The response of bird assemblages to landscape transformation along the northeast coastal plains of southern Africa.

By

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The response of bird assemblages to landscape transformation along the northeast coastal plains of southern Africa.

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Abstract

The fragmentation and loss of natural habitats brings about species losses. These losses may be amplified or reduced by the composition of the habitats surrounding remnant habitat fragments, i.e the matrix. The influence of the matrix on biological assemblages is, however, complex and poorly understood. Therefore, in this dissertation, I aim to determine whether matrix transformation influences bird assemblages within remnant natural habitat fragments and how patterns of bird diversity and the processes which structure those patterns are influenced at the landscape scale.

In the first study component of this dissertation, bird assemblages were surveyed within 29 and 30 forest fragments embedded within contrasting matrix types: natural (grasslands and woodlands) and transformed (sugarcane, agroforestry, human settlements), and categorised as either forest-specialist or habitat-generalist species. I first fitted eight species-area models to evaluate species-area relationships (SARs) in both matrix types. Second, I calculated Pielou's evenness index to determine if the relationship between evenness and area varied among matrix types. Third, I used a nestedness metric based on overlap and decreasing fill to determine if matrix type influences nestedness amongst forest bird assemblages. Finally, I used binomial logistic regressions to determine the relationship between the presence of each species and forest fragment area in each matrix type. I found that SARs for habitat-generalists were weak within transformed and natural matrices. For forest-specialists, the SAR was weak when the matrix was natural, however, when the matrix was transformed the SAR was strong and resembled that of real islands systems. Forest-specialist assemblages were also significantly nested by area within transformed, but not natural matrices. Moreover, fragment area significantly affected the occurrence of 11 forest-specialist species in transformed matrices, compared to only one species in natural matrices.

In the second study component of this dissertation, I made use of a fractal-based design to survey bird assemblages in seven different habitat types (four human-modified and three natural habitats). I calculated and compared estimated species richness (Chao1) for each habitat. I then

investigated and compared patterns of alpha and beta-diversity within each habitat at three different spatial sampling grains, using generalised linear models and multiple comparison tests. I also made use of the Raup-Crick null modelling approach to determine if processes structuring bird assemblages were more deterministic (niche-based) or stochastic (dispersal-based) than expected by chance. My findings suggested that natural habitats did not always support higher species richness. Rural and urban areas were also capable of supporting high species richness comparable with that of natural forests and woodlands. In contrast, grasslands supported reduced species richness comparable to sugarcane and *Eucalyptus* plantations. Patterns of beta-diversity were found to be inconsistent and to decrease with an increase in spatial grain. Therefore, inferences based on beta-diversity were dependent on the scale at which the analysis was conducted. In contrast, patterns of alpha-diversity were not influenced by spatial grain. The processes driving community assembly were found to not be influenced by anthropogenic transformation and were non-random, and influenced by deterministic niche-based processes.

In this dissertation, I therefore show that forest-specialist bird assemblages may conform to island biogeographic predictions of species loss when embedded within transformed, but not natural matrices. Species extinctions from small forest fragments may, therefore, be prevented by conserving natural- or restoring transformed matrices, and not only by increasing forest area. Moreover, I show that while the conservation of natural habitats is important all habitat types in a landscape are important for regional diversity. Therefore, the inclusion of human-modified habitats into conservation planning and the maintenance of structural heterogeneity within these landscapes may be important for maintaining landscape biological diversity in the future. Finally, I show that a multi-scale sampling approach is important when making inferences about patterns of diversity at the landscape scale.

Acknowledgements

Declaration

I, Marc Trevor Freeman, declare that this thesis/dissertation, which I hereby submit for the degree

MSc Zoology at the University of Pretoria, is my own work and has not previously been submitted by

me for a degree at this or any other tertiary institution.

Signature:

Date:

Disclaimer

This dissertation includes two manuscripts. Chapter 2 was submitted for publication to *Landscape Ecology*. Chapter 3 has been prepared for submission to *Diversity and Distributions*. Styles and formatting of the chapters follow the respective journal requirements. Chapters 1,2 and 4 follow the format requirements for the journal *Landscape Ecology*. Chapter 3 follows the format for the journal *Diversity and Distributions*. I hereby declare all the work to be my own and that I have acknowledged all those who helped me and contributed to the production of this dissertation.

Marc T. Freeman

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For Les and Val de Jager

Chapter 1

GENERAL INTRODUCTION

Biodiversity is in decline globally (Hansen et al. 2013). The most imminent threat to the preservation of biodiversity is the fragmentation and loss of natural habitats through the human modification of landscapes (Noss 1987; Foley et al. 2011). The mark of humanity on the biosphere is now so widespread and profound that many consider the Earth to have entered a new geological epoch, the Anthropocene (Smith and Zeder 2013). Typically landscapes are now dominated by agricultural plantations, urban settlements and human infrastructure, while small remnant natural habitat fragments are embedded within this matrix of human land use types (Gardner et al. 2009; Melo et al. 2013). This transformation is affecting an array of taxa, including mammals (Wearn et al. 2016), plants (Botzat et al. 2015), amphibians (Ferrante et al. 2017), insects (Morante-Filho et al. 2016; Sanchez-de-Jesus et al. 2016), reptiles (Driscoll 2004) and birds (Renjifo 2001). As a result, a large proportion of biodiversity may be lost in the near future (Foley 2005; Lees et al. 2015). It is therefore important that we obtain a better understanding of how biological assemblages respond to anthropogenic transformation. However, variability in findings among studies addressing this problem has made it increasingly difficult for scientists to provide conclusive answers to seemingly simple conservation questions (Gardner et al. 2007). For instance, does matrix type influence community structure within remnant habitat fragments? How do human-modified landscapes influence patterns of diversity? Does the spatial scale at which analysis is conducted influence inferences based on patterns of diversity? Do processes underlying community assembly differ between human-modified landscapes and natural landscapes? Providing answers to these questions are important for future conservation management strategies.

How does matrix type influence bird assemblages in coastal forest fragments?

In an attempt to mitigate the effects of habitat loss and fragmentation, conservationists shifted their attention to the establishment of protected areas (i.e. tracts of natural habitats which are actively managed to minimize the impact of people) and the conservation of large remnant habitat fragments as a cornerstone of biodiversity conservation (Gaston et al. 2008). Protected areas now cover ~19.6 million km^2 (15.4 %) of the earth's terrestrial surface (Gaston et al. 2008; Le Saout et al. 2013). These areas are undeniably important and globally support a species richness 10.6% higher and abundances 14.5% higher than the habitats outside of protected areas (Gray et al. 2016). However, projections of human population growth globally suggest that realistically only a fraction of these protected areas are likely to be preserved effectively into the future (Mcdonald et al. 2008; Watson et al. 2014). For instance, only 9.8% of the tropical forest biome is considered to be part of protected areas (Schmitt et al. 2009). Recent reports also suggest that only 22% of protected areas are managed effectively (Leverington et al. 2010). Moreover, species numbers continue to decline, even within the protected area network (Newmark 2008; Craigie et al. 2010; Laurance et al. 2012). This may be as a result of conservation policy and management largely overlooking the importance of the landscapes adjacent to protected areas and remnant habitat fragments (i.e. the matrix) (Wittemyer et al. 2008; Franklin and Lindenmayer 2009).

Biodiversity conservation often focuses on fragments of remnant native vegetation in isolation of the presumably inhospitable matrix of landscapes in which it is embedded (Saunders et al. 1991; Lindenmayer and Fischer 2006). This approach is in agreement with the theory of island biogeography (IBT; MacArthur & Wilson 1967) which was originally proposed to explain patterns of diversity in real island systems surrounded by inhospitable oceans. IBT posits that island species richness is a function both area and isolation (MacArthur and Wilson 1967). Therefore, large well-connected islands should support high species richness because of increased dispersal ability among islands and greater habitat availability. Moreover, the probability of stochastic extinction on such

islands would also be reduced, due to increased immigration (i.e. rescue effect) from surrounding islands (Brown and Kodric-Brown 1977). In contrast, smaller more isolated islands would likely support more species-poor assemblages, where decreased immigration to the island would promote stochastic extinction (MacArthur and Wilson 1967). This would bring about a nested structure among islands where depauperate species assemblages on small islands would constitute proper subsets of species-rich assemblages on larger islands (Patterson and Atmar 1986).

The extension of IBT to terrestrial systems resulted in the human-induced fragmentation being represented as the simple typology of landscape classification into (i) habitat, that is reduced into fragments and (ii) non-habitat, which is extensive enough to form an inhospitable landscape matrix (McIntyre and Hobbs 1999). If this is true then biological assemblages within remnant habitat fragments should conform to a species-area relationship (SAR), where species richness increases with an increase in fragment area and a decrease in isolation (MacArthur and Wilson 1967). Yet, numerous studies show that landscape fragmentation at the terrestrial level is more complex than a simple binary classification of habitat vs non-habitat (Laurance 2008; Didham et al. 2012; Fahrig 2013, 2017). Conversely, some studies even show that the landscapes which constitute the matrix may even have the capacity to support their own biological assemblages and at the same time complement assemblages within remnant habitat fragments. For instance, Daily et al. (2001) found that a substantial fraction of forest species occurred in the intermediate-intensity agricultural landscape bordering old growth forest fragments in southern Costa Rica (Daily *et al.* 2001- Countryside Biogeography Theory). Dunning et al. (1992) also found that matrices which include natural habitats such as secondary growth forests or grasslands may not only represent complementary habitat for generalist species but also for habitat specialists by allowing for dispersal and resource acquisition (see Habitat Complementation Theory).

Complementation theory and countryside biogeography suggest that matrices may therefore not be completely inhospitable, and could potentially have a positive influence on

assemblages within fragments (Ricketts 2001; Kupfer et al. 2006; Didham et al. 2012). The complementation of resources and habitat for fragment species by the matrix could potentially increase species abundances and reduce local extinctions within habitat fragments (Daily et al. 2001; also see the landscape-moderated insurance hypothesis -Tscharntke et al. 2012). However, matrix complementarity is dependent on life history traits and is therefore species specific (Driscoll et al. 2013). This makes it difficult to set expectations about how matrices will influence entire biological assemblage within a fragment (Driscoll et al. 2013). For instance, habitat generalist species (reproduce and acquire resources in multiple habitat types) are able to disperse through an array of landscape types to acquire resources. Therefore, habitat generalists are more likely to conform to a landscape complementation and/or countryside biogeography framework at the terrestrial level (Daily et al. 2001). On the other hand, habitat specialist species (reproduce and occur within a single habitat) may not be able to disperse into or use resources in the matrix due to individual life history traits (Ewers and Didham 2006a). Therefore, habitat specialists may be more likely to conform to an IBT framework because of the disruption of meta-population dynamics (Eycott et al. 2010; Prevedello and Vieira 2010), edge effects (Driscoll and Donovan 2003; Ries et al. 2004), and altered resource availability (Gascon et al. 1999; Brotons et al. 2003). This could bring about the loss of habitat specialists from small habitat fragments which do not provide sufficient resources for their persistence, in line with IBT. Therefore a SAR typical to that of island biogeography may hold for habitat specialist assemblages but not necessarily for habitat generalist assemblages (Hanski 1999; McIntyre and Hobbs 1999). Based on this information I attempt to better understand how bird assemblages in fragmented forested landscapes respond to anthropogenic matrices and natural matrices.

How are patterns of bird diversity influenced by human-modified habitats?

The conservation and protection of natural habitats is undeniably important, however, it is also useful to understand how biodiversity is maintained within the surrounding human-modified

matrix (Norfolk et al. 2017). Much of the uncertainty regarding the future of global biodiversity is driven by a deficit in information pertaining to the patterns of biodiversity within human-modified landscapes (Gardner et al. 2007). Past studies have understandably focused more on areas that support high levels of plant and animal diversity, such as protected areas (Fazey et al. 2005). For decades it was assumed that human-dominated landscapes were incapable of supporting biological assemblages and provided very little conservation value (Greenler and Ebersole 2015). However, a growing body of literature suggests that these landscapes may have the capacity to support higher levels of biodiversity than was originally assumed (Daily et al. 2001; Barlow et al. 2007; Greenler and Ebersole 2015; Norfolk et al. 2017). For example, Wearn *et al.* (2016) found that logged forest landscapes still provided substantial conservation value for mammal communities in Southeast Asia. Moreover, it is now becoming apparent that the fate of biodiversity in natural protected areas and the surrounding matrix are inextricably linked (Perfecto et al. 2009). While this may be true it is still unclear how human-modified landscapes contribute to regional diversity and how diversity is maintained in these landscapes following transformation (Greenler and Ebersole 2015). Therefore, it is important that we have a clear understanding of the patterns of diversity and the processes shaping them in both natural and human-modified landscapes (Chazdon et al. 2009).

The patterns and processes shaping the spatial scaling of beta and alpha-diversity have not been explored thoroughly across an entire region (Barton et al. 2013). Beta-diversity is the component of regional species richness (i.e. gamma diversity) which comes about from variation among local assemblages (i.e. alpha-diversity) within a landscape (Socolar et al. 2015). Patterns of beta-diversity are especially important when investigating how processes shape assemblages within a habitat (Anderson et al. 2011). However, our understanding of the magnitude of biodiversity loss (or gain) and patterns of diversity within a landscape depends on the scale at which we measure it (Socolar et al. 2015). For instance, patterns at at a local scale most often suggest that at diversity is maintained (Vellend et al. 2013; Dornelas et al. 2014), whereas at larger more coarse scales patterns often indicate that we are in the midst of an extinction event (Barnosky et al. 2011; Pimm et al.

2014). For example, Karp *et al.* (2012) found that at large spatial scales beta-diversity declined in human-modified agricultural landscapes, while other studies (Tylianakis *et al.* 2006, Kessler *et al.* 2009) which tested for the same effect but only used fine spatial scales, did not document a decline in beta-diversity. Therefore, if patterns of beta-diversity are to aid conservation strategies reliably, it must be measured appropriately.

Even when measured at the appropriate scale, inferences that are made from patterns of beta-diversity are not straight forward. Obtaining a maximum value for beta-diversity is not necessarily a conservation goal for maintaining high landscape species richness (Socolar et al. 2015). During the initial stages of human modification of a landscape, localised species losses and the invasion of generalist synanthropic species may result in increased levels of beta-diversity within that landscape. For example, the burning of sugarcane during harvesting should result in the formation of a new community assembly during which beta-diversity is initially likely to be high. However, as the sugarcane plantations re-establish and the landscape structure becomes more homogenised, beta-diversity is likely to decrease. Moreover, even when beta-diversity decreases, compensatory changes in alpha-diversity may buffer gamma diversity (referred to as landscape species richness) against declines in beta-diversity. Null models and pairwise beta-diversity metrics are useful for gaining an understanding of how landscape species richness is maintained. Null models are particularly useful in partitioning beta-diversity between the component expected by chance and that driven by landscape structure and ecological filters. Therefore, measuring beta-diversity independently of alpha and understanding how alpha and beta-diversity contribute to landscape species richness are important when interpreting patterns of beta-diversity.

Addressing the problems

The coastal plains of KwaZulu-Natal, South Africa, form part of the Maputaland Coastal Forest Mosaic (Burgess et al. 2004), the Maputaland Centre of Plant Endemism (Van Wyk and Smith 2001) and the Maputaland-Pondoland-Albany biodiversity hotspot (Küper et al. 2004). This region is

therefore of conservation importance. However, like most tropical and subtropical landscapes, these

coastal plains have been subjected to decades of intensive anthropogenic transformation (van Aarde

et al. 2014; Jewitt et al. 2015). Approximately 1.2% of this landscape has been transformed per

annum since 1994 (Jewitt et al. 2015) and ~82% of coastal forests may have been lost (Olivier et al.

2013). As a result, this landscape is now composed of a mosaic of different land-use types, primarily

dominated by humans (Jewitt et al. 2015). Remnant fragments of natural habitats specifically coastal

forest are now mostly small and isolated (Lawes et al. 2007). In contrast, the matrix of landscapes

surrounding these fragments are typically extensive human land use types such as sugarcane

cultivations, exotic tree plantations, urban settlements and to a lesser extent natural mixed

woodlands and grasslands (Van Wyk and Smith 2001). The transformation of this landscape is

unlikely to decline or stop within the foreseeable future with a growing human population and an

increased demand for agriculture, forestry and mining within the region (Mucina and Rutherford

2006).

The landscape in Maputo province of southern Mozambique, however, contrasts with that

of KwaZulu-Natal. Here coastal forests fragments are embedded within a matrix of natural

grasslands, woodlands, and low-density rural settlements. This landscape lies directly north of the

KwaZulu-Natal coastal plains but forms part of the same centres of endemism (Burgess et al. 2004).

Little to no human disturbance has occurred here, and to some extent, this landscape represents

something similar to what we may have expected for the coastal plains of KwaZulu-Natal prior to

extensive anthropogenic transformation. Southern Mozambique also supports a remarkably similar

bird community to that in coastal plains of KwaZulu-Natal (Hockey et al. 2005).

These two contrasting landscapes provided a valuable opportunity to assess some of the

previously mentioned fundamental questions relating to how biological assemblages respond to the

anthropogenic transformation of landscapes. In chapter 2 I attempt to investigate how matrix types

(i.e. anthropogenic and natural) influence bird assemblages in coastal forest fragments by

investigating species-area relationships, patterns of nestedness and evenness and species-specific responses to fragment area. In chapter 3, I investigate how patterns of bird diversity are influenced by human-modified landscapes that make up the matrix surrounding coastal forests. I specifically assess landscape species richness, alpha-diversity, beta-diversity and the processes (stochastic or deterministic) underlying their community assembly (stochastic or deterministic) in the seven most prevalent landscapes along the coastal plains of KwaZulu-Natal.

From previous studies, we can hypothesise how patterns of bird diversity will be influenced within human-modified habitats (e.g. Tscharntke *et al.* 2012, Karp *et al.* 2012, Püttker *et al.* 2015). First I predict that the SAR for forest specialists will conform to the predictions of IBT in the natural and anthropogenic landscape. However, I expect the slope of the SAR to be steeper when the matrix is anthropogenic, compared to when it is natural because specialist species may not be able to disperse through an anthropogenic matrix (Brooks et al. 1997). Conversely, the SAR for generalist species will fit into a countryside biogeography framework, where large and small fragments harbour a similar number of species. Second, I predict that forest specialist bird assemblages will be more nested than habitat generalists. I also expect nestedness to be greater for anthropogenic than natural matrices because of the loss of specialist species from small fragments. Third, I predict that large forest fragments will support rarer forest specialist species, which would increase assemblage unevenness. Conversely, as forest fragments become smaller I expect many forest specialist species to be lost and for a few generalist species to dominate the assemblage, bringing about a more evenly distributed assemblage (Sanchez-de-Jesus et al. 2016). Assemblage evenness should therefore decrease with an increase in fragment area and we expect this pattern to be stronger in anthropogenic than natural matrices. Finally, I investigate species-specific responses to matrix transformation.

By measuring and comparing species richness, alpha and beta-diversity across the predominating landscapes on the coastal plains of KwaZulu-Natal I can make predictions about how patterns of diversity are influenced by human-modified landscapes. First, I predict that avian species

richness (alpha-diversity) would be higher in natural than human-modified landscapes. Second, I

predict that bird assemblages in human-modified landscapes would be more homogenised than

natural landscapes. This is because human land-use intensification often increases similarity in

environmental conditions between distant sites, thereby reducing beta-diversity within a landscape

(Karp et al. 2012; but also see Tscharntke et al. 2012). Mean beta-diversity should, therefore, be

lower in human-modified landscapes than in natural landscapes. Third, I hypothesise bird

assemblages within natural habitats to be structured more through deterministic processes, while in

human-modified landscapes we expected more stochastic processes to shape bird assemblages.

Finally, I predict that although estimates of diversity (alpha and beta) will vary across different

sampling grains, the general patterns amongst landscapes would be similar- i.e. alpha and beta-

diversity would be higher in natural than anthropogenic habitat types and deterministic not

stochastic process would structure communities in natural, but not human habitat types irrespective

of the sampling grain of the investigation.

Chapter 2

Matrix transformation alters species-area relationships in fragmented coastal forests

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Running head: Anthropogenic matrices amplify area effects

ABSTRACT

Context- Ecological theory suggests that large habitat fragments should harbour more species than small fragments. However, this may depend on the surrounding matrix. Matrices in fragmented landscapes may either amplify or reduce area effects, which could influence predicted extinctions based on species-area relationships.

Objective- To determine the influence of matrix type on species-area relationships (SARs).

Methods- We surveyed birds within 59 coastal forest fragments in two matrix types, anthropogenic (South Africa) and natural (Mozambique). We classified species as forest specialists or habitat generalists and fitted species-area models to compare how SAR slopes differed among matrix types. We also calculated nestedness and evenness to determine if these varied among matrix type and used logistic regressions to identify species-specific responses to matrix type.

Results- For habitat generalists, SARs were weak within both matrices, while for forest specialists it was strong in the anthropogenic but weak in the natural matrix. In the former, the SAR was similar to those recorded for real islands within archipelagos. Forest specialist assemblages were nested by area within anthropogenic, but not natural matrices. Matrix type did not influence evenness. Area only affected the occurrence of one species when the matrix was natural, compared to 11 species when it was anthropogenic.

Conclusions- Forest specialist bird species conformed to island biogeographic predictions of species loss in forest fragments embedded in anthropogenic, but not natural matrices. Extinctions from small forest fragments might be prevented by conserving natural- or restoring anthropogenic matrices, as well as by increasing forest area.

