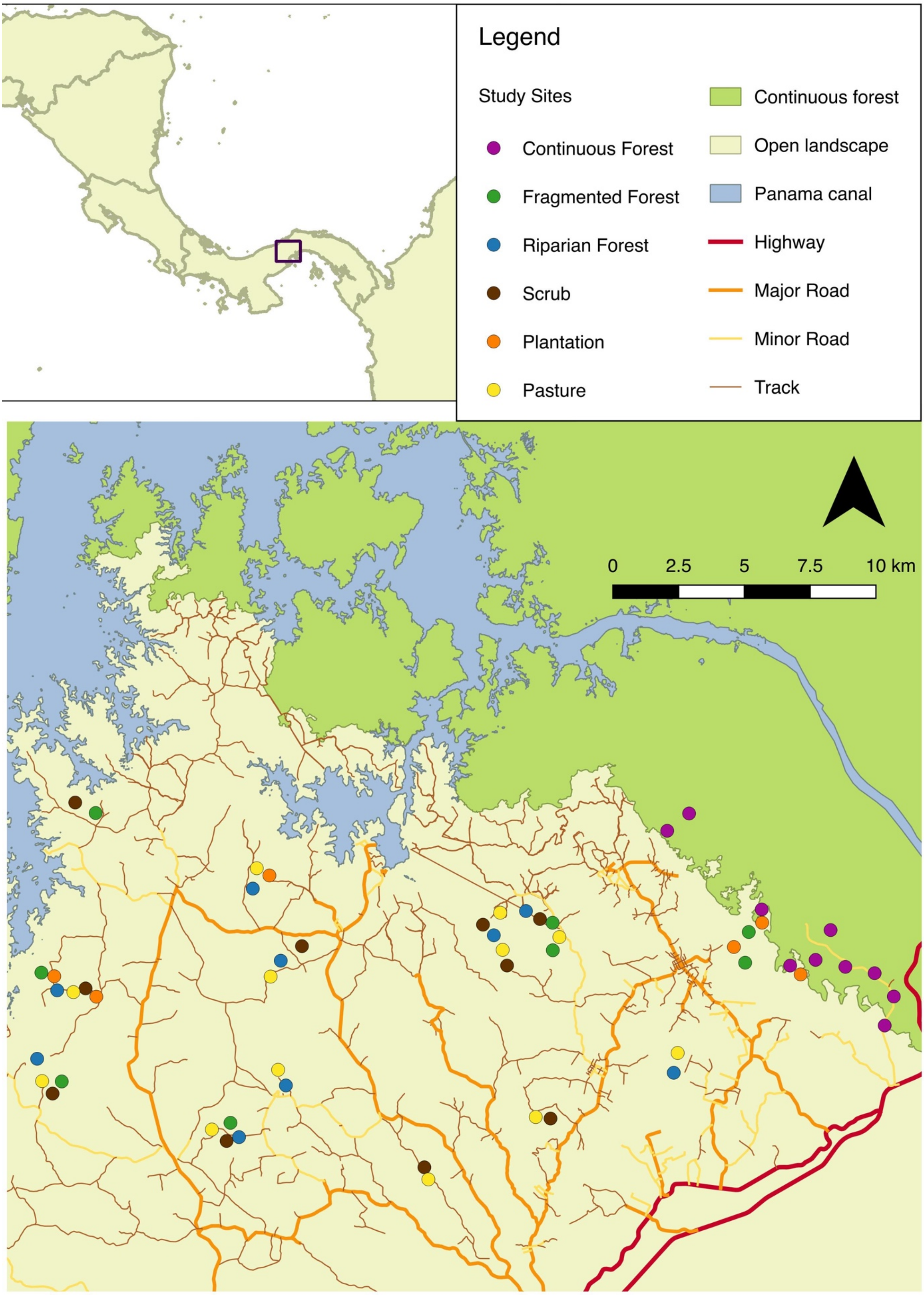


Figure 4.2 - Map of 43 study sites in the Emparador landscape, central Republic of Panama, showing the six habitat types.

4.3.4 Vegetation data

Woody vegetation at each site was assessed with a 20 m x 20 m plot. We recorded: canopy height at nine points, number of stems over 1.3 m tall, and Diameter at Breast Height (DBH) of stems over 1.3 m tall and 5 cm DBH. From these we determined: mean canopy height, ratio of stems over 1.3 m to stems over 5 cm DBH, mean DBH, and basal area. These four values were combined using Principal Components Analysis (PCA) with the package 'vegan' (ver 2.5.2; Oksanen et al. 2018), and the first two axes were used as metrics of vegetation structure in the modelling (Farina & Pieretti 2014).

4.3.5 Modelling

Acoustic indices values cover widely different numeric ranges, and are frequently skewed. To permit comparison among indices, values were scaled by dividing by the maximum value of each index to give relative proportions. The NDSI is on a scale of -1 to +1, so not amenable to this approach, therefore we used (NDSI+1)/2 (Fairbrass et al. 2017). Normalised values were used as the response variable in a generalised mixed model framework with a beta distribution, conducted using the 'glmmTMB' package (ver 0.2.3; Brooks et al. 2017). The beta distribution is continuous between 0 and 1, but has no prior expectations related to the distribution within that range so can cope with asymmetric and heteroskedastic data (Ferrari & Cribari-Neto 2004). Model predictors were mean bird species richness or mean abundance per site, and the first two PCA axes reflecting vegetation structure. To account for potential autocorrelation, models included random effects for site, and day of deployment. The two avian metrics of species richness and abundance were co-linear so could not be included in a single model. Thus, we built two separate sets of models using either species richness or abundance, and then compared them using AIC to determine which was preferred (Burnham & Anderson 2002).

4.4 Results

4.4.1 Bird and vegetation surveys

During point count surveys we detected a total of 4017 individual birds from 188 species. Mean bird species richness per site was 16.2 (range 5.5 - 25), and mean abundance per site was 23.4 (range 7.2 - 39.5). Vegetation structure differed among sites; forest habitats had taller canopies and greater basal area than scrub and pasture habitats (Figure 4.S3). Axis

1 of the vegetation structure PCA accounted for 60.6% of the inter-site variance and reflected vegetation complexity; higher scores were associated with greater canopy height, basal area and mean DBH. Axis 2 accounted for 24.9% of the variance, and higher scores reflected a greater stem ratio; this was particularly marked in the plantation sites where intensive management reduces size variation among stems, with almost all stems part of the mature timber crop.

4.4.2 Soundscape, species richness and detections

Higher mean avian species richness and abundance from point count surveys were strongly associated with significantly higher values of ACI, AEve, Bio, NDSI and NDSI-Bio, and with significantly lower values of H and NDSI-Anthro (Figures 4.3 and 4.S4, Tables 4.S3 and 4.S4). Higher species richness was also significantly associated with lower ADI values, and higher abundance with greater values of M. AIC selection showed the mean species richness model was preferred for Bio, H, M, and the NDSI indices (Table 4.S5). For ACI, ADI and AEve there was no preference between mean species richness and mean abundance models, with delta AIC values of less than two.

Higher vegetation complexity scores on the first PCA axis were significantly associated with lower ACI values when added to both the species richness and abundance models, and with lower NDSI and higher NDSI-Anthro in the species richness model only (Tables 4.S3 and 4.S4). Axis 2 from the PCA, driven by changes in stem ratio, had a positive association with ACI in the species richness model.

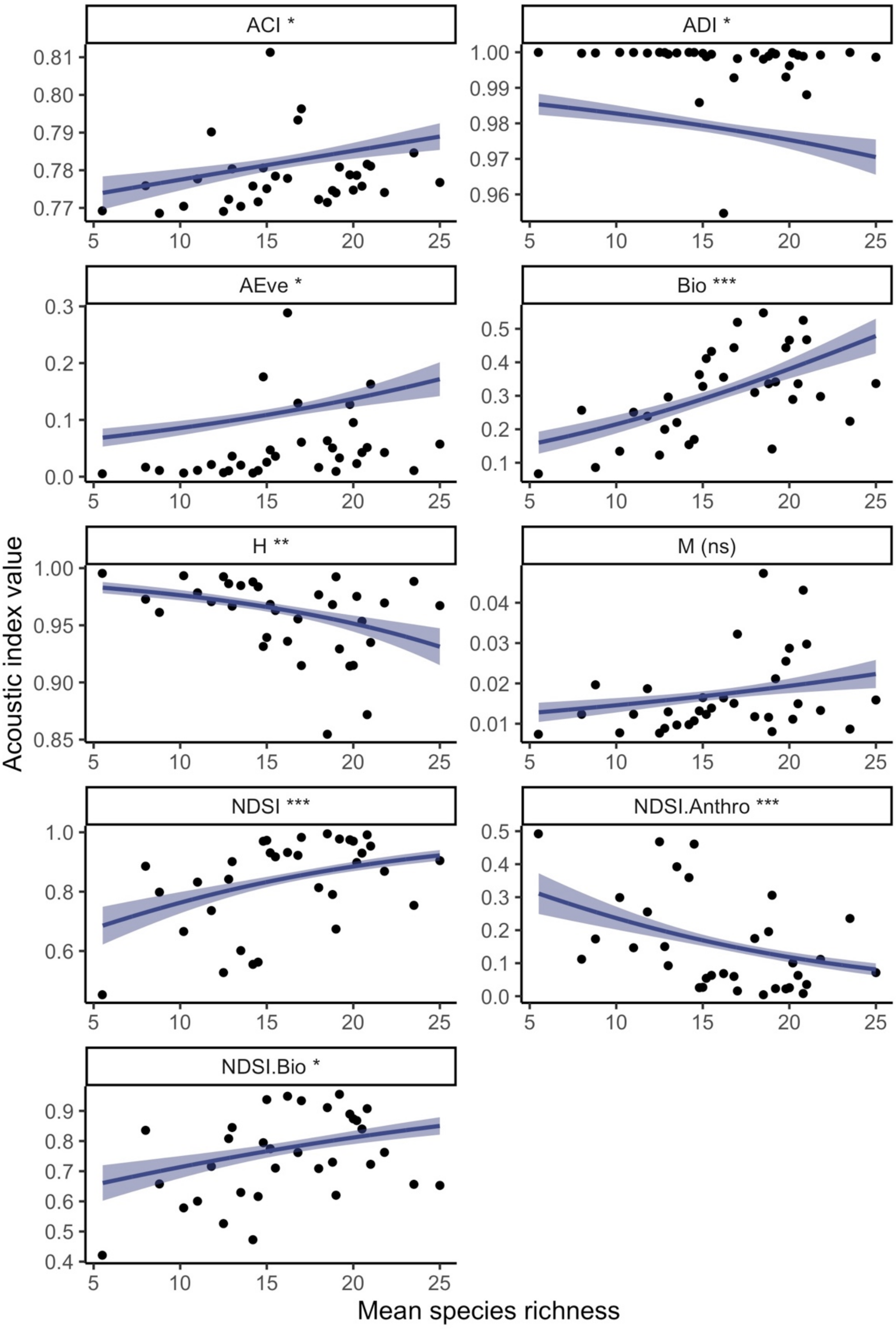


Figure 4.3 - Effect of mean avian species richness on normalised acoustic indices values, with median raw data as points, and predicted values and standard errors from generalised linear mixed models. Note raw data are highly skewed, and hence median points do not lie close to the predicted model fits for ADI and AEve; the long tail of the distributions are key

*to patterns in these indices. Asterisks indicate significance level: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.*

4.5 Discussion

4.5.1 Relationships between biodiversity metrics and acoustic indices

Higher avian species richness and abundance were associated with higher values of ACI, AEve, Bio, NDSI and NDSI-Bio, and lower values of H, and NDSI-Anthro. Despite the correlation between richness and abundance, our models suggested that, overall, acoustic indices were more strongly related to species richness. In line with our hypotheses, sites with higher avian species richness and greater abundance have soundscapes with acoustic energy unevenly distributed among frequency bands. These patterns are evidenced by low ADI values and high Bio and NDSI-Bio values, which all indicate uneven distribution of acoustic energy among frequencies (Table S2). This is consistent with a greater number of birds emitting more calls that span a wider range of frequencies with greater temporal variation (Figure 4.1b). Species-poor sites had impoverished soundscapes, with acoustic energy distributed more evenly across frequency bands (Figure 4.1a). Critically, these patterns were coherent across the different indices, and across sites and habitats, emphasising the potential of acoustic indices for monitoring.

Some existing studies concur with our findings. A recent comparison of temperate and tropical recordings found correlations between species richness and the same indices we considered, emphasising that soundscape evenness declines with greater richness (Eldridge et al. 2018). Similarly, Moreno-Gomez et al (2019) report associations between avian species richness and ADI and AEve. Although the direction of these correlations matches our findings, both studies report only weak relationships in their tropical recordings, perhaps because their sparse recording schedules used there were insufficient data to demonstrate clear patterns (Bradfer-Lawrence et al. 2019). A strong positive association between the Bio index and bird abundance was found in Hawaii (Boelman et al. 2007), and in Papua New Guinea, less disturbed sites had soundscapes with greater acoustic saturation, due to either higher species richness or greater faunal abundance (Burivalova et al. 2018).

Our findings contrast with studies that suggest greater avian species richness, better “ecological condition” and lower disturbance are all associated with more even soundscapes (Sueur et al 2008b; Fuller et al 2015; Mammides et al 2017). We argue that methodological limitations may be responsible for variable findings in previous research, as they are counterintuitive given the soundscape patterns that underlie particular index values (Figure 1). Habitats with rich faunal communities are likely to produce many different sounds at varied frequencies and timing intervals, leading to uneven soundscapes (Figure 4.1b). In contrast, species poor sites are, on average, likely to have fewer vocalisations, and hence the soundscape will be more even (Figure 4.1a).

Vegetation complexity significantly influenced ACI in both species richness and abundance models, and NDSI and NDSI-Anthro values in the species richness model only. Increasing vegetation complexity had the opposite effect to greater avian species richness and abundance on these indices values. The initially counter-intuitive relationship between ACI and vegetation complexity stems from the high ACI values in many of the pasture sites. High levels of tree cover (as remnant trees and living fences) in many Panamanian agricultural landscapes support a species-rich avifauna, and this is apparent in both the avian metrics and the acoustic indices. However, at the 20 m x 20 m vegetation plot scale, structural complexity is very low, leading to the apparent negative influence of vegetation complexity. The NDSI results may stem from more complex habitats having greater acoustic energy, irrespective of avian species richness or abundance. In more complex habitats there is likely to be more biophony from birds and other fauna in the 1 – 2 kHz range that determines NDSI-Anthro values (Eldridge et al 2018). In turn, higher NDSI-Anthro values will reduce the ratio with NDSI-Bio, and thus cause lower overall NDSI.

Previous work has demonstrated further links between vegetation structure and acoustic indices. For example, in Costa Rica, ACI was correlated with liana abundance (Hilje et al. 2017), and ADI with total vegetation complexity measured via LiDAR (Pekin et al. 2012). Higher levels of canopy cover have also been positively linked to Bio in Madagascar (Rankin & Axel 2017). We ascribe the relatively low importance of vegetation in our findings to temporal factors. For example, over a time scale of 24 hours, habitat type and vegetation structure are likely to define the potential range of acoustic indices (Bradfer-Lawrence et al. 2019). However, when restricted to a 15-minute dawn chorus, indices values during an individual minute are more likely driven by vocalising fauna. This supports the use of acoustic indices for biodiversity monitoring, suggesting that by targeted sampling during the period of the day when the focal taxon is most vocal, indices values will be determined by the faunal assemblage rather than just reflecting broader habitat structure.

4.5.2 Using acoustic indices for biodiversity monitoring

Audio recordings can be collected at much greater spatial and temporal scales than most field data, and acoustic indices provide ready means of analysing these data, offering managers an additional method for monitoring biodiversity. For example, ACI has been used to time the arrival of migrant song birds on their breeding grounds (Buxton et al. 2016). A large array of recorders across a region could be employed to track species arrival and relative abundance more readily than traditional survey methods, strengthening the evidence base for management decisions (Blumstein et al. 2011; Sugai et al. 2019). Similarly, the impacts of habitat fragmentation or restoration on animal species could be tracked across entire landscapes. Such a monitoring program could potentially highlight shifts in habitats and species at the landscape scale more rapidly than would be detected using field surveys, and so facilitate management interventions (Gibbs & Breisch 2001; Krause & Farina 2016; Wood et al. 2019).

