Patterns of species diversity in coastal forests: case studies on tree and bird assemblages in KwaZulu-Natal, South Africa

by

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DECLARATION

I, **Pieter Ignatius Olivier**, declare that this thesis/dissertation, which I hereby submit for the degree **PhD 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 thesis contains five manuscripts (Chapters 2-6), prepared for submission to different peer-reviewed journals. This results in some duplication in the study site description and methods between chapters. Chapter 2 has been published as a book chapter in *Coastal Conservation* (2014; Chapter 6, pp. 161-176, ed. by B. Maslo and J.L. Lockwood), Chapter 3 has been published in *Diversity and Distributions* (2013; 19, 1353-1365), and Chapter 6 has been published in the *Journal of Biogeography* (2014; 41, 1428-1439). For consistency, styles and formatting for all Chapters follow the requirements for the journal *Diversity and Distributions*. I hereby declare all the work to be my own and that I have acknowledged all those that helped me and contributed in producing this thesis.

Pieter Ignatius Olivier

"Whatever our passions are, we must feed them, we must invest in them, we must build them, even if they are castles in the sky"

- Hendri Coetzee, *Living the best day ever*

Patterns of species diversity in coastal forests: case studies on tree and bird assemblages in KwaZulu-Natal, South Africa

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ABSTRACT

Habitat loss and fragmentation drives the current extinction crisis. The processes through which it affects biodiversity, however, are complex and poorly understood. This is especially true for spatially complex regions that comprise a mosaic of land-use types, which often range from protected areas to dense human settlements. In such human-modified landscapes, it is important to determine the extent and impact of changing land-use patterns on biodiversity if we are to meet conservation targets or regain ecosystem services.

My analyses of coastal forests in KwaZulu-Natal suggest that extensive loss of forests (82%) incurred an extinction debt, modelled to match the 11 bird species now listed as threatened locally. Forest fragments are now also smaller, fewer, further apart and more encroached by human land uses than in the past. Yet, species interactions with the gradient of habitat conditions that now surround forest fragments may have forestalled the realisation of predicted extinctions. I found that natural matrix habitats adjacent forest fragments (e.g. grasslands and woodlands) may facilitate dispersal, enable species spillover from forest fragments, and buffer forest interiors from changes in abiotic conditions associated with high contrast matrix habitats (e.g. agricultural plantations). However, when natural matrix habitats were transformed, these processes were disrupted, which suggest that the effect of landscape change on coastal forest diversity may stretch beyond forest loss *per se* and the deterministic extinctions predicted by conventional species-area relationships.

Next, I determined that the response of different bird species to habitat fragmentation parameters (i.e. area, connectivity and matrix habitats), depended on life-history traits such as body size, feeding guild and habitat specialization. Extinction risk was, however, not a function of species traits or the fragmentation parameter species responded to. This means that a conservation approach that only focuses on restoring a single fragmentation parameter (e.g. area) may not be successful in halting predicted extinctions, simply because multiple factors may determine extinction risk in coastal forests.

The interpretation of biodiversity patterns in fragmented landscapes may, however, also be influenced by spatial scale. I therefore used a fractal-based sampling design to test how sampling at fine, intermediate and coarse scales influences (1) beta diversity of and (2) inferences from the modelled contribution of niche- versus dispersal-based assembly processes in structuring tree and bird assemblages. I showed that inferences from beta diversity are scale dependent. As a result, studies with similar sampling effort and temporal sampling protocol, but with different sampling grains are likely to report dissimilar ecological patterns, which may ultimately lead to inappropriate conservation strategies.

This thesis provides information of how land-use changes impact on biodiversity patterns and derived processes in a human-modified landscape. It also highlights some conservation opportunities in the coastal forest landscape mosaic, where conservation and restoration actions should focus on both forest fragments and on the surrounding matrices. The conservation of natural matrices may buffer forest communities from impacts associated with high contrast habitat edges, enhance natural plant regeneration through species spillover, provide important linkages between forest fragments, boost regional diversity and allow coastal forests to track environmental change under changing climatic conditions.

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During the last three years, I realised that to complete a PhD you need to solve a trilemma. You need to be (and remain) emotionally stable. You need to figure out solutions for many problems. You need to eat and have somewhere to live. However, I soon understood that this trilemma could only be solved with the help of other people. You need people who support you emotionally, intellectually and financially - and if you are lucky, these three kinds of support will overlap often.

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Chapter 1. General Introduction

Worldwide, many natural ecosystems are being replaced by novel, human-dominated landscape mosaics that are made up of remnant habitat fragments, agricultural plantations, and human settlements (Millennium Ecosystem Assessment MEA, 2005; Gardner *et al.*, 2009; Melo *et al.*, 2013). In such human-modified landscapes, the so-called 'evil quartet' of habitat loss, over-exploitation, invasive species and extinction cascades (Diamond, 1984) may trigger biodiversity losses (e.g. Gibson *et al.*, 2011; Pimm *et al.*, 2014), altered interactions among species (e.g. Tylianakis *et al.*, 2008; Ewers *et al.*, 2013), and a decline in ecosystem services and function (MEA, 2005). However, because of the high variability in findings across studies, scientists have not been able to conclusively answer some of the fundamental questions on how species respond to changing land-use patterns (Chase & Knight, 2013). For example, what is the influence of human activities on biodiversity? To what extent can forest biota persist in human modified landscapes and contribute to ecological processes? How do different ecological and spatial contexts determine our interpretation of biodiversity patterns? What are the most effective management strategies to ensure the persistence of communities? It is therefore important to evaluate patterns, processes, threats and opportunities that relate to biological diversity within affected landscapes if we are to meet conservation targets or regain ecosystem services (Gardner *et al.*, 2009). Indeed, understanding how species respond to human induced land-use changes have become one of the central ecological questions of our time.

Similar to other tropical and sub-tropical forests around the world, forests along the east coast of KwaZulu-Natal, South Africa, have been plagued by decades of intensifying anthropogenic disturbances (van Aarde *et al.*, 2014). Historical records and anecdotal evidence suggest that coastal forests were once more widespread than they are today (Lawes & Eeley, 2000). At present, forest fragments are, however, isolated and disconnected, and vary in size, shape and successional stages. In some fragments, native species have disappeared whereas in others exotic species have established. Surrounding these forest remnants is a variety of matrix habitats that include sugarcane and agroforestry plantations, rural and urban settlements as well as natural grasslands and woodlands.

However, the factors causing forest loss have not disappeared alongside with forest extent. Tourism related development, urban growth, mining, the expansion of agricultural activities, resource extraction and climate change continue to pose a severe threat to the remaining forests (Mucina & Rutherford, 2006). Coastal forests form part of two critically endangered eco-regions: the Maputaland Coastal Forest Mosaic and the KwaZulu-Cape Coastal Forest Mosaic that are renowned for their high levels of endemism (Burgess *et al.*, 2004). These forests are also situated within the Maputaland-Pondoland-Albany biodiversity hotspot (Küper et al., 2004) and the Maputaland Centre of Plant Endemism (van Wyk & Smith, 2000), which further underscore their importance in supporting regional diversity. Indeed, the surrounding landscape may influence much of the diversity within coastal forests because many species that occur within these forests also occur in the adjoining savannah, grasslands and other forest types in the region, or are at the extremes of their distributional ranges. Determining the extent of landscape change and understanding how species respond to current landscape patterns may thus be vital for the development of conservation initiatives that focus on this imperilled forest ecosystem.

Evaluating conservation prospects in a given landscape requires an understanding of how landscape characteristics affect biodiversity patterns and ecological processes at local and regional scales (Tscharntke *et al.*, 2012). However, unravelling how spatial and temporal patterns of biodiversity interact with historical and contemporary human and ecological processes remains an important challenge for ecological science (Gardner *et al.*, 2009). In this thesis, I modified the conceptual framework proposed by Gardner *et al.*, (2009) to understand the challenges and opportunities for conservation in the coastal forest landscape mosaic (Fig. 1). I first attempted to understand how human land-use practices influence patterns of coastal forest biodiversity by investigating historical forest loss and degradation. Second, I attempt to understand the challenge faced by conservation, and investigated how the current landscape structure influences species, communities and ecological processes. Based on this information I attempt to identify opportunities for conservation and restoration within the coastal forest landscape mosaic.

Understanding the problem

To understand the diverse aspects of altered habitat quality as well as habitat quantity scientists turned to a theory originally proposed to explain diversity on oceanic islands. Island biogeography theory (IBT: MacArthur & Wilson, 1967) predicts that area and isolation are drivers of species richness. Large connected islands have higher species richness because they gain more species through immigration and hold larger populations that are less prone to stochastic extinction. Conversely, species on small isolated islands are more prone to stochastic extinctions and gain less species through immigration. Yet, although IBT has been proposed to explain diversity on islands, it has been extended to habitat fragmentation based on the assumption that ‘habitat islands’ will behave similarly to oceanic islands. For instance, MacArthur and Wilson noted that ‘The same principles apply, and will apply to an accelerating extent in the future, to formerly continuous natural habitats now being broken up by the encroachment of civilization’ (MacArthur and Wilson, 1967). As a result, IBT has provided a foundation for much of conservation biology and stimulated a plethora of research on the importance of habitat size and connectivity in the maintenance of species diversity in fragmented landscapes (Laurance, 2008).

By invoking IBT, I can make some predictions of what will happen to species that occur within remaining coastal forest fragments. First, I would expect large forest fragments to have more species than smaller ones. Species may increase with area because habitat heterogeneity increases, which allows a larger number of species with dissimilar ecological requirements to co-occur within larger areas. Furthermore, because larger areas tend to support larger populations, the probability of population survival increases with population size (Hanski & Gyllenberg, 1997). The relationship between species richness and habitat area is described by the power function: $S = cA^z$, where S is species number, A is area, and c and z are constants (Arrhenius, 1921; Preston, 1962). However, whilst the increase in species diversity with area is general, it is not universal to all data sets and circumstances (Lomolino, 2000). What form the relationship takes in particular circumstances is of key concern both for what it reveals of the factors controlling diversity patterns and for the predictive value of species-area relationships (SARs) in relation to the biodiversity consequences of habitat alteration and destruction (Rosenzweig, 1995).

Second, I would expect that because species richness increases with area, a decrease in area would also result in a decrease in species richness. It therefore follows that if I know the proportion of habitat lost from an area, I can theoretically predict the proportion of species that will be lost. For example, if the original habitat area (A_o) is reduced to the new habitat area (A_n) the original number of species (S_o), should decline to a new number (S_n). The fraction of species predicted to remain after habitat loss is then given by $\frac{S_n}{S_o} = (\frac{A_n}{A_o})^z$ where z represent the form of the relationship between species and area (i.e. the slope of the SAR curve). This is particularly important for conservation efforts because in many instances extinction does not immediately follow changes in habitat extent. Instead, a process of time-delayed community ‘relaxation’ usually occurs where species progressively disappear over time (Diamond, 1972). This time delay offers a window of conservation opportunity, during which it is possible to restore habitat or implement alternative measures to safeguard the persistence of species that are otherwise committed to extinction (Wearn *et al.*, 2012). In Chapter 3, I use some of the basic principles of IBT to investigate the influence of human land-use practices on coastal forest biodiversity. I determined the extent of historical deforestation and used species-area relationships to estimate if coastal forests harbour an extinction debt in response to past forest losses.

Understanding the challenge

There has been sustained criticism in the scientific literature that real landscapes are too complex to reflect the rather simplistic reality of IBT (Laurance, 2008; Didham *et al.*, 2012). Unlike oceanic islands where the matrix (ocean) is completely inhospitable, a variety of matrix types surround forest fragments that may, or may not, influence diversity within fragments. Nearly 70 years ago Watt (1947) suggested that 'each habitat patch in a space-time mosaic is dependent on its neighbours and develops under conditions partly imposed on them'. Several studies now emphasize the importance of the surrounding matrix (e.g. Wethered & Lawes, 2003; 2005; Kupfer *et al.*, 2006; Driscoll *et al.*, 2013). For instance, matrix quality can mitigate fragmentation effects by providing a set of resources that are complementary to, and unavailable in, habitat remnants (Tscharntke *et al.*, 2012). In the Amazonian rainforest, for example, 40-80% of frogs, small mammals, birds and ants typical of primary forest were detected outside forest fragments in a matrix composed of pastures and regenerating forest (Gascon *et al.*, 1999). However, the creation of matrix habitats that is highly dissimilar to the original forest habitat, may also allow disturbance adapted species to invade forest fragments and replace forest specialist species (e.g. Chabrerie *et al.*, 2013). Such species replacements could eventually lead to the biotic homogenization of the forest community (Tabarelli *et al.*, 2012). The quality of the matrix may furthermore determine dispersal rates between habitat fragments that are in many instances essential for long-term metapopulation persistence (Prevedello & Vieira, 2010). For instance, Wethered & Lawes (2003) show that matrix type has an influence on bird species richness in Afromontane forest patches in South Africa. Species richness of forests surrounded by commercial plantation forest do not show an island effect, and larger forests are generally more species poor than those surrounded by natural grassland. Matrix habitats may also influence the strength of edge effects. Edges with a high contrast between the fragment and matrix are more likely to generate stronger edge effects than low contrast edges (Ries & Sisk, 2004). This is important as Ewers *et al.*, (2007) show that edge effects may drive area effects in fragmented landscapes. In Chapter 4, I therefore investigated the influence of matrix habitats on coastal forest diversity. I tested how the transformation of matrix habitats adjacent coastal forests influence forest tree and bird communities. I furthermore evaluated if matrix habitat transformation alter interactions among forest tree and bird communities.

Yet, not all species respond to spatial patterns of habitat in the same way. This is because in reality there is a blurring of the boundaries between what constitutes the 'patch' and the 'matrix' from the niche perspective of an organism (Kupfer *et al.*, 2006). As a result, some species may decline or disappear in fragments, others may remain stable, and yet others may increase (Laurance *et al.*, 2008). Such seemingly idiosyncratic responses to fragmentation can be explained by investigating the individual life-history traits that determine species' susceptibilities to land-use changes (Ewers & Didham, 2006). For instance, in a global meta-analysis Newbold *et al.*, (2012) found that long-lived, large, non-migratory, primarily frugivorous or insectivorous forest specialist bird species were less likely to occur and less abundant in landscapes undergoing human driven change than short-lived, small, migratory, non-frugivorous/insectivorous habitat generalists. Recognising these varying responses is important because if species respond idiosyncratically to habitat loss and fragmentation, responses to conservation measures may also differ between taxa and even within functional groups (e.g. Hanski, 2000). Conservation incentives that ignore such idiosyncrasies to changes in habitat may be risky and ultimately fail (e.g. Game *et al.*, 2013). In Chapter 5, I therefore tested if bird species with different life-history traits respond differently to different habitat fragmentation parameters (i.e. area, connectivity and matrix habitats) and if these responses influence extinction risk.

The interpretation of biodiversity patterns in fragmented landscapes may not only be influenced by different life-history traits, but also by the spatial scale of investigation (Wilis & Whitaker, 2002). In the scale concept, five terms: sampling unit, grain, focus, sample size and extent, are of central importance (Schmera & Podani, 2013). Sampling unit is the arbitrarily delimited tract of the community in the real space (synonyms are points, plots, quadrats ext.). Grain is the standardized unit to which all data are adjusted, if necessary, before the analysis. Focus is the scale at which the grains are aggregated and related grains form focal units. Sample size expresses the number of replicates of sampling units at the scale of grain or the number of focal units (at the scale of focus). Finally, extent is the geographical area within which the sampling units are arranged (see Schmera & Podani (2013) and references therein). All of these terms influence the values of biodiversity metrics. For instance, in any given community the number of species increases in a nonlinear way with sampling grain and extent. Therefore, the difference between communities when measured at one grain or extent will differ from that measured at a different grain or extent (Chase & Knight, 2013). This has implications for inferences from biodiversity patterns in fragmented landscapes. For example, Powell *et al.*, (2013) showed that invasive plant species have large effects on native species at fine, but not at coarse sampling grains. Furthermore, Dumbrell *et al.*, (2008) showed a scale-dependent response of butterfly diversity to habitat disturbance – at fine scales logging did not influence butterfly species richness, however, the effect of logging increased at coarser scales.

Yet, despite the growing recognition that spatial scale influence diversity metrics and our interpretation thereof, the patterns and processes shaping the spatial scaling of beta diversity have not been thoroughly explored (Barton *et al.*, 2013). Beta diversity refers to the variation in community composition among sites (Whittaker, 1972) and is at the centre of any investigation that seeks to understand how ecological processes shape patterns of biodiversity (Anderson *et al.*, 2011). For instance, the contribution of niche- versus dispersal-based community assembly processes can be inferred from beta diversity estimates (Tuomisto *et al.*, 2012). Under niche-based assembly, the match between species niches and local environmental conditions controls species distributions. Sites with similar environmental conditions should therefore harbour similar species assemblages (e.g. Tuomisto *et al.*, 2003). Under dispersal-based assembly, dispersal limitation governs whether a species is present or absent from a given site. Sites should therefore harbour increasingly dissimilar species assemblages the further apart they are (Nekola & White, 1999). Dispersal-based assembly is also inherent to Hubbell's (2001) neutral theory, in which spatially limited dispersal and demographic stochasticity determine community assembly. Whether niche- or dispersal-based assembly processes control community composition continues to fuel contemporary debates in ecology (e.g. Chase & Myers, 2011; Fisher & Mehta, 2014) and is important because if these processes vary across taxa and spatial scales conservation efforts that focus on maintaining them will also have to differ (Olivier & van Aarde, 2014). In Chapter 6, I therefore investigated the influence of spatial scale on beta diversity and the processes inferred from beta diversity estimates.