Keywords: birds; extinction; forest specialists; habitat generalists; island biogeography; nestedness; anthropogenic habitats

INTRODUCTION

Habitat loss and fragmentation are accompanied by a loss of species (Fahrig 2003; Haddad et al. 2015). Species losses are usually greatest in the smallest fragments and increase with time (Pardini et al. 2010; Haddad et al. 2015) – however, this may depend on the quality of the surrounding matrix (Öckinger et al. 2012). The matrix is an extensive land cover with different land-use types embedded within it, which may be inhospitable for some, but not all species (Driscoll et al. 2013). For example, matrices made up of human land-use types such as agricultural plantations and urban developments may be inhospitable for habitat specialists, but not habitat generalists. However, matrices, which include natural habitats such as secondary forests or grasslands, may not only represent complementary habitat for generalists, but also for specialists by allowing for dispersal and resource acquisition (Dunning et al. 1992). Consequently, different matrices can either amplify or reduce area effects in remaining habitat fragments (Öckinger et al. 2012). If matrices amplify area effects, predictions based on conventional species-area relationships may underestimate deterministic species losses (Koh and Ghazoul 2010; Jamoneau et al. 2012). Conversely, if matrices reduce area effects, the influence of fragmentation on biodiversity losses may be overestimated (e.g. Tscharntke et al., 2012).

Matrices that are inhospitable to fragment-dwelling species may amplify species-area relationships (SARs). SARs are then likely to conform to island biogeography theory (IBT), i.e. where species richness increases with fragment size, irrespective of the size of the community assemblage (MacArthur and Wilson 1967). This effect is likely to be stronger when dispersal is impaired compared to when it is more frequent (Brooks et al. 1997) and may also be dependent upon the total amount of remaining habitat in a landscape (Fahrig 2003). Some studies suggest SARs may be intensified when the threshold of remaining habitat decrease below one-third of the landscape (e.g. Andrén 1994; Fahrig 2003), but this is not always the case. For example, Pardini et al. (2010) only found strong area effects in landscapes with intermediate amounts of forest cover, but not in forested and deforested landscapes. Area effects may furthermore vary across study locations, taxa

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and spatial scale (Fahrig 2013). This highlights the complexity involved in applying island theory to anthropogenically modified landscapes (Haila 2002) and why SARs are rare for fragments embedded in terrestrial matrices (Drakare et al. 2006). For instance, Mendenhall et al. (2014) found that bats follow island-biogeographic predictions of species loss when water surrounds habitat fragments, but not where coffee plantations and pastures do. It follows that matrices may also reduce area effects in fragmented landscapes, i.e. small and large fragments will harbour a similar number of species. This could be because an increased in landscape heterogeneity provides for higher resilience and stability of ecological processes (Martensen et al. 2012), species are able to utilise matrices through cross-habitat spill-over (Ries et al. 2004), and/or the amount of available habitat increases for some species (Fahrig 2013). If this is the case, SARs are more likely to conform to a landscape complementation (sensu Dunning et al. 1992) and/or countryside biogeography framework (Daily et al. 2001). These frameworks recognises that matrices are not completely inhospitable (as assumed by the island biogeographic model), but could provide resources for many species to increase their abundances and mitigate extinctions of populations and species from habitat fragments (Daily et al. 2001; also see the landscape-moderated insurance hypothesis -Tscharntke et al. 2012).

Generalist species are able to utilize resources in the surrounding matrix because they are more likely to conform to a landscape complementation and/or countryside biogeography framework (Daily et al. 2001). Indeed, anthropogenic matrices may provide generalist species with a platform from which to invade habitat fragments (Bridgman et al. 2012). A few generalist species may, therefore, replace many specialist species (biotic homogenization) and bring about an increase fragment assemblage evenness (Lôbo et al. 2011; Carrara et al. 2015; Ibarra and Martin 2015). This effect may be particularly evident in small fragments where core habitat is lacking (Mac Nally 2007). When habitat generalists replace specialists, the expected SAR may even be reversed, i.e. small fragments may harbour more generalist species than large fragments (Morante-Filho et al. 2015). Specialist species, on the other hand, may be more likely to conform to an island biogeography framework because the disruption of metapopulation dynamics (Eycott et al. 2010; Prevedello and

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Vieira 2010), edge effects (Driscoll and Donovan 2003; Ries et al. 2004), and altered resource availability (Gascon et al. 1999; Brotons et al. 2003) may lead to their disappearance from small forest fragments. As a result, specialist assemblages may be nested within fragments embedded within an anthropogenic matrix (Wethered and Lawes 2005). Nestedness is a type of richness pattern where species present in one site are a subset of species occurring at another more species-rich site (Ulrich et al. 2009). When assemblages are nested, conservation efforts may be better off focusing on large fragments, simply because large fragments will harbour most of the species found in the region (Matthews and Whittaker 2015). This does not, however, imply that smaller fragments do not serve an important role in fragmented landscapes, for example promoting dispersal and the recolonization of species-poor fragments (Dunning et al. 1992; Mueller et al. 2014).

In this study, we tested whether matrices amplified or reduced SARs of birds that occur within fragmented coastal forests along the east coast of southern Africa. We defined matrices as any land-use type that was not coastal forest, but in which coastal forest fragments were embedded. We surveyed birds in 29 coastal forest fragments surrounded by anthropogenic matrices (sugarcane, *Eucalyptus* and *Pinus* plantations, urban settlements) and 30 fragments surrounded by natural matrices (grasslands and woodlands). We categorised all species as either forest specialists or habitat generalists and then tested three hypotheses. First, we hypothesised that the SAR for forest specialists would conform to the predictions of IBT in the natural and anthropogenic landscape (Guldemond and van Aarde 2010). However, we expected the slope of the SAR to be steeper when the matrix is anthropogenic, compared to when it is natural because specialist species may not be able to disperse through an anthropogenic matrix (Brooks et al. 1997). Conversely, the SAR for generalist species would fit into a countryside biogeography framework, where large and small fragments harbour a similar number of species. Second, we hypothesised that forest specialist bird assemblages would be more nested than habitat generalists. We also expected nestedness to be greater for anthropogenic than natural matrices because of the loss of specialist species from small fragments. Third, we hypothesised that large fragments would support rarer forest specialist

species, which would increase assemblage unevenness. Conversely, as forest fragments become smaller we expected many forest specialist species to be lost and for a few generalist species to dominate the assemblage, bringing about a more evenly distributed assemblage (Sanchez-de-Jesus et al. 2016). Assemblage evenness should therefore decrease with an increase in fragment area and we expected this pattern to be stronger in anthropogenic than natural matrices. Finally, we investigated species-specific responses to matrix transformation.

METHODS

Study areas

We studied forest birds within two fragmented landscapes located in South Africa (28°51'51" - 28°28'57"S, 31°38'9" - 32°24'70" E) and Mozambique (26°41'40" - 26°16'15"S, 32°42'23" - 32°54'27"E) (Fig. 1). Both landscapes formed part of the critically endangered Maputaland Coastal Forest Mosaic (Burgess et al. 2004), the Maputaland Centre of Plant Endemism (Van Wyk and Smith 2001) and the Maputaland-Pondoland-Albany biodiversity hotspot (Küper et al. 2004). Climatic conditions at these study areas were similar with hot and wet summers (October– March) and moderate to warm and relatively drier winter periods (April–September). Historically, natural grasslands and woodlands adjoined these forests. However, in many areas sugarcane and *Eucalyptus* plantations, mines, and rural and urban settlements have replaced these habitats. This is specifically true for coastal forests in KwaZulu-Natal, South Africa, where 1.2% of the natural landscape has been transformed per annum since 1994 (Jewitt et al. 2015). However, this has not been the case in the Maputo province of southern Mozambique. Here coastal forests are embedded within a matrix of grasslands, woodlands, and low-density rural settlements. Vegetation types were defined as woodlands when trees dominated the vegetation, but not to the extent that the canopies were continuous or overlapping (less than 50% canopy cover) (Lawes et al. 2004). These two contrasting landscape types provided us with a valuable opportunity to assess the influence of matrices on SARs

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because we could take into account habitat type (coastal forests) within the different matrices (human land-use types in South Africa and natural grasslands and woodlands in Mozambique). We surveyed 29 (range 0.02 km^2 - 30.40 km^2) and 30 (range 0.05 km^2-74.30 km^2) forest fragments in South Africa and Mozambique respectively.

Data collection

Bird communities were surveyed in forest fragments embedded within both matrix types using point counts (Bibby et al. 2000). Both surveys were conducted during the breeding season (Dec, Jan, Feb) during the 2007/2008 and 2014/2015 summer survey seasons. We surveyed 220 points within 30 fragments in the natural landscape and 227 points within 29 fragments in the anthropogenic landscape. Each survey point was visited only once during the study. Both landscapes included dune, swamp, and coastal lowland forests. Thirteen sand forest fragments were surveyed within the natural landscape, but we did not survey any sand forest fragments in the anthropogenic landscape. One scarp forest fragment was surveyed in the anthropogenic landscape. Despite discrepancies in the classification of these different forest types, we opted to recognize coastal forests as comprising these five forest types because they share more than 90% of forest bird species (Von Maltitz et al. 2003; Lawes et al. 2007).

Point counts took place between ~05:00 h and 09:00 h to avoid high midday ambient temperatures that may reduce bird activity. All observers (seven in total) had prior knowledge or were trained to identify coastal forest birds based on calls and appearance. Observers were randomly assigned to forest fragments. More than half (60%) of the survey points in both landscapes were surveyed by the same two observers. Each forest fragment was randomly assigned survey points, which were located using a GPS (Garmin Map 62). The number of survey points per forest fragment ranged from 3-6 for fragments < 5km^2, 6-15 for fragments between 5 and 20km^2 and 15-36 for fragments > 20km^2. Sampling effort varied with fragment size, in an attempt to ensure that the sufficient coverage of bird assemblages within each fragment was achieved. Upon arrival at the

survey point, observers waited for two minutes to allow birds that might have been disturbed to

acclimatise to their presence. The observer then recorded bird species that were judged to be heard

or seen, within an approximate 60m radius for 10 minutes. Surveys were abandoned on windy and

rainy days. Species flying above the canopy were not recorded.

All species recorded during our surveys were categorised as either forest specialist or habitat

generalist species based on Hockey et al. (2005) and the South African Bird Atlasing Project

(www.*sabap2.adu.org.za*) (see table S1 in Appendix S1). We classified forest specialist species as

those that live and reproduce only in forest habitats (also see Lawes et al. 2007). Habitat generalists

were classified as those species that occur within more than one habitat type based on (Hockey et

al. 2005). Consequently, edge species were also classified as habitat generalists because they could

utilize more than one habitat type.

Data analyses

We assessed sampling saturation for each of the 59 surveyed forest fragments using sample-

based accumulation curves calculated in EstimateS 8.2.0 (Gotelli and Colwell 2001; Colwell 2013).

The program uses abundance based data as an input and then calculates rarefied estimated species

richness as Choa1 values for each forest fragment (Colwell 2013). Chao1 is the most commonly used

index for estimating species richness and is based on the frequency of an individual's occurrence

within a sample (Chao 1984). By extrapolating from the recorded observations, estimated species

richness (Chao1) within each of the surveyed forest fragments at both landscapes was obtained.

These values were then used to fit the respective species-area models. We also calculated the

coverage based estimate values for each forest fragment using the iNEXT package in the R

programming environment. Coverage based estimates provide a measure of sample completeness,

giving the proportion of the total number of individuals in an assemblage that belong to the species

represented in the actual sample (Chao and Jost 2012). This ensured that species richness for all

forest fragments was comparable as the set of communities in each forest fragments was based on

samples of equal completeness (Gotelli and Colwell 2001; Chao and Jost 2012). We tested for spatial autocorrelation in each landscape using Mantel tests based on the Bray-Curtis dissimilarity among fragments. Bird assemblages were not spatially auto-correlated in the anthropogenic (Mantel r = 0.07; *P* = 0.25) or natural landscape (Mantel r = -0.06; *P* = 0.91).

Species-area relationships

Numerous functions, which vary in complexity, have been proposed for modelling SARs (Dengler 2009; Triantis et al. 2012). The most widely used of these is the power model $S = cA^z$ where S is species richness, A is area of fragment, and c and z are constants (Arrhenius 1921; Preston 1962). The power model is particular useful when modelling SARs because the z-value, which represent the slope of the SAR, provides information on the spatial arrangement of habitat fragments (Preston 1962). Low z-values that range from 0.12 - 0.18 suggest continuous habitats (Johnson et al. 1968; Brooks et al. 1997) where populations in small habitat fragments are "rescued" from local extinction by the constant immigration of species from surrounding areas (Rosenzweig 1995). Real island systems in archipelagos typically display a z-value which ranges between 0.25 - 0.35 (Johnson et al. 1968). Conversely, high z-values that range from 0.7 - 0.9 suggest fragmented systems with no immigration between fragments (Brooks et al. 1997).

The power model, however, may not always provide the best fit for species-area relationships. To evaluate species-area relationships we fitted eight species-area models to forest specialists and habitat generalist's species richness for forest fragments embedded in the anthropogenic and natural matrices respectively. These models included the power, exponential, negative exponential, monod, rational functional, logist, Lomolino and the cumulative Weibull model (see Triantis et al. 2012) for descriptions of the analytical formulae for each model). Species-area models were fitted using the mmSAR package (Guilhaumon et al. 2010) in the R programming environment (R Development Core Team 2012). SAR models were fitted in arithmetic space employing nonlinear regressions by minimizing the residual sum of squares (RSS) using the unconstrained Nelder–Mead

optimization algorithm (Dennis and Schnabel 1983). Assuming normality of the observations, this approach produces optimal maximum likelihood estimates of model parameters (Rao 1973). We evaluated model fit by statistically evaluating normality and homoscedasticity of residuals. A model is considered not to be valid for a given data set if Pearson's product-moment correlation coefficient and/or Shapiro's normality tests on residuals were significant at the 5% level (Guilhaumon et al. 2010). We also used the information theoretic framework for model selection proposed by Burnham and Anderson, (2002). We compared the fit of the SAR models using the small-sample corrected Akaike's information criterion (AICc), a modification of the AIC that contains a bias correction term for small sample size. The model with the lowest AICc value was considered to fit the data best (Burnham and Anderson 2002). Models with ΔAICc values < 2 of the best model were considered to have similar support (Burnham and Anderson 2002). We also calculated z (the slope of the SAR) and c (a constant) for all of the fitted SAR functions.

Evenness and dominance

We used Pielou's J-value (Pielou, 1967) to calculate evenness of species assemblages within each forest fragment embedded in both matrix types. The J-value ranges from zero to one – a higher J-value reflects less variation between species abundances within a community (i.e. more even), while a lower J-value reflects higher variation (i.e. less even). We may, therefore, expect that assemblages dominated by a few generalist species will have a higher J-value than those with similar numbers of specialists and generalists. We tested if there was a significant difference in the J-values (mean J-value ± SE) calculated for the anthropogenic and natural matrices using a Mann-Whitney test (non-parametric, two-tailed). We then used general linear regressions to evaluate the relationship between evenness and forest fragment area to test if these relationships differed among the natural and anthropogenic landscape. Evenness was calculated with the VEGAN package (Oksanen et al. 2013a) in the R programming environment (R Development Core Team 2012).

Nestedness

We calculated nestedness for forest specialist and habitat generalist assemblages within both matrix types using the nestedness metric based on overlap and decreasing fill (NODF) (Almeida-Neto et al. 2008). The NODF is considered to be the most appropriate metric for measuring nestedness (Ulrich and Almeida-Neto 2012). A score between 0 and 100 is obtained when using NODF, with 100 being completely nested and 0 not nested. The metric calculates nestedness independently for i) sites (numerical matrix rows), ii) species occurrences (numerical matrix columns) and iii) the entire numerical matrix combined ("max matrix") (Matthews and Whittaker 2015). We followed a procedure similar to that of Matthews & Whittaker (2015), by which NODF values were calculated using presence-absence matrices in the VEGAN R package (Oksanen et al. 2013a). Three nestedness values were obtained, namely global NODF (nestedness of entire matrix), maximal NODF (maximum nestedness for rows), and nestedness by area (area NODF). Global nestedness indicates the nestedness for the entire matrix (i.e. nestedness for the entire landscape), while maximal NODF indicates the highest nestedness value recorded within the presence-absence matrix (i.e. the fragment with the highest level of nestedness in the landscape). Nestedness by area indicates the effect that fragment area has on estimates of nestedness.

The global NODF value for the entire presence-absence matrix was calculated initially, and row orders were not held constant. The maximal NODF amongst rows were then calculated, followed by the area NODF value during which rows were held constant and arranged in descending order of area (largest forest fragment as the top row) (Matthews and Whittaker 2015). Using a standard Spearman's correlation test, we were able to determine if the maximal NODF and area NODF values were significantly correlated. A strong correlation suggests that the patterns of nestedness observed in the study were driven by area (e.g. Wang et al., 2010). Therefore, the NODF metric allowed for inferences as to whether the transformation of the matrix leads to a more nested bird community amongst forest fragments, and whether area drives nestedness.

Species presence and forest fragment area

To determine the relationships between the occurrence of each species and the size of forest

fragments in each matrix type we used binomial logistic regressions. We used presence-absence

data to model the relationship between species occurrence and fragment area for each forest

specialist and generalist bird species recorded more than once within each matrix type (17 forest

specialist and 33 habitat generalist species - 100 models that included each species for both matrix

types). This was done for two reasons. First, we wanted to determine if forest specialist species in

anthropogenic matrices were more likely to occur in large forest fragments, while forest specialists

in natural matrices would not be affected by forest fragment size. Second, we wanted to identify

which species were sensitive to fragment area. For each model (i.e. species), we obtained a *P*-value,

which indicated whether the presence of a species was significantly influenced by forest fragment

area. *P*-values > 0.05 indicate no or little effect of area on a bird species, while *P-values* < 0.05

indicate a strong effect of fragment area.

RESULTS

We identified 123 bird species among 5 527 records in 59 forest fragments. Surveys in the

anthropogenic landscape yielded 99 species from 3 200 bird records, of which 33 were forest

specialist and 66 habitat generalist species. Coverage based estimates suggested that in the natural

landscape sampling coverage amongst forest fragments ranged from 67% - 98% with a mean value

of 88%. While in the anthropogenic matrix sampling coverage ranged from 60% - 95% with a mean

value of 82%. The natural landscape yielded 89 species from 2 327 records, of which 27 were forest

specialist and 62 habitat generalist species. Sixty-five out of 123 species were recorded in both

landscapes. However, the overlap in the distributional ranges suggests that 111 out of 123 species

occurred within both landscapes (Hockey et al. 2005). Forest specialist composition between

landscapes was similar with 24 out of 36 species recorded in both landscapes. Thirty of 36 forest

specialists occurred at both landscapes (Hockey et al. 2005). Only about half (41 out of 87) of habitat

generalists were recorded at both landscapes. Yet, based on distributional ranges, 81 out of 87 recorded habitat generalist species occurred within both landscapes (Hockey et al. 2005).

Species-area relationships

The power model yielded the best-fit model for the relationship between forest specialist and generalist's estimated species richness (mean Chao1) and forest area in natural and anthropogenic matrices (Fig. 2). AICc values for the power model were the lowest amongst the eight models or were within ΔAICc values < 2 of the best model (Table 1).

Evaluations of the z-values for the four different models suggest that the relationship between Chao1 estimated species richness and area was strongest for forest specialists in anthropogenic matrices ($z = 0.21 \pm 0.02$). Forest specialist species in natural matrices did not show a strong relationship between species richness and area ($z = 0.02 \pm 0.03$). Generalist species showed a weak relationship between species richness and area in anthropogenic ($z = 0.07 \pm 0.04$) and natural matrices ($z = 0.02 \pm 0.04$) (Fig. 2).

Linear regressions based on log transformed area data indicated that the relationship between forest specialists and area differed significantly (p<0.001) between the anthropogenic (slope = 0.13 ± 0.02, F=38.97, dfn=1, p<0.001) and natural habitat (slope = 0.01 ± 0.01, F=0.51, dfn=1, p=0.47). Conversely, the relationship between habitat generalists and habitat area at the anthropogenic (slope = 0.04 ± 0.02, F=7.05, dfn=1, p=0.01) and natural habitat (slope = 0.01 ± 0.02, F=0.51, dfn=1, p=0.48) was not significantly different (p=0.12).

Evenness and dominance

Bird assemblages within forest fragments were significantly less even when the matrix was anthropogenic (Mean J-value = 0.92 ± 0.004) compared to when it was natural (Mean J-value = 0.95 ± 0.0032) (Mann-Whitney Test, p < 0.001). Linear regressions indicated that evenness of bird assemblages decreased with forest fragment area in both landscape types. Although this effect was

stronger in the anthropogenic (slope = - 0.02 ± 0.002, F=16.51, p < 0.001) than the natural (slope = -0.01 ± 0.001, F=6.34, p=0.018) landscape the slopes were not significantly different (F=1.927, dfn=1, p=0.17) (Fig. 3).

Nestedness

The global NODF for species assemblages was similar between landscapes, with the natural matrix returning a global NODF of 54.65 and the natural matrix a global NODF of 47.68. Global NODF values for forest specialist species in both natural (global NODF=70.05) and anthropogenic (global NODF = 73.21) matrices were also similar. Both these values for forest specialists were higher than habitat generalist species with global NODF values of 48.21 and 43.90 in anthropogenic and natural matrices respectively.

Maximal NODF values for forest specialist species in both anthropogenic and natural matrices were also similar, with values of 77.57 and 72.34 respectively. The difference in nestedness between matrices was only evident in the area NODF values; forest specialist species in the anthropogenic matrix had an area NODF of 67.66, while forest specialists in the natural matrix had an area NODF of 45.53.