There are several important factors land managers should consider when using acoustic indices to monitor biodiversity. Successful use of acoustic indices must be grounded in a thorough understanding of which soundscape characteristics are reflected in changing values. Some acoustic indices are sensitive to geophony and anthrophony, and managers should be aware of potential influences on values, the options for pre-processing recordings to minimise these influences, and the effects this processing might have on acoustic indices values. We demonstrated that greater avian species richness and abundance is associated with more uneven and complex soundscapes. Although we would expect similar soundscape patterns in other systems and with different taxa, land managers and conservationists would need to verify this anticipated link via ground-truth surveys (or manual checking of audio recordings) to establish faunal presence (Gibb et al 2018). With bird monitoring we recommend using mean avian metrics as site features rather than seeking to directly link acoustic indices values and bird surveys. High variability in calling rates and song types limits inference using the latter approach. Again, this pattern might apply with other taxa as well. If using formal statistical tests, we strongly encourage use of analysis techniques appropriate for skewed and bounded data.

Indices with the greatest range among sites were AEve, Bio and NDSI-Bio, suggesting these are potentially most sensitive to detecting spatio-temporal differences in faunal communities and so of greatest utility for monitoring. However, it is still valuable to include other indices that reflect different soundscape elements, as multiple indices offer insight into competing explanations. For example, high AEve values indicate a soundscape with energy unevenly distributed among frequency bands, which could reflect high levels of bird activity or complete dominance by insects such as cicadas. However, if ACI values are also high, this suggests rapid temporal variation lending support to the former interpretation (Pieretti et al. 2011; Bradfer-Lawrence et al. 2019). Some indices are also more robust to non-target noise; for example, ACI has been linked to biotic diversity even when there is substantial anthrophony (Duarte et al. 2015; Fairbrass et al. 2017).

New time- and cost-effective biodiversity monitoring methods are critically needed to provide evidence supporting robust policy decisions, habitat protection and conservation action (Eldridge et al 2018; Burivalova et al 2019a). Earlier failures to demonstrate consistent relationships between acoustic indices and other biodiversity metrics have meant practitioners are understandably reluctant to rely on these new monitoring tools (Browning et al 2017). Here we demonstrated that sites with higher avian species richness and abundance had consistently less even soundscapes, suggesting that acoustic indices can be used as effective conservation monitoring tools.

4.6 Acknowledgements

We thank: the Autoridad de Canal de Panama and the private landowners who granted permission to deploy recorders on their land; the Autoridad Nacional del Ambiente for providing research permits (SE/A-134-16 and SE/A-67-18); the Smithsonian Tropical Research Institute for logistical support; Robbie Whytock and James Christie for helpful support with the Solo audio recorders; Scott Jackson for invaluable IT resources during indices calculations; Jeroen Minderman for valuable suggestions regarding the analysis; two anonymous reviewers for helpful comments that improved an earlier version of the manuscript. TBL was funded by the Natural Environment Research Council UK, and the IAPETUS Doctoral Training Partnership (grant number 1672519).

4.7 Supplementary Information

Example audio recordings

Example audio recordings, illustrating different soundscape patterns are hosted in DataSTORRE, the University of Stirling's online data repository. They can be accessed at http://hdl.handle.net/11667/147.

4.S1 Influence of low-stop filter on acoustic indices values

Low-pass filters are sometimes used in ecoacoustics to reduce microphone self-noise. While using such a filter will remove genuine sources of environmental sound, self-noise may potentially bias indices values. Here we re-analysed the recordings following the same methods as described in the main text but without the low-pass filter. Figure 4.S1 shows predicted indices values depending on mean avian species richness, contrasting indices derived from recordings with and without the low-pass filter. Including the filter appears to have no effect on ACI and Bio indices values, and only a minimal effect on NDSI and its constituents, as sound below 500 Hz makes little contribution to indices values. Trends in ADI, AEve and H demonstrate that the filter reduces soundscape unevenness. Unfiltered recordings were more variable, and the standard errors suggest greater variation. This likely arises from recordings where microphone self-noise is the dominant sound, and the soundscape is otherwise very quiet and even. Models built with mean number of avian detections followed the same pattern (data not shown).

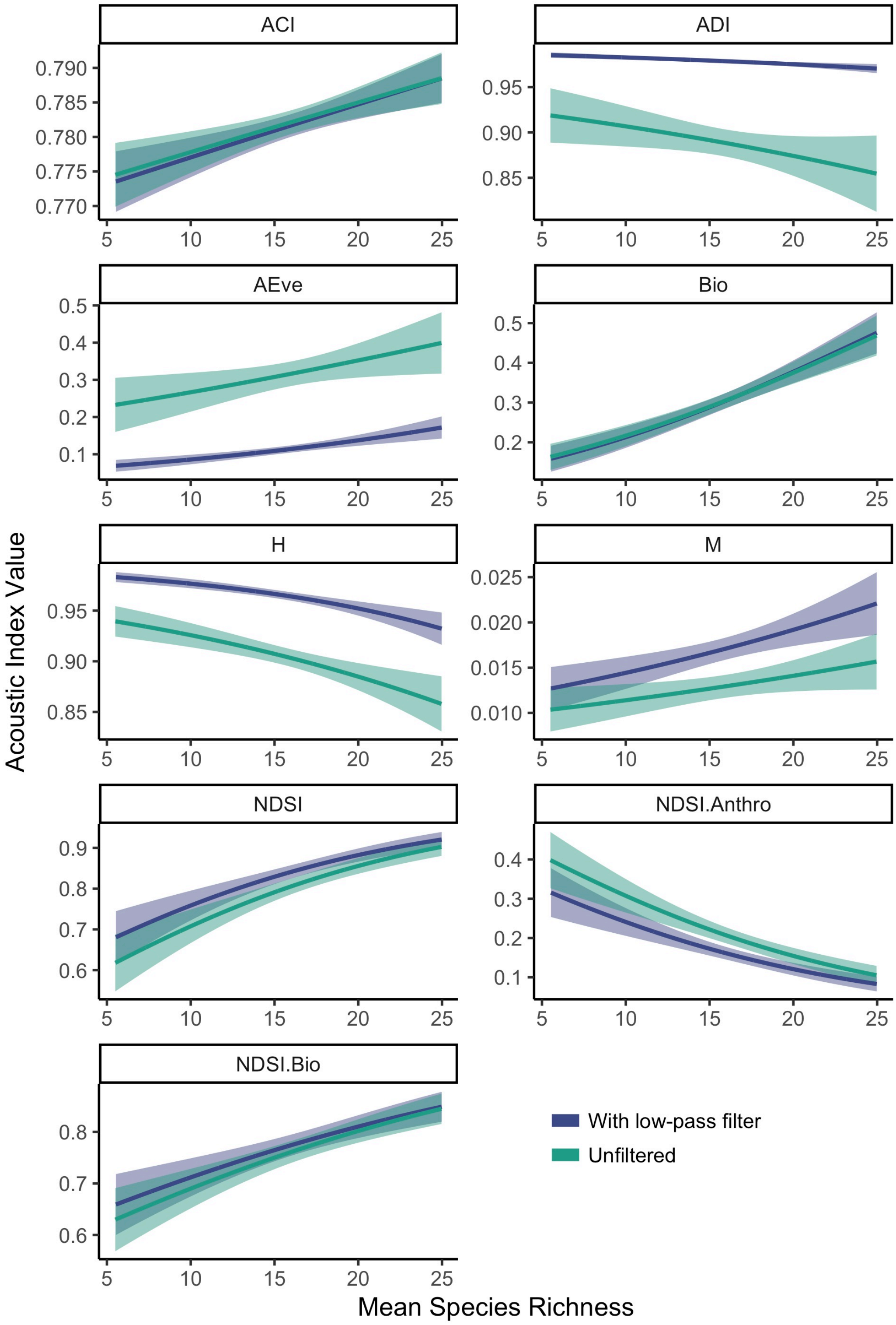


Figure 4.S1 - Effect of low-pass filter on acoustic indices values. Predicted values and standard errors from generalised linear mixed models for normalised acoustic indices values as a function of mean species richness.

4.S2 Acoustic indices table

Table 4.S1 - Summary of the acoustic indices used in this study, the soundscape patterns they reflect, and example recordings demonstrating these patterns. For a further discussion of these acoustic indices, see Eldridge et al. (2016). Example recordings can be accessed from DataSTORRE, the University of Stirling's online research data repository, available at http://hdl.handle.net/11667/147.

Index and reference	R package and function*	Details	Soundscape patterns and example recordings
Acoustic Complexity Index (ACI) Pieretti et al (2011)	soundecology: "acoustic_complexity" **	Designed to reflect the inherent irregularity in biophony, particularly from bird song. This index is relatively impervious to persistent sound of a constant intensity (e.g. machinery or insect choruses). Determines the difference in amplitude between one time sample and the next within a frequency band, relative to the total amplitude within that band.	High values indicate high levels of bird song with many short notes (Example recording 5). Lowest values are associated with minimal bird song and diffuse insect noise (Example recording 6).
Acoustic Diversity Index (ADI)	soundecology: "acoustic_diversity"	Divides recording into frequency bands. Applies the Shannon index to the relative proportion of signals above an amplitude	Highest values from very quiet recordings with little variation in energy among frequency bands (Example recording 1).

Villaneuva-Rivera et al (2011)		threshold within frequency band. Thus greater evenness across frequency bands will give a greater score.	Lowest values reflect uneven soundscapes, with distinct bird and insect biophony (Example recording 2).
Acoustic Evenness (AEve) Villaneuva-Rivera et al (2011)	soundecology: “acoustic_evenness”	As for ADI above, but applies the Gini index to the proportions. This increases with greater relative unevenness among frequency bands, i.e. when more of the sound intensity appears in a restricted range of frequencies.	Converse of the patterns in ADI. High values identify recordings with energy distributed unevenly among frequency bands (Example recording 2). Low values are associated with near silent recordings with only some wind noise, so that energy is even among frequency bands (Example recording 1).
Bioacoustic Index (Bio) Boelman et al (2007)	soundecology: “bioacoustic_index”	Designed to reflect bird biophony, recordings are divided into 1 kHz bands in the 2 – 11 kHz range. Value based on the amplitude of the signal relative to the quietest frequency band. The greater the disparity between bands the higher the values.	The very highest values are produced by recordings with high amplitude bird calls such as army ant following flocks (Example recording 4). Low values arise when there is no sound between 2 and 11 kHz (Example recording 1).
Acoustic entropy (H) Sueur et al (2008b)	seewave: “H”	Similar to ADI but with many more, narrower frequency bands. The Shannon index is applied to	Highest values produced by near-silent recordings, with no wind, and only faint bird calls (Example recording 1).

		two components, spectral and temporal, which are multiplied together to give the final value. Increases with greater evenness of amplitude among frequency bands and over time. An even signal gives a high value, which could be from either uniformly noisy or completely silent recordings. In practice, noisy evenness across the entire frequency range is unlikely.	Lowest values came from recordings with very loud bird calls (Example recording 5).
Median of the amplitude envelope (M) Depraetere et al (2012)	seewave: “M”	Louder recordings will give higher values, and so reflect noisier soundscapes.	Highest values associated with high levels of geophony, particularly storms (Example recording 3). Low levels of M were associated with very quiet recordings, with few faunal vocalisations or geophony (Example recording 1).
Normalised Difference Soundscape Index (NDSI)	Custom function based on soundecology: “ndsi” ***	Gives the ratio of the relative amplitudes between anthrophony (1 – 2 kHz) and biophony (2 – 11 kHz). NDSI values range from -1 to +1, with +1 indicating no	High values reflect high levels of biophony, with minimal noise in the 1 – 2 kHz range (Example recording 2). Low values arise when there is little biophony between 2

Kasten et al (2012)		anthrophony in the soundscape.	- 11 kHz (Example recording 1).

* Indices were calculated using the R packages seewave (ver 2.1.4; Sueur et al 2008) or soundecology (ver 1.3.3; Villanueva-Rivera & Pijanowski 2018).

** ACI can also be calculated using the *seewave* function “ACI”. However, the two packages produce different values and outputs can only be made to agree by altering the default parameters (Villaneuva-Rivera 2015).

*** NDSI can be calculated using the *seewave* function “NDSI” or the *soundecology* function “ndsi”, but again the two packages give different values. Both *seewave* and *soundecology* functions use an alternative formulation to the original proposed by Kasten et al (2012). Here we modified “ndsi” to match that of Kasten et al; see discussion in below.

4.S3 Effect of NDSI formulation

The Normalised Difference Sound Index (NDSI) was proposed by Kasten et al (2012), using the formulation (β - α) / (β + α), where α is the total estimated power spectral density for the 1 kHz anthrophony bin (i.e. 1 – 2 kHz), and β is the total estimated power spectral density for the *largest* 1 kHz biophony bin (i.e. in the range 2 – 11 kHz, our emphasis). However, in both the *seewave* and *soundecology* R packages, the NDSI functions sum all biophony bins together. Summing the biophony bins makes it impossible to assess the evenness among frequency bands, and consequently minimises differences between recordings. Consider the frequency spectra from two example recordings in Figure 4.S2, showing the distribution of acoustic energy in 1 kHz bands.

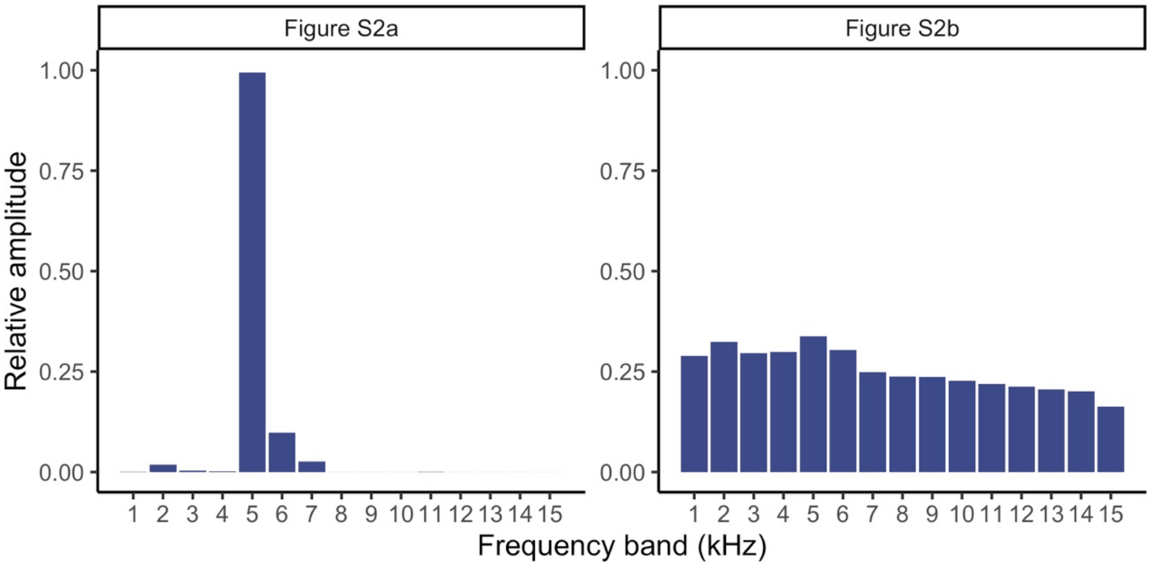


Figure 4.S2 - Comparison of frequency spectra from two recordings.

In Figure 4.S2a the soundscape is uneven with most energy in the 5 – 6 kHz band, so the effect of using the sum of all biophony bins or only the single largest biophony bin is minimal (NDSI with summed bins = 0.999, NDSI with single largest biophony bin = 0.998). In contrast, the acoustic energy in Figure 4.S2b is more evenly distributed among frequency bands. In this latter case, summing across all biophony bins gives a value that implies much greater difference between anthrophony and biophony than is actually the case (NDSI with summed bins = 0.792, NDSI with single largest biophony bin = 0.074). Given these patterns, we opted to follow Kasten et al's (2012) original formulation, using the single largest biophony bin in our NDSI calculations.