Understanding the opportunity

In this thesis, I attempt to unravel some of the fundamental issues associated with the persistence of forest species within human modified landscapes. In the final Chapter (7), I therefore provide a synthesis of my findings and evaluate the future of coastal forest conservation. I present coastal forest loss in the context of forest loss worldwide and propose some ideas for future work.

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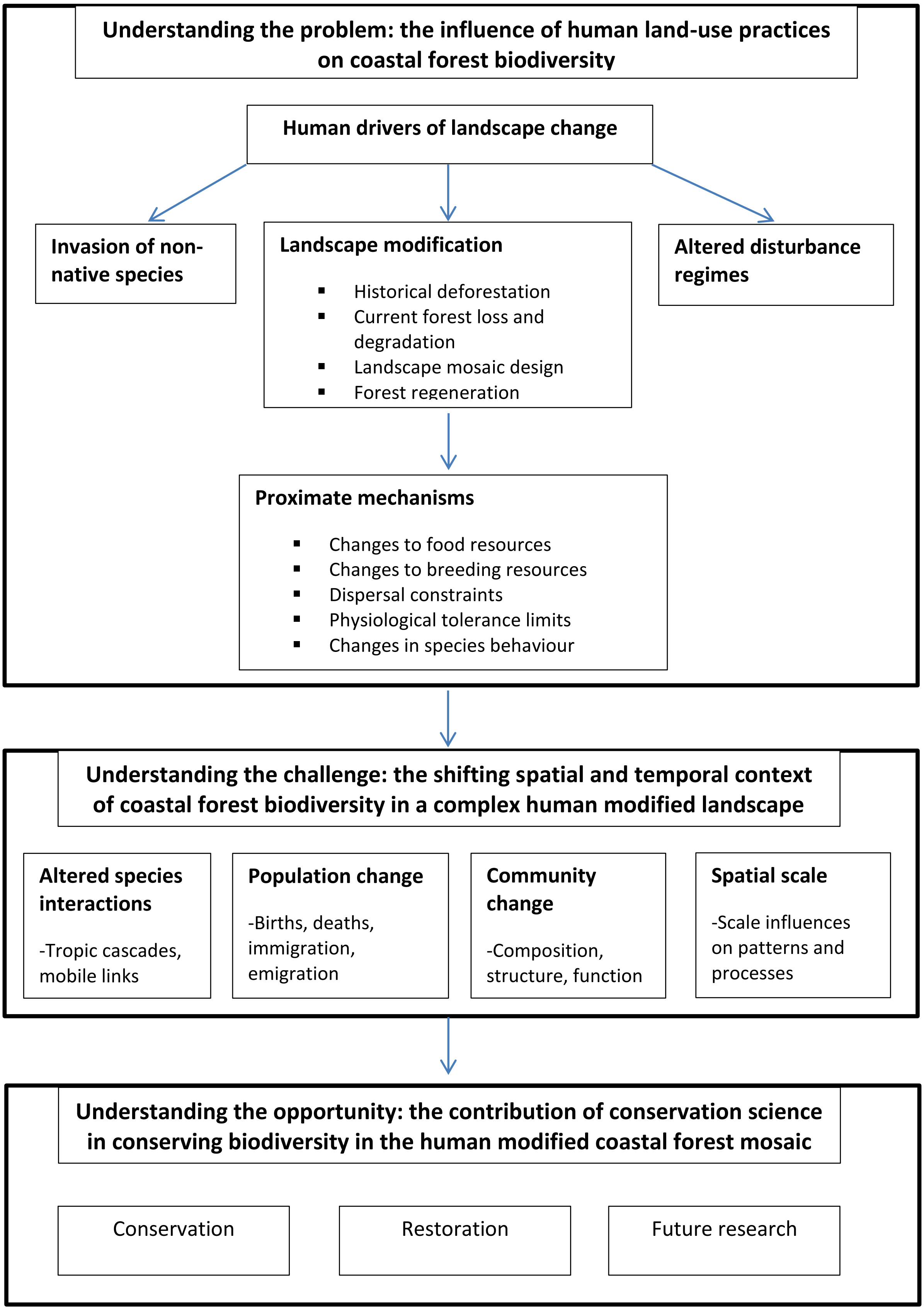
Understanding the problem: the influence of human land-use practices on coastal forest biodiversity
Human drivers of landscape change
Invasion of non-native species
Landscape modification
Historical deforestation
Current forest loss and degradation
Landscape mosaic design
Forest regeneration
Altered disturbance regimes
Proximate mechanisms
Changes to food resources
Changes to breeding resources
Dispersal constraints
Physiological tolerance limits
Changes in species behaviour
Understanding the challenge: the shifting spatial and temporal context of coastal forest biodiversity in a complex human modified landscape
Altered species interactions
-Tropic cascades, mobile links
Population change
-Births, deaths, immigration, emigration
Community change
-Composition, structure, function
Spatial scale
-Scale influences on patterns and processes
Understanding the opportunity: the contribution of conservation science in conserving biodiversity in the human modified coastal forest mosaic
Conservation
Restoration
Future research

Figure 1.1. A broad conceptual framework modified from Gardner *et al.*, (2009) for understanding how landscape characteristics affect biodiversity patterns, ecological processes, and ultimately conservation actions in the coastal forest landscape mosaic.

Chapter 2. Coastal forest in context

This chapter provides an overview of the biodiversity status of coastal forests in South Africa, while also describing the biogeographic forces and historical contingencies that are postulated to have given rise to the current distribution of these forests. I also evaluate the current conservation status and the threats faced by coastal forests. I do not describe the study area *per se* as each of the following chapters contain a description of the habitats and the survey methodologies used for the answering specific study questions. There are, however, some unavoidable overlaps between this chapter and the study area descriptions of the following chapters because they were prepared as separate journal publications.

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INTRODUCTION

People tend to settle close to the sea and hence place disproportionate pressure on coastlines and associated habitats, such as coastal forests. Edge effects, area limitations, isolation, and the ebbs and flows of climatic conditions accentuate the sensitivity of coastal forests to human-made disturbances, which may put extraordinary pressures on species living within them. Associated economic development and reliance on natural resources transform and fragment coastal landscapes and bring about habitat loss that may challenge the persistence of species (Arthurton *et al.*, 2006).

Coastal forests in South Africa are relatively young (Lawes, 1990), harbour few endemic species (van Wyk & Smith, 2001), are naturally fragmented and embedded in matrices of contrasting landscapes (Berliner, 2009). By designation coastal forests are sensitive to disturbance, but relatively high ecological resilience provides for their potential to recover following the withdrawal of local disturbances (van Aarde *et al.*, 1996; Wassenaar *et al.*, 2005, Grainger *et al.*, 2011). Protecting or restoring these forests to meet conservation targets or to regain ecological services makes sense but calls for an evaluation of the prevailing status, as well as identifying the threats and opportunities related to aspects of its biological diversity.

DEFINING SOUTH AFRICA'S COASTAL FORESTS

The 3 650 km long South African coastline runs from Namibia in the west to Mozambique in the east (Fig. 2.1). This coastline is exposed to different climatic and ecological conditions due to the cold Agulhas and warmer Benguela oceanic systems. The western coastline has an arid climate and contains no forests. Forests do, however, occur along the southern and eastern seaboards of South Africa because of a more temperate and sub-tropical climate that sometimes extends to the hinterland across the mountain ranges and coastal plains (Mucina & Rutherford, 2006). Yet, although 7% of terrestrial South Africa is climatically suitable for forests, forests as a biome account for less than 0.6% of the country (Mucina & Rutherford, 2006).

Broadly, parts of South Africa harbours two main forest types, Afromontane and the Indian Ocean Coastal Belt Forests, with an intermediate Coastal Scarp Forest located between the two groups (Lawes *et al.*, 2004). All of these forest types are fragmented and most of the patches are very small (<100 hectares; Berliner, 2009), most likely due to climate conditions and fire over millennia (Geldenhuys, 1992; Eeley *et al.*, 1999) (Table 2.1).

Different sub-types of forests are recognised within Afromontane and the Indian Ocean Coastal Belt Forests, and often a given patch is given different names by authors that use different criteria to classify them (i.e. Lubke *et al*., 1997; Midgley *et al*., 1997; von Maltitz *et al*., 2003). For instance, Indian Ocean Coastal Belt forests include coastal lowland, dune, mangrove, riparian, sand, and swamp forests (Mucina & Rutherford, 2006). In this thesis I use the term 'coastal forests' to refer to coastal lowland and well as coastal dune forests (see von Maltitz *et al*., 2003). I did this because in many instances these two forest types are indistinguishable from one another and also share a number of forest-dependent species (Von Maltitz *et al.*, 2003; Mucina & Rutherford, 2006). Indeed, Ezemvelo KZN Wildlife, (2009) classified some forest fragments as a mixture of coastal lowland and coastal dune forests.

Coastal forests are the southern-most example of the East African Tropical Coastal Forest, which extends northwards along the Mozambican, Tanzanian, Kenyan, and southern Somalian coastline (Burgess & Clarke, 2000). The climate of the Holocene interglacial period provides for the typical tropical affinity of these forests (Mucina & Rutherford, 2006). The southbound shift of the Intertropical Convergence Zone, and the weakening of the high pressure system due to heating of the land surface, cause humid air to flow toward the southern parts of the Africa during the austral summers (Tyson, 1986; Lawes, 1990). These weather systems and the proximity of the warm Agulhas Current close to the eastern coastline enable tropical conditions to persist along this coastline at relatively high latitudes (Mucina & Rutherford, 2006). However, climate conditions undergo gradual changes from north to south along the coast. In summer the northern parts tend to be relatively hot and humid but less so towards the southern regions. Winters are mild in the north and relatively cold in the south. Frost is seldom recorded, and rainfall is fairly consistent across the region at around 1 200 mm per year (Mucina & Rutherford, 2006). Rain falls throughout the year in the northern parts of the region but mostly during the summer months in the southern regions.

Coastal forests are situated on porous and leached sand deposits left by a regressing Indian Ocean during the end of the last glacial period 8 000 to 10 000 years ago (Tinley, 1985). Strong winds during arid periods blew these dunes into a characteristic parabolic shape and rolling topography (von Maltitz *et al.*, 2003). The dunes run parallel to the shoreline and vary in height from a few metres closer to the high water mark to ~80 m high further inland with the highest vegetated dune exceeding 180 m (Tinley, 1985). It follows that these forests by their fragmented nature, their location, and their relatively young age may be disturbance prone, especially in the presence of climate change associated disruptions that are becoming typical of coastlines throughout the world (e.g. Klein & Nicholls, 1999). The extraordinary variety of species associated with these forests, their associations with other biomes, and restrictions imposed by ecological realities are best understood by considering biodiversity at the three popular levels of academic endeavour - species, habitats, and processes.

SPECIES

Vegetation

Coastal forests in South African consist of well-developed tree, shrub and herb layers and has a canopy of 12–15 m high (Ferreira & van Aarde, 2000). The understory is usually between 0.2 m and 2 m high (Ferreira & van Aarde, 2000) with a litter layer that provides niche space for a variety of biological activity, though soils here tend to be relatively poor in minerals and somewhat acidic (van Aarde *et al.*, 1998; Kumssa *et al.*, 2004).

Non-deciduous trees such as coastal red milkwood (*Mimusops caffra*), white milkwood (*Sideroxylon inerme*), white-pear (*Apodytes dimidiata*), Natal apricot (*Dovyalis longispina*) and quar (*Psydrax obovata*) are some of the more common species in the tree canopy layer (Mucina & Rutherford, 2006). The sweet thorn (*Acacia karroo*), a widespread deciduous pioneer tree species, dominates in disturbed as well as new-growth forests less than 50 years old (van Aarde *et al*., 1996). Coastal silver oak *(Brachylaena discolour*), bush-tick berry (*Chrysanthemoides monilifera*) and forest num-num (*Carissa bispinosa*) are also frequently found in the understory, while the herbaceous layer is sometimes dominated by buckweed (*Isoglossa woodii*), Chinese violet (*Asystasia gangetica*), and wart ferns (*Microsorum scolopendria*) (Grainger, 2011). Herbaceous and woody vines such as dwaba-berry (*Monanthotaxis caffra*), Cape grape (*Rhoicissus tomentosa*), and coastal current (*Searsia nebulosa*) add to the structure of these forests (Mucina & Rutherford, 2006).

In some places the vegetation on coastal dunes closely follows progression and erosion of sand from beaches (Lubke *et al*., 1997). Pioneer communities on lower dune ridges close to the high water mark often are dominated by inkberry (*Scaevolia plumieri*) (Peter *et al*., 2003), while grasses such as coastal rat-tail grass (*Sporobolus virginicus*) and blady grass (*Imperata cylindrical*), and the forb, *Helichrysum asperum*, colonise areas behind these dune ridges. Sands behind the foredunes are dominated by woody scrubs such as big num-num (*Carissa macrocarpa*). Bush clumps establish further away from the shoreline and are eventually followed by forests where tall trees dominate; deterministic observations posit this as an alternative successional pathway of regenerating forests to the one described below (Avis, 1992; von Maltitz *et al*., 1991 in Lubke *et al*., 1992a).

On most sand dunes natural and man-made disturbances are followed by ecological succession characterized by a directional progression when senescent pioneer trees (mainly sweet thorn) are replaced by secondary species typical of old-growth forests (Grainger *et al*., 2011; Grainger & van Aarde, 2012a). Coastal forests therefore comprise patches of varying sizes that represent different seral stages ranging in age from a few years to more than 80 years old. Physiognomically older patches represent old-growth forests, and our recent preliminary assessment suggests that there may be 190[*] of these patches along the eastern coastline (Ezemvelo KZN Wildlife, 2009).

Vertebrates

Mammals

Some 15% of the 295 mammals listed for southern Africa may occur in coastal forests, although these species mainly occur in the adjacent savannas and grasslands (Skinner & Smithers, 1990). Large herbivores are mostly absent, whereas bushbuck (*Tragelaphus scriptus*), bushpig (*Potamochoerus porcus*), and red duiker (*Cephalophus natalensis*) are the most prevalent mesoherbivores (Boyes *et al*., 2011). Rodents and shrews are widely distributed in coastal forests, and their numbers vary greatly across space and time (Ferreira & van Aarde, 2000). Early successional stages of new-growth forests are dominated by widespread generalists such as the multimammate mouse (*Mastomys natalensis*) and the pouched mouse (*Saccostomus campestris*), while later stages provide for forest specialists, such as the red veld rat (*Aethomys chrysophilus*) and Angoni vlei rat (*Otomys angoniensis*); albeit always occurring in low numbers (Ferreira & van Aarde, 2000).

Species living in coastal forests that are considered important to conservation in South Africa include a subspecies of samango monkey (*Cercopethicus mitis erythrarchus*), an endemic to the country living mainly in protected areas. The forest shrew (*Myosorex sclateri*) and four-toed elephant shrew (*Petrodromus tetradactylus*) are listed as endangered due to habitat loss, while the tree hyrax (*Dendrohyrax arboreus*), blue duiker (*Philantomba monticola*), and suni (*Neotragus moschatus zuluensis*) are listed as vulnerable species due to habitat loss or being killed for the bush meat trade (Friedman & Daly, 2004).

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[*] This number refers specifically to coastal dune forest patches as classified by Ezemvelo KZN Wildlife (2009).

Birds

Coastal forests support many birds, and during my surveys I recorded 69 species within forests and 139 in the adjacent matrix habitats. Birds of the region appear sensitive to landscape level disturbance, and assemblages in exotic plantations and patches of grasslands (some transient and an apparent seral stage of forest succession) differ from those of new and old-growth forests (see Niemand, 2001). Based on the cumulative abundances calculated from transect surveys in old-growth coastal dune forests (Table 2.2), only the yellow-bellied greenbul (*Chlorocichla falviventris*), green-backed camaroptera (*Camaroptera brachyura*), and the collared sunbird (*Hedydipna collaris*) are considered very common. Six species are common and include yellow-breasted apalis (*Apalis flavida*), dark-backed weaver (*Ploceus bicolour*), terrestrial brownbul (*Phyllastrephus terrestris*), black-backed puffback (*Dryoscopus cubla*), eastern olive sunbird (*Cyanomitra olivacea*), and the yellow-rumped tinkerbird (*Pogoniulus bilineatus*). Eight bird species are considered rare, and an additional 70 species are considered very rare. Few species are restricted to forests here, and may therefore also occur in other forest types or adjacent savanna, woodlands, and grasslands.

Only some of the very rare bird species are of special conservation concern. Coastal forests provide winter habitat for the endangered spotted ground thrush (*Zoothera guttata*), an altitudinal migrant that has experienced extensive range reduction. Two other birds, the eastern bronze napped pigeon (*Columba delegorguei*) and southern-banded snake eagle (*Circaetus fasciolatus*) living in coastal forests also have been listed as vulnerable in South Africa (Barnes, 2000).

Reptiles

Based on the South African Reptile Conservation Assessment (http://sarca.adu.org.za), approximately 10% of the 480 species of reptiles listed for southern Africa may occur in coastal forests. Only Setaro's dwarf chameleon (*Bradypodion setaroi*) was previously thought to be a South African endemic and listed as an endangered species due to a relatively limited distribution and possible habitat loss; however, the IUCN now list it as least concern (www.iucnredlist.org). The gaboon adder (*Bitis gabonica*) has recently been afforded special protective status in South Africa in response to excessive collection for the illegal pet trade. Moreover, and although not directly linked with coastal forests per se, sand dunes above the high tide level provide nesting places for leatherback (*Dermochelys coriacea*) and loggerhead turtles (*Caretta caretta*) (Branch, 1998).