For both forest specialists and habitat generalists in anthropogenic landscape the Maximal NODF and area NODF values were strongly correlated (all Spearman rho > 0.7, p < 0.01). Forest specialist and generalist species in the natural matrix returned significant Spearman's correlations < 0.5 (see Table 2).

Species presence and forest fragment area

Eleven of the 17 forest specialist species in forest fragments in the anthropogenic matrix were influenced by forest fragment size (*P*-value< 0.05) (see Fig. S3 in Appendix S3).In contrast, only 1 out of 17 forest specialists (Narina Trogon, *Apaloderma narina*) was significantly influenced by forest fragment size when the matrix was natural (see Table 3). In forest fragments in the anthropogenic

matrix, only 3 out of 33 habitat generalists were affected by forest fragment size. In the natural

matrix, only 1 out of 33 habitat generalist species was affected by forest fragment area (see Table 3

for reported *P*-values for each species).

DISCUSSION

Large forest fragments should harbour more species than small forest fragments (MacArthur and

Wilson 1967). The reduction and division of extensive forests into smaller fragments should

therefore result in local extinctions (Haddad et al. 2015; but also see Laurance 2008). However, our

results suggest that this effect was stronger when human land-use types surround forest fragments

than when grasslands or woodlands do. When the matrix was natural, small and large forest

fragments harboured a similar number of forest specialist species. Forest area did not affect the

number of habitat generalist species when the matrix was anthropogenic or natural. A landscape

complementation or countryside biogeography framework would therefore be applicable to

generalist species in both matrix types, but only to forest specialist species when natural matrices

surround forest fragments. However, where human land-use types surround forests fragments,

forest specialist species conform to island biogeographic predictions of species loss.

The power model performed slightly better than most SAR models and was therefore

selected to assess SAR for forest specialist and habitat generalist species in both natural and

anthropogenic landscape. This selection was also based on Triantis et al. (2012) who found that the

power model ranked first for 465 island data sets, while Dengler (2009) also suggested that the

power function should be used to describe and compare any type of SAR. The power model

performs well when predicting species richness over a ten-fold increase in area, and may be one of

the reasons why it was the best fit for all four of our datasets (Dengler 2009). However, it is

necessary to exercise caution when assigning an ecological interpretation to the parameters of the

power model (Triantis et al. 2012). For instance, the sampling scheme, spatial scale, taxa and habitat

type may influence the slope of the SAR (z-value) (Drakare et al. 2006). In our study, these variables

were kept constant among landscapes and study fragments. The SAR slopes were thus comparable – specialist species in anthropogenic matrices had a high value of z (0.21), compared to the low z-value of specialists in natural matrices (0.03) and generalists in natural (0.02), and anthropogenic matrices (0.08).

Why do forest specialist species disappear from small forest fragments when the matrix is anthropogenic? Anthropogenic effects on landscapes may homogenize landscape patterns, introduce novel patches and dynamics, and alter patch dynamics (Urban et al. 1987). The heterogeneous, tree-grass matrix typical of the coastal plains of southern Africa may provide forest specialist species with stepping stones that allow them to recolonize isolated forest fragments (Mueller et al. 2014). However, the transformation of the matrix into homogeneous agricultural fields may remove these stepping-stones, and could therefore disrupt dispersal and metapopulation dynamics (Mueller et al. 2014). Following local extinctions, small fragments cannot be recolonized, leading to the absence of forest specialists from small forest fragments. Moreover, natural matrices such as grasslands and woodlands may provide supplementary resources to forest specialist species (Dunning et al. 1992). For example, Trumpeter Hornbills (*Bycanistes bucinator*) nest in large forest fragments but frequently visit fruiting trees in the matrix (Lenz et al. 2011). It may therefore be a mistake to regard natural grasslands and woodlands that surround forest fragments as matrices, as these land-use types may provide additional habitat to forest specialist species. The third reason and one we consider most likely is that matrix transformation alters patch dynamics by influencing tree community composition and structure within forest fragments (Laurance et al. 2006; Botzat et al. 2015). Forests with a high diversity of trees provide for a higher variety of birds (Tews et al. 2004). However, the replacement of natural matrices with human land-use types may lead to the occurrence of more light-tolerant tree species within forest fragments (see Botzat et al. 2015). The increase of light tolerant, early successional trees, as well as invasive plant species, may correlate with a decline of shade tolerant trees and a simplification of forest structure. The absence of large fruiting trees and/or the dominance of pioneers may lead to less specialized and more robust plant-

bird networks (e.g. Menke et al., 2012), where forest specialist species decline with increasing matrix modification. Therefore, even if forest specialist bird species are able to disperse through an anthropogenic matrix, they may not find suitable habitats (Stratford and Stouffer 2015).

Species-specific responses to matrix transformation provide support for this idea that specialist species disappear from small forest fragments in anthropogenic matrices. Seven out of 11 bird species whose occupancy was significantly affected by fragment area were insectivores. Olivier and van Aarde (2017) found a direct link between tree species richness and insectivore bird species richness. If tree species richness therefore declines in response to matrix transformation, insectivore richness should also decline (Olivier and van Aarde 2017), possibly because compositional changes in the tree community lead to changes in vegetation structure on which specialised insectivores depend (e.g. Arcilla et al., 2015; Stratford and Stouffer, 2015). This may hamper the trophic control of herbivorous insects by insectivorous birds, inhibiting tree growth and fecundity and modifying plant assemblage composition (e.g. Peter et al. 2015; Morante-Filho et al. 2016). The three other bird species that were sensitive to forest area in anthropogenic matrices were frugivorous. In our study area, the disappearance of large fruiting trees from forest fragments in anthropogenic matrices may lead to the local extinction of frugivorous species that depend on the availability of fruiting trees (Lenz et al. 2011).

The selective extinction of vulnerable species may explain why forest specialists were nested by area when the matrix was anthropogenically transformed, but not when it was natural. When specialists disappear, a subset of common, more generalized and disturbance-tolerant species may remain (Socolar et al. 2015). When this happens, evenness may increase with a decrease in fragment area because of the loss of rare species. Similar findings were reported for the Lacandona rainforest in Mexico by Sanchez-de-Jesus et al. (2016) who illustrated that the evenness of dung beetle communities increased in small fragments. This suggests that homogenization of coastal forest bird assemblages could be caused by the disappearance of specialists and not because more generalist

species invade forest fragments. The reason could be that coastal forests are young (4000-6000 years BP), dynamic, disturbance-prone (Eeley et al. 1999), and fragmented (Olivier et al. 2013). As a result, coastal forest communities are highly resilient (Lawes et al. 2007) and may be more resistant to generalist invasions than their Neotropical counterparts (e.g. Tabarelli et al., 2012). Moreover, bird communities within these forests represent a mixture of species that are typical of subtropical forests, hinterland habitats (e.g. savannahs) and distant coastal areas (van Aarde et al. 2014). The transformation of the matrix might therefore not lead to the invasion of generalists, simply because many species found within these forests are generalists associated with the surrounding matrix.

Although our results are consistent with our expectations, some limitations of our study should be noted. Fragmented habitats have multiple interacting spatial components, which makes it difficult to isolate the main driver of species richness patterns (i.e. habitat amount, habitat area, connectivity, matrix land-use types) (Didham et al. 2012). In our study area, matrix type, forest amount, and levels of connectivity differed between the two landscapes (see Supplementary Material Table S2 and S3). The habitat amount hypothesis (Fahrig 2013) posits that species richness at a sample site should increase with habitat amount in the landscape where it is embedded. The patterns we recorded could therefore be ascribed to differences in forest amount and not matrix type. However, we consider this unlikely and rather argue that grasslands and woodlands represent additional habitat for forest species. Coastal forests are naturally fragmented (Olivier et al. 2013). Bird species here may therefore be buffered from local extinctions associated with forest loss because they have evolved to utilize resources from the ever-changing assortment of grasslands, bushlands, and woodlands that surround forest fragments. We also do not think that fragment connectivity is driving the patterns we observed as forest fragments in the natural matrix were further apart (mean average nearest neighbour = 3340m) than those in the anthropogenic matrix (mean average nearest neighbour = 442m). Rather fragments in the natural landscape may have been more connected as a result of a more permeable natural matrix through which forest species could disperse (Daily et al. 2001). Another reason for the patterns we found could be the sample

area effect. In a region of continuous habitat, larger sample areas will contain more individuals and, for a given abundance distribution, more species (Fahrig 2013). The occurrence of a SAR is therefore not necessarily related to the delineation of the area as patches, but rather the area sampled (Haila 2002). If this was the case in our study, we would have expected that both specialists and generalists increase with forest area in the anthropogenic landscape. However, only forest specialists, but not generalists increased with area, even though sampling procedures were the same for both groups (e.g. area sampled, the number of survey points). This suggests that specialist species are affected by more than just the sample area effect. We suggest that this is caused by matrix type – natural matrices can be regarded as additional habitat for specialists.

Spatial interactions between species and multiple habitat types represent a conservation challenge, especially where protected area designation focuses on single habitat types to the exclusion of others. Given the fragmented nature of forests in South Africa, much conservation effort focuses on conserving single forest fragments, whilst ignoring the adjacent matrix (e.g. Berliner, 2009). For instance, coastal forests are part of a number of eco-regions to which conservation statuses are assigned (see Burgess et al., 2004). This is problematic because coastal forests form part of a naturally fragmented habitat-matrix landscape mosaic. Therefore, implementing conservation actions at the eco-region scale may not be successful in preventing the bird extinctions we predicted in a previous contribution (Olivier et al. 2013). To prevent local extinctions of forest specialist species, it is important that habitats surrounding coastal forest fragments form part of conservation and restoration plans that focus on these forests. A possible way to accomplish this is to mimic the landscape structure that still exists in southern Mozambique. Here, forest fragments are embedded within a heterogeneous matrix comprised of grasslands, woodlands, and scattered forest trees. In South Africa, this can be achieved within protected areas - the iSimangaliso Wetland Park is a good example of where the matrix surrounding coastal forests fragments are being restored (e.g. Zaloumis and Bond, 2011). However, this landscape structure will be difficult to achieve outside protected areas because, in many instances, forest fragments are the

only natural habitats remaining in an anthropogenic landscape. We suggest that conservation efforts focus on establishing buffer zones around forests fragments embedded within an anthropogenic matrix. These buffer zones may protect forest fragments from high contrast anthropogenic matrices and prevent the invasion of forest fragments by light tolerant tree species. Making the matrix more heterogeneous may be another way to protect forest specialist bird species in small forest fragments.

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TABLES

Table 1 ΔAICc and Akaike weight (ωAICc) values for the eight different SAR models calculated for forest specialists and habitat generalist assemblages in both landscapes. Mean Chao1 were used as estimates of species richness per forest fragment. K refers to the number of parameters associated with each function. Minimum AICc values recorded in the anthropogenic landscape for forest specialists and habitats generalists were 73.02 (Power model) and 135.78 (Negative exponential model) respectively. While minimum AICc values recorded in the natural landscape for forest specialists and habitats generalists were 111.55 (Power model) and 130.81 (Power model) respectively.

Model	Function	K	Anthropogenic matrix				Natural Matrix			
			Forest specialist		Habitat generalist		Forest specialist		Habitat generalist	
			ΔAICc	ωAICc	ΔAICc	ωAICc	ΔAICc	ωAICc	ΔAICc	ωAICc
Power	$S = cA^Z$	2	0	0.74	1.23	0.16	0	0.22	0	0.16
Exponential	$S = c + zlog(A)$	2	5.41	0.05	1.17	0.17	0.02	0.22	0.01	0.16
Negative Exponential	$S = d(1 - \exp(-zA))$	2	19.84	0.00	0.00	0.30	0.47	0.17	0.19	0.15
Monod	$S = d/(1 + cA^{-1})$	2	13.74	0.00	2.18	0.10	0.46	0.18	0.04	0.16
Rational	$S = (c + zA)/(1 + dA)$	3	5.98	0.04	2.87	0.07	3.13	0.05	0.18	0.15
Logistic	$S = D/(1 + \exp(-zA + f))$	3	9.93	0.01	3.94	0.04	2.57	0.06	2.34	0.05
Lomolino	$S = d/1 + (z^{\log(f/A)})$	3	4.39	0.08	2.84	0.07	3.16	0.05	0.23	0.14
Weibull	$S = d/(1 - \exp(-zA^f))$	3	4.44	0.08	2.67	0.08	2.68	0.06	2.69	0.04

Table 2 Nestedness values calculated by using the nestedness metric based on overlap and decreasing fill – a metric that can quantify nestedness for the whole numerical matrix and for rows and columns separately (Almeida-Neto et al. 2008). We calculated three nestedness values for habitat generalists and forest specialists within each matrix type: (i) global nestedness, (ii) maximal nestedness and (iii) area nestedness. We also include the Spearman's correlation between area NODF and maximal NODF along with its associated *P*-value.

	Natural matrix			Anthropogenic matrix		
	All species	Forest specialist	Habitat generalist	All species	Forest specialist	Habitat generalist
Global NODF	54.65	70.05	48.21	47.68	73.21	43.90
Maximal NODF	68.14	72.34	63.43	63.77	77.57	59.53
Area NODF	41.65	45.53	37.93	55.1	67.66	45.23
Spearman's (rho)	0.32	0.41	0.29	0.88	0.86	0.74
p-value (Spearman's)	0.084	0.024	0.012	<0.01	<0.01	<0.01

Table 3 The relationships between the occurrence of each species and the size of forest fragments in each matrix type. Bold-faced characters indicate statistically significant relationships between species presence and forest fragment size). Estimate indicates the slope coefficient and its standard error (SE). The test statistic for the linear regression is represented by z.

Forest specialist species	Anthropogenic matrix				Natural matrix			
	Estimate	SE	z	P-value	Estimate	SE	z	P-value
Notopholia corruscus	0.496	0.530	0.937	0.349	−0.123	0.520	-0.236	0.813
Trochocercus cyanomelas	2.619	1.114	2.351	**0.0187**	0.928	0.599	1.549	0.122
Erythropygia signata	1.835	0.900	2.037	**0.0416**	−0.145	0.638	-0.228	0.82
Ploceus bicolor	3.571	1.319	2.706	**0.0068**	1.451	0.776	1.869	0.062
Nicator gularis	1.867	0.849	2.198	**0.028**	0.205	0.516	1.821	0.069
Ceuthmochares australis	3.318	1.504	2.206	**0.0274**	1.334	0.757	0.397	0.692
Camaroptera brachyura	<0.01	<0.01	0	1	<0.01	<0.01	1.763	0.078
Cyanomitra veroxii	0.5295	0.5318	0.996	0.32	0.838	0.573	0	1
Tauraco livingstonii	1.368	0.673	2.033	**0.042**	1.368	0.673	1.463	0.144
Apaloderma narina	1.724	0.824	2.092	**0.0364**	0.477	0.540	2.033	**0.042**
Cyanomitra olivacea	3.980	1.449	1.625	0.104	1.161	0.638	0.883	0.377
Indicator variegatus	1.3813	0.3432	1.858	0.063	0.937	0.916	1.571	0.116
Dicrurus ludwigii	2.148	0.677	2.45	**0.0143**	1.410	0.898	1.022	0.307
Bycanistes bucinator	2.352	0.263	2.213	**0.0269**	0.397	0.566	1.33	0.183
Chlorocichla flaviventris	3.214	1.557	2.064	**0.039**	0.607	0.703	0.701	0.484
Pogoniulus bilineatus	0.605	0.303	0.002	0.998	2.394	1.632	0.864	0.388
Turtur tympanistria	2.893	1.245	2.324	**0.0201**	0.819	0.616	1.467	0.142
Habitat generalist species								
Treron calvus	0.726	0.653	1.113	0.266	0.232	1.026	0.226	0.821
Terpsiphone viridis	0.595	0.604	0.986	0.324	0.210	1.025	0.205	0.838
Muscicapa caerulescens	0.118	0.760	0.155	0.877	−0.912	0.884	-1.031	0.303
Erythropygia quadrivirgata	−0.222	1.375	-0.161	0.872	0.719	0.618	1.164	0.244
Dryoscopus cubla	1.991	0.977	2.038	**0.0416**	5.017	2.366	0.001	0.999
Tchagra senegalus	0.813	0.619	1.314	0.189	1.244	0.858	1.45	0.147
Oriolus larvatus	0.232	0.542	0.429	0.668	−0.578	0.700	-0.825	0.41
Merops persicus	−1.647	1.91	-0.862	0.389	0.348	1.033	0.337	0.736
Halcyon albiventris	0.662	0.607	1.091	0.276	0.172	0.529	0.325	0.745
Centropus burchellii	−0.437	0.500	-0.872	0.383	0.211	0.512	0.412	0.68
Zosterops capensis	0.414	0.553	0.748	0.454	−0.802	1.028	-0.78	0.435
Hedydipna collaris	3.017	1.366	2.209	0.027	1.236	0.639	1.934	0.053
Pycnonotus tricolor	1.647	1.91	0.862	0.862	0.766	0.649	1.18	0.238
Chrysococcyx caprius	0.886	0.586	1.511	0.131	0.807	0.652	1.236	0.216
Turtur chalcospilos	0.208	0.5429	0.383	0.702	0.391	0.585	0.669	0.503
Dicrurus adsimilis	0.080	0.619	0.129	0.897	0.756	0.681	1.111	0.267
Campethera abingoni	2.423	0.988	2.453	**0.0141**	0.522	0.538	0.969	0.332

Chlorophoneus viridis	0.151	0.507	0.297	0.766	1.105	0.621	1.779	0.075
Bostrychia hagedash	<0.01	<0.01	0.759	0.448	0.082	0.513	0.159	0.874
Chrysococcyx klaas	0.851	0.569	1.495	0.135	1.718	1.067	1.611	0.107
Indicator minor	−0.163	0.973	-0.167	0.867	1.117	1.554	0.719	0.472
Cinnyris bifasciatus	0.334	0.603	0.554	0.58	1.414	0.678	2.087	**0.0369**
Cossypha natalensis	1.443	1.73	0.918	0.359	2.148	1.194	1.799	0.072
Cuculus solitarius	0.322	0.875	0.368	0.713	0.673	0.561	1.2	0.23
Streptopelia semitorquata	−0.040	0.487	-0.082	0.935	−0.749	0.680	-1.102	0.271
Pogoniulus pusillus	1.067	0.603	1.77	0.077	0.753	0.564	1.335	0.182
Apalis ruddi	1.825	0.7904	2.309	**0.0209**	0.509	0.771	0.66	0.509
Andropadus importunus	1.095	0.770	1.422	0.155	0.287	0.683	0.42	0.675
Laniarius ferrugineus	0.807	0.642	1.256	0.209	0.287	0.604	0.475	0.635
Ploceus ocularis	0.135	0.476	0.283	0.777	−0.076	0.745	-0.103	0.918
Cinnyris talatala	0.081	0.918	0.088	0.93	2.805	1.036	2.709	0.007
Stactolaema leucotis	1.146	0.652	1.758	0.079	−0.063	1.015	-0.062	0.951
Milvus parasitus	3.214	1.557	2.064	0.133	−0.684	1.395	-0.49	0.624
Apalis flavida	3.076	1.178	2.611	0.009	0.779	0.781	0.998	0.318

FIGURES

Figure 1 The two landscapes included in our study. In South Africa, coastal forest fragments were embedded within a matrix of human land-use types that included sugarcane, Pine, and *Eucalyptus* plantations, as well as rural and urban settlements. In Mozambique, most fragments were located within the Maputo Elephant Reserve and were embedded within a natural matrix of woodlands and grasslands. Photographs courtesy of Rudi van Aarde.

Figure 2 Species-area relationships for habitat generalists and forest specialists within both matrix types. The power model provided the best fit for forest specialist and generalist species in natural and anthropogenic matrices. Dotted lines represent bird community SAR's for forest fragments embedded within a natural matrix while solid lines represent SAR's for forest bird communities embedded within a transformed matrix.