4.S4 Vegetation PCA

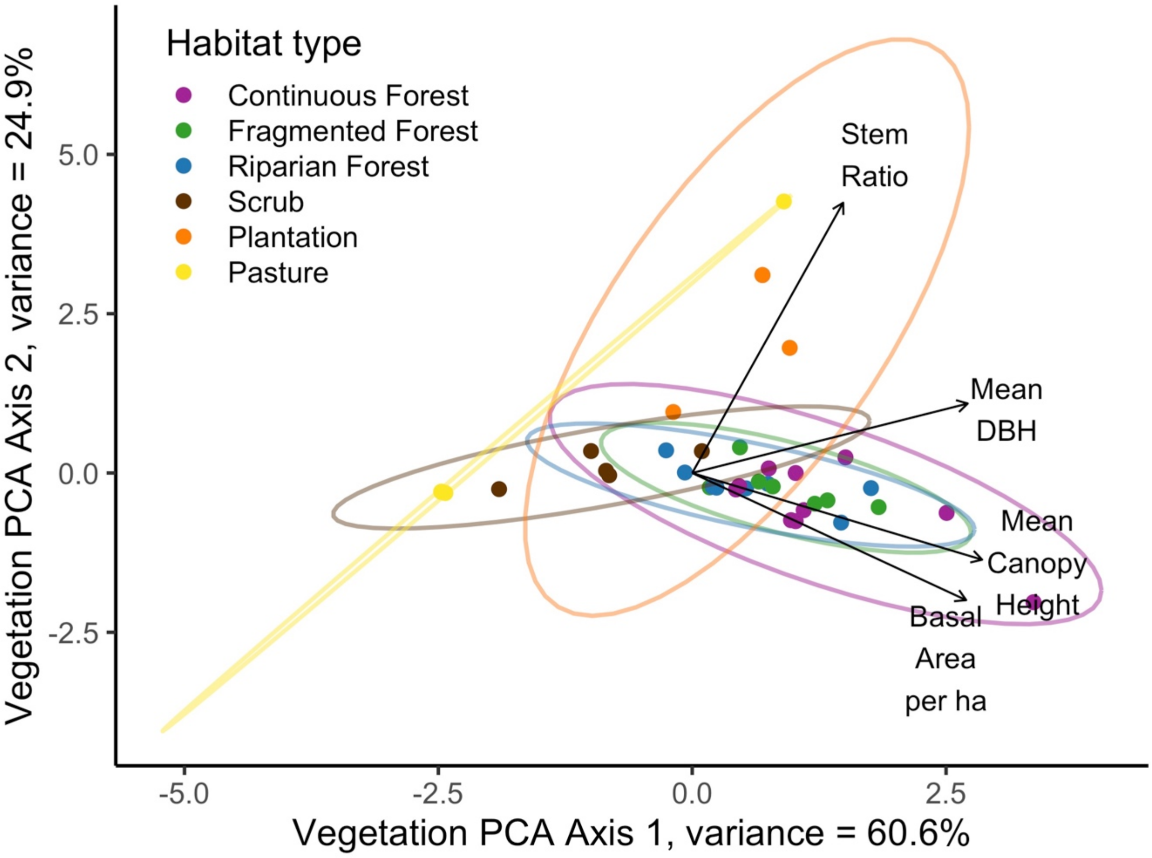


Figure 4.S3 - Principal Components Analysis of the vegetation metrics: mean DBH, mean canopy height, basal area per hectare, and the ratio of stems above and below 5cms DBH. Data from 20m x 20m plots at 43 sites covering six habitat types in a human-modified landscape, central Republic of Panama.

4.S5 Supplementary model outputs and model selection

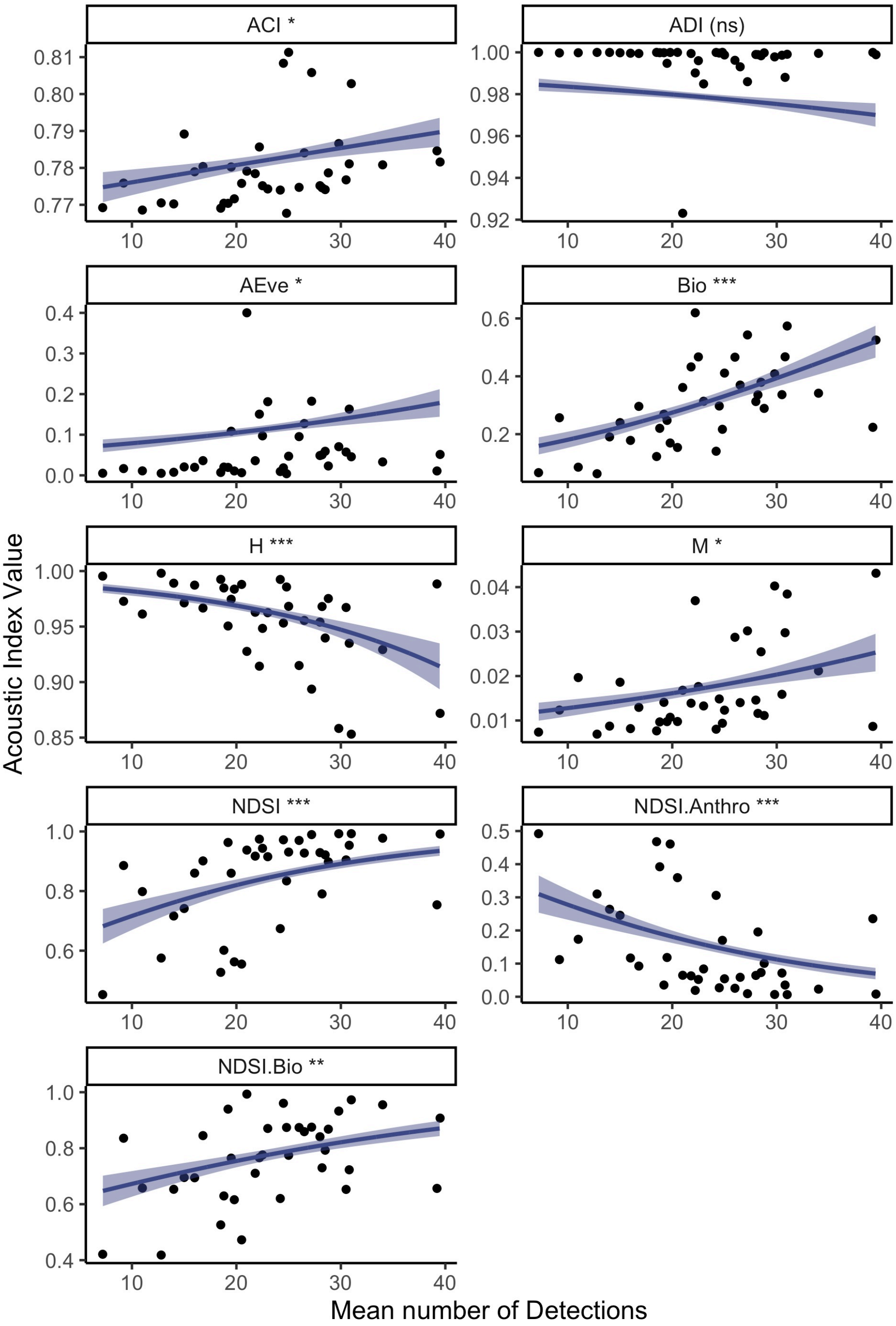


Figure 4.S4 - Effect of mean number of avian detections on normalised acoustic indices values, with median raw data as points, and predicted values and standard errors from generalised linear mixed models. Note raw data are highly skewed, and hence median points do not lie close to the predicted model fits for ADI and AEve; the long tail of the distributions

*are key to patterns in these indices. Asterisks indicate significance level: * p < 0.05, ** p < 0.01, *** p < 0.001.*

Table 4.S2 - Model outputs from generalised linear mixed models for effects of mean species richness and vegetation PCA axes on normalised acoustic indices values.

	Estimate	Std. Error	z value	p value
ACI				
Intercept	1.207	0.036	33.22	< 0.0001
Mean Species Richness	0.004	0.002	2.08	0.0378
Vegetation PCA axis 1	-0.016	0.006	-2.78	0.0054
Vegetation PCA axis 2	0.019	0.009	2.02	0.0434
ADI				
Intercept	4.411	0.296	14.901	< 0.0001
Mean Species Richness	-0.037	0.018	-2.092	0.0365
Vegetation PCA axis 1	-0.007	0.047	-0.158	0.8744
Vegetation PCA axis 2	0.073	0.076	0.962	0.3358
AEve				
Intercept	-2.898	0.359	-8.084	< 0.0001
Mean Species Richness	0.053	0.021	2.486	0.0129
Vegetation PCA axis 1	0.011	0.057	0.19	0.8495
Vegetation PCA axis 2	-0.085	0.092	-0.924	0.3555
Bio				
Intercept	-2.099	0.356	-5.9	< 0.0001
Mean Species Richness	0.081	0.021	3.803	0.0001
Vegetation PCA axis 1	-0.066	0.057	-1.168	0.2429
Vegetation PCA axis 2	-0.0010	0.092	-0.108	0.9144

H				
Intercept	4.454	0.426	10.444	< 0.0001
Mean Species Richness	-0.074	0.025	-2.937	0.0033
Vegetation PCA axis 1	0.083	0.068	1.232	0.218
Vegetation PCA axis 2	0.103	0.109	0.947	0.3438
M				
Intercept	-4.499	0.274	-16.403	< 0.0001
Mean Species Richness	0.029	0.016	1.775	0.076
Vegetation PCA axis 1	-0.065	0.044	-1.482	0.138
Vegetation PCA axis 2	-0.084	0.071	-1.192	0.233
NDSI				
Intercept	0.309	0.426	0.726	0.4680
Mean Species Richness	0.087	0.025	3.456	0.0005
Vegetation PCA axis 1	-0.146	0.068	-2.16	0.0308
Vegetation PCA axis 2	-0.021	0.109	-0.194	0.8464
NDSI-Anthro				
Intercept	-0.344	0.415	-0.829	0.4073
Mean Species Richness	-0.084	0.025	-3.41	0.0006
Vegetation PCA axis 1	0.146	0.066	2.213	0.0269
Vegetation PCA axis 2	0.015	0.106	0.145	0.8845
NDSI-Bio				
Intercept	0.368	0.376	0.978	0.3281
Mean Species Richness	0.055	0.022	2.486	0.0129
Vegetation PCA axis 1	-0.053	0.059	-0.888	0.3748
Vegetation PCA axis 2	-0.053	0.096	-0.559	0.576

Table 4.S3 - Model outputs from generalised linear mixed models for effects of mean number of avian detections and vegetation PCA axes on normalised acoustic indices values.

	Estimate	Std. Error	z value	p value
ACI				
Intercept	1.217	0.032	37.61	< 0.0001
Mean Detections	0.003	0.001	2.05	0.0403
Vegetation PCA axis 1	-0.013	0.006	-2.06	0.039
Vegetation PCA axis 2	0.018	0.009	1.92	0.0543
ADI				
Intercept	4.303	0.265	16.226	< 0.0001
Mean Detections	-0.021	0.011	-1.932	0.0534
Vegetation PCA axis 1	-0.036	0.049	-0.726	0.4681
Vegetation PCA axis 2	0.084	0.075	1.112	0.2661
AEve				
Intercept	-2.800	0.321	-8.736	< 0.0001
Mean Detections	0.032	0.013	2.405	0.0162
Vegetation PCA axis 1	0.057	0.058	0.983	0.3255
Vegetation PCA axis 2	-0.105	0.104	-1.009	0.3132
Bio				
Intercept	-2.052	0.305	-6.717	< 0.0001
Mean Detections	0.054	0.013	4.31	< 0.0001
Vegetation PCA axis 1	0.006	0.057	0.108	0.914
Vegetation PCA axis 2	-0.022	0.088	-0.253	0.8
H				
Intercept	4.539	0.362	12.556	< 0.0001
Mean Detections	-0.055	0.015	-3.757	0.0002
Vegetation PCA axis 1	0.010	0.067	0.145	0.8850
Vegetation PCA axis 2	0.107	0.101	1.042	0.2976

M				
Intercept	-4.579	0.237	-19.331	< 0.0001
Mean Detections	0.024	0.010	2.433	0.015
Vegetation PCA axis 1	-0.033	0.044	-0.756	0.45
Vegetation PCA axis 2	-0.083	0.068	-1.219	0.223
NDSI				
Intercept	0.342	0.367	0.933	0.351
Mean Detections	0.059	0.015	3.959	0.0001
Vegetation PCA axis 1	-0.067	0.068	-0.982	0.326
Vegetation PCA axis 2	-0.033	0.104	-0.319	0.75
NDSI-Anthro				
Intercept	-0.406	0.361	-1.125	0.2606
Mean Detections	-0.056	0.015	-3.785	0.0002
Vegetation PCA axis 1	0.071	0.067	1.066	0.2865
Vegetation PCA axis 2	0.029	0.103	0.282	0.7776
NDSI-Bio				
Intercept	0.317	0.325	0.975	0.3296
Mean Detections	0.040	0.013	3.084	0.0020
Vegetation PCA axis 1	0.001	0.060	0.02	0.9842
Vegetation PCA axis 2	-0.056	0.091	-0.621	0.5348

Table 4.S4 - AIC selection for generalised linear mixed models examining normalised acoustic indices values predicted by either mean species richness or mean number of detections per site. Lower AIC value indicated in bold.

Index	Mean Detections (AIC)	Mean Species Richness (AIC)	Delta AIC
ACI	**-27881.86**	-27881.97	0.11
ADI	**-44809.24**	-44809.83	0.59
AEve	**-14007.93**	-14008.25	0.32
Bio	-9687.62	**-9684.64**	2.98
H	-26414.85	**-26410.51**	4.34
M	-34524.27	**-34521.77**	2.5
NDSI	-11373.55	**-11370.73**	2.82
NDSI-Anthro	-11177.59	**-11175.51**	2.08
NDSI-Bio	-7335.66	**-7332.84**	2.82

Chapter 5. Monitoring an avian taxon of conservation concern across landscape gradients using point counts and automated audio recorders

Research ideas were conceived by Tom Bradfer-Lawrence. TBL and Nick Gardner collected the field data. TBL and Eben Broadbent constructed the land cover map. Daisy Dent, Stephen Willis and Nils Bunnefeld supervised the work. All authors commented on a draft version of this chapter.

5.1 Abstract

Traditional bird survey methods are time-consuming, particularly when assessing speciose communities in complex landscapes comprising multiple habitat types. Recent developments in automated audio recording technology offer the possibility to effectively monitor terrestrial biodiversity on much greater spatial and temporal scales than has previously been possible. However, there have been few tests of the efficacy of audio recordings to track changes in species occupancy across heterogenous landscapes, nor whether results derived from recordings collected in these contexts are comparable with those gathered using traditional survey methods such as point counts.

Here we evaluate the potential of automated audio recorders for surveying assemblages of a disturbance-sensitive Neotropical avian group, the antbirds (*Thamnophilidae*), across a human-modified landscape comprising a range of habitat types. Using audio recording and point count data collected at the same sites, we assessed occupancy of 12 antbird species with Bayesian hierarchical models that accounted for imperfect detectability. We found that occupancy probabilities increased with both greater landscape-scale forest cover and local-scale vegetation productivity. Recording-derived detection probability was higher, and occupancy probability lower, than those of the point count model. Both survey methods provided imprecise estimates for rarer species, with credible intervals surrounding probability of detection and occupancy above 0.5, likely reflecting the restriction of rarer species to continuous forest sites. Increasing the number of sites or replicate surveys would help to improve occupancy estimates for rare species, and scaling monitoring programs in this way is readily achievable with audio recorders.

5.2 Introduction

Automated audio recorders (hereafter “recorders”) hold considerable promise for avian population monitoring. Recorders have been used to track annual life history cycles (Jahn et al. 2017), follow post-reintroduction dispersal (Metcalf et al. 2019), and gauge arrival of migratory birds on breeding grounds (Oliver et al. 2018). Comparisons with point count data suggest that recorders can be as good as human observers for surveying birds (Darras et al. 2018a; Furnas & Callas 2015), and they have been used to assess avian occupancy in a variety of biomes, refine knowledge of species distributions, and estimate population sizes (Abrahams & Denny 2018; Campos-Cerqueira & Aide 2016; Oppel et al. 2014; Pérez-Granados et al. 2019; Wood et al. 2019).

Given that recorders can be deployed at broad spatiotemporal scales (Bradfer-Lawrence et al. 2019; Gibb et al. 2018), they are potentially invaluable for monitoring biodiversity across heterogenous areas such as human-modified landscapes (HMLs), which are complex mosaics of fragmented habitats. This is particularly important in the tropics, where ongoing deforestation and land use change are causing major habitat alterations (Newbold et al. 2014; Wright 2010), potentially threatening the long-term viability of forest-dependent animal species. More research is urgently needed to understand the impacts of anthropogenic disturbances on animal populations in HMLs in order to design conservation interventions (Moura et al. 2016; Powell et al. 2015a).

Before recorders can be widely adopted for animal population monitoring in HMLs, we need to demonstrate that they can provide results comparable with standard field assessment methods such as point counts. There are two aspects of monitoring where recordings data might diverge from point count data: occupancy and detectability. Occupancy is the confirmation of a species' presence at a site, while detectability refers to the probability of that occupancy being confirmed. If a species is not detected this may be a genuine absence, or it may reflect a failure of the monitoring method (Kery & Royle 2016). Unless an individual can be detected with absolute certainty, occupancy estimates are likely to be biased by these false absences. Analyses using hierarchical models can help to account for these false absences (Kery & Royle 2016). However, differences in detectability between recorders and point counts might influence occupancy estimates and thus prevent direct comparisons. It is therefore essential to ascertain whether these monitoring methods are comparable, particularly whether they show equivalent detectability and occupancy patterns when contrasting sites in different habitats.