Amphibians

The 'Maputaland amphibian assemblage', which includes the low lying coastal areas of KwaZulu-Natal, has more species of frogs than any other biogeographic area surveyed during the South African Frog Atlas Project in 2004. On average 30 species were recorded per half-degree grid cell (Minter *et al.*, 2004). Forests along the east coast provide ideal habitat for amphibians and may explain why this region has been identified as a diversity hotspot and region of high endemism for amphibians (Measy, 2011). Trimble & van Aarde (2014) recorded 17 species of frogs in coastal forests and adjacent habitats, including the critically endangered Pickersgill's reed frog (*Hyperolius pickersgilli*), which is considered an endemic species to the region.

Invertebrates

Coastal forests are rich in invertebrates, and systematic or ecological studies in new- and old-growth coastal dune forests include those done on ants (Majer & de Kock, 1992), coleopteran beetles (van Aarde *et al.*, 1996), dung beetles (Davis *et al.*, 2003), millipedes (Redi *et al.*, 2005), soil invertebrates (Kumssa *et al.*, 2004), and spiders (Dippenaar-Schoeman &

Wassenaar, 2002, 2006). Transient and successional vegetation changes that develop either in response to rehabilitation, or spontaneously following disturbances, provide for colonisation by a variety of invertebrate taxa (van Aarde *et al*., 1996; Davis *et al*., 2003; Redi *et al*., 2005; Wassenaar *et al*., 2005). Structured surveys during the last 20 years have recorded 21 millipede species in new and old-growth forests, but these also occur in adjoining forests and woodland habitats. Using structured survey data, a similar pattern to other taxa in species assemblage is prevalent for millipedes (Table 2.1.), with one very common and one common species, two rare species, and 12 very rare species. Only one of the two millipede species listed as endangered for the study region, the Zululand black millipede (*Doratogonus zuluensis*), has been recorded during surveys.

SPATIAL GRADIENTS IN SPECIES COMPOSITION AND RICHNESS

Species richness tends to decline from the lower tropical towards the higher temperate latitudes (Gaston, 2000). Geldenhuys (1992) show a trend of decreasing floristic diversity from north to south for both inland and coastal forests in South Africa. Similarly, Lawes *et al.* (2007a) described a southward decrease in species richness for birds, frogs, and butterflies in coastal forests. However, this pattern is complicated by the close relationship between the coastline and the hinterland where an exchange of coastal species and the adjacent habitats may account for the high species richness observed in coastal forests (Lawes, 1990, Lawes *et al*., 2007a).

Notably, some species reach their northernmost distribution along coastal forest in South Africa, such as the tree hyrax, brown scrub-robin (*Cercotrichas signata*), red-fronted tinkerbird (*Pogoniulus pusillus*), and Natal tree frog (*Leptopelis natalensis*). Coastal forests also have a close affinity with the tropics further north in Africa (Burgess & Clarke, 2000), and several species are at the southern end of their distributional range. Examples here include thick-tailed bushbaby (*Otolemur crassicaudatus*), Livingstone's turaco (*Tauraco livingstonii*), gaboon adder, Setaro's dwarf chameleon, violet worm-lizard (*Zygaspis violacea*), and the sand peawood (*Craibia zimmermannii*).

In some places along the coast, the continuous supply of sand through wave action allow for new coastal habitats to develop (Tinley, 1985). These habitats are colonized by pioneer species at the start of a successional process toward maturely developed thicket or forest communities (Weisser *et al*., 1982). Species richness, cover, stature, and biomass increase as succession progresses, but early seral stages do not support forest specialists, which only reside in later stages (Grainger & van Aarde, 2012). Senescence of the dominant pioneer sweet thorn trees, leave gaps in the canopy which are colonised by secondary pioneer species such as white stinkwood (*Celtis africana*) and coastal red milkwood that are also typical of canopy gaps in old-growth coastal forests (Grainger & van Aarde, 2013). Canopy gaps in new-growth forest, therefore, do not reset succession, but rather are a critical factor in the regeneration of these forests.

HABITAT AND LANDSCAPE REALITIES

Geographic and ecological realities render coastal forests both distinctive and sensitive to regional dynamics and local disturbance. Coastal dune forests, specifically, are narrow and consequently exposed to edge effects, the intensity of which probably depends on how forests differ from the adjoining wetlands, grasslands, savanna, other forest types, stands of exotic plantations or sugarcane fields, and stretches dominated by informal urban developments. Species from different adjoining habitats may structure forest assemblages, some of which originate from the hinterland or from along the coast, most notably the more tropical coastal forests to the north and the temperate forests to the south.

Given this landscape perspective, coastal forests comprise a collection of species assembled from three or more habitat types that existed prior to relatively recent climate conditions (6000 to 8000 BP) that were conducive to forest development. A coastal forest may be a meeting ground, or melting pot, of species that are typical of other habitats that can either withstand, or are favoured by the sub-tropical weather conditions. This idea seems to find support in many species that live in forests, but also occur either in adjoining savanna, grasslands, wetlands in the hinterland, or other forest types in the region, or are at the extremes of their coastal distributional ranges (Table 2.2).

Coastal forests also mark the edge of the distributional range of several hinterland species, and these may occur in numbers well below those recorded in their core distributional ranges (see Caughley & Sinclair, 1994). In addition, the peninsular effect dictates a decrease in species number from the base to the extreme of the peninsula (Simpson, 1964). From this pattern, we can expect coastal forest assemblages to comprise forest specialists at the extreme of their tropical northern or temperate southern distributional ranges, and generalists typical of savanna and grasslands (Table 2.2). It then follows that assemblages in coastal forests are made up of a few common generalists and many apparently rare species, a prediction supported by the summary information in Table 2.1. Collectively, these species contribute to the richness of coastal forests and may play an important, but yet undetermined role in the persistence of assemblages in the greater landscape mosaic.

The proximity of these forests to a variety of other habitats and the expected large species pool in its vicinity accommodates species that can fill niches where forests were disturbed. This pattern may explain the relatively fast rate of ecological succession that marks post-disturbance regeneration of coastal dune forest in particular (see Wassenaar *et al*., 2005, Grainger & van Aarde, 2012). Post-disturbance areas of new growth forests represent a collection of transient habitat and include life forms typical for savanna, shrublands, and grasslands. The rate at which some of these species colonise are a function of landscape features, such as area, distance, and edge, whereas others are driven by local habitat conditions generated during the aging of new-growth forests (Grainger *et al*., 2011). This element adds to the adaptive capacity of forests to changes and may ease regeneration after natural or human-induced disturbances. In part it also may explain the persistence and resilience of coastal forests despite their exposure to a long history of disturbance.

THREATS

Coastal forests have been exposed to exploitation by people since the early Iron Age (around AD 800), when anthropogenic activities such as iron-smelting by using charcoal and agricultural expansion started to play a major role in shaping forest distribution (Feely, 1980). In KwaZulu-Natal (KZN) the arrival of the Zulu people in the 1670s began the rise of Shaka and the Zulu kingdom which had a significant impact on the way forest was distributed. Guy (1980) describes the ecological factors responsible for the rise of Shaka, and suggests that utilization of resources such as the building of homesteads and the production of charcoal to fuel the iron smelting process coupled with agricultural expansion, specifically cattle grazing, all played a major part in shaping the kingdom. Furthermore, fire impacted on the forest margins long before European settlement. However, the arrival of Europeans and the establishment of Durban may have increased the utilization of forests along the KZN coastline (Bews, 1920). Commercial logging became an important economic activity of the province (Fourcade, 1889), but could not provide the colony with all of its timber needs. As a result, plantation forestry was introduced in 1872 and caused large tracts of forests to be cleared and replaced with exotic *Eucalyptus* and *Pinus* plantations (Bews, 1920). Sugarcane production peaked in the early 20th century with more forest cleared for cultivation. More recently urban resort development and dune mining also contributed to the removal of forests.

At present, coastal forests experience some of the highest population pressures in the country with an estimated density of 60 people per hectare living within a 5-km radius of forest patches (Berliner, 2009). Three important exotic invasive plants for the region, triffid weed (*Chromolaena odorata*), lantana (*Lantana camara*), and common guava (*Psidium guajava*) proliferate in areas where people live. The increased population pressure linked to peri-urban and urban development may also degrade forests directly due to timber and fuel-wood extraction, over-exploitation of plants and animals for food and traditional medicines, and land clearance for agriculture, housing, commercial plantations and mining (Lawes *et al*., 2004). The loss of ecosystem services, such as protection from rough seas and storms, erosion control, water catchment and purification, and carbon sequestration may in turn threaten people that depend on these forests for their livelihoods (see Barbier *et al*., 2011).

The modification of wetlands, grasslands, and savanna woodlands adjacent to coastal forests may also have direct effects on forest persistence and development. For instance, if savanna woodlands rather than sugarcane fields surround forest fragments, woodland birds that also occur in coastal forests may benefit from the woodland structure when dispersing, whereas a homogenous and treeless landscape may inhibit such movements (Wethered & Lawes, 2005). Forest fragments may therefore become more isolated due to changes in the surrounding landscape. Furthermore, habitat modification may result from high levels of herbivory by cattle and other herbivores, arresting succession through differential mortality of seedlings (Wassenaar & van Aarde, 2001; Boyes *et al*., 2011). Exposure to disturbed surrounding habitats also increases the probability of invasive plants colonising coastal forests, which may also change natural successional processes (Lubke, 2004; Grainger & van Aarde, 2012). Forests fragmented in this way also become dominated in time by tree species with a coarse-grained scale of recruitment (Lawes *et al*., 2007b).

CONSERVATION

Coastal forests in South Africa fall within a biodiversity hotspot and are situated at the southern end of the Maputaland Centre of Endemism (van Wyk & Smith, 2001; Küper *et al*., 2004). These forests also fall into two critically endangered eco-regions: the Maputaland Coastal Forest Mosaic and the KwaZulu-Cape Coastal Forest Mosaic (Burgess *et al.*, 2004). Coastal forests may be valued for their role in conservation; especially for Maputaland endemic species that tend to have a limited distribution and are consequently sensitive to habitat loss and fragmentation (Guldemond & van Aarde, 2010). Coastal dunes are also excessively exposed to anthropogenic disturbances, such as tourism-related development and extraction of the wealth of minerals in sands contained within them (Lubke *et al*., 1992b). Furthermore, their geographic location in relatively high rainfall regions makes them suitable for commercial forestry, placing even more pressure through the establishment of exotic plantations. For instance, a habitat suitability modelling exercise suggest that suitable forest habitats are now mostly occupied by agroforestry and sugarcane plantations, human settlements and rural subsistence households (Fig. 2.2) (for details on the methodology see Chapter 3 in this thesis). Bush-lands, grasslands and woodlands are, however, also found in areas predicted to be suitable for forests which emphasise the dynamic nature of the coastal forest landscape mosaic.

The coastal forests in South Africa’s northern sectors of the east coast appear to be well protected. However, this is not the case south from Richards Bay towards Durban and beyond (Figure 2.1). Just over 36% of coastal dune forests along the east coast are being conserved (Berliner, 2005). At 23%, the biggest contributor comes from national and provincial parks, wilderness areas, and special protected forests. The iSimangaliso Wetland Park is the largest protected area in the region, a 3320 km^2 World Heritage Site that protects 280 km of coastal dune forests along the coastline stretching from Kosi Bay to the Maphelane

Nature Reserve, just south of St Lucia (Figure 2.1). State forests, where people are allowed to harvest, have almost 13% of the protected forests under their jurisdiction, while private lands contribute to less than 1% of forest protection.

The protection of coastal forest in isolation of other habitat types may lead to misplaced conservation initiatives, especially when considering that these forests and adjoining habitats collectively may provide for the spatial structuring of species populations. Such populations may operate either as a classical metapopulation, partially connected, or a mainland-island system (Olivier *et al*., 2009). Within this paradigm, coastal forests may function either as a source or a sink, but mostly as the latter. The persistence of coastal forests therefore depends on their continuing connectivity to source populations to allow for dispersal through which assemblages are maintained or may regenerate following disturbance. This postulate finds support in a spatial occupancy model, illustrating that the presence of more than half of the tree and bird species in new-growth forests can be explained by landscape parameters such as edge, isolation, and area, while patch age explains presence of the remaining species in these taxa (Grainger *et al*., 2011). Coastal forests therefore do not function in isolation but rather are part of a regional landscape that collectively responds to disturbances and provides for the persistence of both local and regional species pools (see Eeley *et al*., 2001; Fairbanks *et al*., 2001).

The long-term challenge for the preservation of coastal forests in South Africa is to make people understand and appreciate the value of intact forests. For instance, tradition dictates that local people should use and benefit from forests, such as having access to medicinal plants (Grainger & van Aarde, 2011). Coastal forests may also have immediate and future benefit for the people living just inland from them. The most obvious is as a barrier to the destructive forces of the Indian Ocean. In 2007, a storm destroyed some commercial and private property, as well as rural livelihoods along the South African east coast. The worst affected areas were those with no indigenous dune forests to dissipate the force of the waves. With global warming predicted to increase storm events, the value of a barrier to protect human life and livelihood becomes increasingly apparent (e.g. Roberts, 2008).

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TABLES

Table 2.1 - Summary of forest radiations and retractions during the last 200 000 years in southern Africa. In this table, Afromontane forests include coastal scarp forests and Indian Ocean Coastal Belt forests include coastal lowland-, dune-, and swamp forests.

Time before present (BP years)	Afromontane forests	Indian Ocean Coastal Belt forests	References
130 000 – 40 000	-Established in southern Africa since the last interglacial		Lawes 1990; Eeley 1999;
	-Ongoing debate over its extent but because conditions were warm and wet, forests may have occupied a much greater area than at present		Lawes 2000; Lawes 2007
20 000 - 18 000	-Temperatures steadily decline towards the Last Glacial Maximum (LGM) -Conditions during the LGM significantly colder and more dry than present -Cool and dry conditions eliminate some forests	-Sea levels drop and dune formation prevalent on the Agulas bank and Mosambican coastal plains -Conditions intolerable for the formation of forests	Tinley 1985; Lawes 1990; Eeley 1999; Lawes 2007
16 000 – 13 000	-Deglaciation results in the re-radiation of forests		Lawes 1990; Eeley 1999; Lawes 2007
13 000 – 8000	-Arid conditions persist even after the LGM -Conditions not especially favourable for the spread of forests	-Warm interglacial conditions returned that facilitated the establishment of forests on the coastal plain	Martin 1968; Deacon & Lancaster 1988; Lawes 1990; Eeley 1999

Time before present (BP years)	Afromontane forests	Indian Ocean Coastal Belt forests	References
± 10 000 - 8 000*	-Forest range increase again	-Coastal forests radiated into KwaZulu-Natal from the northern tropical latitudes	Tinley 1985; Eely 1999; Von Maltitz *et al.*, 2003; Lawes 2007

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* There is some confusion around this date: Tinley 1985 and Von Maltitz 2003 suggest 10 000 – 8 000 BP, Lawes 2007, Lawes 2000 and Eeley 1999 put the date at around 8000 BP. Lawes 1990 suggest that some coastal forests only established around 6500 - 4000 BP. Following the LGM at 18000 BP there were several short cooling and warming cycles. Conditions suitable for forest radiation therefore only began after 8000 BP. Furthermore, a drop in sea-levels and westerly winds conductive to creating high sand dunes along the coast only occurred after 6000 BP (Hobday 1979; Maud, 1991). Coastal forests may therefore only have established after 6000 BP.

Table 2.2 - The number of species for trees, herbs, millipedes, and birds in each cumulative abundance quartile recorded over 18 years in two patches of old-growth dune forests in the Sokhulu State Forest and Maphelane Nature Reserve. Information extracted from Grainger (2011).

	Very common	Common	Rare	Very rare
Cumulative abundance	>75%	>50 to 74%	>25 to 49%	<25%
Trees	4	6	13	62
Herbs	1	4	6	45
Millipedes	1	1	2	12
Birds	3	6	8	70

Table 2.3 - Number of tree, mammal, bird, reptile, and amphibian species in coastal forests that may also be found in adjoining habitat from the hinterland (savanna, grasslands, and wetlands), other forest types (Afromontane, mangrove, riparian, sand, scarp, and swamp forests), or are at the extreme of their northern or southernmost coastal distributional ranges, South Africa.

Taxon*	Adjoining habitat	Other forest types	Northern most distributional range	Southern most distributional range
Trees	122	24	16	21
Mammals	26	1	2	4
Birds	105	19	8	3
Reptiles	19	0	0	3
Amphibians	18	1	0	4

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[*] The numbers of tree and bird species are from records collected during structured surveys over 18 years in old and new-growth dune forests north of Richards Bay, South Africa. Reptile and amphibian numbers are incidental species records during the same period. Mammal records include 28 species that have been seen in dune forests and 5 more listed in Skinner & Smithers (1990).

FIGURES

Figure 2.1 - Old growth and new growth coastal forests situated at the northern end of the South African east coast. The iSimangaliso Wetland Park, stretching from Kosi Bay in the north to the Maphelane Nature Reserve in the south, is the largest area that formally protects coastal forests. Structured ecological surveys have been conducted for some 20 years in the new growth forests north of Richards Bay and in the old growth Sokhulu State Forests.