Figure 3 Linear regressions fitted to Pielou's evenness indices which were calculated for each forest fragment within both matrix types.
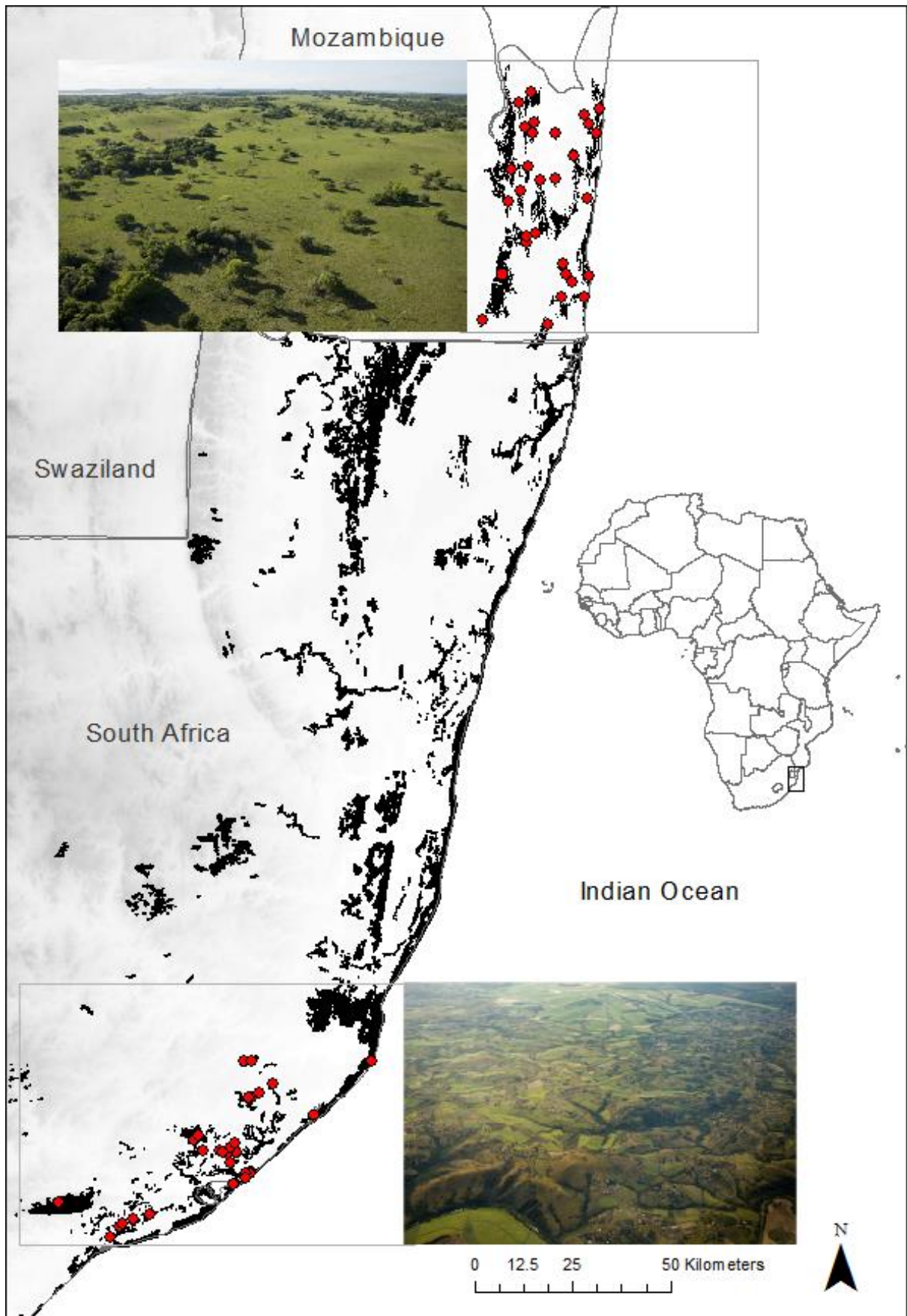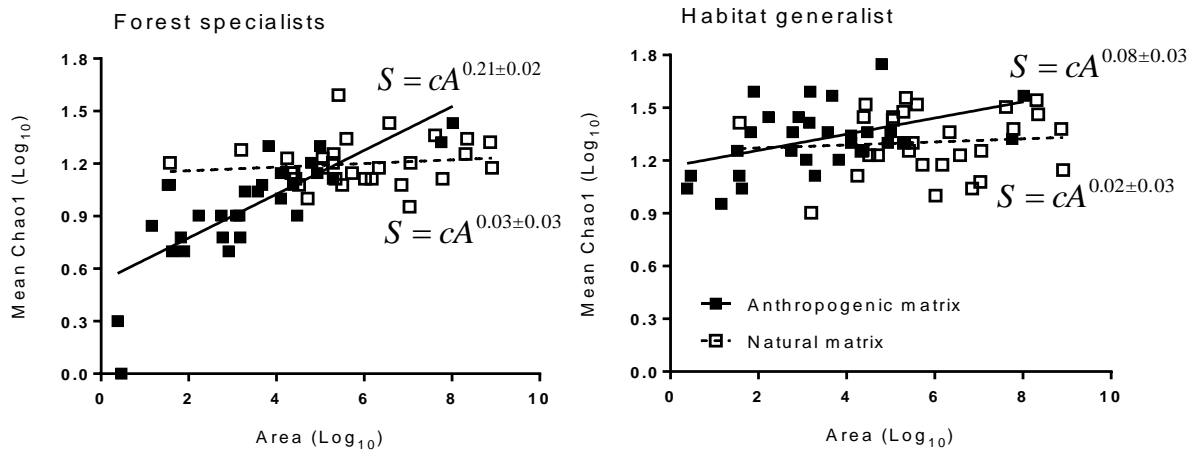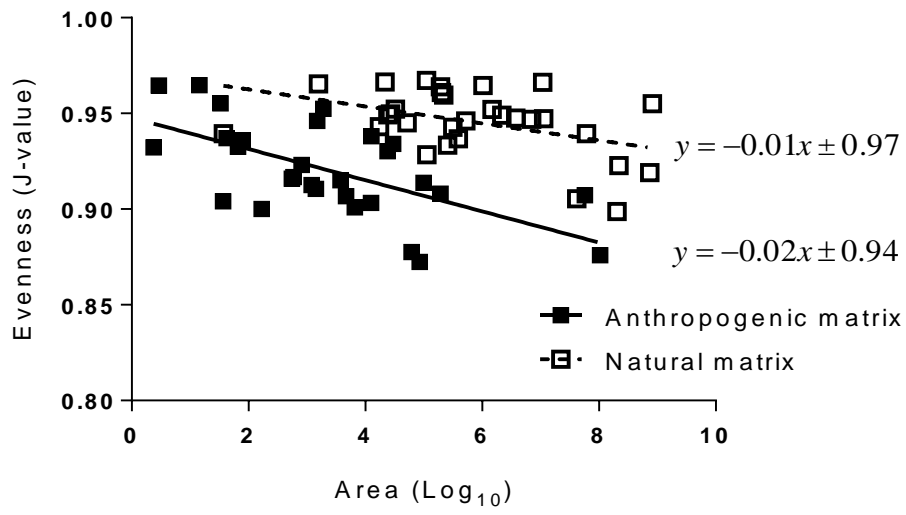
Figure 1

Figure 2

Figure 3.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Spatial structure, bird assemblages and matrix proportions for both study areas.

Appendix S2 Species presence and forest fragment area

Appendix S3 SAR z-values obtained for forest specialists and habitat generalists

SUPPORTING INFORMATION

Appendix S1- Information pertaining to the spatial structure, bird assemblages and matrix proportions for both the natural and transformed landscapes.

Table S2.1 Recorded species from forest fragment surveys at both study areas, categorised into forest specialists and habitat generalist species. An X indicates if a species was recorded within the respective landscape.

Scientific name	English name	Habitat specialisation	Landscape location	
			Anthropogenic	Natural
Accipiter tachiro	African Goshawk	Habitat generalist	x	x
Amblyospiza albifrons	Thick-billed Weaver	Habitat generalist	x	
Andropadus importunus	Sombre Greenbul	Habitat generalist	x	x
Apalis flavida	Yellow-breasted Apalis	Habitat generalist	x	x
Apalis ruddi	Rudd's Apalis	Habitat generalist	x	x
Apalis thoracica	Bar-throated Apalis	Habitat generalist	x	
Apaloderma narina	Narina Trogon	Forest specialist	x	x
Batis capensis	Cape Batis	Habitat generalist	x	
Batis fratrum	Woodwards' Batis	Forest specialist	x	x
Batis molitor	Chinspot Batis	Habitat generalist		x
Bostrychia hagedash	Hadeda Ibis	Habitat generalist	x	x
Bradornis pallidus	Pale Flycatcher	Habitat generalist		x
Bycanistes bucinator	Trumpeter Hornbill	Forest specialist	x	x
Camaroptera brachyura	Green-backed Camaroptera	Forest specialist	x	x
Campephaga flava	Black Cuckooshrike	Habitat generalist	x	
Campethera abingoni	Golden-tailed Woodpecker	Habitat generalist	x	x
Centropus burchellii	Burchell's Coucal	Habitat generalist	x	x
Ceuthmochares australis	Green Malkoha	Forest specialist	x	x
Chalcomitra amethystina	Amethyst Sunbird	Habitat generalist	x	
Chalcomitra senegalensis	Scarlet-chested Sunbird	Habitat generalist		x
Chlorocichla flaviventris	Yellow-bellied Greenbul	Forest specialist	x	x
Chlorophoneus olivaceus	Olive Bushshrike	Forest specialist	x	x
Chlorophoneus sulfureopectus	Orange-breasted Bushshrike	Habitat generalist		x
Chlorophoneus viridis	Gorgeous Bushshrike	Habitat generalist	x	x
Chrysococcyx caprius	Diederik Cuckoo	Habitat generalist	x	x
Chrysococcyx cupreus	African Emerald Cuckoo	Forest specialist	x	
Chrysococcyx klaas	Klaas's Cuckoo	Habitat generalist	x	x
Ciconia episcopus	Woolly-necked Stork	Habitat generalist	x	
Cinnyricinclus leucogaster	Violet-backed Starling	Habitat generalist		x
Cinnyris bifasciatus	Purple-banded Sunbird	Habitat generalist	x	x
Cinnyris neergaardi	Neergaard's Sunbird	Habitat generalist		x
Cinnyris talatala	White-bellied Sunbird	Habitat generalist	x	x
Cisticola chiniana	Rattling Cisticola	Habitat generalist	x	
Columba delegorguei	Eastern Bronze-naped Pigeon	Forest specialist	x	

Scientific name	English name	Habitat specialisation	Landscape location	
			Anthropogenic	Natural
Columba larvata	Lemon Dove	Forest specialist	x	x
Coracina caesia	Grey Cuckoo-shrike	Forest specialist	x	
Corvus albus	Pied crow	Habitat generalist	x	
Cossypha dichroa	Chorister Robin-chat	Forest specialist	x	x
Cossypha heuglini	White-browed Robin-Chat	Habitat generalist		x
Cossypha natalensis	Red-capped Robin-chat	Habitat generalist	x	x
Crithagra mozambica	Yellow-fronted Canary	Habitat generalist	x	
Crithagra sulphurata	Brimstone Canary	Habitat generalist	x	
Cuculus clamosus	Black Cuckoo	Habitat generalist	x	
Cuculus solitarius	Red-chested Cuckoo	Habitat generalist	x	x
Cyanomitra olivacea	Eastern Olive Sunbird	Forest specialist	x	x
Cyanomitra veroxii	Grey Sunbird	Forest specialist	x	x
Dendroperdix sephaena	Crested Francolin	Habitat generalist		x
Dendropicos fuscescens	Cardinal Woodpecker	Habitat generalist	x	
Dendropicos griseocephalus	Olive Woodpecker	Forest specialist	x	
Dicrurus adsimilis	Fork-tailed Drongo	Habitat generalist	x	x
Dicrurus ludwigii	Square-tailed Drongo	Forest specialist	x	x
Dryoscopus cubla	Black-backed Puffback	Habitat generalist	x	x
Erythropygia leucophrys	White-browed Scrub-robin	Habitat generalist	x	x
Erythropygia quadrivirgata	Bearded Scrub-robin	Habitat generalist	x	x
Erythropygia signata	Brown Scrub-robin	Forest specialist	x	x
Estrilda astrild	Common Waxbill	Habitat generalist	x	
Estrilda perreini	Grey Waxbill	Habitat generalist		x
Guttera pucherani	Crested Guineafowl	Forest specialist		x
Halcyon albiventris	Brown-hooded Kingfisher	Habitat generalist	x	x
Hedydipna collaris	Collared Sunbird	Habitat generalist	x	x
Hippolais icterina	Icterine Warbler	Habitat generalist		x
Hirundo rustica	Barn Swallow	Habitat generalist		x
Hypargos margaritatus	Pink-throated Twinspot	Habitat generalist		x
Indicator indicator	Greater Honeyguide	Habitat generalist		x
Indicator minor	Lesser Honeyguide	Habitat generalist	x	x
Indicator variegatus	Scaly-throated Honeyguide	Forest specialist	x	x
Lagonosticta rubricata	African Firefinch	Habitat generalist	x	
Laniarius ferrugineus	Southern Boubou	Habitat generalist	x	x
Lanius collaris	Common Fiscal	Habitat generalist	x	
Lonchura cucullata	Bronze Mannikin	Habitat generalist	x	
Lophaetus occipitalis	Long-crested Eagle	Habitat generalist	x	x
Lybius torquatus	Black-collared Barbet	Habitat generalist	x	x
Malaconotus blanchoti	Grey-headed Bushshrike	Habitat generalist	x	x
Mandingoa nitidula	Green Twinspot	Forest specialist	x	x
Megaceryle maxima	Giant Kingfisher	Habitat generalist	x	

Scientific name	English name	Habitat specialisation	Landscape location	
			Anthropogenic	Natural
Merops apiaster	European Bee-eater	Habitat generalist		x
Merops persicus	Blue-cheeked Bee-eater	Habitat generalist	x	x
Milvus parasitus	Yellow-billed Kite	Habitat generalist	x	x
Motacilla aguimp	African Pied Wagtail	Habitat generalist	x	
Muscicapa adusta	African Dusky Flycatcher	Habitat generalist	x	x
Muscicapa caerulescens	Ashy Flycatcher	Habitat generalist	x	x
Nicator gularis	Eastern Nicator	Forest specialist	x	x
Notopholia corruscus	Black-bellied Starling	Forest specialist	x	x
Oriolus	Eurasian Golden Oriole	Habitat generalist	x	
Oriolus larvatus	Black-headed Oriole	Habitat generalist	x	x
Passer diffusus	Southern Grey-headed Sparrow	Habitat generalist		x
Passer domesticus	House Sparrow	Habitat generalist	x	
Phoeniculus purpureus	Green Wood-hoopoe	Habitat generalist		x
Phyllastrephus flavostriatus	Yellow-streaked Greenbul	Forest specialist	x	
Phyllastrephus terrestris	Terrestrial Brownbul	Forest specialist	x	x
Phylloscopus trochilus	Willow Warbler	Habitat generalist	x	
Platysteira peltata	Black-throated Wattle-eye	Forest specialist	x	x
Ploceus bicolor	Dark-backed Weaver	Forest specialist	x	x
Ploceus ocularis	Spectacled Weaver	Habitat generalist	x	x
Ploceus velatus	Southern Masked-weaver	Habitat generalist		x
Ploceus xanthops	Golden Weaver	Habitat generalist		x
Pogoniulus bilineatus	Yellow-rumped Tinkerbird	Forest specialist	x	x
Pogoniulus pusillus	Red-fronted Tinkerbird	Habitat generalist	x	x
Pogonocichla stellata	White-starred Robin	Forest specialist	x	
Prinia subflava	Tawny-flanked Prinia	Habitat generalist	x	
Prodotiscus regulus	Brown-backed Honeybird	Habitat generalist	x	
Pycnonotus tricolor	Dark-capped Bulbul	Habitat generalist	x	x
Sarothrura elegans	Buff-spotted Flufftail	Forest specialist	x	
Smithornis capensis	African Broadbill	Forest specialist		x
Stactolaema leucotis	White-eared Barbet	Habitat generalist	x	x
Stactolaema olivacea	Green Barbet	Forest specialist	x	
Stephanoaetus coronatus	Crowned Eagle	Forest specialist	x	
Streptopelia capicola	Cape Turtle-Dove	Habitat generalist		x
Streptopelia semitorquata	Red-eyed Dove	Habitat generalist	x	x
Sylvietta rufescens	Long-billed Crombec	Habitat generalist		x
Tauraco livingstonii	Livingstone's Turaco	Forest specialist	x	x
Tauraco porphyreolophus	Purple-crested Turaco	Habitat generalist	x	x
Tchagra senegalus	Black-crowned Tchagra	Habitat generalist	x	x
Terpsiphone viridis	African Paradise Flycatcher	Habitat generalist	x	x
Tockus alboterminatus	Crowned Hornbill	Forest specialist		x
Trachyphonus vaillantii	Crested Barbet	Habitat generalist	x	

Scientific name	English name	Habitat specialisation	Landscape location	
			Anthropogenic	Natural
Treron calvus	African Green Pigeon	Habitat generalist	x	x
Trochocercus cyanomelas	Blue-mantled Crested Flycatcher	Forest specialist	x	x
Turdus olivaceus	Olive Thrush	Habitat generalist	x	
Turtur chalcospilos	Emerald-spotted Wood Dove	Habitat generalist	x	x
Turtur tympanistria	Tambourine Dove	Forest specialist	x	x
Zosterops capensis	Cape White-eye	Habitat generalist	x	x
Zosterops senegalensis	African Yellow White-eye	Habitat generalist		x

Table S1.2- Number of bird species recorded in South Africa and Mozambique categorised into species richness, forest specialist and habitat generalist species based on presence-absence data and distributional data (Hockey et al., 2005; *www.*sabap2.adu.org.za). The composition of the two landscapes indicating the total survey site area, mean forest fragment area, total forest cover, average nearest neighbour, survey points and number of surveyed forest fragments are also provided.

	Anthropogenic landscape	Natural landscape
Species richness	99	89
Forest specialist species	33	27
Habitat generalist species	66	62
Mean forest fragment area	226 ± 128 ha	1170 ± 361.6 ha
Total forest area	28 744 ha	47 600 ha
Average nearest neighbour	442 m	3 340m
Survey points	227	220
Surveyed forest fragments	29	30

Table S1.3-Proportion of different matrix types in each landscape calculated from landcover images for KwaZulu-Natal (Jewitt et al. 2015) and Mozambique (Guldemond and van Aarde 2010).

	Natural landscape	Anthropogenic landscape
Woodland	14.7%	2.15%
Mangrove	1.2%	0.26%
Grassland	35.1 %	9.91%
Forest	35.9 %	6.13%
Eucalyptus plantation	<0.1%	14.22%
Sugarcane plantation	<0.1%	8.57%
Rural settlements	<0.1%	14.18%
Urban settlements	<0.1%	2.39%

Appendix S2- Species presence and fragment area using binomial general linear models
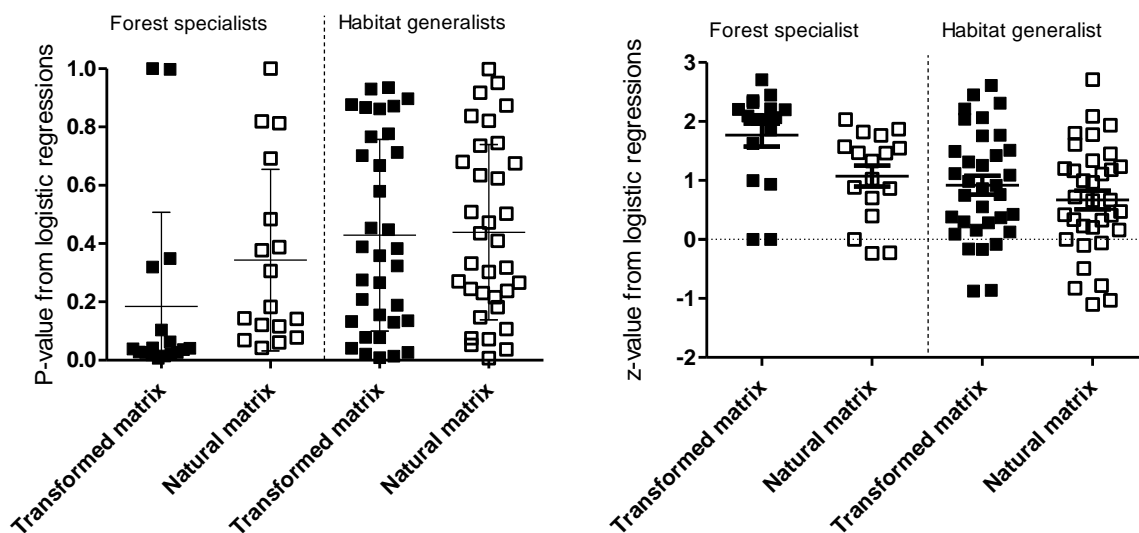
Figure S2.1 Species responses to fragment area using binomial general linear models for 50 species at each landscape. The probability of a species presence or absence being significantly influenced (p-value < 0.05) by forest fragment size is indicated by the p-value. Seventeen forest specialists and 33 habitat generalist species were included in this analysis.

Appendix S3- Figure illustrating the returned z-values of the power model from calculating SAR for forest specialists and habitat generalists in both landscapes.
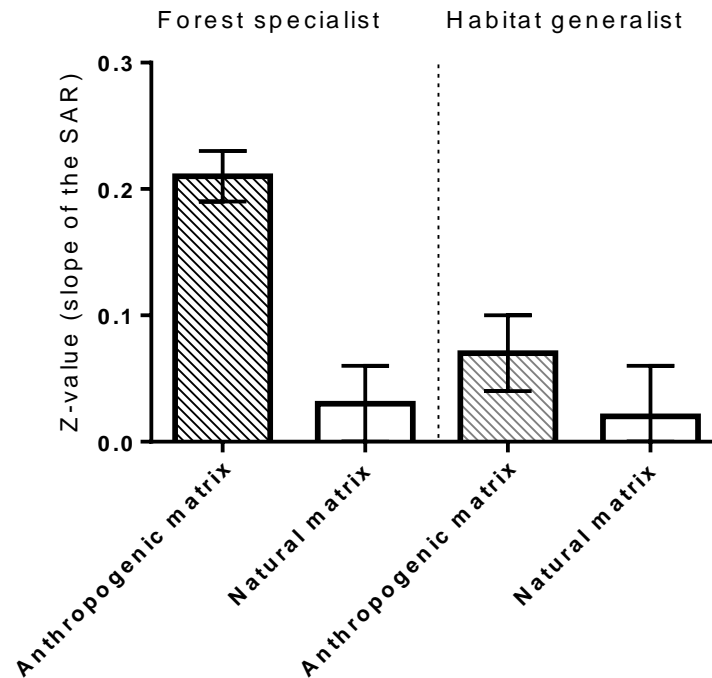
Figure S3.1 z-values obtained from the power model SAR. These values represent the slope of the SAR. High z-values suggest isolated habitats with infrequent movements, while low z-values suggest continuous habitats with frequent movements (see Brooks et al. 1997 and references therein). A z-value of 0.25 is associated with a real island system.

Chapter 3

The response of avian assemblages to human-modified landscapes at three different spatial grains

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Running head: Human-modified habitats are capable of supporting diverse bird assemblages

ABSTRACT

Aim: To assess patterns of bird diversity and the processes which drive their assembly in a human-modified landscape. Also to determine whether the spatial grain at which analysis is conducted influences inferences based on patterns of diversity.