Thus far, studies using recorders to assess inter-habitat differences have generally focused on disparities in detectability among sites rather than comparing methods across habitat types or landscape contexts (Celis-Murillo et al. 2012; Hutto & Stutzman 2009; Kułaga & Budka 2019; Van Wilgenburg et al. 2017). Several studies have successfully used recorders to track changes in bird communities over elevational gradients (Campos-Cerqueira et al. 2017; Leach et al. 2016; McGrann & Furnas 2016), but less research has explicitly examined the effects of vegetation structure on bird occupancy (Pillay et al. 2019; Vold et al. 2017). Moreover, there appears to be no research with recorders that integrates habitat quality and composition of the surrounding landscape, despite the fact that landscape matrix likely dictates occupancy for the majority of avian species (Bhakti et al. 2018; Carrara et al. 2015; Lees & Peres 2010; Moura et al. 2013). Further tests are needed to determine whether recorders are an appropriate tool for detecting variations in species occupancy with changing vegetation structure and landscape composition.

To investigate the potential of recorders for tracking changes in animal populations across a HML, we focus here on the Neotropical antbird family. Antbirds are understorey insectivores, and the family name originates from some species' attendance at army ant (*Eciton burchellii*) swarms, where they feed on invertebrates fleeing from the ants (Brumfield et al. 2007; Willis & Oniki 1978; Willson 2004). Some antbird species are highly sensitive to habitat change, with strong declines following forest clearance, and the family has been the focus of considerable scientific attention (Canaday & Rivadeneyra 2001; Lees & Peres 2010; Moura et al. 2016; Robinson 1999; Stouffer et al. 2011; Stouffer & Bierregaard 1995b; Visco et al. 2015; Visco & Sherry 2015). However, there is distinct within-family variation in terms of level of forest dependence and response to landscape composition (Lees & Peres 2010). For example, spotted antbird (*Hylophylax naevioides*) is typically never found outside large tracts of forest, while dusky antbird (*Cercomacroides tyrannina*) is often found in forest edge habitat, and barred antshrike (*Thamnophilus doliatus*) can persist in disturbed habitats such as young scrub in fragmented landscapes (Gorrell et al. 2014; Zimmer et al. 2019a, 2019b).

The range of antbird responses to habitat change may stem from species' sensitivity to vegetation structure. Influences might be at the site-scale (<10 ha), for example as seen in the strong positive correlation between antbird abundance and number of stems in regenerating forest patches in Colombia (Castaño-Villa et al. 2014), or the correlation between antbird occupancy and canopy height in the Brazilian Atlantic Forest (Bhakti et al 2018). Sensitivity may also occur at the microhabitat-scale, as some antbird species specialise in feeding from particular substrates; for example, checker-throated antwren (*Epinecrophylla fulviventris*) is strongly associated with presence of aerial leaf litter (Gradwohl & Greenberg 1980; Rosenberg 1993). Thus antbird declines following forest disturbance and loss may be due to changes in vegetation structure (Harper et al. 2005; Lees & Peres 2010; Powell et al. 2015a; Stratford & Stouffer 2015). Alternatively, the impact of disturbance may be indirect; for example, loss of army ant swarms from forest fragments has been shown to trigger extirpations of obligate ant-following species (Harper 1989; Stouffer & Bierregaard 1995). These ecosystem changes can be tracked using proxy measures of habitat integrity, such as vegetation productivity. Normalised Difference Vegetation Index (NDVI) and other satellite-derived measures of vegetation health are closely correlated with total avian species richness (Hurlbert & Haskell 2003; Nieto et al. 2015; Ranganathan et al. 2007), and antbird occupancy in Brazilian Atlantic forest fragments has been linked with higher NDVI (Bhakti et al 2018).

In addition to the influences of site-scale habitat structure and quality, factors at the landscape scale (i.e. 500 ha) have been strongly implicated in dictating antbird occupancy. Many antbird species are dispersal limited (Sekercioglu et al. 2002) and have home ranges of less than a hectare (Gorrell et al. 2014; Losada-Prado et al. 2014). Even in intact forest, natal dispersal of chestnut-backed antbirds (*Poliocrania exsul*) is estimated to be less than 2 km (Woltmann et al. 2012) and that of black-crowned antshrike (*Thamnophilus atrinucha*) less than 1.5 km (Tarwater 2012). Many antbird species are also reluctant to cross even small open areas such as road clearings (Laurance et al. 2004; Lees & Peres 2009; Moore et al. 2008), may struggle to persist in isolated fragments (Stouffer et al. 2011; Stouffer & Bierregaard 1995b), and can be slow to recolonise regenerating secondary forest or isolated forest patches (Bradfer-Lawrence et al. 2018; Mayhew et al. 2019; Powell et al. 2013; Robinson 1999). These sedentary behaviours mean antbirds are poorly adapted to cope with landscape-scale forest clearance and are often unable to persist in the non-forest matrix in HMLs. Hence the proportion of remaining forest cover and extent of fragmentation at the landscape scale are likely to be important drivers of antbird occupancy in HMLs (Antongiovanni & Metzger 2005; Lees & Peres 2010; Moura et al. 2013; Rompré et al. 2007).

Here we test the potential of recorders to survey assemblages of antbirds across a HML in central Panama. Antbirds are an ideal focal taxon because they are vocal, territorial and have small home ranges (Mathias & Duca 2016; Woltmann & Sherry 2011), suggesting they will be readily detected with recorders. Moreover, the range of antbird responses to habitat disturbance allows us to test whether recorders can detect intra-taxon differences in occupancy probability across the landscape gradients in a HML. We selected 40 sites with a range of local and landscape contexts according to measures of vegetation structure (number of stems), habitat integrity (NDVI) and landscape composition (forest cover and fragmentation). We ask the following questions;

1. Are the data from recorders sufficient to show variation in antbird species occupancy across a HML?

2. Are antbird occupancy patterns derived from recorders equivalent to those from point count surveys, and thus are recorders suitable for monitoring these understorey insectivores in HMLs?

5.3 Methods

5.3.1 Study landscape

This study was conducted in the Emparador landscape in central Panama. This region covers approximately 700km^2, and is bordered by the Panama Canal to the North and East, and the Interamericana highway to the South. A large area of relatively undisturbed continuous forest borders the canal, but beyond the forest boundary lies a highly heterogenous human-modified landscape (Figure 5.1). Here, the landscape is comprised of cattle pasture, non-native teak plantations, remnant forest fragments, regenerating scrub, urban areas and pineapple plantations.

We selected 40 survey sites in the Emparador landscape, spanning a gradient of habitat complexity. We selected 10 sites in each of the following classes: continuous forest, fragmented forest, scrub, and pasture (Figure 5.1). Each survey site was located in an area of uniform habitat of at least one hectare in size, and was at least 500m from any other site. This separation ensured independence; antbirds' territoriality makes it very unlikely that the same individuals were detected at more than one site (Campos-Cerqueira & Aide 2016).

5.3.2 Data collection

5.3.2.1 Audio recordings

At each survey site, we deployed Solo audio recorders with an omnidirectional Primo microphone (Whytock & Christie 2017) for a minimum of six days between January and May 2017. We collected a total of 8329 hours of audio recordings, mostly at a sampling rate of 32 kHz (although at nine sites recordings were at 16 kHz, a rate still sufficient to capture all antbird calls). From the first three days of each deployment, we subset recordings to one minute in every ten minutes during the two hours corresponding to the peak in dawn chorus (6:30 – 8:30 am). This gave 36 minutes of recording per site, and a total of 1440 minutes of audio recordings for the analyses. We opted to subset longer recordings rather than use a single continuous recording to minimise interference from geophony that might obscure the

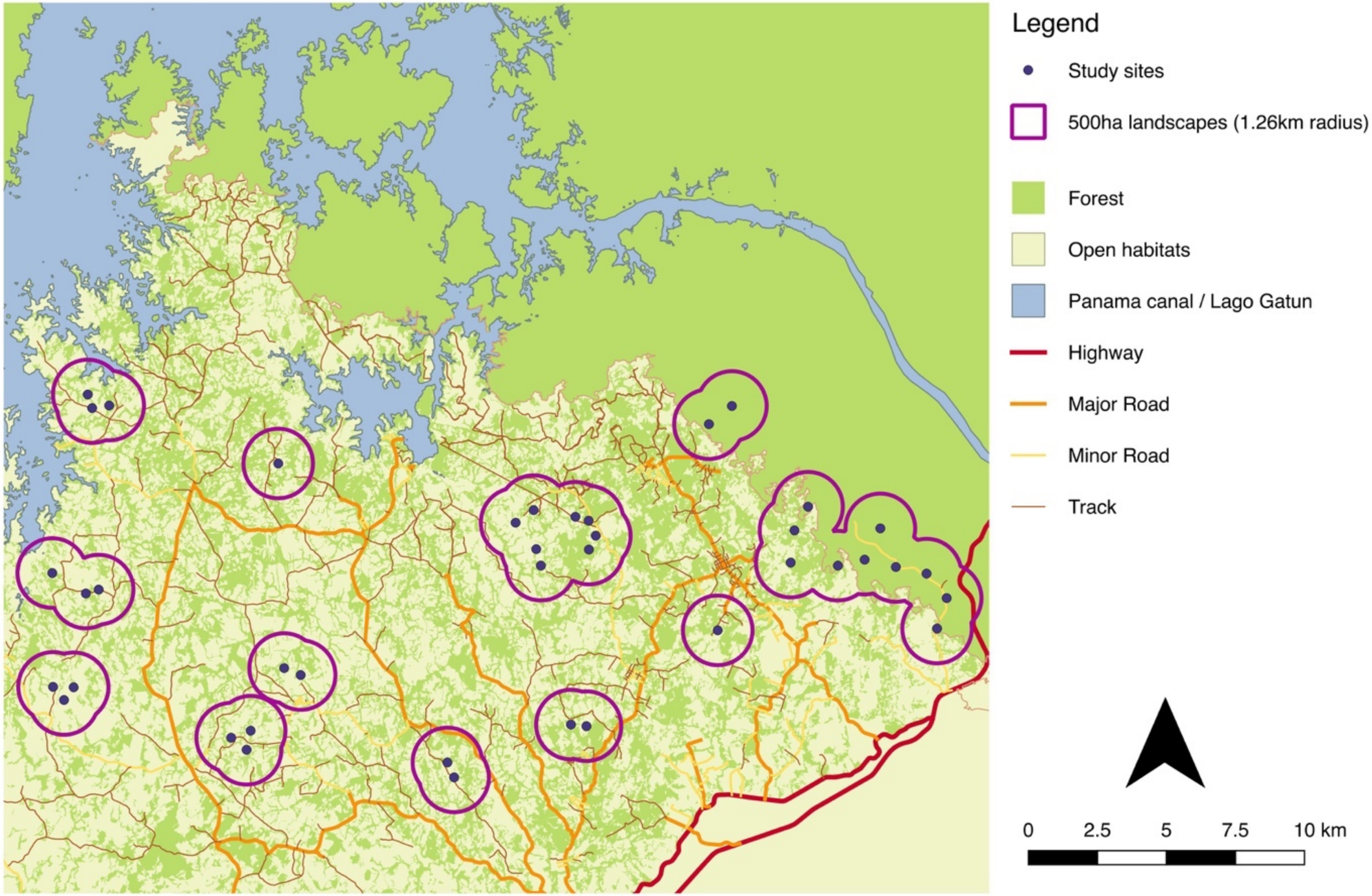


Figure 5.1 - Map of the Emparador landscape, showing the 40 study sites.

target species, and because it increases likelihood of detection (Cook & Hartley 2018; Thompson et al. 2017). One person (TBL) used Audacity (ver. 2.1.1) to simultaneously playback recordings and scan spectrograms, noting all antbird species detected (Table 5.2). Occupancy data could also be derived using automated recognisers (Furnas & Callas 2015; Trifa et al. 2008; Venier et al. 2017), however, there are still concerns regarding their accuracy (Priyadarshani et al. 2018) and hence we opted for the manual listening approach. The presence – absence records for each minute of recording were amalgamated at the dawn scale, so that each morning was treated as a replicate survey.

5.3.2.2 Point count surveys

During the same 2017 field season, two expert observers (TBL and NG) conducted 10-minute, unlimited radius point counts at the same 40 survey sites. We recorded all antbirds seen or heard. In practice, all detections were auditory or, in 3% of cases, auditory and visual. Each site was surveyed three times, giving 30 minutes of survey time per site, and a total of 1200 minutes for analyses. Surveys were conducted between 30 minutes after morning nautical twilight and 10 am. There was a mean of 21 days between revisits to the same site, so point counts were not always conducted concurrently with recordings.

5.3.2.3 Landscape and habitat variables

We constructed a landcover map for the Emparador landscape from PlanetLabs and Sentinel 1 satellite imagery from 2017. This imagery was segmented using eCognition software (ver 9.2, Trimble). We built a random forest classifier to assign polygons to one of six landcover classes: forest, scrub, plantation, pasture, urban and water. We collected over 200 ground-truthed data points per habitat class in the field, and used 70% of these for building the model and the remainder for testing. We tuned the model to find the best parameter values with the "caret" package (ver 6.0.84; Kuhn 2019) in R (ver 3.6.0; R Core Team 2019), and used 10-fold cross-validation. The model was found to be 92.5% accurate.

We extracted landscape compositional data from the landcover map, calculating proportion of forest cover and forest edge density (as a measure of fragmentation) in the 500 ha landscape surrounding each survey site (i.e. 1260 m radius). To reflect vegetation productivity, and hence habitat integrity, we used mean Normalised Difference Vegetation Index (NVDI) values. We determined this for the 10 ha (i.e. 180m radius) surrounding each survey site from Sentinel 2 satellite imagery from 2017. The 180 m radius was chosen because it encompassed the maximum range at which an antbird was likely to be detected during point counts. Although NDVI can saturate in highly vegetated tropical environments (Ranganathan et al. 2007), testing showed this was not an issue in the Emparador HML. Finally, as a measure of vegetation structure, we also assessed woody vegetation at each site in a 20 m x 20 m plot recording all stems over 1.3 m high. This plot was centred on the point where audio recordings and point counts were collected. We tested for collinearity between the four variables; forest cover and fragmentation had a correlation coefficient above 0.6, suggesting collinearity might inflate uncertainty in parameter estimates in this case (Frishkoff & Karp 2019). The four variables were used as parameters in the occupancy modelling.

5.3.3 Occupancy modelling

We fit hierarchical occupancy models to account for both observation processes (i.e. detection/non-detection) and state processes (i.e. presence/absence; Kery & Royle 2016). We fit separate models to the recording and point count data, with the occupancy parameters reflecting landscape composition, and local vegetation productivity and structure. The observation process of each antbird species (*i*) at each site (*j*) for each visit (*k*) was modelled as:

$$y_{i,j,k} \mid z_j \sim \text{Bernoulli}(z_j, p_{i,j,k})$$

Where z_j is the true occupancy state, and p is the probability of detection. Occupancy state z_j was modelled as:

$$z_j \sim \text{Bermoulli}(\mathit{\Psi}_j)$$

Where $\mathit{\Psi}_j$ is a function of landscape structure:

$$\begin{gathered}\log(\Psi_j) = \beta 0_i + \beta 1_i \text{ x forest \_cover}_j + \beta 2_i \text{ x fragmentation}_j + \\ \beta 3_i \text{ x NDVI}_j + \beta 4_i \text{ x No\_of\_Stems}_j + \gamma_{\text{site}j}\end{gathered}$$

Where “forest_cover” refers to proportion of forest within the surrounding 500 ha, “fragmentation” indicates the edge density in the same area, “NDVI” the value within the surrounding 10 ha, and “No_of_Stems” the stem density at the survey point. All parameters were scaled prior to analysis. To account for any potential spatial autocorrelation, we included a random effect of "site". Replicates for visit were either day of deployment for the recording data, or survey number for the point count data.

We fit occupancy models in JAGS (ver 4.3.0; Plummer 2017) via R using the package "jagsUI" (ver 1.5.0; Kellner 2018). In all cases we used diffuse priors. All models were run with 100,000 iterations, with 50,000 discarded as burn in samples, and a thinning rate of 100, giving 4000 samples of the posterior. We ensured model convergence via visual inspection of trace plots and confirmed that $\hat{R}$ values were all < 1.1 (Gelman & Rubin 1992).

We compared outputs from the null models to examine the ability of recording and point count data to discern differences in species detectability and hence apparent differences in occupancy. For each species we examined variation in occupancy as a response to the environmental parameters. From the posterior, we determined 95% Bayesian Credible Intervals (BCIs) around each parameter; where BCIs did not encompass zero, effects were deemed "significant" (*sensu* Kery & Royle 2016). Finally, to illustrate how the two data sets might show differing occupancy patterns, we created regional maps showing predicted antbird occupancy as a function of landscape composition and habitat structure.

Effective sample area could vary between the two data collection approaches. To attempt to standardise for potential differences, we ran a second series of analysis with point count observations truncated to a maximum detection distance of 100 m, which we estimated to be the effective distance of the microphones (see supplementary material). However, truncation had minimal effects on occupancy patterns, and so we report only the main recorder-point count comparison here.