Figure 2.2 - The proportion of modelled forest area that are currently occupied by other land-use types. Open bars represent transformed habitat types, while shaded bars represent natural habitat types found throughout the study area. For details on the modelling approach see Chapter 3 of this thesis.

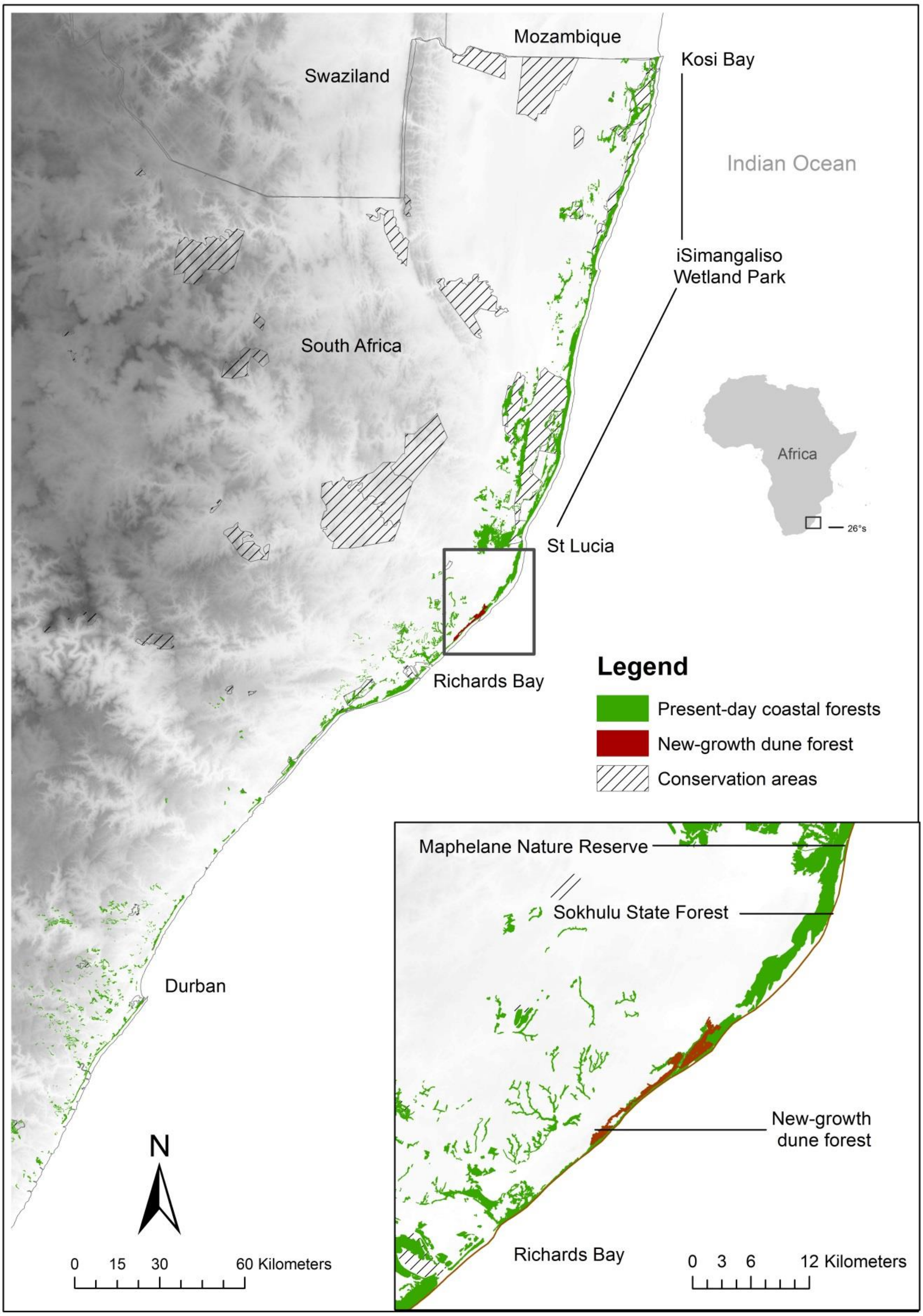
Mozambique
Kosi Bay
Swaziland
Indian Ocean
iSimangaliso
Wetland Park
South Africa
Africa
26°s
St Lucia
Richards Bay
Legend
Present-day coastal forests
New-growth dune forest
Conservation areas
Maphelane Nature Reserve
Sokhulu State Forest
New-growth
dune forest
Durban
N
0 15 30 60 Kilometers
Richards Bay
0 3 6 12 Kilometers

Figure 2.1

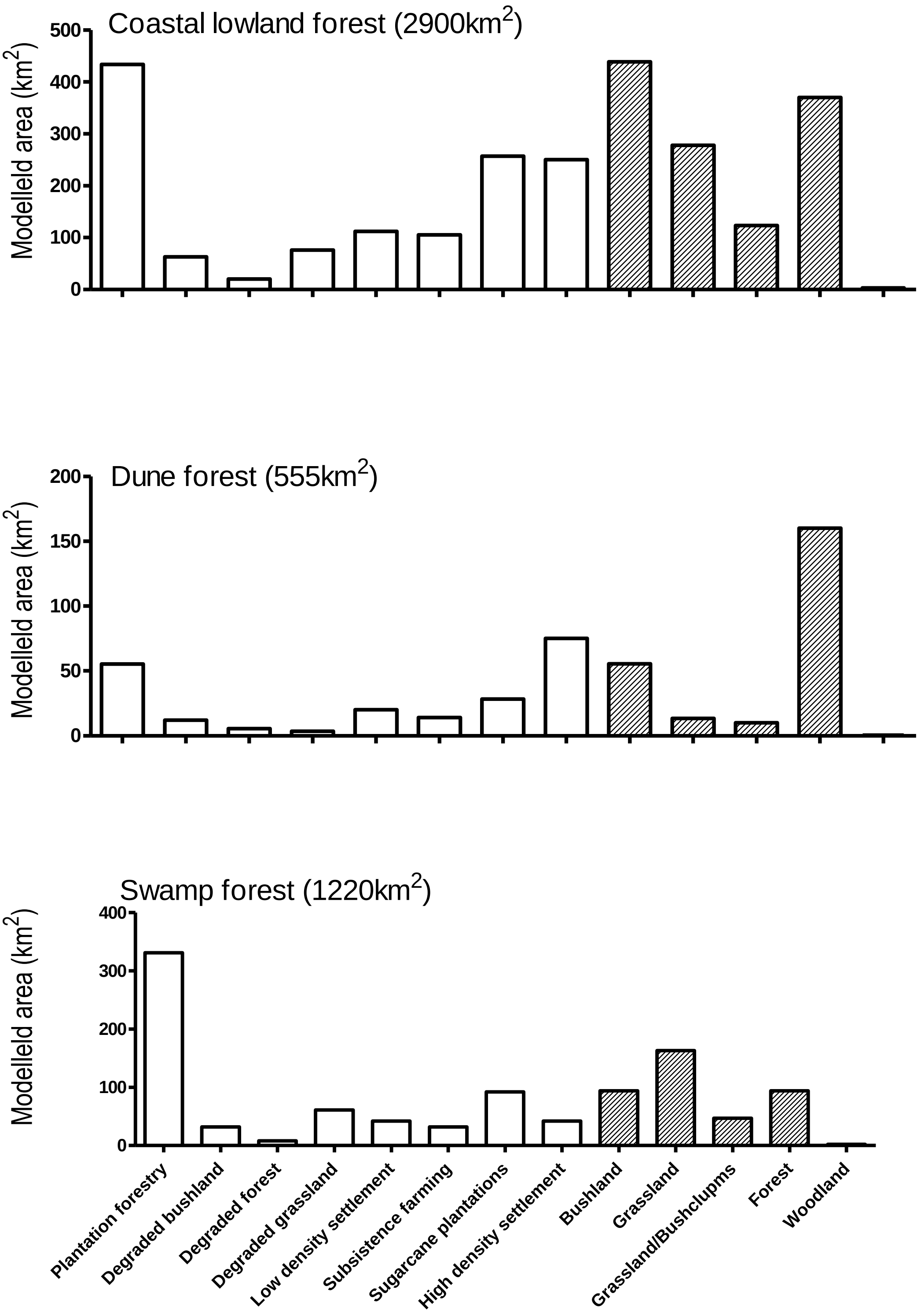
Coastal lowland forest (2900km^2)
Modelleld area (km^2)
500
400
300
200
100
0
Dune forest (555km^2)
Modelleld area (km^2)
200
150
100
50
0
Swamp forest (1220km^2)
Modelleld area (km^2)
400
300
200
100
0
Plantation forestry
Degraded bushland
Degraded forest
Degraded grassland
Low density settlement
Subsistence farming
Sugarcane plantations
High density settlement
Bushland
Grassland
Grassland/Bushclupms
Forest
Woodland

Figure 2.2

Chapter 3. The use of habitat suitability models and species-area relationships to predict extinction debts in coastal forests, South Africa

Publication details

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ABSTRACT

Aim Predicting extinctions before they are realised has proven difficult, yet is increasingly important for biodiversity conservation as habitat destruction continues unabated around the world. We evaluated whether habitat suitability models can be used in conjunction with species-area relationships (SAR) to detect apparent extinction debts as implicated by the conservation status assigned to bird species.

Location KwaZulu-Natal province, South Africa

Methods We modelled historic distributions of coastal forests using MaxEnt, a presence-only technique for modelling species distributions. The model provided an estimate of forest loss. We then conducted 293 point counts to survey birds within remaining forest fragments and employed an information-theoretic framework to test for the best fit SAR model. Extinction debts were calculated using the estimate of forest loss and the empirical SAR data.

Results Our model suggests extensive forest loss (82%) within a naturally fragmented landscape. The power function provided the best fit for bird SAR. Fourteen bird species are predicted to go extinct from coastal forests. Predicted extinctions closely matched the number of threatened species locally but not globally. Predicted extinctions also only matched globally threatened species that reach their northernmost distribution limit within coastal forests but not species that reach their southernmost distribution limit here.

Main conclusions We found that habitat suitability models could be used in conjunction with SAR to estimate extinction debt implied by conservation statuses of extant species. Our approach assumed that forest loss drives extinction debts but also provided opportunity to link forest loss and the likelihood of extinction. Models of historical forest distribution may provide guidelines of where to implement restoration actions. Maintaining matrix habitats that link forest fragments and targeted landscape level restoration that increases fragment area and link isolated fragments will be important to prevent predicted extinctions.

Key words: conservation; forest loss; fragmentation; MaxEnt; metapopulation; restoration.

INTRODUCTION

Extinction debt is the expected future losses of species in response to present habitat loss, yet it is a phenomenon that can easily go unnoticed (Kuussaari *et al.*, 2009). Predicting extinction debts has important implications for conservation planning, as the associated time delay provides the opportunity to enact conservation measures which may mitigate future species losses (Wearn *et al.*, 2012). Because habitat loss is the main driver of species extinction (Pimm & Raven, 2000), mitigation measures often relate to habitat restoration or preservation (Hanski, 2000; Lamb *et al.*, 2005). These proactive initiatives protect species from extinction

(Brooks *et al.*, 1999). However, even though extinction debts may be common in many remaining natural communities, verifying the existence of extinction debts remains problematic (Hanski & Ovaskainen, 2002; Kuussaari *et al.*, 2009).

Species-area relationships (SAR) have been used to estimate extinction debt and depend on four variables: 1) the habitat area prior to loss, 2) the number of species that occurred within the habitat prior to loss, 3) the area of habitat that remains and 4) an estimate of z that is determined by the slope of the power law that describes the SAR (e.g. Pimm & Askins, 1995; Brooks *et al.*, 1997; Cowlishaw, 1999; Wearn *et al.*, 2012). The problem, however, is that many threatened habitats are poorly studied with limited data on historic land cover and land use (Brooks *et al.*, 2002; Trimble & van Aarde, 2012). Therefore, estimates of the original habitat area and the number of species that occurred there prior to habitat loss are rarely available. In such instances, indirect approaches based on modelling may provide a way to delineate habitat area and evaluate species responses to habitat loss.

Habitat suitability models entail the geographic modelling of bio-spatial patterns in relation to environmental gradients. These models can contribute to conservation (Hirzel & Lay, 2008) and have been used to select sites for ecological restoration (e.g. Franklin *et al.*, 2005), predict the biological effects of climate change and invasive species (e.g. Thomas *et al.*, 2004; Ficetola *et al.*, 2007) and design corridors (e.g. Roever *et al.*, 2013). However, despite their wide range of applications their usefulness in predicting extinction debts has not been evaluated. Combining spatially explicit modelling with empirical data may prove a potentially powerful approach to predict extinction debt (Kuussaarri *et al.*, 2009). In the absence of historical data that describe land use history, habitat suitability models can be used to estimate the original area covered by a habitat. The effect of a reduction in habitat area on species occupancy can then be investigated with SAR.

Here we test this idea by studying a coastal forest along the east coast of South Africa. Coastal forests fall into two critically endangered eco-regions: the Maputaland Coastal Forest Mosaic and the KwaZulu-Cape Coastal Forest Mosaic which both support exceptionally high levels of floristic endemism as well as a high number of narrowly endemic species, including relict species (Burgess *et al.*, 2004). Anecdotal evidence (e.g. McCracken, 2008; Skead, 2009) and published reports (e.g. Cooper, 1985; Avis, 1992; Lawes, 2002; Thomson, 2002) suggest that coastal forests were once more widespread than they are today. However, we do not know to what extent. Current estimates of forest loss vary widely because they are not derived from consistent methodologies, but depend on expert opinion and their definitions of forest types (Berliner 2009). For example, estimates of coastal forest loss vary from ‘greater than 35%’ (Berliner, 2009), 65% (Lawes, 2002) and 90% (Cooper, 1985). Yet despite more than two centuries of intensifying human disturbances, species have not gone extinct from coastal forests in the region. Could these forests therefore harbour an unpaid extinction debt?

We used habitat suitability models that include information on remaining coastal forest distribution to model past forest distribution under assumed similar environmental conditions (e.g. Guisan & Zimmermann, 2000; Elith & Leathwick, 2009; Franklin, 2009). We compared modelled and current distributions of coastal forests to quantify forest loss and fragmentation. We then used our modelled estimate of forest loss to calculate extinction debts based on the SAR. Studies have shown that the number of extinctions predicted from deforestation and the number of species actually threatened are in many instances strikingly similar (Brooks *et al.*, 1997; Wearn *et al.*, 2012). Therefore, the number of species classified as threatened may represent the extinction debt of the habitat if these species match the number of species predicted to have become extinct based on SAR (e.g. Brooks *et al.*, 1997). We therefore compared the extinction debt based on our estimate of forest loss with the number of species listed as conservation concern in a) South Africa (locally) and b) on the

IUCN Red List of Threatened Species (globally). We assumed that our estimate of modelled forest loss can be used to calculate extinction debt if the number of species predicted to go extinct matched the number of species classified as threatened in South Africa. We conclude with recommendations to improve coastal forest conservation and restoration in South Africa.

METHODS

Study area

Lawes (1990), Eeley *et al.*, (1999) and Lawes *et al.*, (2007) reviewed the climatic history, palaeo-climatic change and biogeographic forces that explain the distribution of coastal and Afromontane forests in KwaZulu-Natal (KZN). Despite discrepancies in the classification of coastal forest types (see Moll & White, 1978; Lubke *et al.*, 1997; Midgley *et al.*, 1997; Mucina & Rutherford, 2006) we opted to recognise coastal forests as comprising lowland forests, dune forests and swamp forests. We included swamp forests in our analysis because of their close proximity to lowland and dune forests, with which they also share a number of forest-dependent species (von Maltitz *et al.*, 2003; Mucina & Rutherford, 2006).

Historical records and published reports suggest that coastal forests were once more widespread than what they are today. Archaeological records indicate that agricultural activities have been widespread in the region from the late Iron Age (1300’s). These probably intensified as the region experienced an influx of people as well as political and social unrest (Feely, 1980; Sundes, 2013). Forest clearing for agriculture, iron smelting and stock farming may also have caused an increase in grass-fuelled fires that promoted the spread of grassy ecosystems by carving holes in existing forest fragments (Acocks, 1953; Bond *et al.*, 2003; Bond & Keeley, 2005). Subsistence farming, cattle grazing, unregulated burning, commercial logging, agricultural plantations, and urban developments, all which accelerated since Europeans arrived in the region contributed to further forest losses (Fourcade, 1889; Bews, 1920; Feely, 1980; Avis, 1992; Thompson, 2002; Mucina & Rutherford, 2006). By 2010 these forests comprised 3087 patches (range 0.002 – 80km^2) that collectively accounted for 663km^2 (KZN Indigenous Forest Map, 2009) of the ~16300km^2 flat coastal plain (altitude 0-450m) along the east coast of KZN (Mucina & Rutherford 2006). These fragments are embedded within a matrix of mixed habitat and land-use types that range from natural grasslands and woodlands to agricultural plantations and human settlements.