Location: Coastal plains of north east KwaZulu-Natal, South Africa

Methods: I made use of a fractal-based design to survey bird assemblages in seven different habitat types (four human-modified and three natural). I investigated and compared patterns of alpha and beta-diversity within each habitat at three different spatial sampling grains, using generalised linear models and multiple comparison tests. I then used the Raup-Crick null modelling approach to determine if the processes structuring bird assemblages were more deterministic (niche-based) or stochastic (dispersal-based) and if these processes differed between natural and human-modified habitats.

Results: Natural habitats did not always support the highest species richness. Rural and urban areas also supported high species richness comparable with that of primary forest and woodlands. In contrast, grasslands supported one of the lowest species richness similar to sugarcane and *Eucalyptus* plantations. Patterns of beta-diversity were idiosyncratic and values decreased with an increase in spatial grain. In contrast, patterns of alpha-diversity were not influenced by spatial grain. Community assembly processes in both humans modified and natural habitats were predominantly non-random and influenced by deterministic, niche-based processes.

Main conclusions: Preserving natural habitats is important, however, human-modified habitats surrounding natural habitats are also important for regional species richness and should be considered when assessing the conservation value of habitats within a landscape. Further, my study shows the importance of assessing patterns of diversity at multiple spatial grains.

INTRODUCTION

The transformation of natural habitats into human-modified land-use types is widespread globally (Foley 2005; Sodhi et al. 2010; Wang and Foster 2015). The expected negative effects thereof on native species are also well documented (Tilman et al. 2002; Foley 2005). However, what is less well known is the capacity of transformed habitats to support diverse biological assemblages (Vandermeer and Perfecto 1997; Daily et al. 2001; Donald and Evans 2006; Greenler and Ebersole 2015). For example, bird assemblages in habitats adjacent forest fragments may not only be simple subsets of forest assemblages, but could also harbour a substantial number of unique species (Greenler and Ebersole 2015). Determining the contribution of human-modified habitats to regional diversity is therefore important because they could complement conservation strategies. In contrast, these habitats may also decrease species richness, homogenise biological assemblages, disrupt ecological processes, or act as ecological traps that reduce regional diversity and community resilience (Karp et al. 2012; Tabarelli et al. 2012; Greenler and Ebersole 2015). It is therefore important to understand patterns and processes of biological diversity to inform future conservation strategies (Bhagwat et al. 2008; Vellend 2010).

When a natural habitat is transformed to a human land-use type (e.g. agricultural fields, agroforestry) it is often accompanied by a reduction in species richness (Foley 2005; Tscharntke et al. 2005; Karp et al. 2012). Natural habitats are generally heterogeneous with many potential niches and are therefore more likely to be species-rich than transformed habitats which are often structurally more homogenous (Tscharntke et al. 2005). Furthermore, high species richness in natural habitats could be attributed to an increased number of rare specialist species (i.e habitat unique species). For example, in sub-tropical coastal forests in South Africa 89% of species can be considered rare or very rare and may depend on specific habitat requirements (Grainger et al. 2011). When habitats are transformed these specialised niches may be lost and consequently these species could disappear, thereby reducing habitat species richness (Haddad et al. 2015). When this happens, one would expect that only a few wide-spread generalist species remain (Karp et al. 2012). However,

this is not always the case. Some studies have shown that human-modified habitats can maintain, and in some instances, even increase diversity after losing habitat specialists. For example, Hugo and van Rensburg (2009) found a positive correlation between human modification of habitats and avian diversity, but also found that functionally specialised species were less likely to persist in human-modified habitats.

If habitat specialist species disappear following landscape transformation, the variation in species composition among sites (beta-diversity) should decrease (Karp et al. 2012; Tabarelli et al. 2012; Tscharntke et al. 2012). Beta-diversity refers to the variation in community composition among sites (Whittaker 1972) and is important for any study that aims at better understanding how ecological processes shape patterns of biodiversity (Anderson et al. 2011). Indeed, beta-diversity within human land use types such as intensive agriculture is likely to decrease (Karp et al. 2012). These habitats are also likely to be depauperate in rare species. A decrease in beta-diversity and the absence of rare specialist species may bring about a biotic homogenisation effect within habitats, where many habitat specialist species are lost and replaced by a few disturbance-tolerant species that dominate the assemblage (Olden 2006; Karp et al. 2012; Tabarelli et al. 2012). However, beta-diversity between different habitat types may subsequently increase in a landscape comprising of patchy different land use types, thereby increasing regional species richness. This idea, the beta-diversity dominance hypothesis, has been postulated by Quinn et al. (1988) but also recently by Tscharntke et al. (2012). This is specifically likely in areas where low-density agriculture is practised i.e. a land sharing approach (Tscharntke et al. 2012). Increased beta-diversity between habitats may override the negative local effects of habitat loss and fragmentation on regional biodiversity (Quinn et al. 1988). Alternatively, generalist species may spill over from adjacent habitats within the landscape mosaic thereby decreasing between habitat beta-diversity – the cross-habitat spillover hypothesis (Ricketts 2001; Tscharntke et al. 2012; Driscoll et al. 2013). For example, Daily et al. (2001) found that a substantial fraction of forest species occurred in the intermediate-intensity agricultural landscape bordering old growth forest fragments in southern Costa Rica.

Beta-diversity patterns also allow for inferences on the processes that structure biodiversity. For example, the contribution of stochastic (neutral) versus deterministic (niche-based) community assembly processes can be inferred from patterns of beta-diversity (Püttker et al. 2015). Under stochastic assembly, the presence of a species at a site is influenced by random extinction, dispersal and ecological drift (Raup and Crick 1979; Chase and Myers 2011). Therefore, sites that are further away from each other should harbour increasingly dissimilar biological assemblages (Nekola and White 1999). In contrast, under deterministic assembly, a species niche and local environmental conditions determine the presence or absence of a species. Therefore, sites with similar environmental conditions would likely support similar biological assemblages (e.g. Tuomisto et al. 2003). Determining which processes underlie community assembly has proven to be a contentious topic (Chase and Myers 2011). However, understanding which processes structure communities is important especially if they differ between human-modified land use types and natural habitats. For example, Püttker et al. (2015) found that deterministic processes structure assemblages in both human-modified and natural habitats. However, this study was only conducted at a single spatial scale. Gaining a better understanding of the processes driving community assembly in human-modified and natural habitats is important, specifically to inform process-based approaches to conservation.

Many studies have shown that inferences based on indices of diversity are influenced by the spatial grain at which the analysis is conducted (the size of the sampling unit) as well as spatial extent of the study area (the total area encompassed) (Mac Nally et al. 2004a; Barton et al. 2013; Olivier and Van Aarde 2014). For example, studies which accounted for spatial scale found that alpha-diversity was unchanged (Vellend et al. 2013) or even increased (Dornelas et al. 2014) in human-modified landscapes. Conflictingly, studies which did not account for spatial scale reported that alpha-diversity declined in response to anthropogenic transformation (Dunn 2004; Gibson et al. 2013). Similarly, we know that patterns of beta-diversity are dependent on sampling grain (Mac Nally et al. 2004). In most cases, beta-diversity decreases as sampling grain increases (Karp et al.

2012; Socolar et al. 2015). This may be because of a sampling effect where the proportion of a community included in a sample increases with sampling scale because the focal unit size increases (Olivier and Van Aarde 2014). This apparent decrease may also be ascribed to the species-area effect where the number of species increases with area sampled (Fahrig 2013). It follows that inferences from beta-diversity would also be dependent on the sampling scale at which studies were conducted. Indeed, Olivier & van Aarde (2014) found that inferences based on beta-diversity for bird and tree assemblages in South African coastal forests were dependent on spatial grain. Moreover, Wearn et al. (2016) found a similar result for mammal communities in response to logging in South East Asia. Therefore, assessing patterns of diversity at a single spatial scale could be misleading (Tylianakis et al. 2006). Instead, using multi-spatial scale analyses could provide better insight and improve inferences based on the patterns of diversity observed at the landscape scale (Olivier and Van Aarde 2014).

In this study I investigate i) how bird assemblages respond to human-modified landscapes, ii) if the processes that structure community assembly differ between natural and human-modified landscapes and iii) if inferences on their responses are dependent on sampling grain. I studied seven bird assemblages that occur within a mosaic of natural and anthropogenic habitat types along the coastal plains of the KwaZulu-Natal Province of South Africa. These coastal plains have undergone an extensive anthropogenic transformation in the past two decades (Olivier et al. 2013; Jewitt et al. 2015). Human land-use types now dominate this landscape with few remnant natural habitat fragments embedded within them (Van Wyk and Smith 2001; van Aarde et al. 2014). I tested four hypotheses. First, I hypothesised that bird species richness (alpha-diversity) would be higher in natural than human-modified habitat types. Second, I hypothesized that bird assemblages in human-modified habitats would be homogenised because habitats converted to human land-use types (especially agriculture landscapes) are generally more environmentally homogeneous compared to natural habitats (Karp et al. 2012; but also see Tscharntke et al. 2012). Estimates of beta-diversity should, therefore, be lower in human-modified landscapes relative to natural landscapes. Third, I

hypothesised bird assemblages within human-modified habitats to be structured more through deterministic, niche-based processes than assemblages in natural habitats which we expected to be influenced by more stochastic processes (Tilman 2004; Püttker et al. 2015). Finally, I hypothesised that although estimates of diversity would vary across different sampling grains, the general patterns amongst habitats would be the same, i.e. alpha and beta-diversity would be higher in natural than human-modified habitat types and deterministic processes would structure communities in both natural and human-modified habitat types irrespective of the sampling grain of the investigation.

METHODS

Study Area

The study area was located in northern KwaZulu-Natal on the east coast of South Africa between the Tugela River in the south and Lake Sibaya in the north (29°13'56" - 27°17'7"S, 31°27'49" - 32°44'47"E) (Fig. 1). This area forms part of the Maputaland Coastal Forest Mosaic (Burgess et al. 2004), the Maputaland Centre of Plant Endemism (Van Wyk and Smith 2001) and the Maputaland-Pondoland-Albany biodiversity hotspot (Küper et al. 2004). Historically, coastal forests, grasslands as well as mixed acacia/broadleaf woodlands dominated this region (Van Wyk and Smith 2001). However, sugarcane, forestry, mines, rural habitats and urban settlements have replaced much of these natural habitats (van Aarde et al. 2014; Jewitt et al. 2015), with ~1.2% of the natural habitats being transformed per annum since 1994 (Jewitt et al. 2015) and 82% of coastal forests potentially lost (Olivier et al. 2013). This region may therefore now also harbour an extinction debt (Olivier et al. 2013). I selected and surveyed seven habitat types that occurred across the study area. These included three natural (coastal forests, woodlands and grasslands) and four anthropogenic habitat types (sugarcane plantations, *Eucalyptus* plantations and rural and urban settlements). The landscape comprised of the following proportions of habitats; coastal forests (7.6%), woodlands

(7.2%), grasslands (8%), sugarcane plantations (14%), *Eucalyptus* plantations (19.2%), rural (14.2%)

and urban settlements (8.4%) (see supplementary material Appendix S3).

Survey design

A fractal-based survey design provides a clearly defined structure for accumulating data on

ecological phenomena that vary over spatial scales (Ewers et al. 2011). I therefore made use of a

fractal-based survey design to assess patterns of alpha and beta-diversity at three different spatial

sampling grains (fine, intermediate and coarse) across seven different habitat types (Fig.1) (Marsh

and Ewers 2013; Wearn et al. 2016). Each sampling grain included a number of accumulated survey

points. At the finest sampling grain was fine scale (FS) which included individual survey points

(sample sizes n = ~162 survey points per habitat type, 1240 number of points in total). These survey

points were then arranged into equilateral triangles or plots (three points per plot) with sides of

178m (sample size n=54 plots per habitat) to form first order fractals. Plots or first order fractals

represent the intermediate spatial scale (IS) component for this study. Second order fractals were

formed by clustering three first order fractals together (500m apart) to form a larger equilateral

triangle (see Figure 1). Second order fractals represent the coarse scale (CS) component of this study

(sample size n = 18 per habitat type). The distance between second order fractals varied but was

~1500m across habitat types. Distances between plots (500m) and survey points (178m) remained

constant. To evaluate survey effort I generated species accumulation curves using the rarefaction

software program EstimateS 8 (Colwell 2013). Survey effort was deemed sufficient when at least 162

points had been surveyed and species assemblage saturation (proportion of the assemblage actually

observed) exceeded 85%.

Data collection

Birds were surveyed within each habitat type using point counts (Bibby et al. 2000). All surveys were

conducted during the summer breeding season (December-April 2016) between ~05:00h and 09:00h

to avoid high ambient temperatures that may reduce bird activity. Surveyors had prior experience in

identifying birds based on both auditory cues and observation. Survey points were located using a GPS (Map 62, Garmin). To reduce potential observer bias, surveyors 'shared' fractal points, i.e. second order fractal were surveyed twice, each time by different observers. Upon arrival at a survey point, observers waited two minutes to allow birds to acclimatise to their presence. The observer then recorded all species seen and heard within ~60m radius (Nikon Laser 550As; Nikon, Tokyo, Japan) for ten minutes. The distances of observed bird species from the observer were also measured by the rangefinder. Birds flying over the habitat without settling were not recorded. Surveys were abandoned on windy and rainy days.

Data analyses

Alpha-diversity

Sampling saturation was assessed using sample-based accumulation curves in the software program EstimateS 8.2.0 (Colwell 2013) (Supplementary material Appendix 1). The program uses abundance based data as an input and then calculates rarefied estimated species richness as Choa1 values for each forest fragment (Colwell 2013). Bird diversity within each habitat type was estimated by six non-parametric species richness estimators: four abundance-based [Chao1, abundance-based coverage estimator (ACE), Jack1, and Jack2] and two incidence-based [Chao2 and incidence-based coverage estimator (ICE)] estimators. Based on these values, I calculated the range of the estimated species richness which was actually observed. The range of species richness values was derived from the lowest and highest values of the six species richness estimators. Estimated species richness per habitat type was then compared using the estimated Chao1 values obtained during the rarefaction process. The asymmetrical 95% confidence interval (CI) of Chao1 were used to determine whether habitats species richness (γ-diversity) differed significantly among habitat types (Lande 1996). Chao1 is the most commonly used index for estimating species richness and is based on the frequency of an individual's occurrence within a sample (Chao 1984).

Alpha-diversity is defined as the species richness at each sampling unit (number of species recorded at survey point, first order fractal and second order fractal). For the purposes of this study, alpha-diversity and beta-diversity correspond to the spatial scales of my hierarchical fractal sampling design (Marsh and Ewers 2013). Bird records were organised into the respective sampling unit in which they were recorded and presence-absence matrices for each spatial scale were constructed. An alpha-diversity value was then obtained for each survey site (species richness at that site). These alpha-diversity values were utilised to calculate a mean alpha-diversity value at each spatial scale for all seven habitats with its respective 95% CI.

Beta-diversity

Beta-diversity was calculated at each spatial scale within the respective habitat types. Bray-Curtis dissimilarity was used as my index of beta-diversity as this allowed for the inclusion of abundance data at the respective sampling units. The Bray Curtis dissimilarity index provides an index value ranging from zero to one. High values of β_{bray} (close to 1) indicate high levels of dissimilarity between assemblages (heterogeneous assemblage). Conversely, low β_{bray} values (close to 0) indicate that local assemblages have a similar species composition (homogenised assemblage). Each sampling unit within a habitat was compared using this criterion. From the returned absolute beta-diversity values, I then again calculated the mean β_{bray} value and the 95% CI for each habitat type at the three respective spatial grains. Analysis of beta-diversity was conducted in the R programming environment (R Development Core Team 2012) using the VEGAN package (Oksanen et al. 2013b).

To evaluate whether habitat type was a good predictor of alpha and beta-diversity, I made use of Poisson generalised linear models (GLM) and analysis of deviance based on the χ2-value at each spatial scale. Further ANOVA step-wise multiple comparison tests were conducted to allow for direct comparisons of alpha and beta-diversity to be made amongst habitat types. This provided more information about the variation in diversity indices which between specific habitat types. Finally, habitats were categorised respectively under natural and anthropogenic habitats and then

compared using a two-tailed non-parametric T-test in in the software program GraphPad Prism 6 (Graph-Pad Software, San Diego, CA, USA; http://www.graphpad. com/).

Community assembly processes

Beta-diversity metrics (e.g. Jaccard, Sorenson and Bray Curtis) are often sensitive to alpha-diversity (Koleff et al. 2003; Vellend et al. 2007). For instance, sites that have lower alpha-diversity will appear more dissimilar as a result of sites that support high alpha-diversity, even if the species present at the species-poor site are all present in the species-rich site. This is problematic as alpha-diversity may be influencing the observed patterns of beta-diversity.

To correct for this, I calculated beta-diversity using a null-model approach and modified Raup-Crick metric following a similar procedure to that of Raup and Crick (1979) and Chase et al. (2011). Raup-Crick dissimilarity is an incidence-based, probabilistic metric that calculates beta-diversity independently of alpha-diversity (Vellend et al. 2007). The Raup-Crick metric between two sample units is calculated by repeated random sampling (species frequencies as weights) of the number of species at each site from a habitat species pool. This is followed by a comparison of pairwise similarity (i.e. the number shared species) between random samples and the observed similarity between units (Püttker et al. 2015). The returned value or β_{RC} is the proportion of random samples that result in equal or higher number of shared species compared to the observed. In other words, β_{RC} measures the deviation from the null expectation that community assembly is stochastic (Chase et al. 2011). The Raup-Crick metric creates a re-scaled probability metric (β_{RC}) which ranges from -1 to 1 (Raup and Crick 1979). The β_{RC} is indicative of whether compared assemblages are more dissimilar (approaching 1), as dissimilar (approaching 0), or less dissimilar (approaching -1) than expected by random chance (Chase et al. 2011). Moreover, my use of the Raup-Crick metric was dual purpose. Raup-Crick is also useful in determining if processes driving community assemblage are more deterministic (niche based) or stochastic (Chase et al. 2011). A mean β_{RC} close to 0 indicates

community assemblage is more stochastic, while, a β_{RC} approaching -1 or 1 indicates deterministic processes in community assemblage (Chase et al. 2011; Püttker et al. 2015).

β_{RC} was calculated in the vegan package of R (Oksanen 2016). The metric makes use of presence-absence matrices unlike that used to calculate beta-diversity using the Bray-Curtis approach (abundance matrices). Mean β_{RC} was calculated for each habitat at the three respective spatial grains. Non-metric multi-dimensional scaling (NMDS) was then utilised to visually represent the spread of β_{RC} at each spatial scale within each habitat (Püttker et al. 2015).

RESULTS

I recorded 171 species from 10 345 records in the seven different habitat types sampled in my study (see Appendix 1 Supplementary material for species list). Most species were recorded in woodlands (n = 84), while sugarcane (n = 28) had the lowest number of species records. Natural habitats, forest (n = 21), woodlands (n =18) and grasslands (n = 13), supported more unique species (i.e. species only recorded in a single habitat type) than human-modified habitat. Human-modified habitats such as sugarcane (n= 13), rural (n = 8) and urban (n = 7) settlements and *Eucalyptus* plantations (n = 1) also supported unique species, but fewer than natural habitats. Combined, I recorded 110 species in human-modified habitats and 134 in natural habitats of which 36 (21%) and 63 (36%) were unique to human and natural habitats respectively. Just less than half (72 out of 171) of the species were recorded within both anthropogenic and natural habitats. Only the widespread generalist *Pycnonotus barbatus* (Dark-capped Bulbul) was recorded within all habitat types.

Alpha-diversity

Survey saturation approached but did not reach asymptotic density for any habitat type. The proportion of expected species observed during surveys ranged from 77% - 97% for the different habitats (see Table 1). Saturation in sugarcane came closest to reaching asymptotic density while forests were the least saturated (See Appendix 2 Supplementary Material). Estimates of species richness varied amongst habitat types for incidence-based and abundance based estimators (Table

1). Chao1 suggested that species richness was highest in woodlands ($Chao1_{woodland}$ = 90), followed by forests ($Chao1_{forest}$ = 74), rural areas ($Chao1_{rural}$ =75), and urban habitats ($Chao1_{urban}$ = 69). The habitats that supported the lowest estimated species richness were *Eucalyptus* plantations ($Chao1_{planatation}$ = 50), grasslands ($Chao1_{grassland}$ = 35) and sugarcane ($Chao1_{sugarcane}$ = 30). Alternative estimates of species richness were consistent with that of Chao1 in ranking species richness amongst habitat types and all suggested that woodlands, forests, rural and urban areas respectively, supported the greatest number of species.

Alpha-diversity was significantly different amongst surveyed habitat types for all spatial scales (Poisson GLM, FS: ($\chi2$= 520, df = 6, P < 0.001), IS *($\chi2$= 366, df = 6, P < 0.001)* CS *($\chi2$= 197, df = 6, P < 0.001)* (Fig. 3). Mean values of alpha-diversity also increased with an increase in sampling spatial grain. However, patterns of alpha-diversity amongst habitat types remained similar irrespective of the spatial scale at which analysis was conducted. Alpha-diversity was significantly higher (P > 0.001) in woodlands than any other habitat type at all spatial scales (FS_α =12.51 ± 0.46; IS_α =23.41 ± 1.21 and CS_α = 38.63 ± 2.65). In contrast, grasslands (FS_α =3.84 ± 0.21; IS_α =7.20 ± 1.21 and CS_α = 12.5 ± 1.38) and *Eucalyptus* plantations (FS_α =4.83 ± 0.22; IS_α =7.83 ± 0.42 and CS_α = 13.12 ± 0.89) were not significantly different (P > 0.155) and supported the lowest alpha-diversity amongst habitats for all spatial scales (Fig. 3).