5.4 Results

We detected 12 antbird species during the study, of the 16 species likely present in the region (Table 5.1). We found 30 of the 40 sites to be occupied by at least one antbird species using the recordings, and 32 occupied using point counts. This was despite the survey time with the recordings being 20% longer than the point counts (36 versus 30 minutes per site). There was a high level of overall agreement between the two data sets; of 480 potential site-by-species occupancy combinations (i.e. 12 species at 40 sites), the datasets matched for 436 of these. Of the remaining 44 occupancy states, 13 occupancies were detected in recordings but missed by point counts, and 31 detected during point counts but not recordings. These missed occupancy states were not associated with a particular habitat type, and all species

Table 5.1 - The sixteen antbird species present in central Panama (Angehr & Dean 2010), details of their forest dependence according to Birdlife International (BirdLife 2019, Buchanan et al 2011), and numbers of detections and occupied sites from the two datasets. Four species were not recorded in the Emparador landscape during this study (great antshrike, spot-crowned antvireo, Pacific antwren, jet antbird). All species are classified as "Least Concern" in the IUCN Red List (IUCN 2019).

Common name	Scientific name	Forest dependence	Recorded in Emparador?	Point counts			Recorders		
				Total number of detections	Number of known occupied sites	Number of predicted occupied sites	Total number of detections	Number of known occupied sites	Number of predicted occupied sites
Fasciated antshrike	*Cymbilaimus lineatus*	Medium	Yes	6	4	9	7	3	9
Barred antshrike	*Thamnophilus doliatus*	Medium	Yes	11	4	16	11	2	6
Black-crowned antshrike	*Thamnophilus atrinucha*	Medium	Yes	106	27	29	204	24	24
Checker-throated antwren	*Epinecrophylla fulviventris*	High	Yes	7	5	13	6	4	12
White-flanked antwren	*Myrmotherula axillaris*	High	Yes	5	2	7	1	1	9
Dot-winged antwren	*Microrhopias quixensis*	High	Yes	11	5	13	1	1	8
Dusky antbird	*Cercomacroides tyrannina*	Medium	Yes	53	16	22	120	11	12

Chestnut-backed antbird	*Poliocrania exsul*	High	Yes	8	3	14	9	3	9
White-bellied antbird	*Myrmeciza longipes*	Medium	Yes	39	18	34	97	17	19
Spotted antbird	*Hylophylax naevioides*	High	Yes	36	11	13	25	9	11
Bicoloured antbird	*Gymnopithys bicolor*	High	Yes	9	5	10	5	3	7
Ocellated antbird	*Phaenostictus mcleannani*	Medium	Yes	1	1	7	0	0	4
Great antshrike	*Taraba major*	Medium	No	-	-	-	-	-	-
Spot-crowned antvireo	*Dysithamnus puncticeps*	High	No	-	-	-	-	-	-
Pacific antwren	*Myrmotherula pacifica*	Medium	No	-	-	-	-	-	-
Jet antbird	*Cercomacra nigricans*	Medium	No	-	-	-	-	-	-

except chestnut-backed antbird were missed on at least one occasion. Table 5.1 shows the number of times each species was detected, the number of sites with confirmed occupancy, and number of sites predicted occupied by each model. Ocellated antbird (*Phaenostictus mcleannani*) was only detected once during a point count, and not at all with the recorders, probably because of its relative rarity in the region.

There were clear differences in detectability and apparent occupancy between the two models, at least for the more commonly detected species (Figure 5.2). Detectability was generally higher using recorders (mean 0.12 +/- 0.22 SD), but estimates of occupancy were much lower than with point counts (mean -0.13 +/- 0.14 SD). However, the Bayesian credible intervals (BCIs) for occupancy were wide for many species, ranging from 0.3 to 0.95, reflecting considerable variation in probability of occupancy among sites (Figure 5.2).

Species' responses to the landscape and habitat parameters were qualitatively similar in recording and point counts models (Figure 5.3). However, higher estimated occupancy in the point count model resulted in stronger parameter effects for individual species. Greater forest cover at 500 ha was associated with significantly greater probability of occupancy for five species according to the recording model and nine species in the point count model (mean response in occupancy probability for recordings = 2.7, for point counts = 4.4). Responses to fragmentation were smaller but generally negative, although the BCIs for all species included zero (mean response in occupancy probability for recordings = -3.1, for point counts = -1.4). Higher habitat integrity, measured using mean NDVI at 10 ha, positively affected occupancy of four species when using the recordings, and of seven species when using point counts (mean response for recordings = 1.7, for point counts = 2.6). Vegetation structure, i.e. number of stems over 1.3 m, appeared to have minimal effect.

Predicted occupancy maps constructed using the two models demonstrated that most antbird species are reliant on forest cover (Figures 5.4 and 5.S2). Some species were strongly limited to the area of continuous forest bordering the Panama Canal; for most species occupancy probability only approached 0.5 in continuous forest. The two models gave similar patterns in predicted occupancy, although probability of occupancy across the open habitat portion of the landscape was often greater in one model than the other. For example, the recording model predicted greater occupancy for dusky antbird and spotted antbird beyond the continuous forest, while the point count model showed a similar pattern for black-crowned antshrike and chestnut-backed antbird (Figure 5.4). However, increased occupancy probability in the open habitats were accompanied by higher occupancy probability in the

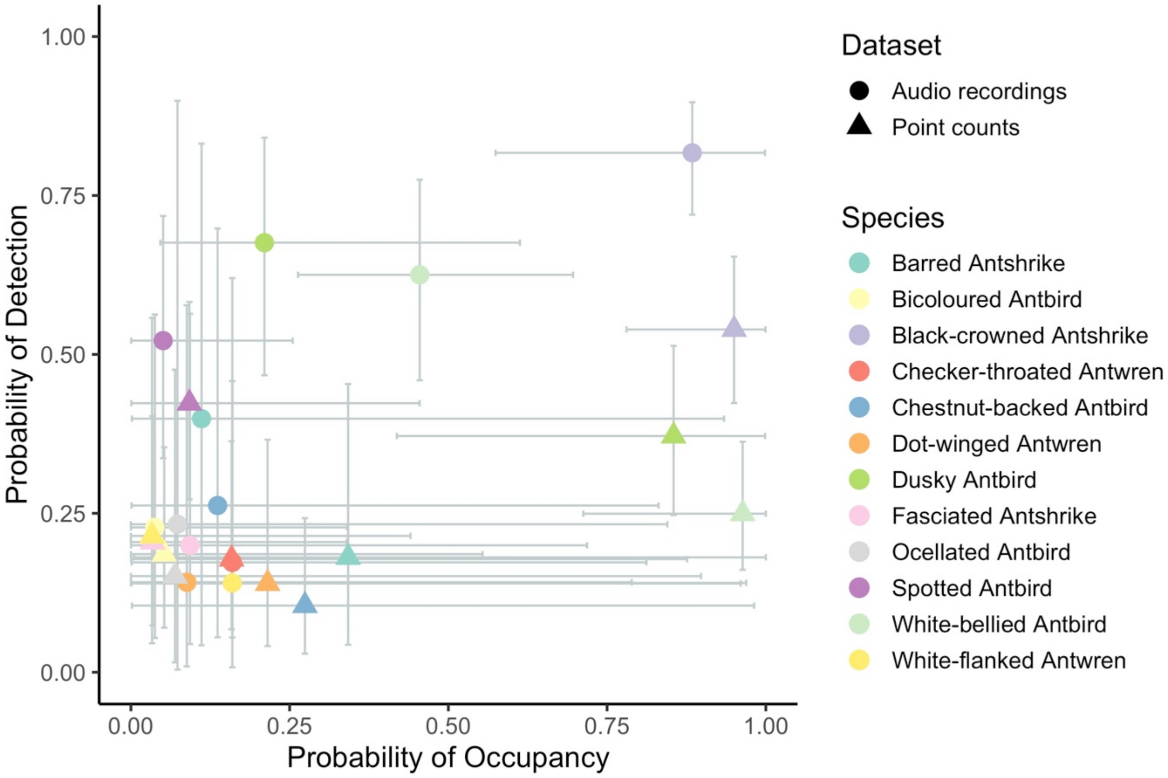


Figure 5.2 - Probability of detectability and occupancy for each antbird species from data collected with either point counts or automated audio recorders, bars show 95% CRIs.

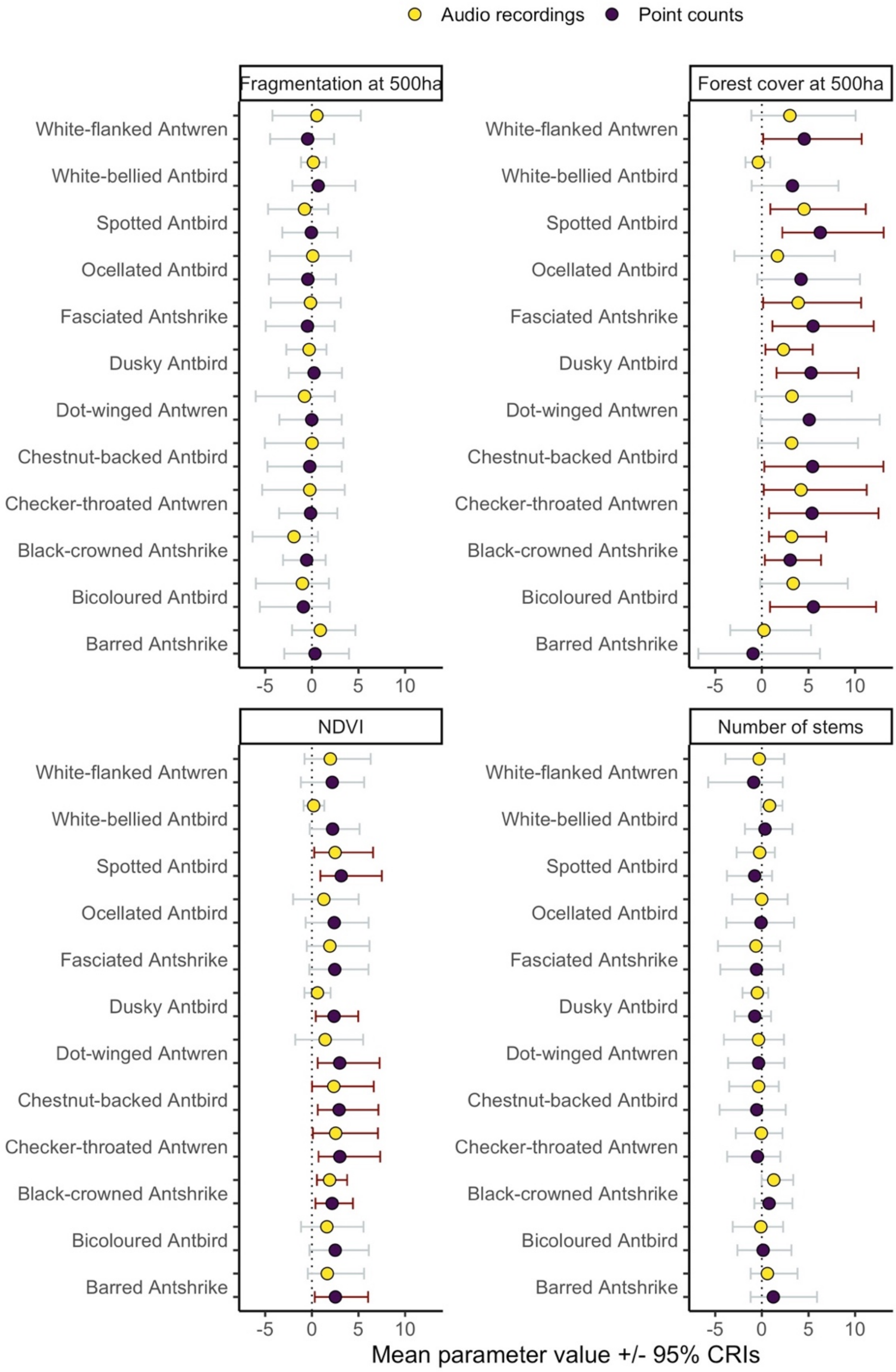


Figure 5.3 - Antbird species parameter responses to the proportion of forest cover and fragmentation at 500 ha, NDVI at 10ha, and number of stems over 1.3m high in 20m x 20 m plot. Shaded error bars denote species with 95% BCIs that do not include zero (implying a significant response).

continuous forest, so that relative patterns of occupancy across the HML were very similar between models. In a few cases, the recording model over predicted occupancy, giving unrealistic results for dot-winged antwren (*Microrhopias quixensis*) and white-bellied antbird (Figure 5.S2).

5.5 Discussion

5.5.1 Comparison of point count and recorder data

We found recorder data to be suitable for assessing antbirds' occupancy status across a HML, with predicted occupancy maps similar to those produced using point count data. As anticipated, occupancy patterns were driven by changing forest cover at the landscape scale and habitat integrity at the local scale. There were no major disparities between the two models in terms of species' parameter values. However, responses to landscape-scale forest cover and habitat integrity were generally greater in the point count model. This is probably due to the higher estimates of occupancy in the point count model, which results from multiple sampling visits over a prolonged season (see below). There were no significant effects of landscape-scale fragmentation or patch-scale number of stems in either model.

Recording and point count models both produced similar, low estimates of detectability and occupancy for rarer species. These species had very wide BCIs, indicating substantial variation in probability of occupancy among sites. This was closely associated with differences among habitat types, as these rarer species were only recorded in forest sites. For more common species, the recording model had higher levels of detectability than the point count model. This is likely because of the temporal subsampling of the recordings; by pooling samples from across each morning (i.e. 1-minute samples from every 10 minutes between 6.30 and 8.30 am), there was a greater chance that a species would be detected on multiple days and hence detectability was high. However, by limiting recordings to three consecutive days, antbirds might be missed if calling rates were low during this relatively brief sampling window. Thus, according to the recording model, apparently unoccupied sites were more likely to be true absences and so occupancy rates were lower. Conversely, species were often detected on only one occasion during the point counts. Although a bird might not call during a single 10-minute count, and the site would appear unoccupied on that occasion, multiple visits over a prolonged season meant that eventually a species would be detected. With lower detectability, occupancy was therefore more likely across all sites. In consequence, the point count model predicted higher levels of site occupancy for 10 of the 12 antbird species. Inflated occupancy estimates often reflect violation of the closure assumption that underlies hierarchical models, i.e. the population must be constant with no movement of individuals in to or out of the study area. This issue can be circumvented by reframing the occupancy parameter as probability of use rather than permanent residence (Kery & Royle 2016).

5.5.2 Determinants of occupancy

Landscape-scale forest cover was a key determinant of occupancy for most antbird species in our study region. The prediction maps demonstrate the area of continuous forest adjacent to the Panama Canal to be the stronghold for antbirds in the Emparador HML, particularly for forest-dependent species such as spotted antbird and checker-throated antwren. Previous research has found that large areas of forest are critical for maintaining populations of antbirds and other Neotropical understorey insectivores (Lees & Peres 2010; Morante-Filho et al. 2015; Stouffer et al. 2011). This may be because army ant swarms tend to be restricted to large areas of forest, and many obligate ant-following species, particularly ocellated antbird and chestnut-backed antbird, are unable to persist without army ants (Harper 1989; Stouffer & Bierregaard 1995). In this study, only species associated with non-forest habitats, notably barred antshrike, had an even occupancy probability beyond the continuous forest. However, even species associated with open habitats were positively influenced by higher NDVI, suggesting that these species select areas of higher habitat integrity within the HML matrix. This compliments existing studies showing that antbirds are sensitive to local-scale habitat quality (Bhakti et al. 2018; Lees & Peres 2010).