Habitat suitability modelling

Environmental data

We assembled digital maps of 10 environmental variables (Schulze, 2006) relating to four principal traits associated with coastal forest distribution: temperature (maximum daily temperature in winter), precipitation (daily rainfall in winter, humidity, plant available water), geology (soil type, geology, soil clay content) and topography (aspect, elevation, slope) (Mucina & Rutherford 2006). The maps were 200m x 200m raster (grid cell) layers for KZN. A digital map (LandSAT 2010) that covered the distribution of coastal forest was converted to a 200m x 200m raster format for analysis. Grid cells that contained forest were coded separately for lowland, dune, and swamp forests. Each coded grid cell represented a single observation of forest presence. Grid cells that comprised both forest and non-forest were coded as forest. Where more than one forest type occurred within a grid cell, the grid cell was coded for the forest type that made up the largest proportion of the cell. For our models we assumed that there was no significant change in climate since the end of the 18th century when the development of Iron Age commercial centres caused the number of settlements in

KZN to increase rapidly and the first Europeans began to settle along the coast (Holmgren & Öberg, 2006).

Modelling algorithm and evaluation

We used MaxEnt version 3.3.2 (http://www.cs.princeton.edu/~schapire/maxent) to construct separate models for each forest type (see Phillips *et al.*, 2006 and Elith *et al.*, 2010). We used a presence-only modelling approach because we could not classify the absence of forests with certainty. In our study area, absence of forest could be due either to unsuitable environmental conditions or anthropogenically driven causes. We relied on recommended default values for the convergence threshold (10^{-5}) and maximum number of iterations (1000) (Phillips & Dudík, 2008). The program automatically selected suitable regularization values to reduce over-fitting. A jackknifing procedure was used to examine the importance of each variable, by comparing models with a particular variable absent, or present.

We evaluated modelling performance based on the area under the curve (AUC) (Fieldling & Bell, 1997). The value of an AUC index varies between 0 (performance worse than random) and 1 (perfect discrimination), with 0.5 being indistinguishable from random. Consequently model performance can be ranked as fair (0.7 - 0.8), good (0.8 - 0.9) and excellent (0.9 – 1.0) (Phillips *et al.,* 2006). We used a cross-validation procedure to evaluate the performance of our models by modelling each forest type 10 times and splitting the data in each partition between calibrations (70% training data) and evaluation (30% test data) for all three data sets. The AUC, average AUC and standard deviation of the AUC were calculated for all 10 models per forest type.

To aid model validation and interpretation it is necessary to distinguish ‘suitable’ areas from ‘unsuitable’ areas by setting a decision threshold above which model output is considered to be an accurate prediction of presence (Pearson *et al.,* 2004). This is important because when the logistic model output is converted to only forest presence and forest absence, the choice of threshold determines the amount of area classified as suitable for forest occurrence. We evaluated five optimal threshold criteria that have been found to produce accurate predictions when compared with other threshold criteria (Liu *et al.*, 2005; Jimènez-Valverde & Lobo, 2007; Bean et *al.*, 2012): 1) sensitivity-specificity equality, where positive observations are just as likely to be wrong as negative observations, 2) sensitivity-specificity sum maximisation, where the mean error rate for positive observations and the error rate for negative observations is minimized, 3) lowest presence threshold, which is the lowest value associated with any of the observed presence records, and 4) observed presence equals predicted presence, where the predicted presence is equal to the observed presence. We also evaluated the 10th and 20th percentile training presence threshold where the suitability threshold selects the value above which 90% and 80% of training locations are correctly classified. We then conducted a sensitivity analysis on threshold selection by calculating the amount of forest cover predicted based on each threshold value that we evaluated. We opted to underestimate rather than overestimate forest distribution because of the uncertainty associated with a modelling approach (Pearson *et al.*, 2006). We therefore selected the threshold that minimized the predicted area of forest cover for each forest type. Subsequent analyses were based on this estimate of forest cover. Optimal thresholds were calculated using R software (R Development Core Team, 2012) along with the Presence-Absence Model Evaluation package (Freeman, 2007).

Spatial structure of coastal forests

We calculated the fragmentation parameters; 1) number of fragments, 2) mean fragment size and 3) average nearest neighbour distance (ANND) for modelled and present-day coastal forest distributions. Modelled fragment parameters were then compared with present-day fragments using Mann-Whitney U tests. All calculations were done in Geospatial Modelling

Environment (Beyer, 2011) in combination with ArcGIS 10 (ESRI, 2011) and R (R Development Core Team, 2012).

Extinction debts

Field surveys

We conducted bird surveys using point counts (Bibby *et al.*, 2000) within 11 randomly selected coastal forest fragments that ranged in size from 0.29 to 80km^2. Survey sites were stratified by forest type and forest area resulting in two swamp, three lowland and six dune forest fragments. The number of survey points per fragment ranged from 3 to 9 for fragments < 5km^2, 9 to 18 for fragments between 5 and 20km^2 and 27 to 54 for fragments > 20km^2. In total 293 point counts were conducted between November 2011 and March 2012.

Point counts were conducted between 04:00 h and 10:00 h by the same three observers. Each observer surveyed 4 to 5 points per day. Observers were trained in, and had prior experience of local bird identification. Point counts were at least 180m apart and were located using handheld GPSs. An observer allowed for a 2min period for birds that may have been disturbed upon arrival at the survey point to resettle and thereafter recorded birds for 10min. All birds seen or heard within a 60m radius were recorded, but those that flew above the forest canopy were excluded. Point counts were also not surveyed during rain or windy conditions.

SAR model evaluation

We fitted a power function (Arrhenius, 1921) to our survey data of birds that occurred within coastal forests fragments of varying sizes. As our focus was on the effect of forest loss, we only included forest dependent species in our model evaluations. We then evaluated the model fit against seven other functions that have been proposed to model SARs

(Guillhaumon *et al.*, 2010; Triantis *et al.*, 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 & Schnabel, 1983). Assuming normality of the observations, this approach produces optimal maximum likelihood estimates of model parameters (Rao, 1973). Model fit was evaluated in two ways. First we statistically evaluated normality and homoscedasticity of residuals. A model is considered not to be valid for a given dataset if Pearson's product-moment correlation coefficient between residuals and/or Shapiro normality tests on residuals was significant at the 5% level (Guillhaumon *et al.*, 2010). Second, we used the information-theoretic framework for model selection proposed by Burnham & Anderson (2002). We compared the fit of the SAR models using the small-sample corrected Akaike's information criterion (AIC_c), a modification of the AIC that contains a bias correction term for small sample size. The model with the lowest AIC_c value was considered to fit the data best (Burnham & Anderson, 2002). For each model we obtained a model selection profile and an adequate fit profile, and we used these to evaluate how the different species-area functions compared to the power function when fitted to our data. We also calculated z (the slope of the SAR) and c (a constant) for all of the fitted SAR functions. Analyses were done using the 'mmSAR' package (Guilhaumon *et al.*, 2010) in R (R Development Core Team 2012).

Extinction debts

We used the SAR to estimate extinction debts rather than the endemics area relationship (EAR) (He & Hubbell, 2011) because we were modelling a community-level process of relaxation in remnant habitat, rather than a sampling process within continuous habitat (also see Wearn *et al.*, 2012). The SAR integrates the effects of increased isolation and density compensation in smaller habitat patches, such that a species may be committed to extinction before its entire habitat has been lost, whilst the EAR requires every individual of a species to lose its habitat for extinction to occur. As we also only focused on species that are dependent on forest habitat we opted to use the SAR and not the countryside SAR proposed by Pereira & Daily (2006) that takes into account the ability of species to persist in human-modified habitats.

The SAR presents a modelling framework that can be used to predict the number of species to go extinct after habitat loss by using an extension of the power function: $\frac{S_n}{S_o} = (\frac{A_n}{A_o})^z$ where S_n is the new number of species occurring within the habitat after disturbance, (S_o) the original number of species that occurred within the habitat prior to disturbance, (A_n) the new habitat area after disturbance, (A_o) the original habitat area prior disturbance and z the slope of the log-log plot of the power-law SAR. We based (A_o) on our modelled estimate of the original extent of coastal forest and (A_n) on the present extent of coastal forests derived from a 2010 LANDSAT image. For (S_o) and z we only included bird species that are dependent on coastal forests. Forest-dependent species were those that live and reproduce only in forest habitat (see Lawes *et al.*, 2007). There are no records of bird extinctions from these forests and we therefore assumed that species found here now are similar to those that occurred prior to forest losses. Species lists were compiled from the literature and nomenclature followed Hockey *et al.* (2005). We calculated three estimates of extinction debts by using the lower, mean and upper value of z.

Threatened species and extinction debts

We used conservation assessments published on birds (Barnes, 2000) as a tally of the numbers of coastal forest species likely to become extinct in South Africa (locally). We used the IUCN Red List of Threatened Species (IUCN, 2012) to count species likely to go extinct globally. These were species classified as critically endangered, endangered, vulnerable or near-threatened within both sets of assessments. As South Africa directly follows the IUCN categories when assigning conservation statuses to bird species (Barnes, 2000) we assumed that the two sets of assessments would be comparable. We then compared estimates of extinction debt for each group with a) the number of species classified as threatened in South Africa (locally) and b) the number of species classified as threatened on the Red List (globally). The IUCN Red List is widely regarded as the most authoritative list of globally threatened species (Rodrigues *et al.*, 2006). However, because the IUCN system is a probabilistic assessment of the likelihood that a species within a particular threat category will go extinct within a particular time frame, it is inevitable that certain species will be listed as at risk yet do not actually go extinct. Furthermore, because the system is precautionary, it is inevitable that there will be some over-listing (see Mace *et al.*, 2008). We attempted to overcome uncertainty associated with the listing process by evaluating the reasons why species were listed as threatened on the Red List as well as in South Africa.

The second part of this analysis distinguished between forest-dependent species that reach their northernmost distribution within coastal forests in KZN (hereto referred as southern species) and species that reach their southernmost distribution in KZN (hereto referred as northern species). We used IUCN range maps (IUCN, 2012) to assess the distribution patterns of forest-dependent species that occur within coastal forests. We defined a southern species as a species that had all or most of its range within South Africa. However, we also considered a species ‘southern’ when it had a South African population that was geographically isolated from populations further north in Africa with no possibility of dispersal between sub-populations. We then calculated extinction debts by considering southern and northern species separately in the analysis and evaluated their local and global conservation statuses. We also used the Red List to assess if the population was stable, declining, increasing or if the population status was unknown.

RESULTS

Habitat suitability models

Model evaluations

Modelling performance ranked from good to excellent for all three models as indicated by high AUC values that ranged from 0.819 (lowland forest) to 0.953 (swamp forest) (Table 3.1). The predicted amount of forest cover based on the optimal thresholds evaluated ranged from 3595km^2 – 44054km^2 which suggest that the models are sensitive to the threshold metric used (see Appendix S3.1 in Supporting Information). The threshold that yielded the smallest fraction of predicted area was predicted presence = observed presence (Table 3.2).

Jackknife tests revealed that median winter rainfall, minimum humidity in winter, elevation and plant available water contributed more than 70% to the lowland, dune and swamp forest models. For all three models aspect was of least importance. Maximum daily temperature in winter contributed significantly to the lowland (23.2%) and swamp forest (13.2%) models but not at all to the dune forest models.

Model output

Coastal lowland forest was predicted to be the most widespread (2900km^2), followed by swamp (1220km^2), and dune forest (555km^2) (Fig. 3.1 & Fig. 3.2). These values suggest that potential areas for 85% of lowland, 94% of swamp, and 70% of dune forest are not made up by these forests. Coastal forests therefore occupied 663km^2 (18%) out of a possible 3595km^2 that had suitable environmental conditions for forest occurrence (Table 3.3).

Our results suggest that lowland, dune and swamp forest have always been naturally fragmented (Table 3.3 & Fig. 3.2) as indicated by similar size class distributions of modelled and current forest fragments (Fig. 3.3). However, lowland, dune and swamp forest may have lost as much as 23%, 53% and 75% of fragments respectively. Current fragment sizes were also significantly smaller than modelled fragment sizes and indicate forest loss rather than increased fragmentation (P<0.0001, Mann-Whitney U-tests).

Extinction debts

Field surveys

Our survey resulted in 2018 records of 65 bird species found within 11 coastal forest fragments that ranged in size from 0.29km^2 to 80km^2. Of these 65 species, 28 were categorised as forest dependent. Species accumulation curves suggest sampling saturation despite few records in the smallest forest patches.

Model evaluation and estimates of z

The power model was considered the single 'best' model for our data set, as judged by the lowest AIC$_c$ value, followed by the Lomolino, Weibull and exponential models (Table 3.4). The non-significance of both the normality and homoscedasticity tests also suggest our assumption that coastal forest bird diversity follows the relationship $S = cA^z$ was met. A mean z value of 0.23 (95% CI: 0.16-0.30) was calculated by fitting the power model to the bird diversity data (Fig. 3.4).

Threatened species and extinction debt

We identified 45 forest-dependent bird species that may occur within coastal forests. Using the extent of forest loss calculated from our models coastal forests in KZN are predicted to have an extinction debt of 14.4 (95% z: 10.6 – 17.9) bird species (Fig. 3.5). The number of predicted extinctions closely matched the number of locally threatened species (11) but not the number of globally threatened species (5). In addition, 12.2 (95% z: 9.0 – 15.1) northern bird species were predicted to go extinct compared with the eight that were classified as threatened locally. However, none of these species was globally threatened. Conversely, 2.3 (95% z: 1.7 – 2.8) southern species were predicted to go extinct but three species (spotted ground thrush (*Zoothera guttata*), Knysna woodpecker (*Campethera notate*) and the bush blackcap (*Lioptilus nigricapillus*)) were classified as threatened – both locally and globally (Fig. 3.5). Furthermore, five out of seven southern bird species were declining compared with 13 out of 38 northern species. Only one northern bird species (African crowned eagle (*Stephanoaetus coronatus*)) were classified as threatened on the Red List (globally). Forest loss, degradation and fragmentation were the main reason for the listing of 10 out of 11 locally threatened species. In addition, forest loss and small population sizes were the main reasons for the listing of all five globally threatened species (see Appendix S3.2 in Supporting Information).

DISCUSSION

One of the goals of conservation scientists is to predict which species are most likely to be threatened with extinction, understand why, and then act to improve the situation (Manne & Pimm, 2000). Our findings suggest that by combining a simple modelling approach with empirical SAR data, scientists can detect extinction debts, determine the driver(s) behind extinction debts, identify species that are threatened with extinctions, and develop guidelines to spend limited conservation resources effectively and efficiently.

The number of threatened species that occur within coastal forests closely matched the number of species predicted to go extinct. This is nothing new as others have illustrated the same pattern for birds in south-east Asia and birds, mammals and amphibians in the Brazilian Amazon (Brooks *et al.*, 1997; Wearn *et al.*, 2012). However, it is the first time that similar results have been found with the use of a modelled estimate of forest loss. There are, however, potential caveats associated with our approach. First, species distribution modelling are subject to uncertainty which can arise from assumptions associated with a presence-absence modelling framework, conceptual and numerical model formulations, parameter estimates, model evaluation, and the potential for adaptation of living systems (Planque *et al.*, 2011; Yackulic *et al.*, 2013). For instance, our results suggest that predicted forest cover differ markedly depending on the threshold criteria selected. We suggest that to calculate extinction debts, researches should evaluate a range of threshold criteria and settle on the value that is relevant to their study area. Second, extinction debt and locally listed species might be similar, but not casually linked. For our study area, forest loss was the foremost reason for the listing of nearly every locally threatened species. This suggests that the listing of species here is a function of forest loss. This is supported by our observation that none of the species with a range that extended north of KZN, were considered threatened globally. We therefore propose that habitat suitability models could be used in conjunction with SAR to detect extinction debts if we assume that extinction debt is driven by habitat loss.

Given the amount of forest loss predicted by our models, why have we not seen species go extinct and can we maintain this status quo? The absence of realised extinctions may be related to the fragmented nature of coastal forests in South Africa. Our *z* value of 0.23 for forest dependent species is similar to 0.25 that has been calculated for islands within an archipelago (Drakare et al., 2006) and which has been widely used as a model for the habitat fragmentation process (Pimm & Askins, 1995; Rosenzwieg, 1995). However, because forests here may have been fragmented for considerable time, shaped by thousands of years of climate change, fire and human activities (Bond *et al.*, 2003), forest dependent species may have evolved to persist in fragmented habitats where forests are surrounded by an ever changing assortment of grasslands, bush-lands, and woodlands (Von Maltitz, 1996). Some species may therefore be able to disperse through, or utilize resources in the surrounding matrix and be buffered from extinctions associated with forest loss. This has been shown by Pereira & Daily, (2006) who illustrated that the number of predicted extinctions derived from the SAR decrease when the areas of the surrounding matrices are incorporated in calculations.

Metapopulation processes such as dispersal and colonization may also drive species occupancy in fragmented landscapes (Hanski & Ovaskainen, 2000). Under such conditions local extinction rates (within fragments) decline with increasing fragment area and the colonization rate increases with connectivity (Hanksi, 1998; Prugh *et al.*, 2008). We speculate that these processes of extinction and re-colonisations through constant dispersal may have always maintained species populations within coastal forests in South Africa. This idea is supported by our SAR calculations when we include all the species recorded during our survey. The resultant *z*-value of 0.16 suggest continuous habitat where immigration constantly 'rescues' species populations in smaller areas (Watling & Donnelly, 2008). Extinctions may therefore not have occurred because even with the loss of habitat and increased levels of fragmentation species could still persist by dispersing through the natural matrix and re-colonizing empty fragments. However, based on our modelling exercise coastal forest fragments are now smaller, fewer, further apart and more 'hemmed in' by human land-uses than what could have been the situation in the past. In addition, matrix habitats are also being transformed at alarming rates and are under no less pressure than forests (CERU unpublished data). The conversion of natural matrix habitats to anthropogenically transformed habitats, together with forest loss may eventually result in the formation of non-equilibrium metapopulations where sub-population (fragment) extinction rates exceed colonization rates (Hanski & Ovaskainen, 2000). This process may be happening within coastal forest fragments in KZN. For one study site where long term monitoring data were available, Trimble & van Aarde (2010) recorded that the densities of 57% of species declined in new and old growth dune forests over the last two decades. Without management interventions non-equilibrium metapopulations will eventually go extinct, locally as well as regionally (Harrison, 1991).