Beta-diversity

The β_{bray} for all landscape types decreased as spatial sampling grain became courser. β_{bray} also differed significantly amongst landscape types at all spatial scales FS *($\chi2$= 61, df = 6, P < 0.001)*, IS *($\chi2$= 4.098, df = 6, P = P < 0.001)* and CS *($\chi2$= 1.39, df = 6, P = P < 0.001)* (Fig. 3). However, unlike alpha-diversity, patterns of beta-diversity were not similar at different spatial scales. At fine scales, forest assemblages supported the highest β_{bray} (FS_β = 0.65 ± 0.0009), followed by rural (FS_β = 0.60 ± 0.003), and woodlands (FS_β = 0.59 ± 0.003). Bird assemblages within sugarcane (FS_β = 0.57 ± 0.003),

plantations ($FS_\beta = 0.57 \pm 0.004$) and urban ($FS_\beta = 0.57 \pm 0.0023$) habitats had similar levels of β_{bray} while grassland supported the lowest levels β_{bray} ($FS_\beta = 0.55 \pm 0.0023$) at fine spatial scales.

At intermediate scales, patterns of beta-diversity amongst landscapes were different than at fine scales. Assemblages within grasslands now supported the highest β_{bray} ($IS_\beta = 0.53 \pm 0.007$), which was significantly higher than any other habitat type. This was followed by plantations ($IS_\beta = 0.49 \pm 0.01$), woodlands ($IS_\beta = 0.49 \pm 0.004$) (that were not significantly different), forest ($IS_\beta = 0.47 \pm 0.002$), rural ($IS_\beta = 0.46 \pm 0.005$) and urban habitats ($IS_\beta = 0.41 \pm 0.008$). β_{bray} in sugarcane ($IS_\beta = 0.38 \pm 0.008$) was significantly lower than within any other habitat type ($P < 0.03$).

At coarse scales, grasslands ($CS_\beta = 0.48 \pm 0.02$) and plantations ($CS_\beta = 0.44 \pm 0.01$) were not significantly different and supported the highest β_{bray} among habitat types. This was followed by woodlands ($CS_\beta = 0.39 \pm 0.01$), rural ($CS_\beta = 0.39 \pm 0.009$) and forest habitats ($CS_\beta = 0.32 \pm 0.009$). The lowest β_{bray} at coarse scales was recorded in urban ($CS_\beta = 0.22 \pm 0.01$) and sugarcane ($CS_\beta = 0.22 \pm 0.01$) habitats. β_{bray} in natural habitats was significantly higher than anthropogenic habitats at fine ($P_{FS\beta} < 0.0001$) and intermediate ($P_{IS\beta} < 0.001$) spatial scales but not at coarse scales ($P_{CS\beta} = 0.17$).

Community assembly processes

Mean β_{RC} within all seven habitat types were similar for fine (-0.68 to -0.91), intermediate (-0.84 to -0.97) and coarse spatial scale (-0.72 to -0.96). Therefore, mean β_{RC} values were generally close to or approaching -1 for all habitat types at all spatial scales. This provides two sets of results. Firstly, this indicates that community composition was more similar between sample units within habitat types than expected by chance. Secondly, estimates of β_{RC} indicate community assembly within habitat types were more influenced by deterministic processes (approaching -1) than stochastic processes for both natural and human-modified habitat types. However, patterns of mean β_{RC} differed amongst habitat types at different spatial scales. Moreover, as spatial grain became finer, community assembly processes became more stochastic (approaching 0) (Fig 4). This resulted in estimates of β_{RC} at intermediate and coarse spatial scales becoming nested within fine scale β_{RC} values (Fig 5).

At fine scales I found that community assembly, while still deterministic, was more stochastic than at intermediate and coarse spatial scales. The habitat with a mean β_{RC} closest to 0 at fine scales and therefore the least deterministically structured was sugarcane [β_{RC}= -0.68 (95% CI: -0.70 to -0.67)] and became more deterministic for plantations [(β_{RC}= -0.77 (95% CI: -0.79 to -0.76)], grasslands [(β_{RC}= -0.78 (95% CI: -0.80 to -0.77)], forests [(β_{RC}= -0.79 (95% CI: -0.79 to -0.78)], urban [(β_{RC}= -0.87 (95% CI: -0.89 to -0.86)], rural [(β_{RC}= -0.88 (95% CI: -0.89 to -0.87)] and woodlands [(β_{RC}= -0.92 (95% CI: -0.93 to -0.91)].

At intermediate spatial scales β_{RC} values were similar and indicated that all assemblages amongst habitats were structured by deterministic processes. The habitat with a mean β_{RC} closest to 0 at intermediate scales and therefore the least deterministically structured was grasslands [β_{RC}= -0.84 (95% CI: -0.86 to -0.82)]. Community assembly processes became more deterministic in sugarcane [β_{RC}= -0.85 (95% CI: -0.87 to -0.81)], plantations [β_{RC}= -0.86 (95% CI: -0.89 to -0.81)], urban [β_{RC}= -0.96 (95% CI: -0.97 to -0.94)], rural [β_{RC}= -0.96 (95% CI: -0.97 to -0.98)], forest [β_{RC}= -0.96 (95% CI: -0.96 to -0.96)], and woodland [β_{RC}= -0.97 (95% CI: -0.98 to -0.95)] respectively.

At coarse spatial scales mean β_{RC} amongst habitat were again similar and also indicate deterministic community assembly with the exception of grasslands [β_{RC}= -0.72 (95% CI: -0.82 to -0.61)] where β_{RC} was lower than at intermediate scales, however, the 95% CI here was large. Plantations [β_{RC}= -0.91 (95% CI: -0.96 to -0.82)], sugarcane [β_{RC}= -0.92 (95% CI: -0.95 to -0.87)], rural [β_{RC}= -0.92 (95% CI: -0.97 to -0.87)], woodlands [β_{RC}= -0.94 (95% CI: -0.98 to -0.89)], urban [β_{RC}= -0.95 (95% CI: -0.98 to -0.82)] and forest [β_{RC}= -0.96 (95% CI: -0.99 to -0.93)] all supported very similar β_{RC} values (see figures 4 and 5).

DISCUSSION

What happens to bird assemblages when humans transform habitats? I found partial support for my first hypothesis that species richness declines in human-modified habitats relative to natural habitats. The exception was natural grasslands where species richness was low and comparable to

that of sugarcane, which supported the lowest habitat species richness. I also found partial support

for my second hypothesis that human-modified habitats may homogenise assemblages. However,

this was only the case for sugarcane at intermediate and coarse spatial scales. Other human-

modified habitats such as plantations, urban settlements and rural habitats supported levels of beta-

diversity comparable with natural habitats. I found no support for my third hypothesis that

community assembly processes are more deterministic in human-modified habitats than natural

habitats. Rather community assembly in both human-modified and natural habitats were

predominantly non-random and influenced by deterministic, niche-based processes (Püttker et al.

2015). I did, however, find that processes driving community assembly became more stochastic as

spatial sampling grain became finer for all habitats. My final hypothesis that spatial scale would

influence estimates but not patterns of diversity was only true for alpha-diversity. Conversely,

patterns of beta-diversity varied at different spatial scales. My findings (β_{Bray} and β_{RC}) also indicated

that beta-diversity decreased as spatial sampling grain became coarser.

In response to the human modification of habitats, bird assemblages may be more

influenced by the habitat structure and the type of activities taking place in the habitat as opposed

to a simple binary approach of whether the habitat is natural or human-modified. For instance, not

all natural habitats in my study supported high species richness. Grasslands contrasted with

woodlands and forests by supporting the lowest alpha-diversity at all spatial scales and the second

lowest habitat species richness. Moreover, rural and urban habitats supported surprisingly high

levels of species richness, comparable to that of the species-rich woodland and forest habitats.

These findings provide some support for the emerging consensus that certain human-modified

habitats may be capable of supporting diverse biological assemblages (Donald and Evans 2006;

Greenler and Ebersole 2015; Wearn et al. 2016). The reason for this may be that some human-

modified habitats may maintain certain niches following anthropogenic transformation while also

provide new niches, therefore, overriding the effects of species loss following habitat transformation

(Ehlers Smith et al. 2015). However, in support of my first hypothesis intensively managed human

habitats such as sugarcane and plantations supported decreased habitat species richness and alpha-diversity.

Niche-based correlates of species loss in a habitat were not directly tested for in my study, however, previous studies assessing alpha and gamma diversity have suggested that assemblage responses to habitat transformation and loss may be associated with available niches within a habitat (Pardini et al. 2010; Ehlers Smith et al. 2015). For example, Ehlers Smith et al. (2015) found that when natural heterogeneous habitats were replaced by comparatively homogenous human-modified habitats the reduction in vegetation structure and niche availability, brought about a reduction or loss of various foraging strategies, associated with 35% of the species in their study. This may explain why grasslands, sugarcane and plantations which are more structurally homogeneous, supported reduced alpha-diversity and overall habitat species richness (Tilman 2004). In contrast, forests and woodlands which are more structurally heterogeneous may provide a wider variety of niches specifically for habitat specialist species and therefore promote increased species richness and possibly functional diversity (Carrara et al. 2015). Similarly, rural and urban habitats which comprise an array of different land use types such as suburban gardens, human infrastructure, greenbelt areas, and subsistence agriculture may compensate for species losses following anthropogenic transformation by providing similar or increased habitat availability relative the natural habitat which it replaced (Ehlers Smith et al. 2015). Therefore, increased habitat availability may increase within habitat beta-diversity and maintain or increase species richness as posited by the dominance of beta-diversity hypothesis (Quinn et al. 1988; but also see Tscharntke et al. 2012). This may further explain high levels of beta-diversity for rural and urban habitats in my study.

Increased species richness following anthropogenic transformation, however, does not imply an increase in functional diversity or regional diversity (Karp et al. 2012). Conversely, these human-modified habitats may be comprised of mostly synanthropic generalist species (i.e. species commonly associated with human-modified habitats) which have similar functional traits and are

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capable of exploiting a commonly available resource (Tscharntke et al. 2005). As a result

representation of functional traits in these habitats could be impaired (De Coster et al. 2015). For

example, Flynn et al. (2009) found that functional diversity in high-intensity agriculture systems was

low beyond what would be expected given the number of species in the present in the habitat.

Decreased functional diversity in human-modified habitats may reflect that only a subset of traits

allows for the persistence of species in human-modified conditions (Ekroos et al. 2010). Moreover,

human-modified habitats may also provide a platform for generalist species to spill over and invade

adjacent natural habitats decreasing between habitat beta-diversity (Bridgman et al. 2012). This

invasion could result in the further selective extirpation of habitat specialist species and the success

of a few generalist species across the landscape bringing about a regional biotic homogenisation

effect (McKinney and Lockwood 1999). My study supports this by showing that very few habitats

apart from forests and woodlands supported many unique species. This was particularly true for

plantations, rural and urban areas where most of the species recorded were recorded in other

habitats too. However, only one species the *Pycnonotus barbatus* (Dark-capped Bulbul) was

recorded in all of the habitats which were surveyed. The exception to this was sugarcane which

supported low habitat species richness (n = 28) but 13 of those species were unique to the

sugarcane habitat. Moreover, human-modified habitats have also been shown to have strong

influences on species occurrence and spatial dynamics in adjacent natural habitats (Ricketts 2001;

Tscharntke et al. 2012). For instance, Freeman et al. (2018) found that coastal forest fragments were

more likely to lose forest specialist species from smaller forest fragments when embedded within an

anthropogenic matrix compared to natural matrices. The expected contribution of human-modified

habitats to regional species richness may therefore be overshadowed by their negative effects on

within habitat functional diversity and the occurrence of specialist species in the natural habitats

adjacent to them (Driscoll et al. 2013; Ferrante et al. 2017).

Estimates of beta-diversity decreased with sampling grain using both Bray Curtis and Raup–

Crick in human-modified and natural habitats. This finding is consistent to that found by other

studies (e.g. Mac Nally et al. 2004; Martiny et al. 2011; Olivier and van Aarde 2014). This may be as a result of a sampling effect whereby as the area of the focal unit increases so too does the proportion of a community included in a sample (Olivier and Van Aarde 2014). This increases the probability of the species composition between sampling units becoming more similar at coarser spatial grains (i.e. decreased beta-diversity). However, unlike alpha-diversity patterns of beta-diversity were also variable across spatial scales. For example, grassland supported assemblages with the lowest beta-diversity amongst habitats at fine scales but contrastingly supported the highest beta-diversity at intermediate and coarse spatial scale. A possible explanation for this is that grassland habitats are dominated by a few generalist species which were recorded consistently at survey points. Specialist or rare grassland species, however, were only recorded occasionally in larger sampling units (i.e. within first of second order fractals). Due to the robustness of sampling units at fine scales, the presence of rare species would likely have little influence on mean beta-diversity. However, at coarser spatial grains the presence of rarer species would hold more weight and possibly bring about an increase in mean beta-diversity. The opposite may be true for an intensively managed human-modified habitat such as sugarcane. Species assemblages at survey points were similar and rare species were very seldom recorded. This may also explain why beta-diversity within sugarcane was low especially at coarse scales suggesting a biotic homogenisation effect (Tabarelli et al. 2012). This supports the findings of Karp et al. (2012) that agricultural intensification (specifically monocultures) brings about a decrease in habitat beta-diversity but is only apparent at coarse spatial scales.

Do we disrupt community assembly processes when we transform natural habitats? My results suggest that this is not the case and that community assembly is most often deterministic and niche based in both natural and transformed habitats. Püttker et al. (2015) also found that niche based community assembly processes were more prevalent in small mammal communities than stochastic processes in all landscape types within their study. However, these deterministic processes may not be the same between human-modified and natural habitats. This suggests that the while the specific community assembly processes may differ between human-modified and

natural landscapes, community assembly in both these habitat types is likely a product of ecological filtering and habitat niche breadth but not random extinction and colonisation (Püttker et al. 2015). We did, however, find that assembly processes become more stochastic as spatial grain became finer. This is almost definitely a sampling effect similar to that observed for my β_{Bray} metric, whereas spatial grain increased the proportion of the community included at a sampling unit increased thereby reducing beta between sampling units. I, however, never obtained a β_{RC} that indicated processes were conclusively more stochastic than deterministic in any habitat. This result again demonstrates the sensitivity of beta-diversity metrics to spatial sampling scale which is of particular importance especially when making inferences about community assembly process.

Some limitations of my study should, however, also be noted. Different habitat types have multiple interacting spatial components, which makes it difficult to isolate the main driver of species richness, patterns of diversity and community assembly processes (i.e. habitat amount, habitat area, edge effects, matrix land-use types) (Didham et al. 2012). Moreover, the habitats adjacent to the surveyed habitats were not always constant and spill-over effects from various neighbouring habitats may have influenced patterns of diversity (Tscharntke et al. 2012). This is particularly true for coarse scales where small sample sizes may introduce errors particularly relating to estimates of beta-diversity (Crist et al. 2003; Tuomisto 2010). Moreover, my study only assessed the seven most prevalent habitat types along the coastal plains of KwaZulu-Natal. There are, however, a number of other habitat types both human-modified and natural within this landscape that may contribute or impede regional species richness. Moreover, as discussed while I found that species richness and beta-diversity was high within certain human-modified I did not test for the influence of habitat transformation on functional diversity.

The transformation of landscapes to human land use types is unlikely to slow down in the foreseeable future (Petit and Petit 2003; Foley 2005; Jewitt et al. 2015). My findings suggest that preserving natural habitats such as forests, woodlands and grasslands is important for the future preservation of diverse biological assemblages. However, the landscapes surrounding these natural

habitats are also important for regional species richness and should be considered when assessing the conservation value of habitats within a landscapes (Greenler and Ebersole 2015; Freeman et al. 2017). Further research on these habitats may provide insight into their roles of maintaining functional diversity, ecosystem services and their capacity to provide habitats for various taxa. However, it is true that human-modified habitats are unlikely to ever provide the same conservation value as pristine natural habitats (e.g. Gibson et al. 2013). This is particularly true for intensively managed monoculture habitats such as sugarcane (Karp et al. 2012). However, promoting a mosaic landscape approach where land-use types vary and maintaining heterogeneous vegetation structure or high niche availability in these habitats (e.g. indigenous trees, see Bhagwat et al. 2008) may promote increased beta-diversity both within and between habitats and therefore bring about increased regional species richness (Quinn et al. 1988). This is in line with the landscape moderated insurance hypothesis which suggests that the complexity of a landscape provides both spatial and temporal insurance by increasing the resilience and stability of ecological processes in a landscape following landscape disturbances such as anthropogenic transformation (Yachi and Loreau 1999). Therefore if considered and integrated properly into a management strategy and landscape design the associated negative impact of human-modified habitats may be overridden by the composition and spatial structure of habitat types within a landscape (Tscharntke et al. 2012).

Tables

Table 3 Observed species richness (Species obs., include auditory records and sightings) and abundance (Ind. obs.), abundance- and incidence-based richness estimators, percentage of predicted richness actually observed, and Shannon diversity of birds across seven habitat types

Habitat	Species obs.	Ind. obs.	Abundance-based estimators				Incidence-based estimators		Percentage observed (range)	Shannon diversity
			Chao1(95% CI)	ACE	Jack1	Jack2	Chao2 (95% CI)	ICE		
Sugarcane	28	888	29.50 (29.03-37.25)	29.77	32.98	34.96	30.99 (29.25-44.92)	31.54	82-95%	1.37
Rural	69	1556	74.50 (71-89.6)	76.19	82.92	84.96	76.46 (71.74-93.98)	79.26	81-93%	1.49
Urban	58	2029	69.16 (62.29-96.64)	68.39	72.92	77.91	68.61(62.36-91.49)	72.13	77-87%	1.63
Plantation	43	732	50.53 (39.19-103.39)	46.7	45.95	49.92	47.31 (38.74-83.41)	47.11	85-93%	0.92
Grassland	34	749	35.11 (34.14-42.69)	38.19	41.95	40.04	36.53 (34.48-47.33)	40.09	82-97%	0.63
Woodland	84	1789	89.5 (86.03-104.6)	89.76	97.92	96.04	89.84 (86.26-103.55)	93.85	86-94%	1.78
Forest	68	2602	74.11(69.51-92.73)	77.06	78.96	81.97	74.09(69.50-92.65)	77.15	83-91%	2.02

ACE, abundance-based coverage estimator; CI, confidence interval; ICE, incidence-based coverage estimator.

Table 2 Analysis of variance (ANOVA) stepwise multiple comparisons (Tukey test). (2a) Comparing alpha-diversity (presence-absence data) and (2b) beta-diversity values (Bray-Curtis dissimilarity) among seven different habitat types at three different sampling spatial scales (fine, intermediate and coarse scale) based on fractal sampling design.