Forest fragmentation had a negative influence on occupancy for nearly all species, although this was not significant. Fragmentation can affect antbird occupancy and abundance (Chapter 2 of this thesis; Martensen et al. 2012; Stouffer et al. 2011), but may perhaps be less critical than changes in total forest cover. If forest loss has already triggered shifts in occupancy of more sensitive species, configuration of remaining habitat and extent of fragmentation may be relatively unimportant (Martensen et al 2012). Habitat structure also had a weaker influence on antbird occupancy than predicted. Higher stem density in regenerating forest has been linked with increased antbird abundance in Colombia (Castaño-Villa et al. 2014). However, the mature forest sites studied here often had a low number of

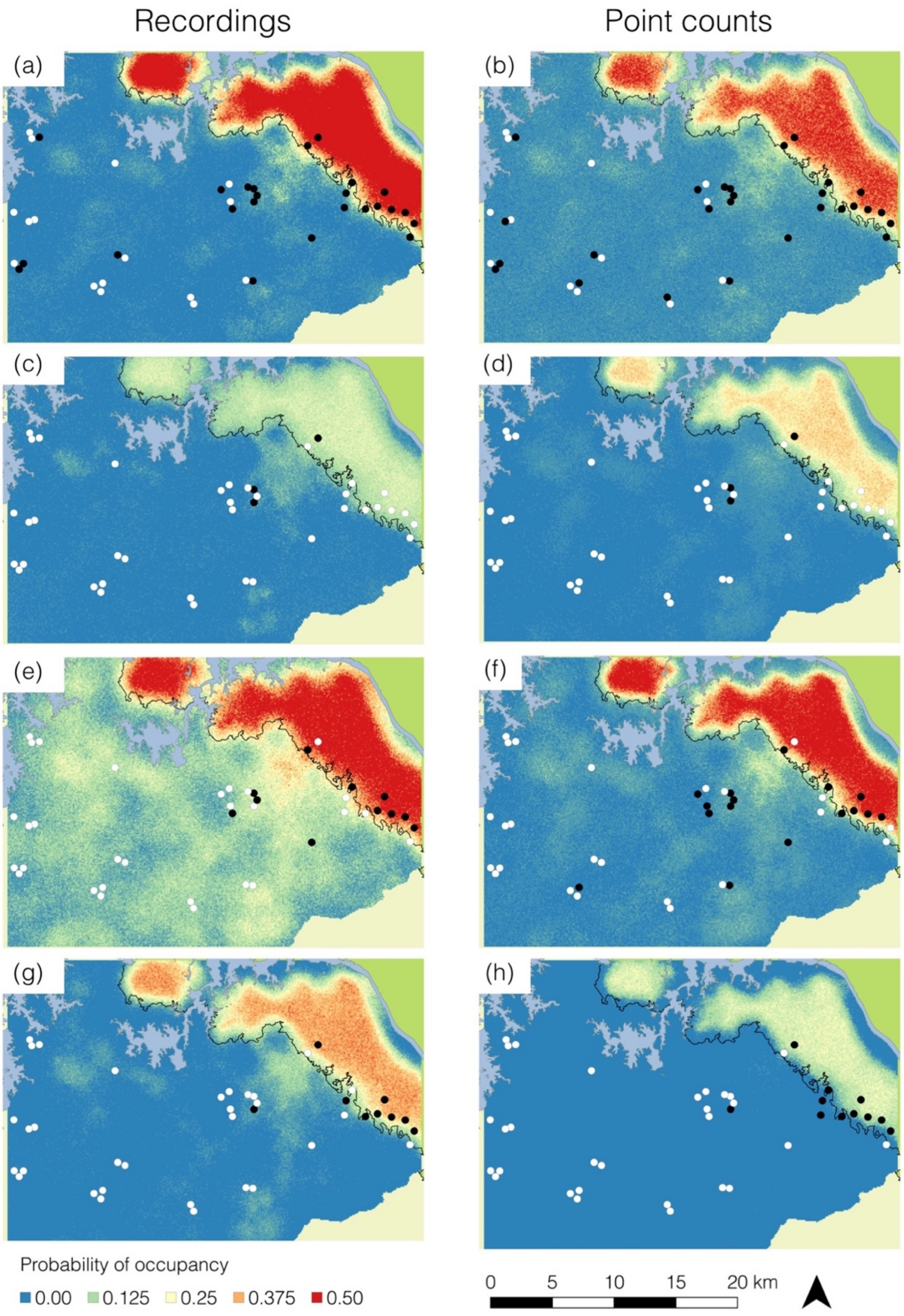


Figure 5.4 - Probability of occupancy for four antbird species, with predictions from Bayesian hierarchical occupancy models constructed with data from automated audio recorders (left) and point counts (right). (a & b) Black-crowned antshrike, (c & d) Chestnut-backed antbird, (e & f) Dusky antbird, (g & h) Spotted antbird. Black points identify sites where the species was detected, white points where they were not. Black line shows boundary of continuous forest.

stems, so antbirds may be responding to other aspects of habitat structure such as canopy height (Bhakti et al 2018) or microhabitat niches (Marcotullio & Gill 1985; Rosenberg 1993; Stratford & Stouffer 2015).

Both models still predicted antbird occupancy in some of the more isolated forest patches in the HML. Given the sensitivity of antbirds to habitat disturbance (Powell et al 2015a, Stouffer et al 2011), and our familiarity with the avian assemblages in the region, we deem antbird occupancy of these patches to be unlikely. Although the combination of forest cover, fragmentation and NDVI reflect gross habitat suitability, there are probably other aspects of patch quality that influence antbird occupancy. These might include matrix context and patch connectivity, as individuals' ability to move among patches in the matrix is critically important for maintaining bird populations in HMLs (Lees & Peres 2010; Martensen et al. 2012; Mayhew et al. 2019; Powell et al. 2015b; Wolfe et al. 2015a). Alternatively, the overprediction may be because transient anthropogenic disturbances are not well reflected in satellite-derived measures of landscape composition and habitat quality (Burivalova et al. 2019a; Peres 2000). Forest fragments in HMLs are susceptible to fire, timber extraction and hunting (Cochrane 2001; Wright et al. 2000); such pressures may not be apparent with the parameters used in our models, but could indirectly influence antbird populations through subtle habitat alterations (Barlow & Peres 2004; Wright 2003).

5.5.3 Caveats and recommendations

In both recording and point count datasets, some antbird species were only detected on a few occasions, or not at all in the case of ocellated antbird in the recordings dataset. Small numbers of recorder sites, or short deployment times make detecting rarer species with audio recordings unlikely (Holmes et al. 2014), and much larger arrays are necessary to detect small changes in occupancy (Wood et al 2019). Although a Bayesian occupancy modelling framework can cope with rare species, inference can be limited with data from a relatively small number of sites, which may explain the overpredictions of occupancy for dot-winged antwren and white-flanked antwren (*Myrmotherula axillaris*). These two species each occupied only a single site, so the recording model could not produce realistic predictions. Analysis of a larger number of recordings would likely help to refine occupancy patterns (Campos-Cerqueira & Aide 2016).

Traditional survey approaches for understorey birds in the tropics include mist-netting as well as point counts (Martensen et al. 2012; Stouffer et al. 2011; Stouffer & Bierregaard 1995a). These approaches generate highly detailed data, but are time-consuming to collect. Recorders should be seen as complimentary monitoring tools rather than replacements for these more established methods. Recorders are suitable for surveying any bird species provided they are sufficiently numerous and vocal (Darras et al. 2018b) and recorders can be deployed at much greater spatio-temporal scales than other methods. However, just as mist nets are most useful for surveying species in lower forest strata, recorders are likely best suited for vocal, territorial and sedentary species such as antbirds. There are many bird species without these characteristics, and further testing would be required to determine how best to employ recorders if interested in these other species. For example, longer deployments and more recordings would likely be necessary to produce meaningful occupancy estimates for species with less frequent vocalisations. While for species with prominent leks such as manakins (*Pipridae*), individuals are clustered in space, and thus measures of occupancy are not equivalent with those of territorial species.

However, recorders do have additional benefits; circumventing potential observer-avoidance effects (Darras et al. 2018a), and providing permanent, unbiased evidence, allowing reanalysis in the future (Deichmann et al. 2018; Sugai & Llusia 2019). Moreover, recent developments, such as inferring avian abundance via vocal activity rates, will allow fresh insights from existing recordings (Pérez-Granados et al. 2019).

5.5.4 Summary

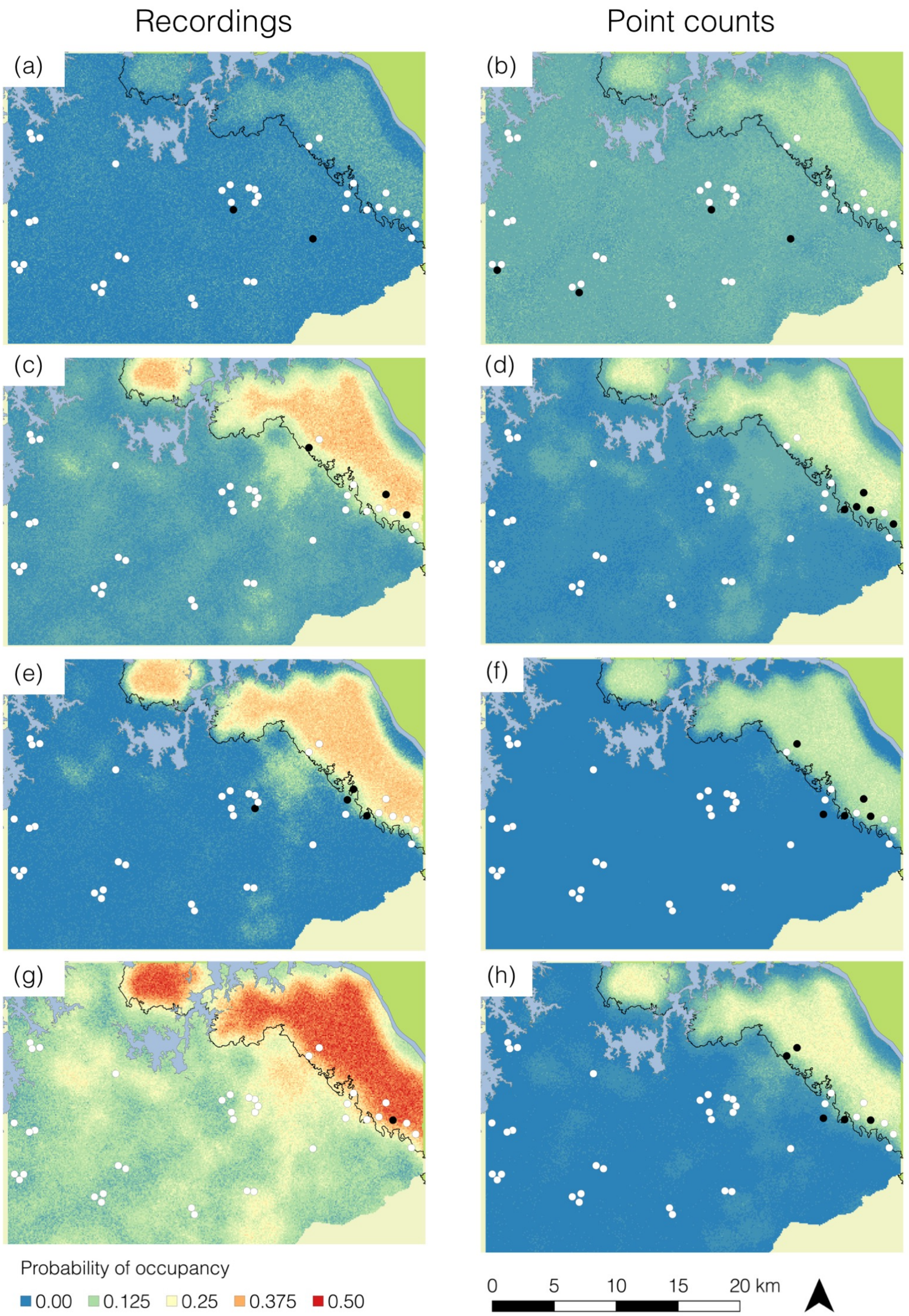
Here we used datasets collected with automated audio recorders and conventional point count methodology to examine occupancy patterns in Neotropical antbirds across a range of habitat types. We found significant influences of both landscape composition and habitat quality on antbird occupancy in both models. Predicted occupancy patterns across a HML were also similar between the two models, suggesting that recorders are as suitable as point counts for surveying antbirds. However, recorders may struggle to provide meaningful estimates for rarer species if data collection is limited to a small number of sites or for short deployments.

5.6 Acknowledgements

Our thanks to the Autoridad de Canal de Panama and the private landowners who granted permission to deploy recorders on their land; the Autoridad Nacional del Ambiente for providing research permits to work in Panama (permits SE/A-134-16 and SE/A-67-18); the Smithsonian Tropical Research Institute for logistical support; Robbie Whytock and James Christie for helpful support with the Solo audio recorders; TBL was funded by the Natural Environment Research Council UK, and the IAPETUS Doctoral Training Partnership.

5.7 Supplementary Information

5.S1 Occupancy maps for additional species



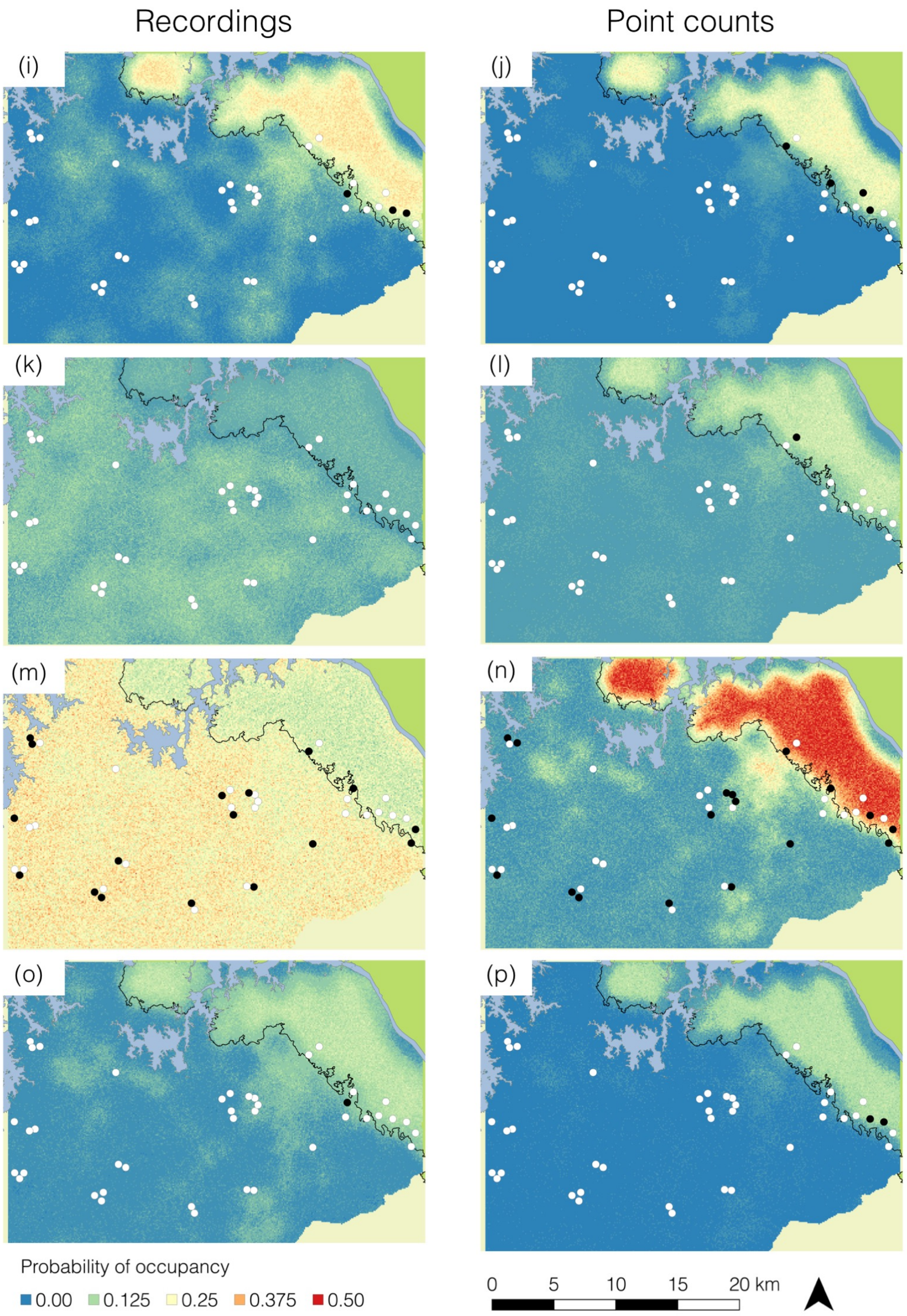

Recordings
Point counts
(i)
(j)
(k)
(l)
(m)
(n)
(o)
(p)
Probability of occupancy
0.00
0.125
0.25
0.375
0.50
0
5
10
15
20 km

Figure 5.S2 - Probability of occupancy for eight antbird species, with predictions from Bayesian hierarchical occupancy models constructed with data from automated audio recorders (left) and point counts (right). (a & b) Barred antshrike, (c & d) Bicoloured antbird, (e & f) Checker-throated antwren, (g & h) Dot-winged antwren, (i & j) Fasciated antshrike, (k & l) Ocellated antbird, (m & n) White-bellied antbird, (o & p) White-flanked antwren. Black points identify sites where the species was detected, white points where they were not. Black line shows boundary of continuous forest.

5.S2 Supplementary analysis with truncated point counts

Unlimited radius point count surveys generally have greater detection distances than audio recorders, although this might be offset because of observer-avoidance effects (Darras et al. 2018a). Disparities in detectability and occupancy estimates may have arisen because of differing detection distances with the two survey methods. To investigate this potential effect, we truncated point count detections to a maximum distance of 100 m, this resulted in 242 observations, rather than 292 in the full dataset.