Colonization and extinction may also be driving patch occupancy in other taxa (e.g. Lawes *et al.*, 2000; Olivier *et al.*, 2009). For instance, even though we did not have empirical data to evaluate extinction debts for other taxa, the same pattern observed for birds also held for mammals. Ten out of 13 forest dependent mammal species were considered locally threatened, but none of these were threatened globally. If we assume that this represents an extinction debt it would mean that the slope of mammal SAR within coastal forests approach 0.75. Such a high z value suggests that mammals in these forests occur within small isolated patches that contain very few individuals of each species, with limited dispersal between patches. The large differences in our z-values for mammals and birds reflect on differences in their susceptibility to forest lost, some of which may be ascribed to differences in life history properties associated with dispersal. In addition, mammals may also be facing high levels of subsistence hunting pressure in disturbed fragments (Hayward, 2009) that result in them being particularly vulnerable to local extinction (e.g. Canale *et al.*, 2013).

How long will it take threatened forest species to go extinct? The time to extinction depends on variables such as population size, the colonization processes maintaining metapopulations, the magnitude of forest loss, as well as the future rate of deforestation (Wearn *et al.*, 2012; Hylander & Ehrlén, 2013). We have no information on past rates of forest lost or on the bird species that occupies the remaining forest fragments in KZN. We therefore can only speculate on the time it will take for predicted extinctions to be realised. However, we do know from historical records that five bird species have gone locally extinct, purportedly, due to the clearance of coastal forest (Siegfried *et al.*, 1976; Brooke, 1984). Predicting future forest cover under different land use scenarios as well as long-term monitoring of forest fragments therefore may enable us to set timeframes of conservation opportunities to protect species threatened by extinction.

In view of our findings, the good news is that there is still time to carry out conservation actions such as the active management of threatened species, the protection of remaining forests from disturbance, and restoration of degraded forests. The bad news, however, is that the existence of extinction debts implies that even with no further habitat loss some species may go extinct locally (see Kuussaari *et al.*, 2009). The prevention of future extinctions may therefore depend on restoring and conserving natural landscapes. This could be achieved by maintaining or enhancing the coastal forest cordon as a migration corridor that may facilitate dispersal from north to south, thereby reducing extinction risk due to the loss of forests in KZN.

Furthermore, geographical isolation, small range sizes and high levels of historical habitat loss render southern species particularly vulnerable to extinction. Targeted habitat restoration efforts may therefore be the best strategy to ensure the persistence of these species, even though the selection of restoration sites remains a challenge (Thompson, 2011). Our analysis gives some indication of where one should target restoration efforts to complement remaining forest fragments, protected areas and other natural habitats in the human modified landscape mosaic. Fragments that are surrounded by an inhospitable matrix may be linked with other fragments through restoration corridors or stepping stones (e.g. Baum *et al.*, 2004; Kupfer *et al.*, 2006). Conversely fragments that are surrounded by a permeable matrix may benefit more from an increase in area (e.g. Wethered & Lawes, 2003). Given the naturally fragmented nature of these forests, conserving natural habitats that link forest may also be just as important to prevent future extinctions as conserving remaining forests fragments. Knowing where forest occurred in the past and where they do not occur at present will be crucial for getting the best return on efforts to regain some forests and restore important ecological processes to prevent future extinctions.

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TABLES

Table 3.1 - Area under the curve (AUC) scores for lowland, dune, and swamp forests for all model runs. Models were calibrated using training data (70% of occurrence points, randomly selected), and AUC values were calculated from test data (30% of occurrence points, randomly selected).

	Lowland forest		Dune forest		Swamp forest	
	Training AUC	Test AUC	Training AUC	Test AUC	Training AUC	Test AUC
Full model	0.819	0.818	0.901	0.900	0.953	0.951
Cross validation models						
1	0.790	0.791	0.882	0.877	0.953	0.951
2	0.790	0.789	0.882	0.876	0.953	0.953
3	0.790	0.799	0.882	0.886	0.953	0.952
4	0.790	0.789	0.882	0.885	0.953	0.954
5	0.790	0.796	0.882	0.886	0.953	0.949
6	0.790	0.785	0.882	0.879	0.953	0.951
7	0.790	0.787	0.882	0.875	0.953	0.950
8	0.791	0.790	0.882	0.885	0.953	0.952
9	0.791	0.779	0.882	0.880	0.953	0.950
10	0.790	0.792	0.881	0.886	0.953	0.950
Mean	0.790	0.789	0.882	0.881	0.953	0.951
Standard deviation	0.0004	0.006	0.0003	0.005	0	0.002

Table 3.2 - Thresholds of occurrence evaluated for each of the forests models. The thresholds that minimized the predicted area of forest cover were used in all the subsequent analyses and are highlighted in bold.

Threshold criteria	Lowland forest	Dune forest	Swamp forest	Predicted forest area (km^2)	Estimate of forest loss (%)
Sensitivity-specificity equality	0.498	0.517	0.446	5013	86.7
Sensitivity-specificity maximisation	0.337	0.301	0.235	13094	94.9
Lowest presence threshold	0.001	0.005	0.007	44054	98.5
Predicted prevalence equals observed prevalence	**0.508**	**0.533**	**0.514**	**3595**	**81.5**
Percentiles					
10th percentile	0.447	0.499	0.452	8236	91.9
20th percentile	0.491	0.528	0.482	5128	87.1

Table 3.3 - Fragmentation parameters calculated for modelled and present-day coastal forest fragments.

Forest type	Area (km^2)		Number of fragments		Mean fragment size (km^2) (SD)		Average Nearest Neighbour (km)	
	Modelled	Present	Modelled	Present	Modelled	Present	Modelled	Present
Lowland	2900	370	3317	2549	0.87 (18.68)	0.17 (1.52)	0.66	0.42
Dune	555	160	411	191	1.34 (9.44)	0.88 (4.89)	0.91	1.57
Swamp	1220	94	1404	347	0.86 (13.98)	0.21 (0.78)	0.70	1.36

Table 3.4 – Comparison of the performance of eight SAR functions for the number of bird species that occur within coastal forest fragments. Note that *c* (a constant) and *z* (the exponent of the SAR) are fitted model parameters.

Function	AIC_c	R^2	*c* (95% CI)	*z* (95% CI)	Homogeneity of variance	Residuals
Power	22.40	0.85	2.63 (1.20-4.06)	0.23 (0.16-0.30)	-0.09	0.22
Exponential	27.81	0.82	-4.20 (-9.44-1.03)	2.62 (1.79-3.44)	-0.02	0.93
Negative exponential	38.27	0.52	15.75 (11.97-19.52)	0.01 (0.001-0.01)	0.48	0.16
Monod	34.60	0.66	17.26 (13.42-21.09)	135.04 (1.06-269-02)	0.36	0.12
Logistic	25.00	0.83	21.72 (16.41-27.03)	0.0006 (0.0001-0.001)	-0.26	0.16
Rational	32.18	0.83	7.00 (4.39-9.61)	0.009 (-0.02-0.02)	-0.19	0.19
Lomolino	24.39	0.84	41022.63 (28.32-47.56)	1.26 (0.72-1.80)	-0.10	0.20
Weibull	24.39	0.84	3.9e+07 (-3.8e+08-4.6e+08)	6.8e-07 (-6.9e-07-8.3e-07)	-0.01	0.20

FIGURES

Figure 3.1 - Map of KZN indicating where coastal forests (lowland, dune, and swamp forest) are predicted to occur by the three forest models. Different shades of green represent different forest types. Black squares are linked to Figure 3.2 which illustrates how modelled coastal forest distributions differ from present day coastal forest distributions within selected areas.

Figure 3.2 - Map's showing the modelled and current distributions of coastal forests for selected areas in KZN. Each forest model is shown independently from other forest models. Red indicates areas that are predicted to be suitable for forest occurrence while shades of green indicate present-day forest occurrence.

Figure 3.3 - Histograms showing the size distribution of forest fragments for the three different forest types considered in our analysis. Open bars represent the number of modelled fragments while shaded bars represent the number of present-day fragments.

Figure 3.4 - Species-area relationship for forest dependent bird species that occur within remaining coastal forest fragments. The fit of the power function $S = cA^z$ is shown where z is the exponent of the SAR and c is a constant.

Figure 3.5 - Comparison between the numbers of bird species predicted to go extinct based on our modelled estimate of forest loss and the number of locally and globally threatened species. Predictions of extinction debts closely matched the number of species classified as threatened in South Africa (locally) but not the number of species classified as threatened on the Red List (globally). Northern species were only locally threatened. For southern species predictions of extinction debts closely matched the number of both locally and globally threatened species.

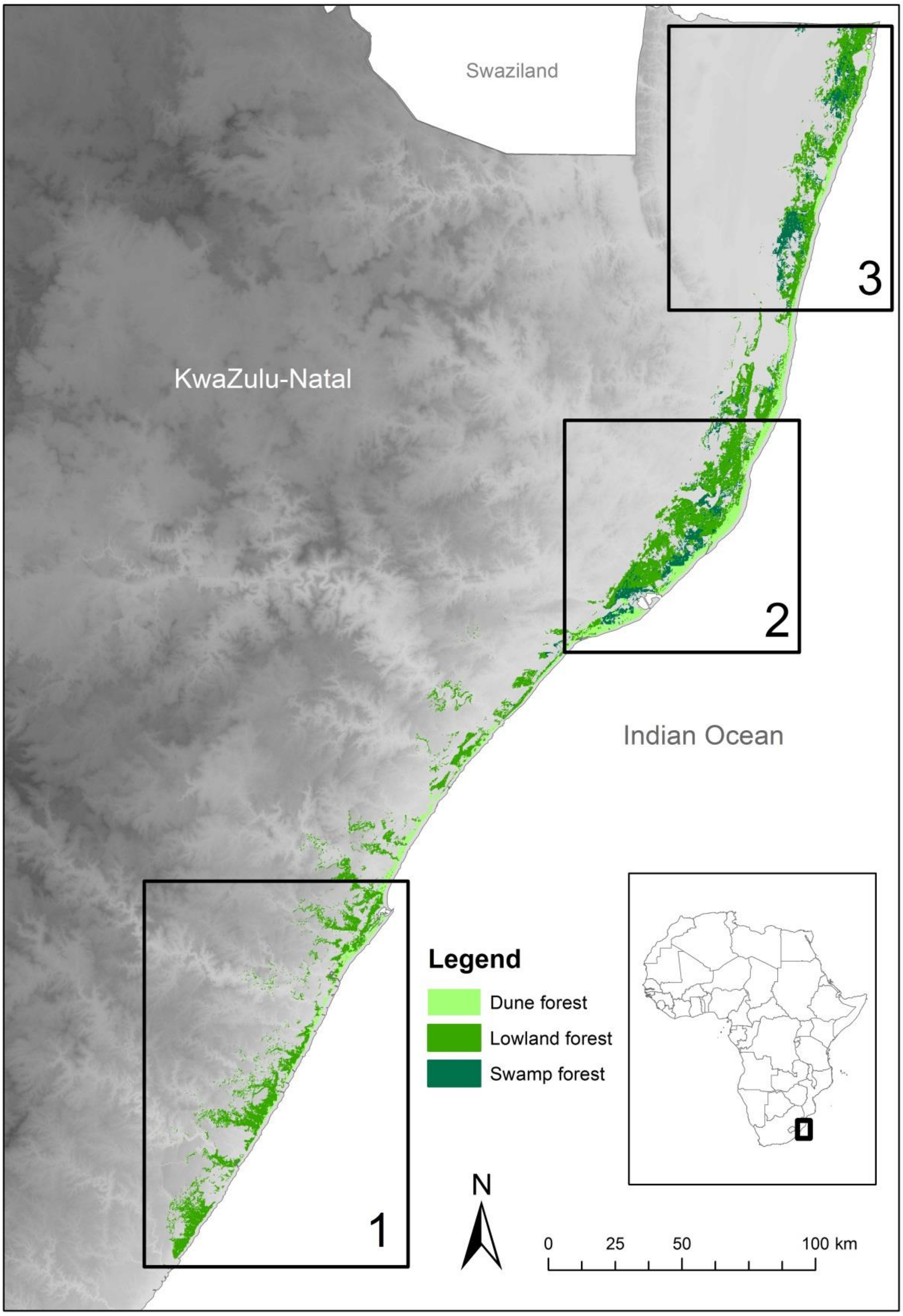
Swaziland
KwaZulu-Natal
Indian Ocean
1
2
3
Legend
Dune forest
Lowland forest
Swamp forest
N
0
25
50
100 km

Figure 3.1

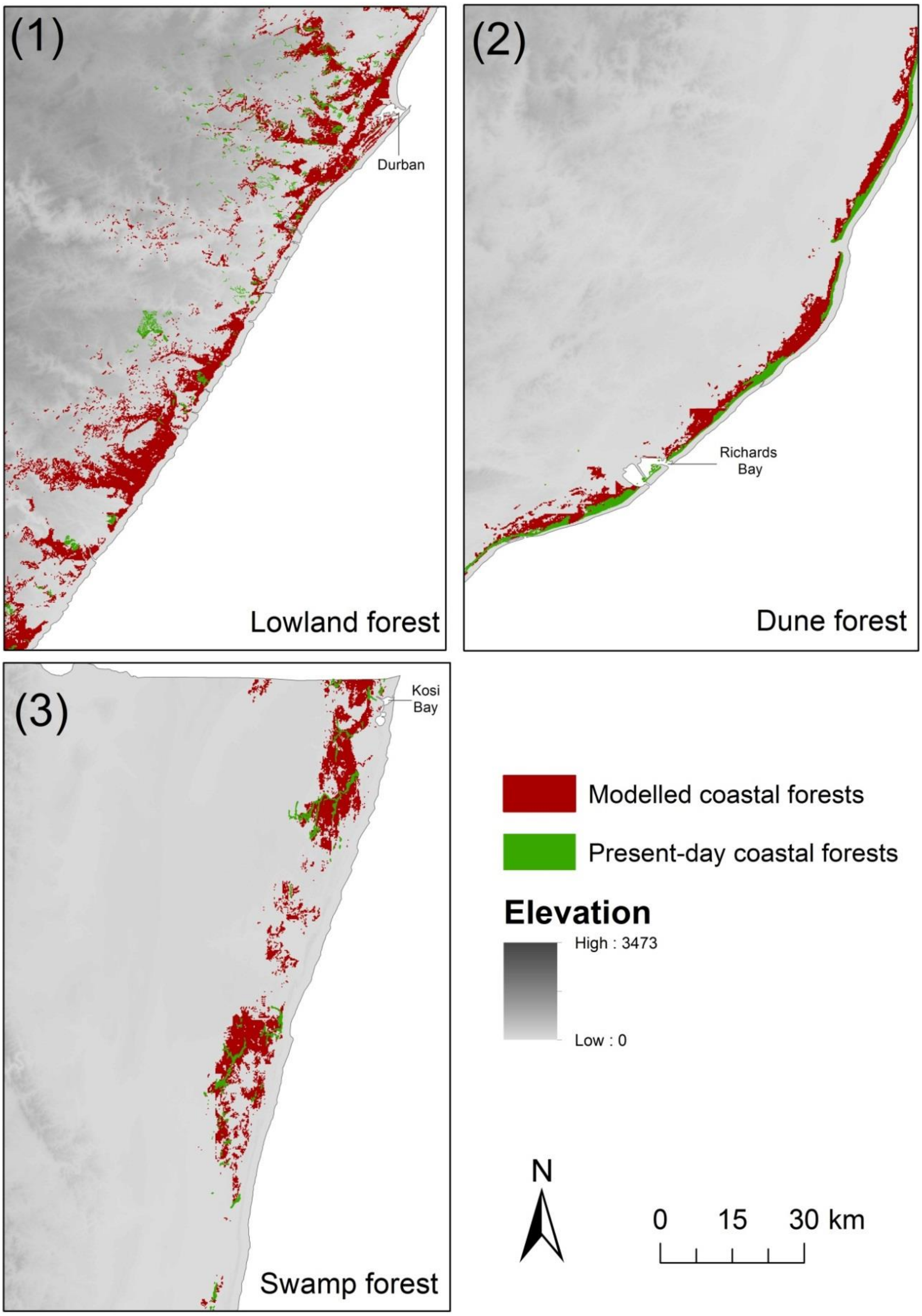
(1)
Durban
Lowland forest
(2)
Richards Bay
Dune forest
(3)
Kosi Bay
Swamp forest
Modelled coastal forests
Present-day coastal forests
Elevation
High : 3473
Low : 0
N
0 15 30 km