2a

	Fine sampling scale			Intermediate scale			Coarse scale		
	Estimate	Z-value	p-value	Estimate	Z-value	p-value	Estimate	Z-value	p-value
Forest - Grasslands	-0.761	-11.951	< 0.001 ***	-0.757	-9.293	< 0.001 ***	-0.677	-6.005	<0.001 ***
Forest - Plantations	-0.561	-9.739	< 0.001 ***	-0.674	-8.576	< 0.001 ***	-0.628	-5.680	<0.001 ***
Forest - Rural	0.131	3.019	0.038	0.181	3.240	0.019 *	0.243	2.973	0.044 *
Forest - Sugarcane	-0.183	-3.717	0.00347 **	-0.261	-3.951	0.00142 **	-0.312	-3.179	0.024 *
Forest - Urban	0.210	4.983	< 0.001 ***	0.170	3.024	0.03723 *	0.152	1.801	0.536
Forest - Woodlands	0.391	9.912	< 0.001 ***	0.421	8.203	< 0.001 ***	0.451	5.851	<0.001 ***
Grasslands - Plantations	0.200	2.484	0.155	0.083	0.789	0.985	0.049	0.349	0.999
Grasslands - Rural	0.892	12.550	< 0.001 ***	0.938	10.459	< 0.001 ***	0.920	7.782	<0.001 ***
Grasslands - Sugarcane	0.578	7.743	< 0.001 ***	0.496	5.140	< 0.001 ***	0.365	2.801	0.0717
Grasslands - Urban	0.971	13.809	< 0.001 ***	0.927	10.316	< 0.001 ***	0.829	6.913	<0.001 ***
Grasslands - Woodlands	1.151	16.758	< 0.001 ***	1.178	13.551	< 0.001 ***	1.128	9.806	<0.001 ***
Plantations - Rural	0.692	10.533	< 0.001 ***	0.855	9.818	< 0.001 ***	0.871	7.498	<0.001 ***
Plantations - Sugarcane	0.378	5.436	< 0.001 ***	0.413	4.388	< 0.001 ***	0.316	2.461	0.167
Plantations - Urban	0.771	11.885	< 0.001 ***	0.843	9.671	< 0.001 ***	0.780	6.616	<0.001 ***
Plantations - Woodlands	0.951	15.073	< 0.001 ***	1.095	12.997	< 0.001 ***	1.079	9.555	<0.001 ***
Rural - Sugarcane	-0.313	-5.370	< 0.001 ***	-0.442	-5.816	< 0.001 ***	-0.556	-5.315	<0.001 ***
Rural - Urban	0.079	1.498	0.732	-0.011	-0.169	1	-0.092	-1.004	0.951
Rural - Woodlands	0.260	5.142	< 0.001 ***	0.240	3.778	0.003 **	0.208	2.447	0.172
Sugarcane - Urban	0.392	6.830	< 0.001 ***	0.431	5.654	< 0.001 ***	0.464	4.362	<0.001 ***
Sugarcane - Woodlands	0.573	10.328	< 0.001 ***	0.683	9.375	< 0.001 ***	0.764	7.567	<0.001 ***
Urban - Woodlands	0.181	3.660	0.004 **	0.252	3.944	0.001 **	0.300	3.436	0.0101 *

	Fine sampling scale			Intermediate scale			Coarse scale		
	Estimate	Z-value	p-value	Estimate	Z-value	p-value	Estimate	Z-value	p-value
Forest - Grasslands	-0.098	-28.409	<0.001 ***	0.068	9.044	<0.001 ***	0.164	9.060	<0.001 ***
Forest - Plantations	-0.080	-23.762	<0.001 ***	0.027	3.570	0.006 **	0.119	6.595	<0.001 ***
Forest - Rural	-0.047	-13.891	<0.001 ***	-0.002	-0.242	1	0.065	3.627	0.005
Forest - Sugarcane	-0.080	-23.523	<0.001 ***	-0.080	-10.521	<0.001 ***	-0.099	-5.490	<0.001 ***
Forest - Urban	-0.060	-24.059	<0.001 ***	-0.048	-6.330	<0.001 ***	0.001	0.090	1.000
Forest - Woodlands	-0.018	-16.646	<0.001 ***	0.028	3.685	0.004 **	0.068	3.764	<0.001 ***
Grasslands - Plantations	0.018	3.905	0.002 **	-0.041	-4.054	<0.001 ***	-0.044	-1.961	0.430
Grasslands - Rural	0.051	11.028	<0.001 ***	-0.070	-6.877	<0.001 ***	-0.099	-4.324	<0.001 ***
Grasslands - Sugarcane	0.019	4.077	<0.001 ***	-0.148	-14.489	<0.001 ***	-0.264	-11.580	<0.001 ***
Grasslands - Urban	0.017	3.690	0.004	-0.116	-11.385	<0.001 ***	-0.163	-7.138	<0.001 ***
Grasslands - Woodlands	0.042	9.040	<0.001 ***	-0.041	-3.969	0.0013 **	-0.096	-4.214	<0.001 ***
Plantations - Rural	0.033	7.226	<0.001 ***	-0.029	-2.823	0.066	-0.054	-2.362	0.208
Plantations - Sugarcane	0.0008	0.175	1	-0.107	-10.435	<0.001 ***	-0.220	-9.618	<0.001 ***
Plantations - Urban	-0.001	-0.218	1	-0.074	-7.331	<0.001 ***	-0.118	-5.177	<0.001 ***
Plantations - Woodlands	0.024	5.210	< 0.001 ***	0.0008	0.085	1	-0.051	-2.253	0.260
Rural - Sugarcane	-0.032	-7.051	< 0.001 ***	-0.078	-7.612	<0.001 ***	-0.166	-7.256	<0.001 ***
Rural - Urban	-0.034	-7.444	< 0.001 ***	-0.046	-4.508	<0.001 ***	-0.064	-2.815	0.07
Rural - Woodlands	-0.009	-2.016	0.382	0.029	2.908	0.052	0.002	0.109	1.000
Sugarcane - Urban	-0.002	-0.393	1	0.032	3.104	0.029 *	0.101	4.441	<0.001 ***
Sugarcane - Woodlands	0.023	5.035	< 0.001 ***	0.108	10.520	<0.001 ***	0.168	7.365	<0.001 ***
Urban - Woodlands	0.024	5.428	< 0.001 ***	0.076	7.416	<0.001 ***	0.067	2.924	0.05

[a] Significance of each comparison is indicated by *P < 0.05; **P < 0.01; ***P < 0.001.

Figures

Figure 1. (a) The study area along the north east coast of South Africa (KwaZulu-Natal province). The location of surveyed habitat types is represented by triangles. Dark grey areas on the map highlight coastal forest fragments. At each habitat type, a minimum of nine second order fractals were surveyed. (b) Hierarchical fractal sampling design (Marsh and Ewers 2013). Black circles indicate survey points (fine scale) which were arranged into equilateral triangles with sides of 178m. Each equilateral triangle represents a first order fractal (intermediate scale). Three first order fractals arranged into a larger equilateral triangle with sides of ~564m formed a second order fractal (coarse scale). Second order fractals were therefore made up of nine survey points.

Figure 2 (a) Chao1 estimated habitat species richness and (b) Beta-diversity and 95% confidence intervals of bird assemblages within the seven surveyed habitat types.

Figure 3 Mean alpha- and beta-diversity with 95% CI for seven different habitat types at fine, intermediate and coarse sampling spatial scales. Habitats are ranked from a-e with a representing the significantly highest diversity index value and e representing the significantly lowest diversity index value. Habitats that share the same ranking are significantly non-different (ANOVA). Gamma diversity has been partitioned into its alpha and beta components.

Figure 4. Mean raup-crick null model values. A β_{RC} value is indicative of whether compared assemblages are more dissimilar (approaching 1), as dissimilar (approaching 0), or less dissimilar (approaching -1) than expected by random chance (Chase et al. 2011). Moreover, a mean β_{RC} value of 0 indicates processes driving community assemblage are more stochastic (neutral), while, a β_{RC} approaching -1 or 1 indicates deterministic processes (niche based) in community assemblage (Chase et al. 2011; Püttker et al. 2015). Fine-scale (FS), Intermediate scale (IS) and Coarse-scale (CS).

Figure 5. Non-metric multi-dimensional scaling (NMDS) ordinations of sites for each of the seven different landscapes at the three respective spatial grains based on β_{RC} between sampling units. Polygons enclose sites for each of the sampling grains tested.
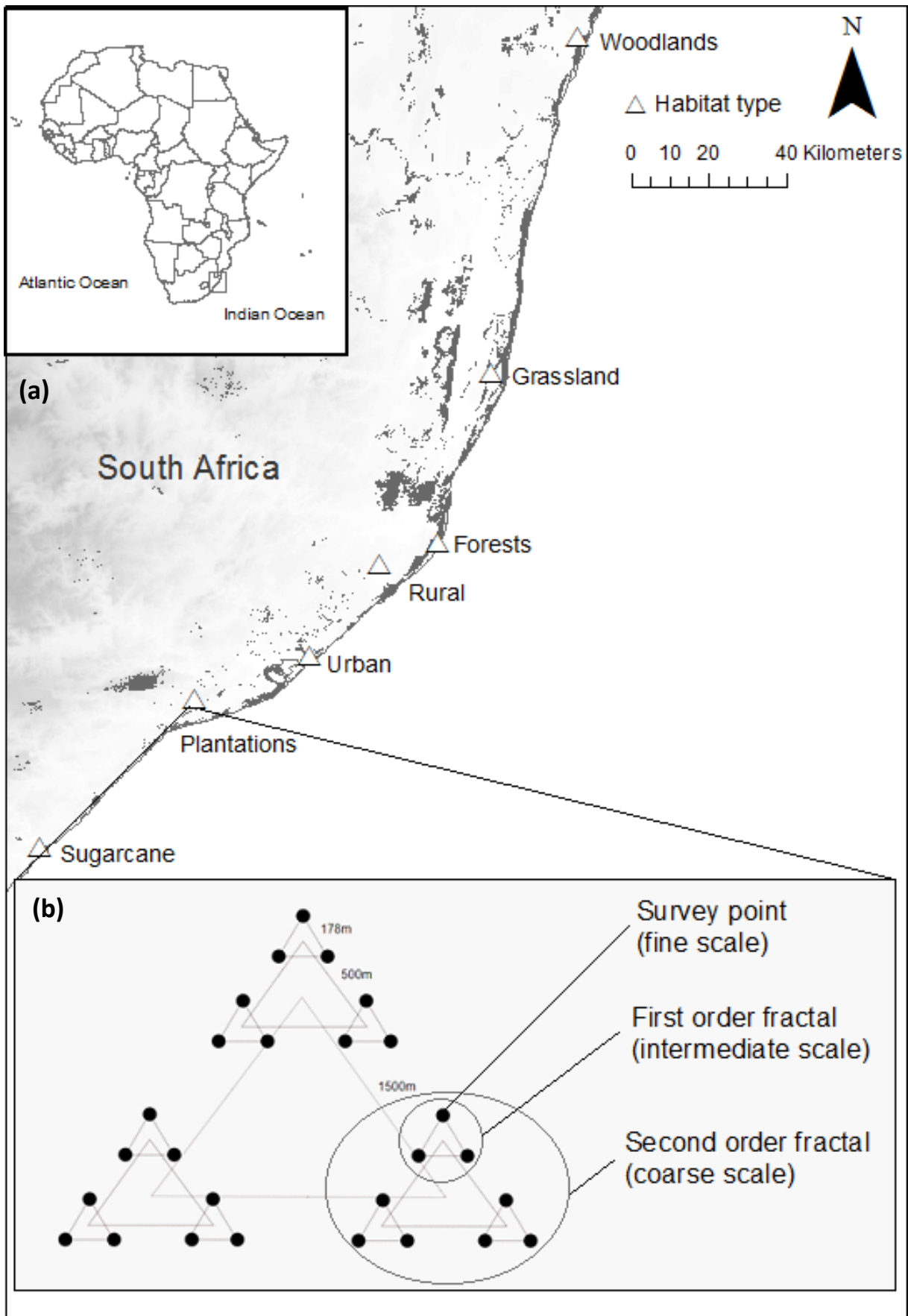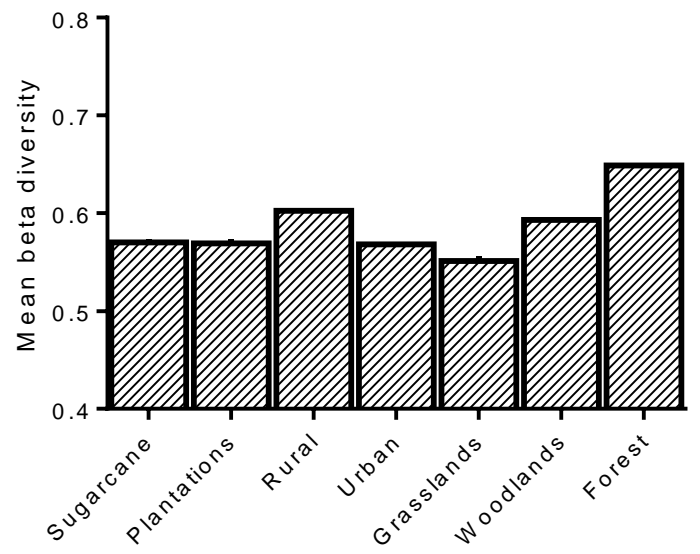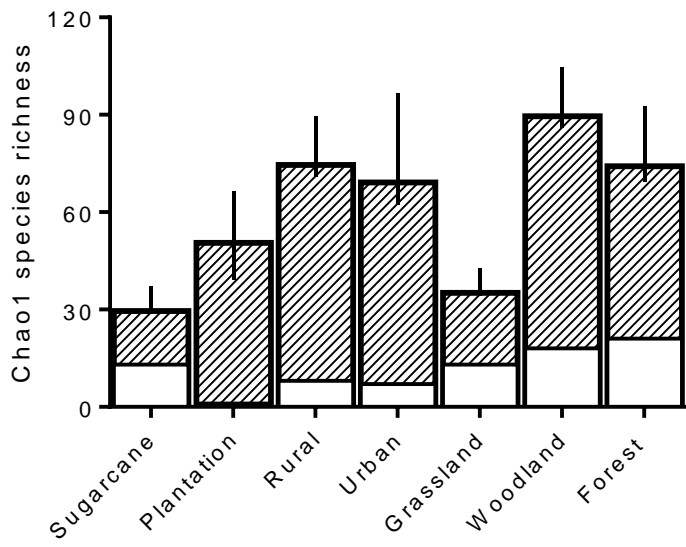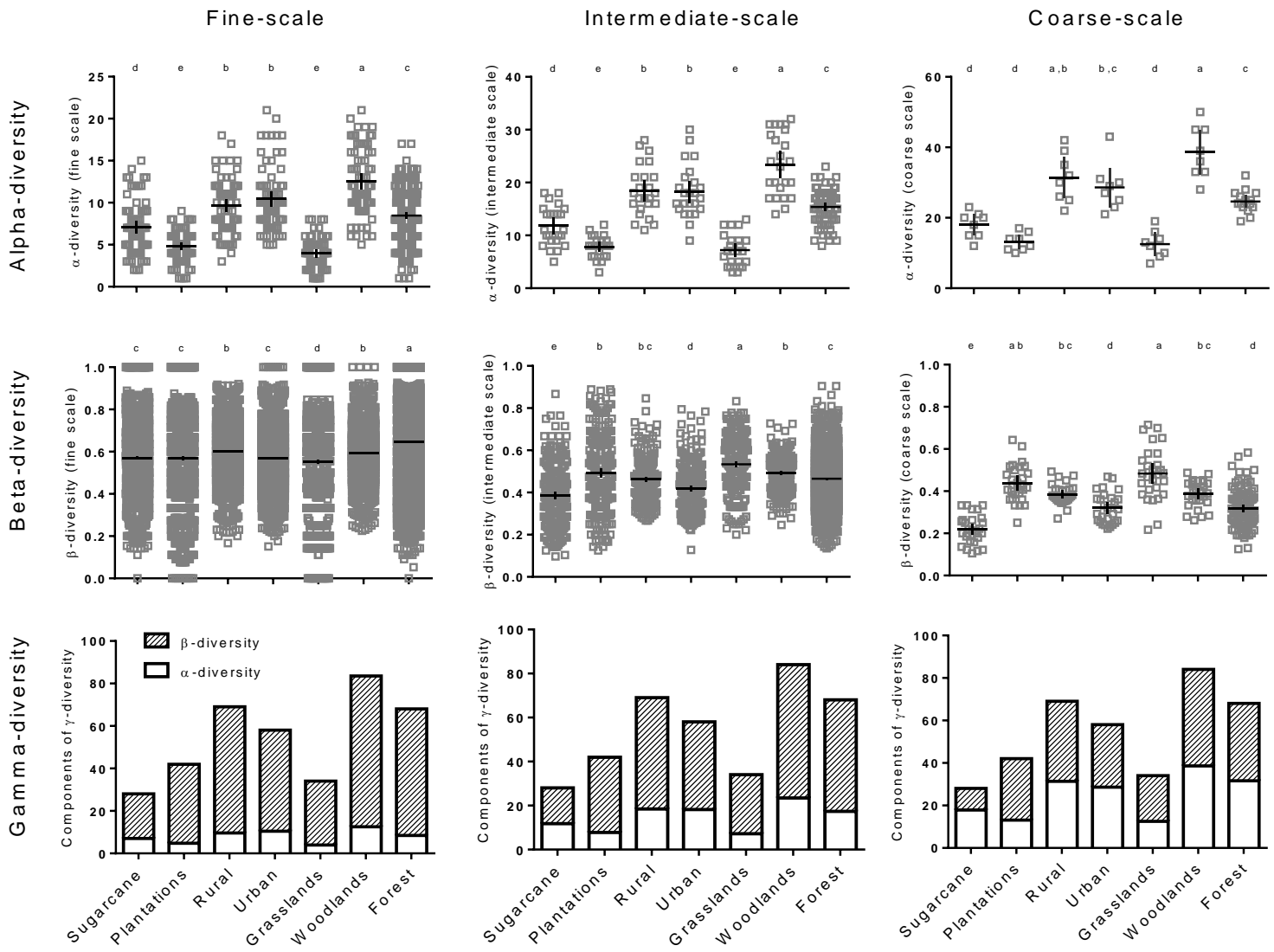
Figure 1

Figure 2

Figure 3
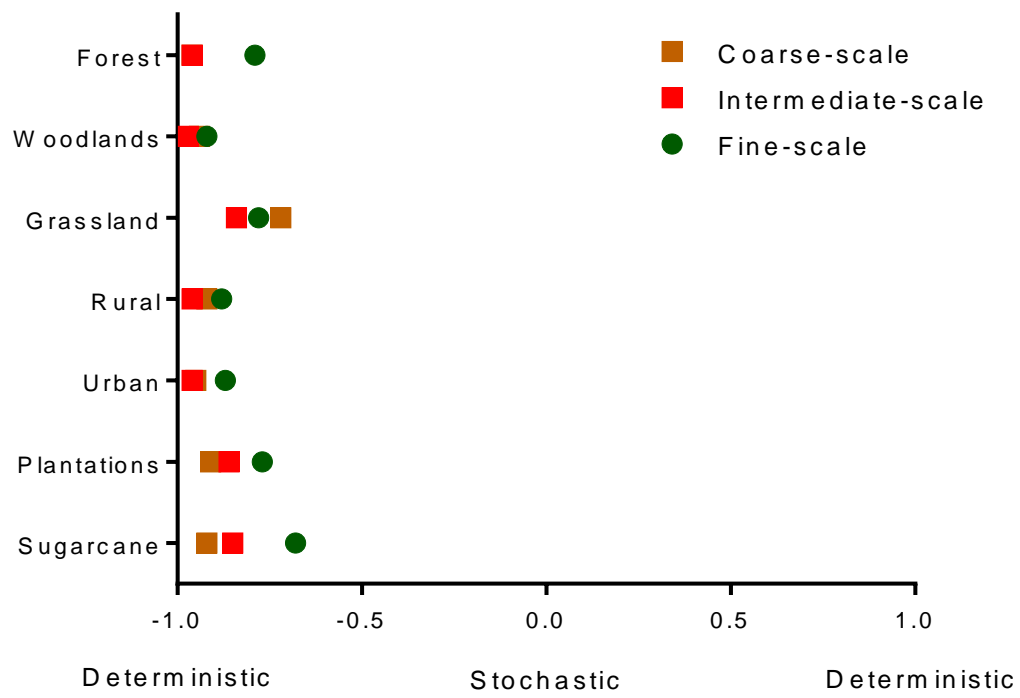
Figure 4
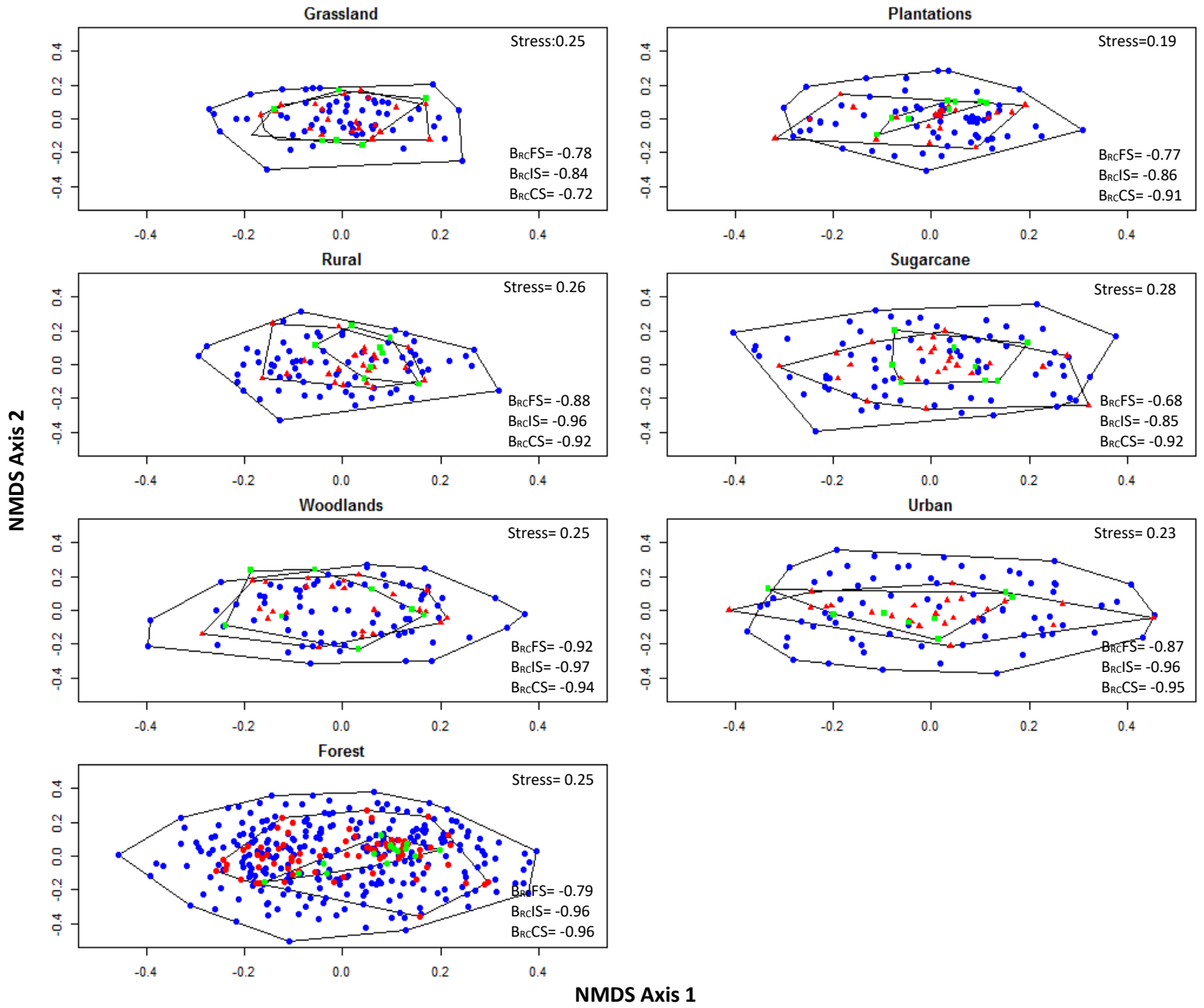
Figure 5