We re-ran the analyses as detailed in the main Methods section. Truncating the point data set led to very slight declines in probability of detection compared to the unlimited radius point counts (mean = -0.02), but there was no clear pattern in the probability of occupancy (mean = - 0.03; Figure 5.S3). Parameter estimates for forest cover were very similar between the two point count datasets (Figure 5.S4). However, parameter estimates for NDVI were substantially larger (truncated point count mean = 5.0, unlimited point count mean = 2.6), although only bicoloured antbird became significant. In consequence, we conclude that truncating the point count dataset had a minimal influence on occupancy patterns already described in the main text.

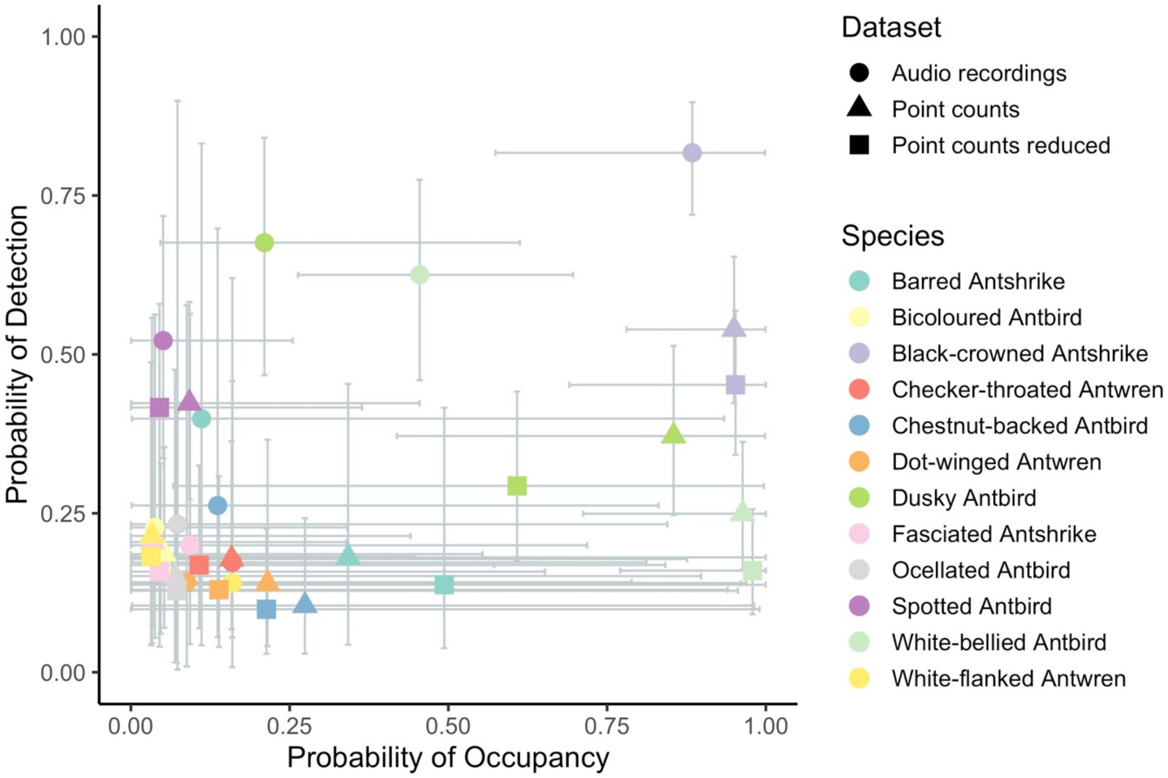


Figure 5.S3 - Estimated probability of detection and occupancy of 12 antbird species, from models built with three datasets: automated audio recorders, unlimited radius point counts, and 100m fixed-radius point counts.

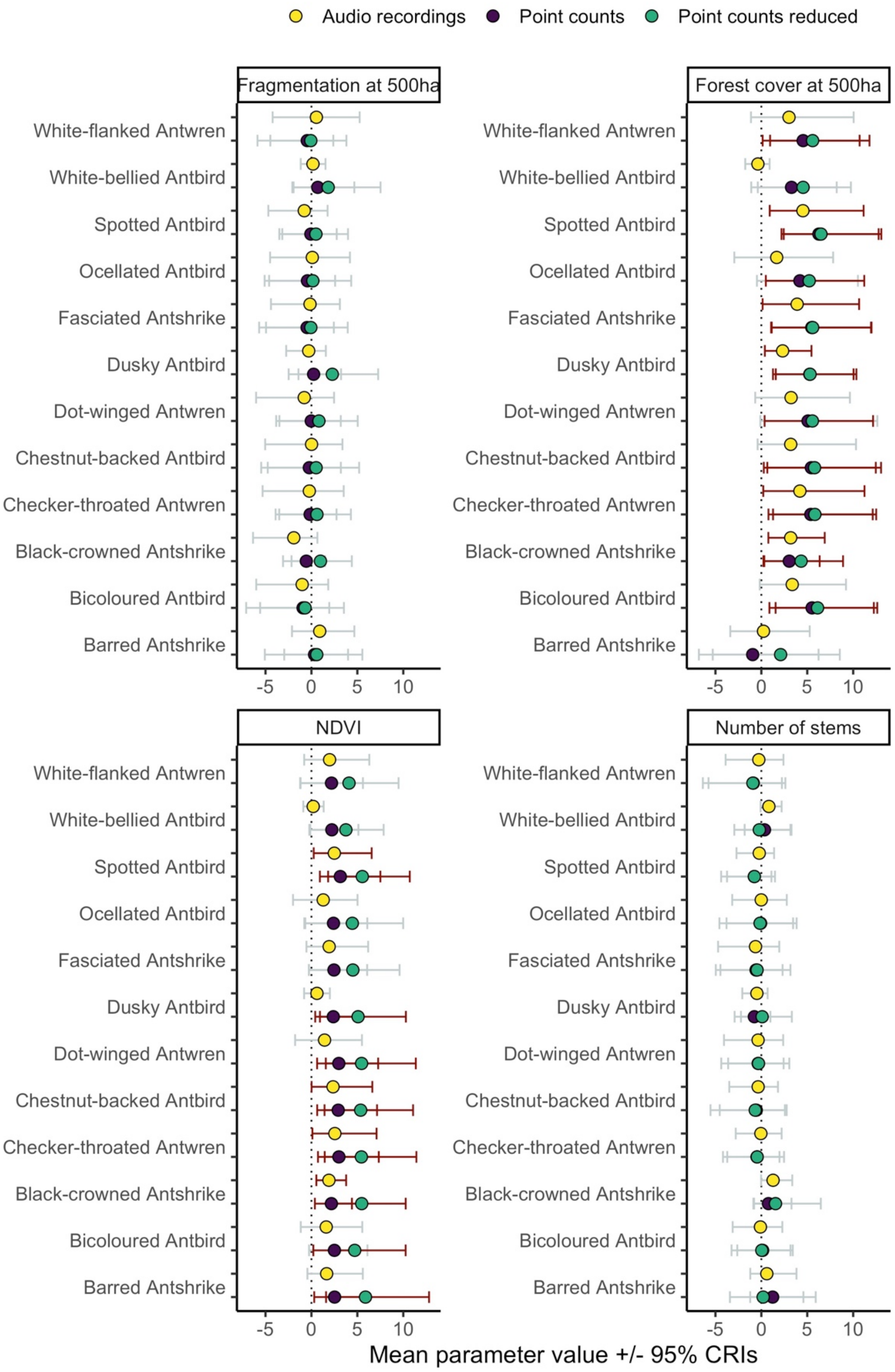


Figure 5.S4 - Antbird species parameter responses from three datasets for the proportion of forest cover and fragmentation at 500 ha, NDVI at 10 ha, and number of stems over 1.3 m

high in 20 m x 20 m plot. Shaded error bars denote species with 95% BCIs that do not include zero (implying a significant response).

Chapter 6. General Discussion

6.1 Background

Throughout the tropics, large areas of tropical forest have been converted to human-modified landscapes (HMLs). The original continuous forest cover has been replaced with a heterogenous mix of other habitats, including cattle pasture, non-native timber plantations, croplands and urban settlements. Any remaining forest in HMLs is generally restricted to isolated fragments or riparian strips. These habitat changes have profound consequences for wildlife populations in HMLs, and likely concomitant impacts on ecosystem processes such as seed dispersal.

Tropical forest continues to be cleared at dramatic rates (Achard et al. 2014), and preventing extinctions necessitates effective conservation action aimed at minimising the effects of forest loss. Protected areas are vital for conservation, and although globally nearly 15% of land and inland waters have some form of conservation designation (Lewis et al. 2019), protected area networks are inevitably limited (Schleicher et al. 2019). Therefore conservation actions also need to take place outside protected areas. Encouraging wildlife-friendly management practices in surrounding landscapes maximises the effectiveness of protected areas, through improving connectivity in the protected area network and providing additional habitat and resources (Cottee-Jones et al. 2015; Harvey et al. 2006; Norris 2008; Sekercioglu et al. 2019). With effective management, HMLs can support considerable wildlife populations and provide valuable ecosystem services, thus supporting the conservation value of protected areas (Chazdon et al. 2009; Edwards et al. 2019).

The challenge of conserving biodiversity in HMLs has never been more urgent. Agricultural intensification has been a major driver of biodiversity loss in recent decades, and this trend is likely to continue without careful management and mitigation (Edwards et al. 2019; Norris 2008). Furthermore, population growth throughout the Neotropics is resulting in spreading urbanisation. In this context of rapid change, refining our understanding of species and ecosystems in HMLs is critical for conservation (Harvey et al. 2008). However, there are still considerable uncertainties surrounding how species, communities, and ecosystem processes respond to habitat disturbance and HML structure, and how conservation interventions might best be designed and implemented.

6.2 “Beyond reserves” – Conservation in HMLs

In 2009, Chazdon et al. published a paper entitled “Beyond reserves: A research agenda for conserving biodiversity in human-modified tropical landscapes”. They list 12 research areas in which scientists could contribute to greater understanding of wildlife dynamics in tropical HMLs and hence biodiversity conservation. A substantial volume of research in this field has been conducted in the last decade, and the work in this thesis provides additional contributions to four of these areas that I will discuss here: population biology and monitoring; animal dispersal and habitat use; effectiveness of corridors and buffer zones for conservation and ecosystem services; and the relationship between biodiversity and ecosystem functions.

6.2.1 Population biology and long-term monitoring within HMLs

Chazdon et al (2009) ask “Which taxa can persist in human-modified landscapes and which cannot?” Although forest clearance can lead to species extirpations, some forest-affiliated species are apparently able to persist in HMLs (Chapter 2 of this thesis; Frishkoff & Karp 2019; Karp et al. 2019; Walter et al. 2017). However, determining which species are more robust to disturbance, and why, are still key questions.

The role that species traits play in determining avian responses to HMLs has received considerable attention (Newbold et al. 2014). General patterns have been reported, such as the persistence of wide-ranging omnivorous species in HMLs following habitat fragmentation (Graham 2001; Newbold et al. 2013). Conversely, understorey insectivores and large-bodied frugivores are often highly sensitive to fragmentation (Bregman et al. 2014; Lees & Peres 2010; Morante-Filho et al. 2015; Newbold et al. 2013; Vidal et al. 2019). Behavioural traits have also been used to identify sensitive species, for example, migratory and bark gleaning species persist more readily in HMLs than sedentary and ground foraging species (Sekercioglu et al. 2019; Tobias & Pigot 2019). Thus, certain suites of traits may predispose some species to greater disturbance sensitivity than others.

Although such trait patterns might be useful for predicting changes in avian communities in HMLs, and for planning conservation interventions, the work presented in Chapter 2 of this thesis cautions against over-reliance on these coarse patterns. We demonstrated that species’ abundances varied significantly within functional group at both local and landscape scales in response to forest cover and fragmentation. There were no clear trait patterns that could be used *a priori* to predict species responses to landscape structure. This mirrors Hatfield et al. (2018) who contrasted two bird community datasets collected in the same region in Brazil; they found that traits identified as important predictors of avian responses to forest loss in one dataset were not significant predictors in the second dataset. Careful choice of morphological or behavioural traits may reveal consistent patterns, but it seems likely that responses of individual species will evade stable classifications that hold across all landscapes (Bueno et al. 2018).

One possible explanation for the lack of trait patterns may be the confounding influence of landscape features on avian persistence. Chazdon et al (2009) ask "How are population processes affected by different land-use practices, landscape configurations, and levels of landscape modification and degradation?" HMLs tend to be highly complex across multiple spatial scales, and habitat influences likely compound and negate one another across scales (Frishkoff & Karp 2019; Hatfield et al. 2019). As discussed in Chapter 1, local-scale patch quality will be mediated be mediated by intermediate- and landscape-scale effects. Determining the relative importance of land-use, configuration and disturbance is still problematic, despite a large number of recent studies from multiple HMLs in Central and South America (Carrara et al. 2015; Frishkoff & Karp 2019; Hatfield et al. 2019; Karp et al. 2019). We demonstrated in Chapters 2 and 5 that HML forest cover at both intermediate- and landscape-scales was particularly important for persistence of many birds, not only forest-affiliated species. These findings parallel other research that reports thresholds of 20 – 50% landscape-scale forest cover as a critical habitat level (Melo et al. 2018). Below the threshold, forest-affiliated bird species are more likely to be extirpated, leading to major shifts in community composition (Banks-Leite et al. 2014; Martensen et al. 2012; Morante-Filho et al. 2018; Vidal et al. 2019).

As the discussed in chapter 1, forest connectivity is often highlighted as being particularly important for avian persistence in HMLs (Eycott et al. 2012; Leon & Harvey 2006; Vergara et al. 2013). However, we were unable to explicitly consider connectivity in either chapter 2 or 5. Tree cover in the Emparador landscape is so extensive that almost all forest patches are connected to the wider landscape, making it impossible to examine this aspect of landscape structure. Moreover, much of the Emparador landscape is a relatively benign matrix, so that there is no dramatic gradient of land management intensity.

The second component of this research area highlighted in Chazdon et al (2009) is the critical importance of long-term biodiversity monitoring in providing evidence for conservation (Stroud & Thompson 2019). Developments in audio recording technology over the last decade represents a major change in the way that scientists can collect data, opening up new avenues for long-term monitoring at much greater spatiotemporal scales than has hitherto been possible (Burivalova et al. 2019a). The work presented in Chapters 3 and 4 illustrates the potential of this new technology. However, the novelty of audio recording technology means that researchers have yet to reach consensus on the most appropriate way to collect and analyse audio recordings (Bradfer-Lawrence et al. 2019; Gibb et al. 2018; Sugai et al. 2019). In particular, the efficacy of collection protocols has major implications for the long-term value of these datasets (Deichmann et al. 2018; Sugai & Llusia 2019). Acoustic indices have received a fair amount of research attention, perhaps because of the ease with which they can be calculated and compared (Gibb et al. 2018). However, they have often been used inappropriately, and without a clear understanding of the patterns they represent, an argument we present in this thesis.

In Chapter 3 we sought to resolve some of the methodological questions surrounding collection of sound recordings, demonstrating the minimum amount of recordings required to capture a soundscape, and the benefits of continuous recordings rather than sub-sampling. Moreover, we found habitat-distinct soundscapes, suggesting that these soundscapes reflect differences in vegetation structure and wildlife among habitat types. We developed this aspect in Chapter 4, where we show clear patterns in acoustic indices values that depend on avian species richness and abundance. Critically, these recordings represent a permanent record, not only providing a baseline for repeat monitoring, but allowing future re-analysis with as yet undeveloped tools (Deichmann et al. 2018; Sugai & Llusia 2019). As such, they are invaluable for long-term biodiversity monitoring.

6.2.2 Animal dispersal and habitat use within HMLs

As we demonstrated in Chapter 2, the ability of birds to use HMLs varies considerably. While some species have readily adapted to anthropogenic habitat disturbance, others appear particularly sensitive to loss of forest cover. This includes many insectivore species, such as the antbirds assessed in Chapter 5. Antbirds and other understorey insectivores often have restricted natal dispersal and small home ranges (Gorrell et al. 2014; Losada-Prado et al. 2014; Sekercioglu et al. 2002; Tarwater 2012; Woltmann et al. 2012). In translocations experiments with forest-affiliated birds, many species were reluctant to cross open areas, and were often physically incapable of traversing distances of more than 200 m (Gillies & St. Clair 2008; Moore et al. 2008). Hence, reductions in forest cover and increased fragmentation are likely to hinder avian dispersal in HMLs (Ibarra-Macias et al. 2011; Laurance et al. 2004; Lees & Peres 2009; Moore et al. 2008). To gain full understanding of species' use of HML habitats, we need both greater knowledge of both avian dispersal abilities, particularly interspecific differences (Van Houtan et al. 2007), and the relative importance of patch- and intermediate-scale effects on persistence of sensitive species.