Figure 3.2

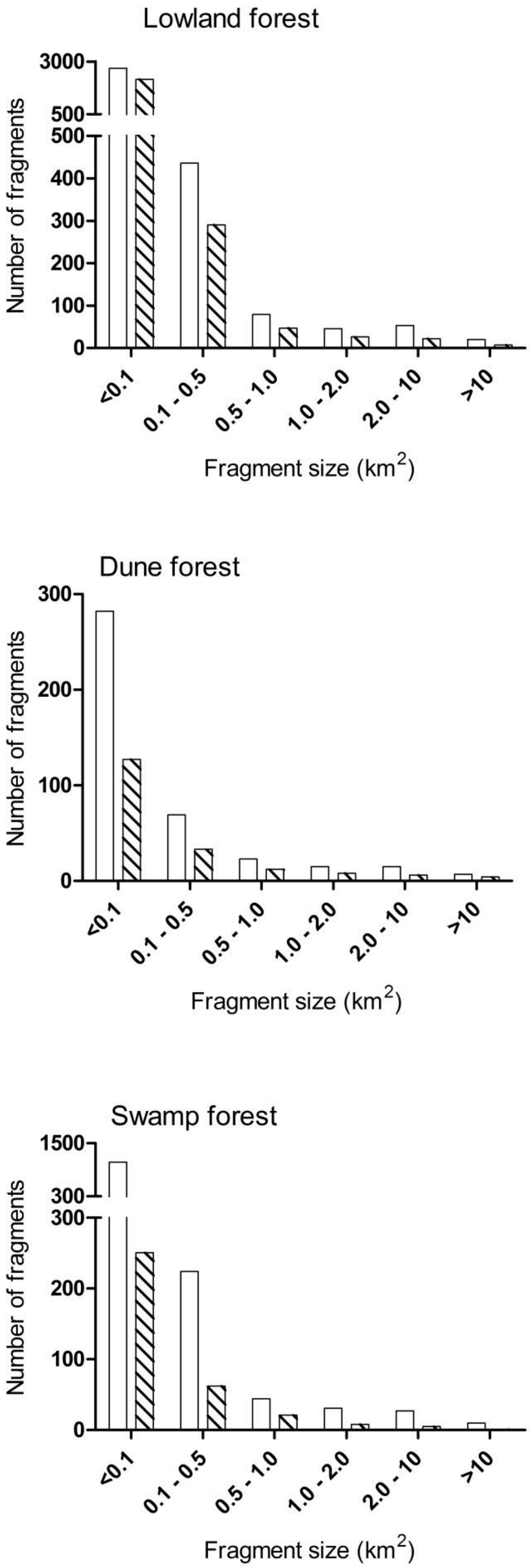
Lowland forest
Number of fragments
3000
500
500
400
300
200
100
0
<0.1
0.1 - 0.5
0.5 - 1.0
1.0 - 2.0
2.0 - 10
>10
Fragment size (km^2)
Dune forest
Number of fragments
300
200
100
0
<0.1
0.1 - 0.5
0.5 - 1.0
1.0 - 2.0
2.0 - 10
>10
Fragment size (km^2)
Swamp forest
Number of fragments
1500
300
300
200
100
0
<0.1
0.1 - 0.5
0.5 - 1.0
1.0 - 2.0
2.0 - 10
>10
Fragment size (km^2)

Figure 3.3

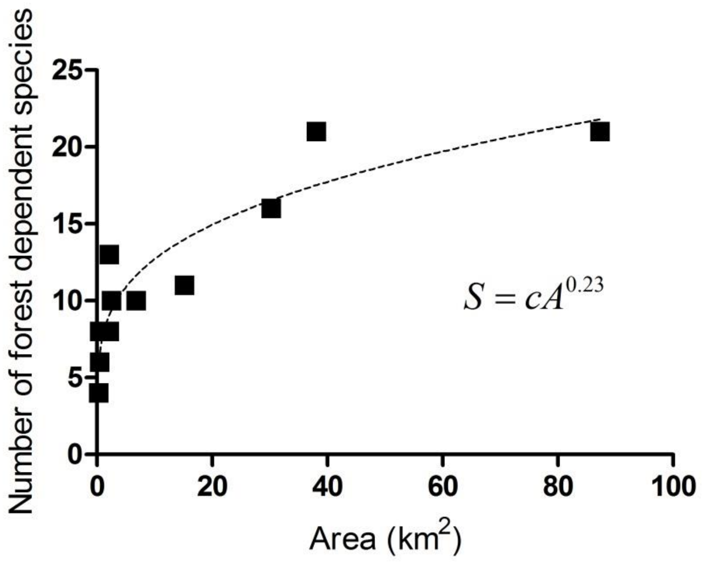
Number of forest dependent species
25
20
15
10
5
0
0
20
40
60
80
100
Area (km^2)
$S = cA^{0.23}$

Figure 3.4

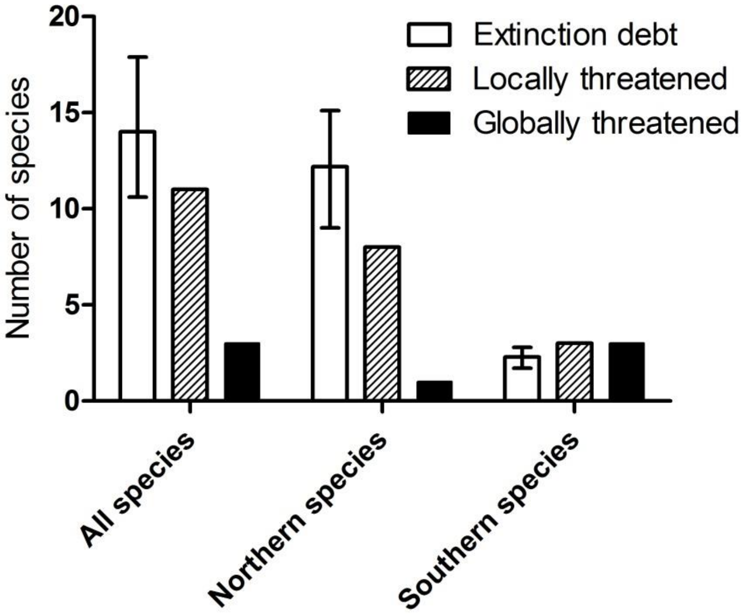
20
15
10
5
0
Number of species
Extinction debt
Locally threatened
Globally threatened
All species
Northern species
Southern species

Figure 3.5

SUPPORTING INFORMATION

Appendix S3.1 Maps of KZN indicating the predicted extent and occurrence of coastal forests (lowland, dune, and swamp forest) based on the optimal thresholds evaluated.

Appendix S3.2 Table of forest dependent bird species that are categorized as threatened in South Africa with the motives for their listing in South Africa and the IUCN Red List.

Appendix S3.1

Table S3.1 - Predicted forest cover for dune, lowland and swamp forest based on the optimal thresholds evaluated.

Optimal threshold	Dune forest (km^2)	Lowland forest (km^2)	Swamp forest (km^2)	Total forest cover (km^2)
Sensitivity-specificity equality	799	3910	2694	5013
Sensitivity-specificity maximisation	2548	12844	4681	13094
Lowest presence threshold	10296	44071	14940	44054
Predicted prevalence equals observed prevalence	555	2900	1220	3595
Percentiles				
10th percentile	1094	7925	2607	8236
20th percentile	620	4577	2004	5128

Figure S3.1a – e: Maps of KZN indicating where coastal forests (lowland, dune, and swamp forest) are predicted to occur by the three forest models based on the optimal thresholds evaluated. Each map represents the predicted occurrence based on a specific optimal threshold. The threshold that resulted in the smallest fraction of predicted forest cover, observed prevalence equals predicted prevalence, is not shown because it is included in the manuscript.

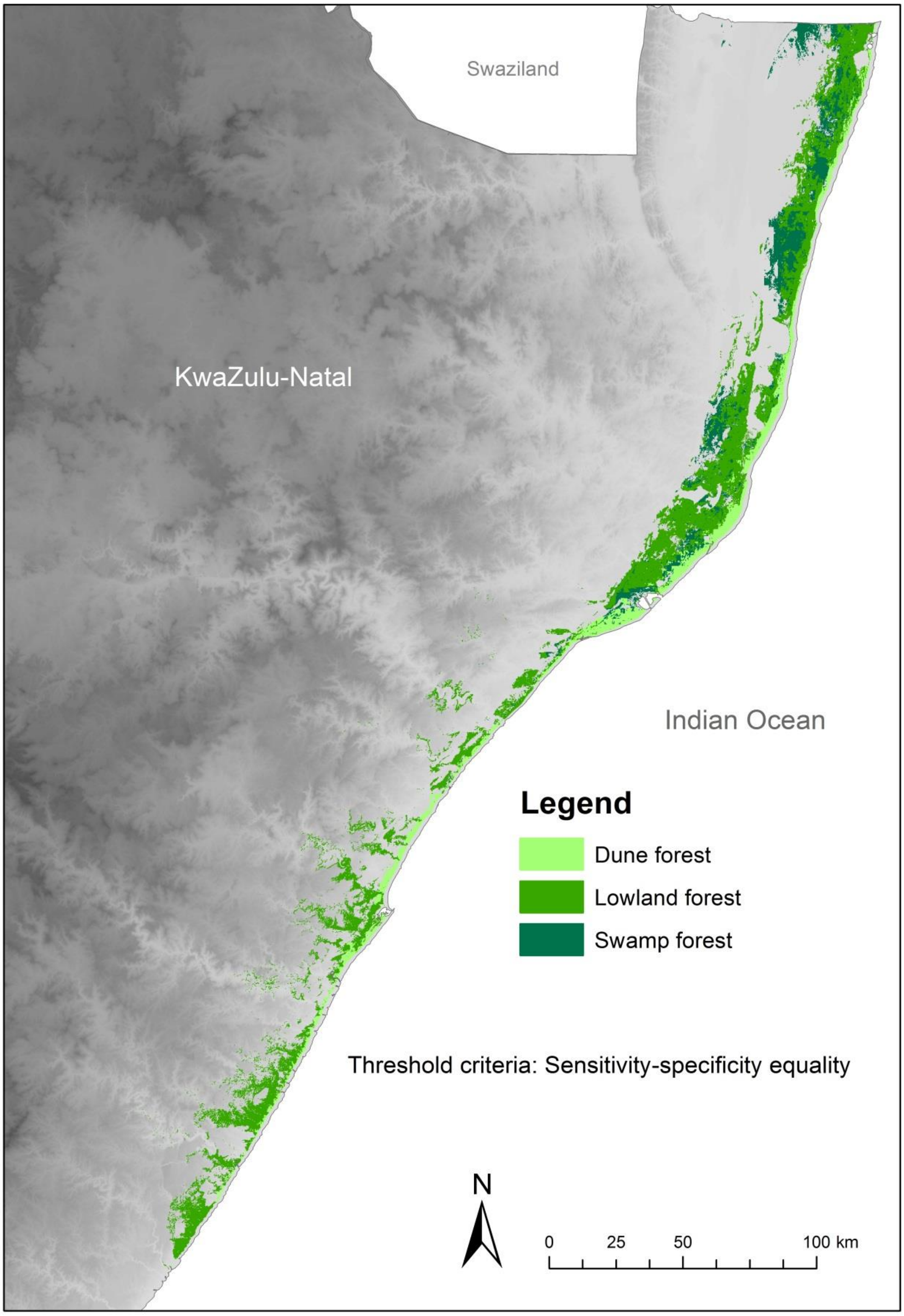
Swaziland
KwaZulu-Natal
Indian Ocean
Legend
Dune forest
Lowland forest
Swamp forest
Threshold criteria: Sensitivity-specificity equality
N
0
25
50
100 km

Figure S3.1a

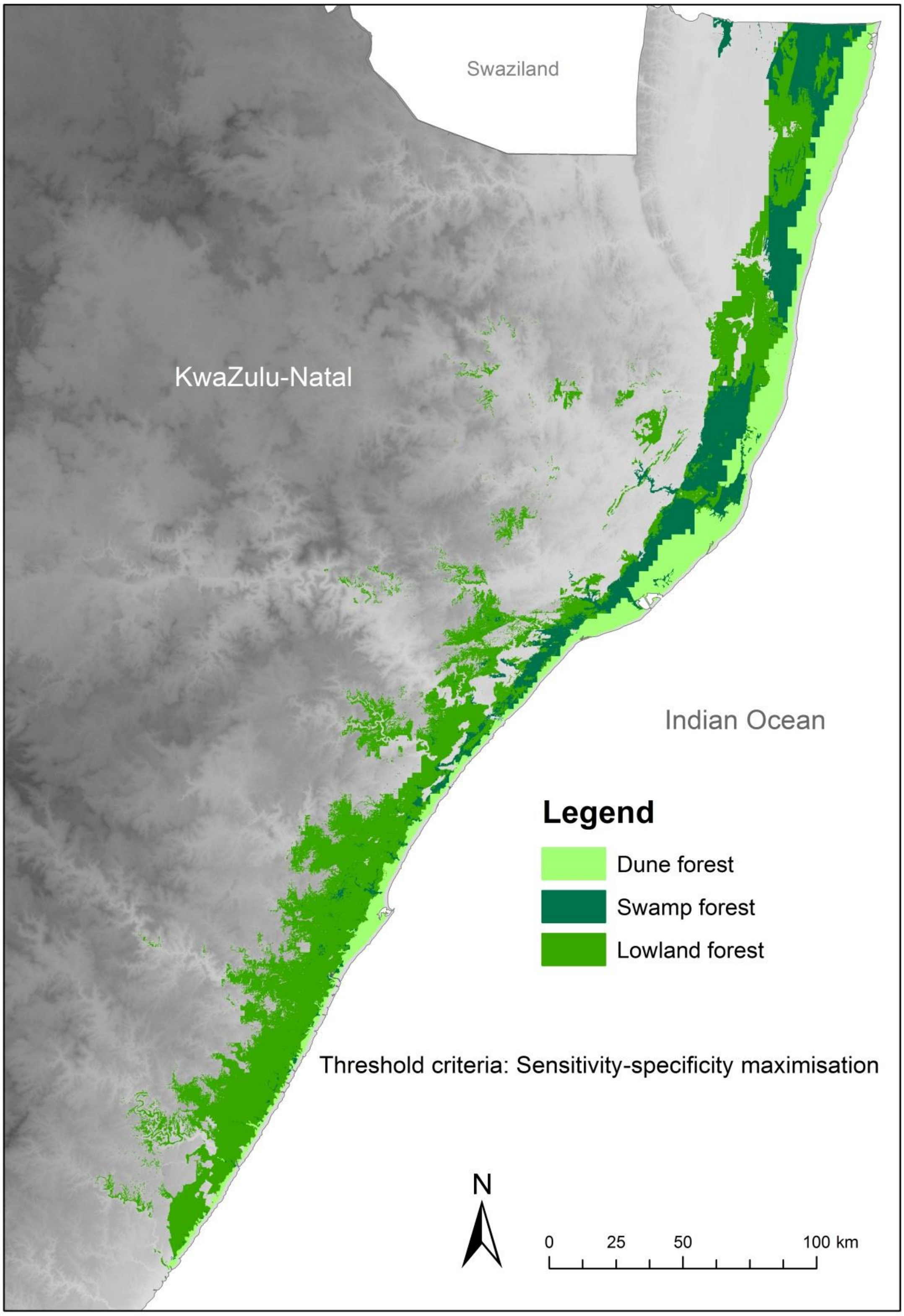
Swaziland
KwaZulu-Natal
Indian Ocean
Legend
Dune forest
Swamp forest
Lowland forest
Threshold criteria: Sensitivity-specificity maximisation
N
0
25
50
100 km

Figure S3.1b

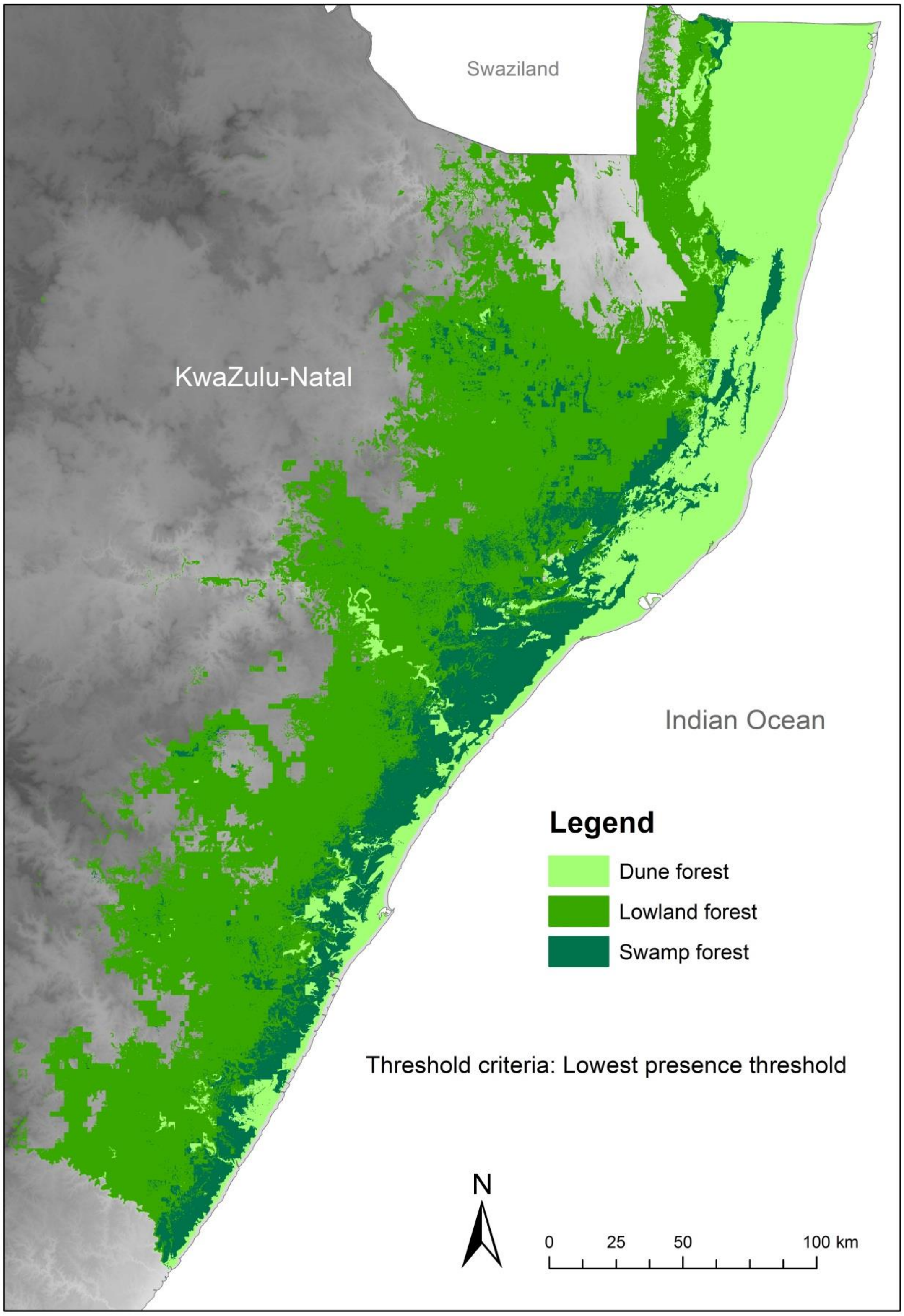
Swaziland
KwaZulu-Natal
Indian Ocean
Legend
Dune forest
Lowland forest
Swamp forest
Threshold criteria: Lowest presence threshold
N
0
25
50
100 km