SUPPORTING INFORMATION

Appendix S1- Habitat saturation curves.
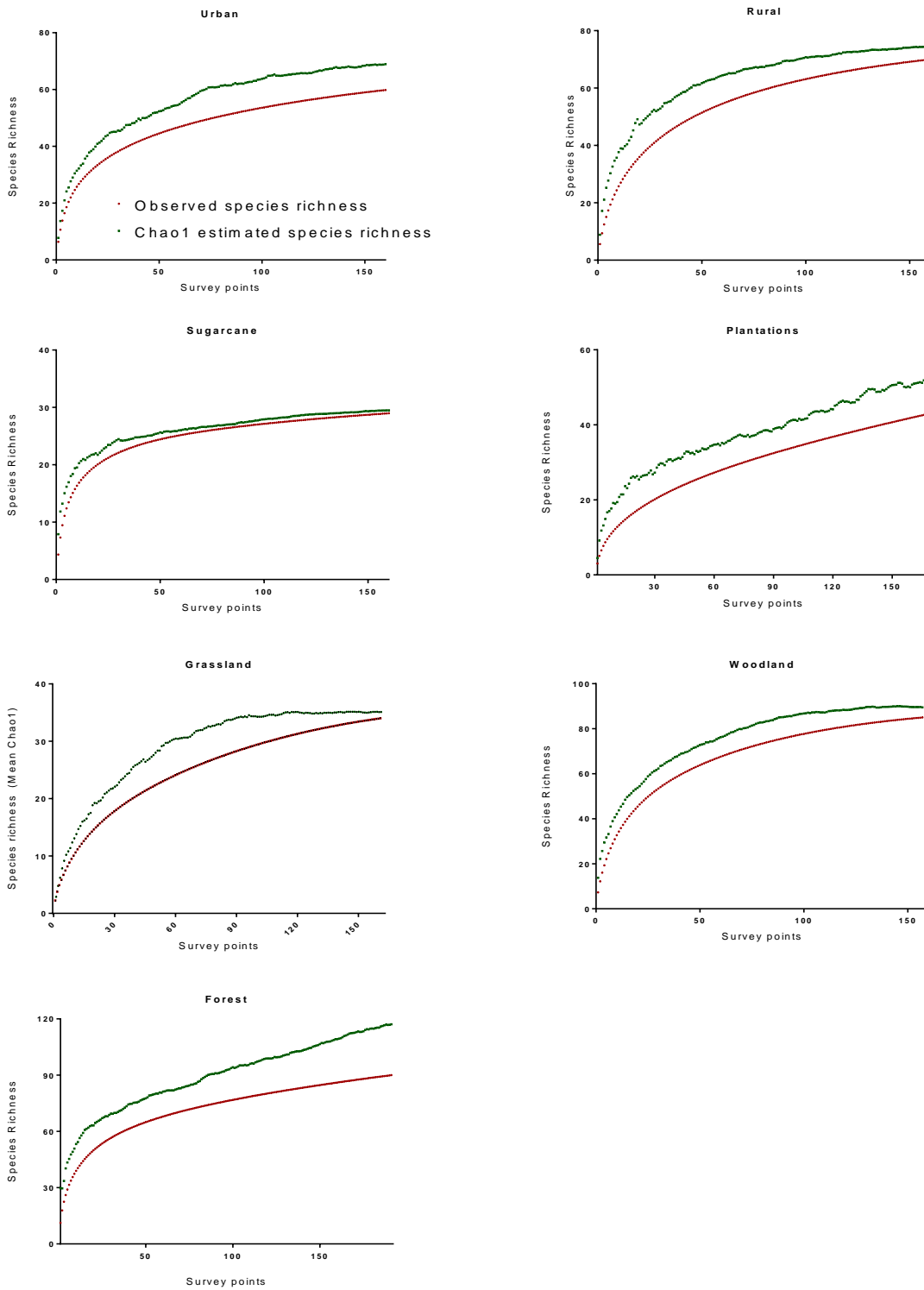
Figure S2.1 Saturation curves based on Chao1 estimated species richness calculated using Estimate S 8.2.0 compared to observed species richness.

Appendix S3 – Proportion of different habitat types in my human-dominated landscape Along the coastal plains of KwaZulu-Natal, South Africa. Calculated using land-cover images for KwaZulu-Natal from Jewitt et al (2015).

Figure 3.1 Percentage habitat type coverage for study landscape in KwaZulu-Natal, South Africa.

Chapter 4

GENERAL CONCLUSIONS

Much of the natural habitat along the northeast coastal plains of southern Africa such as grasslands, woodlands and forests have given way to human land-use types such as urban infrastructure, timber plantations and agricultural cultivations (Olivier et al. 2013; Jewitt et al. 2015). The conversion of natural habitats to human land use types influences bird community assembly both within remnant fragments of natural habitat (Chapt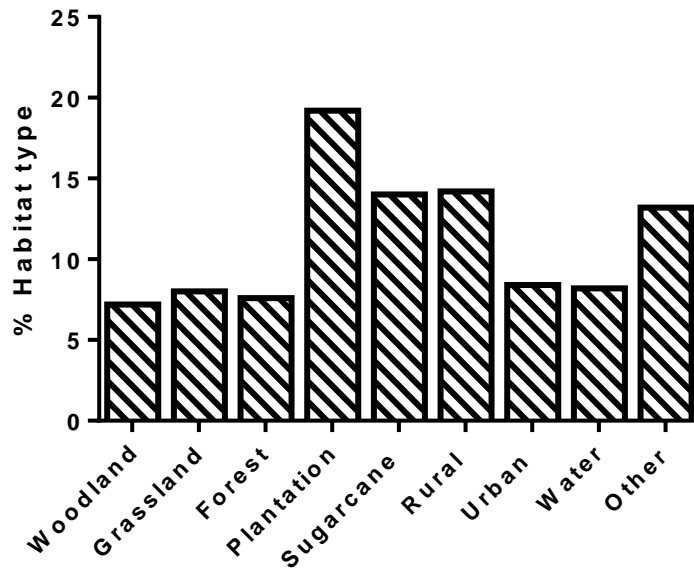er 2) and within the matrix of habitats adjacent to them (Chapter 3). Attempting to recover large proportions of lost natural habitats, however, may not be a viable conservation strategy at the landscape scale especially considering the growing human population and with it an increased demand for agricultural products, natural resources and living space (Foley 2005). Moreover, the conservation of protected natural areas alone is unlikely to preserve large proportions of biodiversity moving into the future (Mcdonald et al. 2008). Instead, global biodiversity will likely become increasingly dependent on the ability to persist in the face of anthropogenic landscape transformation (Petit and Petit 2003). This persistence may hinge on the effective management of both natural habitats and the matrix of human-modified habitat types which surround them (Pereira et al. 2010). However, evidence that anthropogenic matrices influence community assembly processes in remnant habitat fragments provide some hope that sustainable and well-informed management could have the capacity to reduce biodiversity losses even in the face of landscape transformation (Bhagwat et al. 2008). For this reason, scientists have increasingly begun assessing how human-modified habitats influence biological assemblages and whether they could potentially augment conservation efforts in conjunction with protected areas and remnant natural habitat fragments (Daily et al. 2001; Petit and Petit 2003; Ehlers Smith et al. 2015; Fahrig 2017). Further evidence that human-modified habitats may also have the capacity to support their own diverse assemblages provides an incentive to incorporate them into future conservation management planning (Ehlers Smith et al. 2015; Greenler and Ebersole 2015).

In this chapter, I aim to provide a synthesis of the scientific insights obtained during the preparation of my thesis which assesses how human-modified habitats influence bird assemblages. I base my synthesis on a selection of hypotheses. First, I address the findings of my second chapter regarding how anthropogenic matrices influence coastal forest bird assemblages relative to natural matrices. I place particular emphasis on island biogeography theory (IBT) (MacArthur and Wilson 1967), landscape complementarity theory (Dunning et al. 1992) and countryside biogeography theory (Daily et al. 2001). Next, I address my third chapter and discuss how patterns of bird diversity in the matrix of habitats surrounding coastal forest fragments are influenced by anthropogenic transformation. I discuss the observed patterns of diversity, the landscape moderated insurance hypothesis (Tscharntke et al. 2012) and the dominance of beta-diversity hypothesis (Quinn et al. 1988). I also emphasise the importance of using multiple spatial scales when making inferences regarding patterns of diversity across a landscape. In conclusion, I discuss potential conservation strategies and draw on my findings from both my second and third chapters to potentially identify further ecological questions which may improve the effectiveness of landscape conservation efforts in the future.

The reduction and fragmentation of continuous forests into smaller more isolated fragments results in local extinctions (Haddad et al. 2015; but also see Laurance 2008). However, the anthropogenic transformation of matrices surrounding forest fragments may also affect forest bird assemblages by disrupting dispersal ability, ecological functioning and community assembly (Kupfer et al. 2006; Didham et al. 2012; Tscharntke et al. 2012). To test this, I surveyed bird assemblages in 29 coastal forest fragments surrounded by anthropogenic matrices (sugarcane, *Eucalyptus* and *Pinus* plantations, urban settlements) and 30 fragments surrounded by natural matrices (grasslands and woodlands) along the east coast of southern Africa. I then modelled and compared the relationship between species richness and fragment using area eight different species-area models to determine which model was best suited to analyse my collected data. I also calculated and compared nestedness, assemblage evenness and species-specific response to fragment area for each fragment

in each landscape type. In agreement with Triantis et al. (2012) and Dengler (2009), I found that the Power model performed better than most other SAR models based on AICc values. Therefore, using the Power model, I determined the species-area relationships (SAR) for forest specialist species and habitat generalist in both landscapes. My results suggested that SAR's for forest specialist assemblages were amplified when the matrix was transformed and assemblages conformed more to predictions set out by Island Biogeography Theory (IBT) i.e. large forest fragments harboured many species relative to smaller forest fragments where species richness was impoverished (MacArthur and Wilson 1967). Therefore, matrix transformation may have a similar effect to flooding the area between forest fragments (e.g. Gibson, 2014) and cause forest specialists to disappear from small forest fragments. However, when matrices were natural, both small and large forest fragments supported a similar number of forest specialist and generalist species in agreement with that found by Guldemond and van Aarde (2010). This finding suggests that forest fragments embedded within a natural matrix may function as continuous habitat with the matrix adjacent to them (Dunning et al. 1992; Daily et al. 2001). We may then also expect that forest species to also be present to some extent in the surrounding natural matrix. This idea, however, has yet to be tested but may provide insight into how large populations of forest bird species are maintained in small forest fragments. If this is the case then it would be in line with that expected by the landscape complementation (Dunning et al. 1992) or countryside biogeographic theory (Daily et al. 2001) where fragment species regard the matrix as additional habitat and the species richness within a fragment is not a function of the area of that fragment (Tscharntke et al. 2012). It is then also possible that that the entire landscape is the scale at which species richness is determined (Lawes 2000).

What are the implications of matrix transformation for forest bird assemblages? My findings suggest that the type of matrix surrounding a forest fragment may alter forest bird community assembly through a number of mechanisms (Driscoll et al. 2013). First, the anthropogenic transformation of natural matrices may reduce the dispersal ability of forest specialist species further isolating assemblages and disrupting metapopulation and community dynamics (Hanski and

Gilpin 1991; Ricketts 2001; Driscoll et al. 2013). This increases the probability of local extinctions

from forest fragments, especially with regards to forest specialist species (Haddad et al. 2015). My

results further support this idea in showing that forest specialist assemblages were nested by area

when the matrix was anthropogenic but not when it was natural i.e. bird assemblages in smaller

fragments were a subset of those occurring within larger more species-rich fragments (Ulrich et al.

2009). Further species-specific analysis regarding fragment area and matrix type also showed that 11

of the 17 forest specialist species in forest fragments embedded within in an anthropogenic matrix

were influenced by forest fragment size. While in contrast only 1 out of 17 forest specialists (Narina

Trogon, *Apaloderma narina*) was significantly influenced by forest fragment size when the matrix

was natural. Therefore, natural matrices such as grass-woodland complexes may be more permeable

than anthropogenic matrices and could potentially facilitate dispersal between forest fragments

through the use of stepping stones (Mueller et al. 2014). This could potentially also reduce the

occurrence of local extinctions through rescue effects (Brown and Kodric-Brown 1977). However, my

SARs for the anthropogenic matrix may still not yet represent the full extent of local extinctions as

smaller forest fragments may harbour an extinction debt where future species losses in response to

past disturbances such as anthropogenic matrix transformation may bring about a significant

challenge for conservation management but go undetected (Kuussaari et al. 2009). Second,

anthropogenic matrix transformation may alter or remove the availability of supplementary

resources in the matrix for fragment dwelling species (Dunning et al. 1992; Ries et al. 2004). This

could have consequences for fragment species who may rely on such resources to sustain larger

populations within a fragment (Dunning et al. 1992; Bhagwat et al. 2008). This in conjunction with

decreased dispersal ability could also amplify local extinctions especially amongst forest specialist

species which are restricted to a specific niche that may no longer be available following

anthropogenic transformation. Third, anthropogenic matrices may alter forest edge dynamics

(Strayer et al. 2003) and may alter species interactions between assemblages within forest

fragments and the adjacent matrix (Fagan et al. 1999). For instance, altered edge effects could

potentially provide a platform for habitat generalist species to spill over from the anthropogenic

matrix and invade a forest fragment (Saunders and Hobbs 1991). Because generalist species are

better adapted to disperse, acquire resources and persist in human-modified habitats, they may

replace or out-compete forest specialist species. This may result in biotic homogenisation effect

where many specialist species are replaced by a few habitat generalist species and may compromise

functional diversity within a fragment (Ibarra and Martin 2015). Counterintuitively altered edge

dynamics could also promote forest species spilling over into the matrix and acquiring potential

supplementary resources which may benefit some forest specialist species to the detriment of

others. Therefore the composition and habitat quality of the matrix may be an important

determinant of how biological assemblages respond to anthropogenic transformation (Driscoll et al.

2013).

The importance of the matrix surrounding habitat fragments may, therefore, have been

underestimated in the past (Ricketts 2001; Franklin and Lindenmayer 2009; Driscoll et al. 2013).

Rather these matrices may be of great importance for the future persistence of biological diversity. If

managed appropriately the matrix surrounding remnant habitat fragments could potentially provide

alternative or supplementary habitat (Daily et al. 2001) and resources (Dunning et al. 1992) for

forest birds assemblages (Franklin and Lindenmayer 2009). At least, well managed matrices could

facilitate the dispersal of species between suitable habitat fragments (Neuschulz et al. 2013).

Matrices could, therefore, complement conservation efforts within protected natural areas by

allowing for the immigration of previously lost species and the re-establishment of a metapopulation

dynamic (Gilpin and Hanski 1991; Mueller et al. 2014). The effective management of the matrix

could, therefore, be used as a conservation tool to limit or exacerbate the effect of habitat loss and

fragmentation on biological assemblages (Prugh et al. 2008; Franklin and Lindenmayer 2009).

However, to ensure that these management strategies are effective, it is important that we also

have an understanding of how patterns of biological diversity and the processes which structure

these patterns are influenced by the human-modified habitats compared to natural habitats (Petit and Petit 2003; Foley et al. 2011).

I therefore in my third chapter investigated patterns of bird diversity and the processes which drive these patterns in four human-modified habitats (urban settlements, rural, *Eucalyptus* plantations and sugarcane cultivations) and three natural habitats (forests, woodlands and grasslands) along the coastal plains of northern KwaZulu-Natal, South Africa. Assessing patterns of diversity at the landscape scale is important in understanding how regional diversity is maintained following a disturbance (Franklin and Lindenmayer 2009; Mendenhall et al. 2014; Wearn et al. 2016). However, making inferences about these patterns can be complex (Wang and Foster 2015; Wearn et al. 2016). For instance, the biogeographic complexity of a landscape and the close proximity of adjacent habitats types could influence the observed patterns of diversity through coincidental spill-over effects (Quinn et al. 1988; Thies and Tscharntke 2003). Moreover, a number of studies have shown that patterns of diversity are a function of the spatial grain at which analysis is conducted (Karp et al. 2012; Olivier and Van Aarde 2014; Wearn et al. 2016). I therefore used a standardised fractal sampling design for this component of the study which reduced sampling artefacts and issues regarding imperfect detection (Marsh and Ewers 2013). Replication of survey points and rarefaction analysis also ensured that sampling saturation was achieved (Ewers and Didham 2006b; Chao and Jost 2012). Alpha (local species richness) and beta-diversity (dissimilarity between local species assemblages) were calculated at three different spatial scales and compared to determine if patterns of diversity were indeed influenced by spatial grain. I then used the Raup Crick null modelling metric to determine whether processes driving these patterns of diversity were more deterministic (niche based) or stochastic (dispersal based) than expected by chance (Chase and Myers 2011; Püttker et al. 2015).

The findings in my third chapter suggest that the influence of human-induced landscape transformation on bird assemblages may be more complex than the rudimentary assumption that

human-modified habitats support reduced homogenised biological assemblages relative to natural habitats (Laurance 2008; Fahrig 2017). Rather biological diversity may be more influenced by the structure and type of activities taking place within habitats as well as the niche breadth of that habitat (Wang and Foster 2015a). For instance, rural and urban habitats supported habitat species richness, alpha-diversity and beta-diversity comparable to that of natural woodland and forest habitats. However, it is important to mention that rural and urban habitats in my study comprised of an array of different land use types such as suburban gardens, human infrastructure, greenbelt areas, subsistence agriculture and also the remnants of natural vegetation which may have increased or maintained habitat availability relative the natural habitat which it replaced (Ehlers Smith et al. 2015). In contrast, I found that grasslands and sugarcane cultivations supported similar but reduced diversity compared to most other habitats. However, it should be mentioned that both these habitats supported a high number of unique species with 13 of the 29 species in sugarcane and 13 of the 34 species in grasslands. These findings therefore illustrate that species richness may not only be a function of whether a habitat is natural or transformed, but rather the structural complexity and niche breadth of that habitat (Sekercioglu 2012). Certain human-modified habitats could therefore potentially also provide suitable habitat for a species and/or stepping stones which promote dispersal of habitat specialist species between remnant natural fragments in agreement with that concluded in my second chapter (Greenler and Ebersole 2015). Moreover, while we did not directly test for this my findings also suggest that all surveyed habitat types contributed to regional bird diversity. This supports the idea of the landscape moderated insurance hypothesis by Tscharntke et al. (2012) where it is proposed that a landscapes composed of an array of intermediate habitats with varying structural complexities may provide the greatest conservation gains as opposed to one homogenised landscape or even a single pristine natural habitat (Tscharntke et al. 2005; Rundlöf and Smith 2006). If this observed increase in taxonomic diversity across the landscape is analogous with an increase in functional group diversity it could buffer ecosystem functionality against further environmental changes and loss in ecological functioning brought about

by anthropogenic transformation (Lawton 1994; De Coster et al. 2015) Also if the dissimilarity amongst habitat assemblages within a landscape is high it could also potentially override the negative local effects of anthropogenic landscape transformation on biodiversity losses in line with the dominance of beta-diversity hypothesis (Quinn et al. 1988). Possibly making use of a functional diversity approach in conjunction with taxonomic diversity may provide more insight into how biological assemblages are influenced anthropogenic transformation. Finally, my analysis suggested that human modification of landscapes did not influence or alter the processes driving community assembly. Rather community assembly in both humans modified and natural habitats were non-random and influenced by deterministic, niche-based processes. This was similar to that found by Püttker et al. (2015) where niche-based community assembly processes were more prevalent than stochastic processes in all habitat types. Therefore processes driving community assembly in both human-modified and natural habitats, were most likely a product of ecological filtering and habitat niche breadth (Püttker et al. 2015).

The interaction between species and multiple habitats types represents a considerable challenge for conservationists moving into the future. This is especially true for highly fragmented landscapes (Fahrig 2003). It is, however, important to acknowledge that while human-modified habitats may potentially have the capacity to support diverse assemblages, natural habitats undeniably support a larger proportion of the biological diversity within a landscape. Therefore, the conservation of natural habitats remains an important objective for conservationists in the future (Gibson et al. 2013). However, the implementation of conservation strategies at an eco-region scale may be unsuccessful in preventing local extinctions. Rather a regional landscape complementation approach should be adopted whereby all habitats (both human-modified and natural) within a landscape are considered and included in conservation planning. My findings suggest that if managed appropriately certain human-modified habitats may have the capacity to complement current conservation efforts centred around natural habitats and protected areas (Greenler and Ebersole 2015). For instance, in my Chapter 2, I suggest that a possible way to reduce the effect of

matrices on forest specialist species is to attempt to mimic the matrix surrounding coastal forest

fragments in southern Mozambique. In this landscape, SARs are reduced and forest fragments are

embedded within a matrix of grasslands and woodlands. However, it is true that realistically in a

human-dominated landscape that we cannot completely restore all natural grasslands and

woodlands in the matrix surrounding coastal forests. It is also true that the anthropogenic

transformation of landscapes is unlikely to slow down in the foreseeable future (Petit and Petit

2003; Foley 2005; Jewitt et al. 2015). However, it may be possible to maintain or increase

structurally heterogeneity in anthropogenically transformed landscapes (e.g. Rural and Urban

habitats). This may provide supplementary habitat, resources and stepping stones for habitat

specialist species to utilise. Therefore, promoting a mosaic landscape approach where land-use types

vary and maintaining heterogeneous vegetation structure in matrix habitats (e.g. indigenous trees,

see Bhagwat et al. 2008) may re-establish a meta-population dynamic, promote increased regional

species richness and maintain ecological functioning (Quinn et al. 1988; Hanski and Gilpin 1991;

Bhagwat et al. 2008; De Coster et al. 2015).

Chapter 5

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