Within the broader topic of animal dispersal and habitat use, Chazdon et al (2009) also ask "To what extent do remnant habitats serve as refugia?" In Chapters 2 and 5 we show that many species, and particularly antbirds, were heavily influenced by the presence of remnant forest patches and higher vegetation quality in HMLs. Even generalist bird species often responded positively to increased forest cover. This is mirrored in many other studies, that show the importance of forest fragments in fostering avian persistence in Neotropical HMLs (Arroyo-Rodríguez et al. 2017; Bueno et al. 2018; Carrara et al. 2015; Frishkoff & Karp 2019; Ruffell et al. 2017; Walter et al. 2017). This underlines the importance of retaining forest fragments, even in low intensity HMLs. The high tree cover found in Emparador and many other Mesoamerican HMLs are critical for providing refugia for wildlife (Colorado Zuluaga & Rodewald 2015; Harvey & Haber 1998; Pulido-Santacruz & Renjifo 2011).

Unexpectedly, we found forest fragmentation, i.e. the configuration of forest patches, to be of lesser importance than forest cover in dictating species' presence and abundance. There are three potential explanations for this. First, it may be that there is insufficient variation in the level of fragmentation at the landscape-scale to reveal specific response patterns (Villard & Metzger 2014). Second, fragmentation may only influence species' distributions when overall forest cover is very low, i.e. below a critical threshold (Pardini et al. 2010). Or third, increased resources at ecotones may counteract the loss of core forest habitat for some species (Morante-Filho et al. 2018). In the Emparador landscape we predict that a combination of insufficient landscape-scale variation, and the relatively high forest cover and connectivity underlies the lower importance of fragmentation.

6.2.3 Effectiveness of buffer zones and corridors for the conservation of target species, sources of forest regeneration, and production of ecosystem services

Areas of the Emparador HML with greater forest cover supported a richer and more intact avifauna. In general terms, buffer zones and corridors are key to supporting forest-affiliated species and ecosystem services, by improving connectivity and providing additional habitat and resources. However, Chazdon et al (2009) highlight the "lack [of] experimental studies to determine the most effective design and management of buffer zones and biological corridors". In the tropics, large-scale experimental forest fragmentation has only been conducted at the Biological Dynamics of Forest Fragments Project (BDFFP) in Brazil (Laurance et al. 2011) and the Stability of Altered Forest Ecosystems (SAFE) project in Sabah (Ewers et al. 2011). Findings from the BDFFP supplement findings from HML surveys, providing evidence for the design and management of wildlife-friendly areas in HMLs. Specifically, avian recovery in the regenerating scrub surrounding forest fragments in the BDFFP highlights the importance of semi-natural vegetation in the matrix (Antongiovanni & Metzger 2005; Powell et al. 2013; Wolfe et al. 2015a).

For many species, connectivity to other forest patches is more important than forest age in determining the value of a forest patch for birds (Mayhew et al. 2019). While any increase in forest cover is likely to have some wildlife benefit (Cazetta et al. 2019), careful siting of buffer zones and corridors will be most cost effective. Such interventions are likely to be of greater utility in HMLs with lower levels of connectivity and forest cover than the Emparador landscape. As outlined above, the low intensity land management in the study region means that connectivity levels are high. Species persistence is therefore likely driven by factors such as patch quality. As outlined in chapter 1, edge effects can reduce the value of a forest patch for many species. Although there are high levels of tree cover, there is very little non-edge forest habitat in the open areas of the Emparardor landscape. Therefore targeted buffer zones expanding existing forest patches would likely be of greatest benefit for some of the more sensitive forest-affiliated bird species The predicted distribution maps shown in Chapters 2 and 5 would be ideal for targeting interventions of this type. Corridors and buffer zones must be sufficiently large to ensure effectiveness, although determining the exact size will be context dependent (Luke et al. 2019), and contingent on the species of interest (Lees & Peres 2008b).

6.2.4 Relationship between biodiversity and ecosystem functions: How does functional richness relate to species richness?

Although functional richness and species richness are related, function may be maintained in the face of habitat disturbance and declines in species richness. This is because multiple species may be able to perform the same ecosystem functions in HMLs. For example, plant-frugivore interaction networks are frequently robust; frugivores are often generalists that consume a wide variety of fruits (Levey 1987). There are exceptions to these patterns, with large-seeded fruits such as nutmegs (*Virola* sp.) reliant on large-gaped species likes toucans (*Rhamphastos* sp.) for dispersal (Howe 1981). However, larger species are also more likely to be able to traverse HMLs; we recorded toucans in even relatively isolated forest fragments across the Emparador landscape. This capacity for movement may make interactions between large-seeded trees and their frugivores particularly resilient in the face of habitat disturbance (Moreira et al. 2017). From the perspective of ecosystem function, does it matter whether seed dispersal is conducted by a forest specialist or habitat generalist? Reductions in forest-affiliated frugivores may be balanced by increases in agriculture-affiliated frugivores, as we found in Chapter 2. Predicted frugivore abundance was highest when landscape-scale forest cover was either very high or very low. Thus ecosystem functioning may be maintained in HMLs despite species turnover (Karp et al. 2011; Reid et al. 2014).

Frugivore abundance rather than species' identity often appears to be key for the majority of seed dispersal, and is the best predictor of the richness of dispersed seeds (Pejchar et al. 2008; Stevenson et al. 2015). This pattern in richness of dispersed seeds occurs even when fragmentation has driven changes in community-level functional trait composition (Quitián et al. 2019). Many frugivores undertake movements across HMLs (Chapter 2 of this thesis; Graham 2001; Moreira et al. 2017), so at the landscape scale seed dispersal may be occurring effectively (Carlo & Morales 2016; Díaz Vélez et al. 2015; Holbrook 2011; Moreira et al. 2017; Neuschulz et al. 2011), provided there are sufficient remnant forest fragments to support frugivore populations (Chapter 2 of this thesis; Walter et al. 2017). Thus ecosystem functions such as seed dispersal might be maintained in low-intensity HMLs like the Emparador landscape, where there is still an abundant avifauna.

Chazdon et al (2009) also consider "What agroecosystems and landscape configurations provide the highest levels of ecosystem functions?" It seems reasonable to expect that high levels of heterogeneity and low intensity land management will likely support the greatest levels of biodiversity. Whether this translates in to improved ecosystem functioning is less clear (Luke et al. 2019), nor does it imply which landscape configurations might maximise function. In Emparador, forest-affiliated species were most abundant close to continuous forest, in the less intensively managed areas of the landscape. At increasing distance from continuous forest and closer to urban areas, avian richness and abundance declined. HMLs are inherently dynamic and with the added uncertainties around future patterns of land use and climate change (DeClerck et al. 2010), increasing landscape resilience by improving connectivity and matrix quality is probably the best approach for promoting ecosystem functions (Tambosi et al. 2014).

6.3 Scope for future research

Although the last decade has seen a growth in the understanding of bird community dynamics in tropical HMLs, many of the questions posed by Chazdon et al (2009) are yet to be answered satisfactorily. Bird communities can persist in HMLs, and ecosystem functions can be maintained, but we are still uncertain about their sensitivity to further disturbance. Do the landscape thresholds that predict changes in avian community composition also apply to ecosystem functions? Which ecosystem services are most at risk in the face of ongoing habitat disturbance? Addressing these questions requires a solid understanding of the effects of landscape structure on both community composition, and individual movement patterns. Given the difficulties associated with large-scale experiments, a combination of simulation studies and individual based models might help to clarify these issues (Gelmi-Candusso et al. 2019; Nield et al. 2019; Pegman et al. 2017).

Furthermore, there is a need for finer-scale understanding of the effects of specific land-use practices on wildlife populations. Land management is highly heterogenous at multiple spatial scales, and as Chazdon et al (2009) state; “Few studies have examined how agrochemicals, fire, machinery, introduced plant species, rotational grazing, tree pruning, poly-cropping, harvesting of natural products, or combinations of these practices affect biodiversity in the agricultural matrix.” In addition to these practices, urbanisation, hunting and climate change also require consideration. Although a substantial volume of research has considered many of these factors, they are generally examined in isolation (Barlow et al. 2006; Costantini 2015; Wright 2003). Yet critically, there will be synergies between these elements, likely compounding effects (Arroyo-Rodríguez et al. 2017; Melo et al. 2013).

Recent developments in multifactor experimental approaches may offer new options for investigating such interactions (Rillig et al. 2019). Disentangling these multiple drivers will be essential in improving our understanding of complex HML systems and their wildlife.

6.4 Historical context and future change

6.4.1 The Emparador landscape

Humans have lived in central Panama for millennia, and are likely to have influenced natural habitats and wildlife for much of that time. Archaeological evidence indicates that by 11,000 years BP humans were already exploiting forest resources, and conducting widespread slash-and-burn agriculture (Piperno 1994, 2011). Infectious diseases brought by Europeans led to a population crash in the 17th century, and the decline in anthropogenic pressures allowed forests to regenerate (Koch et al. 2019; Piperno 1994). Whilst forest cover in Emparador has expanded and contracted before, the latest phase of human presence is likely to be far more detrimental (Harvey et al. 2008).

The “forest transition” model posits that globalisation will lead to an increase in afforestation, facilitated by agricultural intensification and increased rural-urban migration (Aide & Grau 2004; Wright & Muller-Landau 2006). However, many consider this scenario overly optimistic (Melo et al. 2013; Perfecto & Vandermeer 2010), and it is unlikely to apply in Emparador because of human population growth. Panama’s population has doubled in the last 35 years, to over 4 million people (UNSD 2019). This has triggered an exponential increase in forest disturbance. Forest cover in Panama declined by 2% between 1990 and 2000 (Kaimowitz 2008) but nearly 20% between 2000 and 2013 (Potapov et al. 2017). While the importance of agriculture to local livelihoods is declining in Emparador, half of Panama’s population lives in Panama City or surrounding the canal region. Emparador is too close to the city to remain undeveloped and major urbanisation is already taking place, including the spread of high-density urban developments on what was previously low-intensity farmland. This will likely have dramatic effects on bird populations (Newbold et al. 2014), and even urban-associated species decline with loss of remnant vegetation and increased building density (Amaya-Espinel et al. 2019; de Toledo et al. 2012).

6.4.2 The wider Neotropics

Patterns of land ownership and management intensity in central Panama are typical of Mesoamerica (DeClerck et al. 2010; Harvey et al. 2008). However, this is in stark contrast to much of the rest of the Neotropics, including the “pristine” forests of Amazonia, where (pre)historic anthropogenic impacts are likely to have been minimal across large areas of the basin (Barlow et al. 2012; Koch et al. 2019). Similarly, the widespread deforestation taking place in the Amazon (Hansen et al. 2013; Potapov et al. 2017) is probably far more destructive than the piecemeal forest loss that has occurred in Panama. Until now, different land-use practices between Mesoamerica and South America have resulted in diverging patterns of species loss following habitat disturbance, and of biodiversity retention in HMLs. Unfortunately, the growth in global consumer markets is concentrating land ownership and encouraging agricultural intensification across both Mesoamerica and South America (Aide et al. 2013; Laurance et al. 2014; Rudel et al. 2009). These changes may mean that Mesoamerican biodiversity begins to follow wider Neotropical patterns, with extinctions, extirpations and declining ecosystem functions (Harvey et al. 2008).

6.5 Policy implications

Robinson et al. (2004) called for greater protection of the forests in central Panama, but no further designations have occurred in the last two decades. Instead the region’s wildlife is threatened by ongoing forest loss and disturbance. In areas such as this, where much of the original forest cover has been cleared, only modification of the HML matrix can secure conservation benefits (Driscoll et al. 2013). Conservation policy should focus on interventions that improve the quality of the HML matrix; restoring habitat to provide additional wildlife resources and to effectively link forest fragments and protected areas.

Forest restoration is key to improving forest cover and connectivity in HMLs, but given the inevitable financial constraints on conservation it is important to consider when it is necessary to actively restore ecosystems (Brancalion et al. 2019; Holl & Aide 2011). In some situations, preventing cattle grazing and fire will be sufficient to permit natural regeneration (Letcher & Chazdon 2009). In others, soil degradation and extreme isolation may inhibit successful floral colonisation (Aide & Cavelier 1994; Zahawi & Augspurger 1999). If this is the case, then interventions such as planting small tree islands of native species can rehabilitate degraded pastures (Petit & Montagnini 2004; Cole et al. 2010). Griscom &

Ashton (2011) argue for further enrichment planting in HMLs, both of fast-growing, nitrogen-fixing species to improve the soil, and late-successional, shade-tolerant species to supplement species composition and structure. Even small amounts of forest-like habitat can be important; increasing the area and structural complexity of forest patches should provide the greatest benefit for birds (Arroyo-Rodríguez et al. 2017; Gillies & St. Clair 2008; Ruffell et al. 2017). Such small-scale actions can represent significant steps towards restoration and encourage the persistence and colonisation of birds, whilst minimising impacts on productivity.

Funding protection and restoration could be achieved through a Payment for Ecosystem Services (PES) framework (DeClerck et al. 2010; Edwards et al. 2019; Garbach et al. 2012). This might come from national government, such as Panama's reforestation of the canal watershed (Van Bael et al. 2013), or from international organisations such as the World Bank, or the United Nations Reduced Emissions from Deforestation and Degradation program (REDD+; Kaimowitz 2008; Pagiola et al. 2005). Compensating landowners has proven an effective means of influencing management practices (Garbach et al. 2012; Pagiola et al. 2005; Wunder 2007), and offering technical assistance can be important in influencing uptake of the scheme (Garbach et al. 2012). However, a PES scheme must be designed carefully, as restoration may not simultaneously optimise conservation and ecosystem service provision (Karp et al. 2015; Reid et al. 2014).

Conservation policy will only be effective if there is widespread engagement with land managers to both assess the feasibility and effectiveness of interventions, and to foster an understanding of the importance of intact functional networks and rich biodiversity (Brancalion et al. 2019; Chazdon 2019; Chazdon et al. 2009; Harvey et al. 2008; Mesquita et al. 2010; Senior et al. 2015). Management actions can have wide-ranging impacts, for example using fire to clear land during drought conditions resulted in the loss of more than a million hectares of forest in Mexico and Nicaragua in 1998 after management fires burnt out of control (Griffith 2000). Similarly, hunting can significantly impact wildlife populations, even in areas of relatively undisturbed habitat (Holbrook & Loiselle 2009; Peres 2000; Suarez & Zapata-Ríos 2019; Whitworth et al. 2018). In situations such as this, it may be possible to improve management practices through the use of educational initiatives and by guaranteeing land tenure (Cruz & Segura 2010; Edwards et al. 2019; Scherr & McNeely 2008). Despite some adverse impacts, it must be emphasised that land managers play an important and positive role in HML conservation. For example, Harvey & Haber (1998) interviewed famers in Costa Rica about retaining trees in pasture, finding farmers were frequently aware of the ecological benefits of retaining trees, and interested in increasing tree cover in their pastures. This suggests that if well-designed policies and incentive structures are in place, successful conservation in HMLs is possible.

Conservation efforts embedded within HMLs can yield advantages for both wildlife and human inhabitants, promoting bird abundance and improving ecosystem services such as pest control (Chazdon et al. 2009b; Karp et al. 2011; Reid et al. 2014). Minimising detrimental management practices should bring biodiversity benefits and improve ecosystem functioning. Whilst knowledge of HML systems is critical to the conservation of both species and functioning ecosystem services, to succeed in regions with a long history of anthropogenic settlement and agriculture any conservation policy must balance wildlife requirements with those of humans. Hence holistic strategies are required for landscape conservation, combining ecology and socio-economics (Melo et al. 2013; Tanentzap et al. 2015).

6.6 Concluding remarks

The Neotropics supports an enormously diverse avifauna, with complex interdependencies between species, and between birds and other taxa. Despite dramatic and sustained disturbance of the original forest habitats, many bird species have successfully adapted to living in HMLs. Up until now, the high heterogeneity of Mesoamerican HMLs has facilitated the maintenance of critical ecosystem services and key interaction networks. However, changing land use patterns threaten these systems. To prevent mass species extinctions, it is essential to preserve and restore the landscape elements that have so far permitted the survival of biodiversity in HMLs. The work presented in this thesis demonstrated the importance of forest fragments and low-intensity management in HMLs to fostering avian communities. Forest fragments and riparian strips should be protected, live fences encouraged, and connectivity fostered. Spreading urbanisation, agricultural intensification and large crop monocultures will likely destroy the biodiversity that has so far persisted in HMLs. Further losses will have detrimental impacts on ecosystem services as well as wildlife populations. Long-term monitoring, with traditional field techniques or audio recorders, are essential to provide evidence supporting conservation. The value of HMLs for wildlife conservation is reliant on retention of forest fragments and connectivity, and this forest cover will only persist if its value is recognised and encouraged.

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