Figure S3.1c

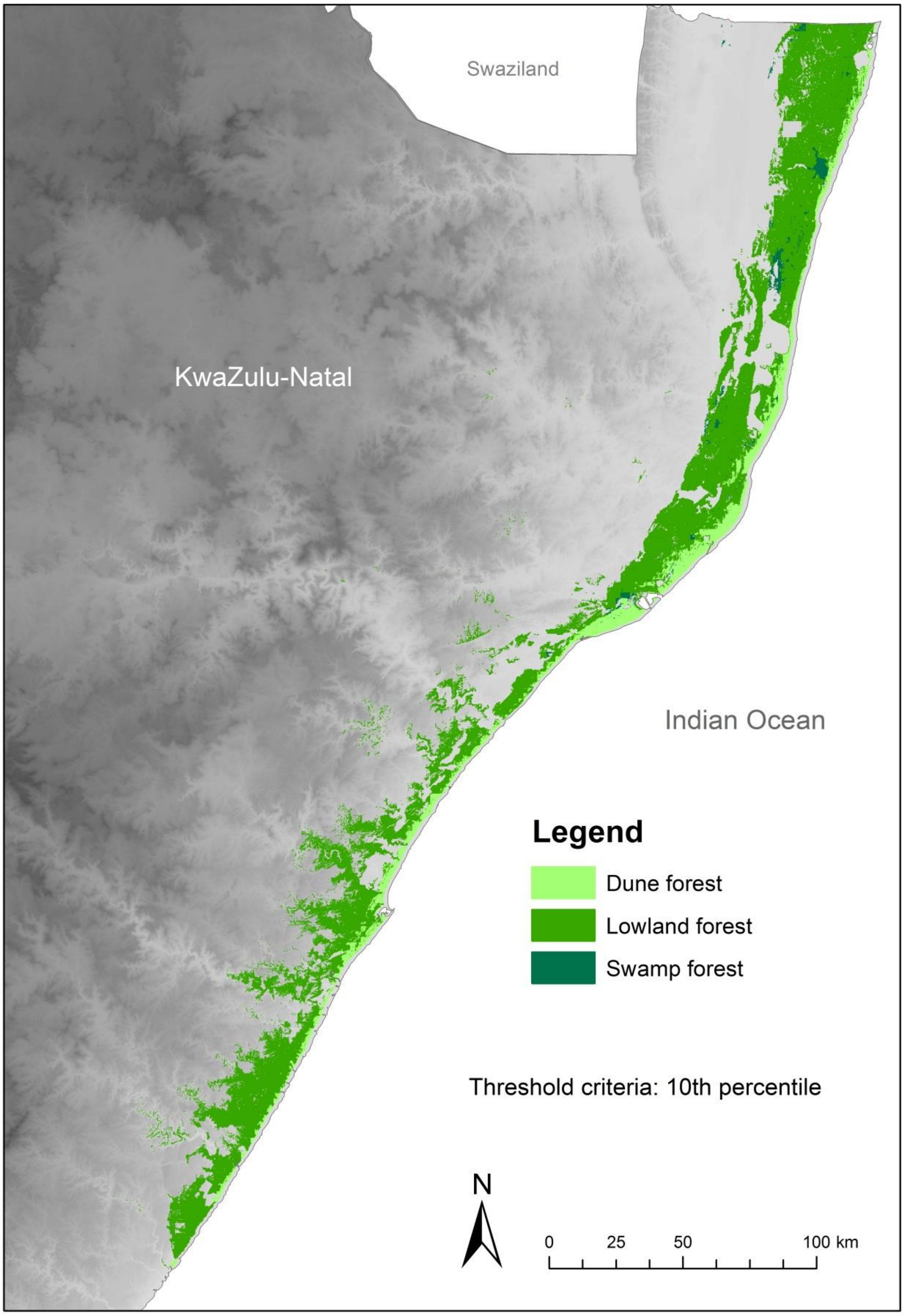
Swaziland
KwaZulu-Natal
Indian Ocean
Legend
Dune forest
Lowland forest
Swamp forest
Threshold criteria: 10th percentile
N
0
25
50
100 km

Figure S3.1d

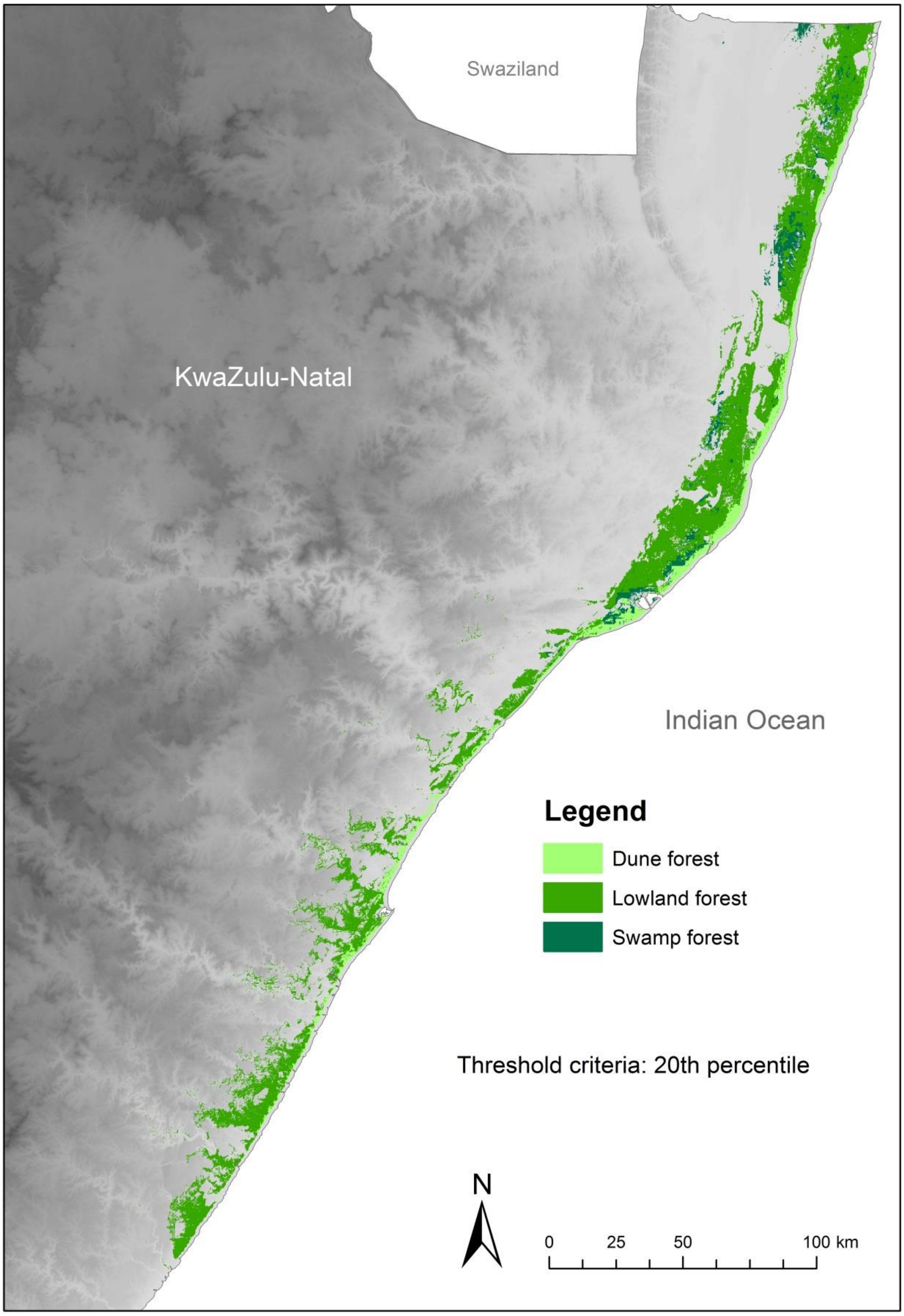
Swaziland
KwaZulu-Natal
Indian Ocean
Legend
Dune forest
Lowland forest
Swamp forest
Threshold criteria: 20th percentile
N
0
25
50
100 km

Figure S3.1e

Appendix S3.2

Table S3.2 - Forest dependent bird species that are categorized as threatened in South Africa. The reasons for their listing in South Africa and the IUCN Red List are also given. The South African conservation statuses only started following IUCN categories in 2000 – statuses before 2000 are therefore difficult to compare with those of the IUCN Red List. Information extracted from Siegfried *et al.*, (1976), Brooke, (1984), Barnes, (2000) and the IUCN Red list of Threatened Species (www.iucnredlist.org).

Common name	Scientific name	IUCN status	Reasons for IUCN listing (latest)	SA status	Reasons for SA listing (2000)	IUCN Population trend
African Broadbill	*Smithornis capensis*	2009: Least concern 2008: Least concern 2004: Least concern	- Large range and population size of >10 000 mature individuals	2000: Near-threatened 1984: Vulnerable 1974: Not listed	- Habitat destruction through dense human settlement and agriculture	Decreasing
African Crowned Eagle	*Stephanoaetus coronatus*	2012: Near-threatened 2009: Least concern 2008: Least concern 2004: Least concern	- Deforestation - Competition from humans for prey species - Direct persecution	2000: Near-threatened 1984: Not listed 1974: Not listed	- Range contractions through habitat destruction for commercial plantations - Direct persecution by stock farmers	Decreasing

Common name	Scientific name	IUCN status	Reasons for IUCN listing (latest)	SA status	Reasons for SA listing (2000)	IUCN Population trend
Black-throated Wattle-eye	*Platysteira peltata*	2009: Least concern 2008: Least concern 2004: Least concern	- Large range and population size of >10 000 mature individuals	2000: Near-threatened 1984: Indeterminate 1974: Peripheral	- Habitat destruction through dense human settlement and agriculture	Black-throated Wattle-eye
Eastern Bronze-naped Pigeon	*Columba delegorguei*	2009: Least concern 2008: Least concern 2004: Least concern	- Large range and population size of >10 000 mature individuals	2000: Vulnerable 1984: Indeterminate 1974: Rare	- Habitat loss through destruction and fragmentation of coastal forests - Selective removal of favoured tree species	Eastern Bronze-naped Pigeon
Bush Blackcap	*Lioptilus nigricapillus*	2008: Near-threatened 2004: Near-threatened	- Small population - Threatened by afforestation and habitat loss	2000: Near-threatened 1984: Not listed 1974: Not listed	Small range and low numbers	Decreasing
Knysna Woodpecker	*Campethera notata*	2008: Near-threatened 2004: Near-threatened	- Small population - Historical range contractions through forest clearance	2000: Near-threatened 1984: Not listed 1974: Not listed	- Small population sensitive to old growth removal - Range retraction through habitat destruction	Decreasing

Common name	Scientific name	IUCN status	Reasons for IUCN listing (latest)	SA status	Reasons for SA listing (2000)	IUCN Population trend
Neergaard's Sunbird	*Nectarinia neergaardi*	2008: Near-threatened 2004: Near-threatened 1988: Near-threatened	- Small population - Threatened by clearance of native forest habitats, commercial logging and afforestation with non-native tree species	2000: Near-threatened 1984: Rare 1974: Vulnerable	- Restricted range that have suffered habitat destruction and degradation	Decreasing
Pel's Fishing Owl	*Scotopelia peli*	2009: Least concern 2008: Least concern 2004: Least concern	- Large range and population size of >10 000 mature individuals	2000: Vulnerable 1984: Rare 1974: Rare	- Habitat loss and degradation of riverine vegetation - Reduction of water flow through commercial afforestation, water extraction and damming	Stable
Southern Banded Snake Eagle	*Circaetus fasciolatus*	2008: Near-threatened 2004: Near-threatened 1988: Near-threatened	- Small population - Threatened by habitat loss and degradation	2000: Vulnerable 1984: Rare 1974: Peripheral	- Habitat loss through destruction and fragmentation of coastal forests	Decreasing

Common name	Scientific name	IUCN status	Reasons for IUCN listing (latest)	SA status	Reasons for SA listing (2000)	IUCN Population trend
Spotted Ground-Thrush	*Zoothera guttata*	2008: Endangered 2006: Endangered 2004: Endangered 2000: Endangered 1996: Endangered 1994: Endangered	- Very small, fragmented population - Threatened by destruction and degradation of habitat	2000: Endangered 1984: Vulnerable 1974: Rare	- Extensive range reduction - Threatened by clearing and alteration of forests and mortalities associated with annual migrations	Decreasing
Woodwards' Batis	*Batis fratrum*	2009: Least concern 2008: Least concern 2004: Least concern 1988: Near-threatened	- Large range and population size of >10 000 mature individuals	2000: Near-threatened 1984: Indeterminate 1974: Rare	- Range retraction through habitat destruction	Decreasing

Chapter 4. Matrix habitat transformation disrupts assembly processes of tree and bird communities in coastal forest fragments

Publication Details

Olivier, P.I. & van Aarde, R.J. (2014) Matrix habitat transformation disrupts assembly processes of tree and bird communities in coastal forest fragments. *Diversity and Distributions*. In review.

ABSTRACT

Aim To determine how matrix habitats influence the variation in tree and bird species composition (beta diversity) and inferences on the processes that structure these communities.

Location Fragmented coastal forests in South Africa.

Methods We used a hierarchical, fractal-based sampling design to survey forests adjoined by transformed and natural matrices at two sampling scales. We investigated patterns of beta diversity by comparing the slopes of dissimilarity-distance relationships among forests adjoined by transformed and natural matrices. We then partitioned beta diversity into its turnover and nestedness components to test if matrix type influenced the proportion these components contribute to overall beta diversity. Finally, we used partial Mantel tests and variance partitioning to test if the relative contribution of niche- and dispersal-based assembly processes in structuring tree and bird communities varied in response to matrix type.

Results Estimates of forest tree and bird beta diversity were similar along natural and transformed matrices. Bird beta diversity was, however, consistently higher within matrix than forest habitats. For trees, the contribution of nestedness increased and community assembly became more random (i.e. dispersal-based) along transformed matrices. As a result, the structure of the bird community also became more random and less dependent on environmental factors (i.e. niche-based) than what was the case along natural matrices.

Main conclusions We found that matrix habitat transformation result in unstable, randomly assembled forest communities. These communities may be prone to invasions and possible collapse because of an adaptive response to changing living conditions that benefit habitat generalists, but impair specialists. The number of predicted extinctions inferred from conventional species-area relationships might therefore be underestimates in severely transformed landscapes, simply because the effects of landscape change on forest species stretch beyond those predicted from habitat loss alone. Our findings highlight the importance of including matrix habitats within conservation plans that focuses on forests.

Keywords: Beta diversity; dispersal-based assembly; extinction; landscape change; nestedness; niche-based assembly; spatial turnover; spillover.

INTRODUCTION

Worldwide, novel, human-dominated landscapes made up of remnant habitat fragments, agricultural plantations and human settlements are replacing natural ecosystems (Gardner *et al.*, 2009; Newbold *et al.*, 2014). The loss and fragmentation of habitat, coupled with the emergence of new human-modified habitats may not only influence species richness (i.e. estimates of alpha diversity) (e.g. Hill *et al.*, 2011; Pimm *et al.*, 2014), but also patterns of beta diversity (Dornelas *et al.*, 2014). Beta diversity describes the variation in species composition among sites and allows inferences on the processes that structure biological communities (Anderson *et al.*, 2011). Within fragmented landscapes, the size, shape and spatial arrangement of remaining habitats may influence estimates of beta diversity (e.g. Tscharntke *et al.*, 2002; Cook *et al.*, 2005). Beta diversity may, however, also be influenced by the structure and composition of the land cover surrounding habitat remnants (Jamoneau *et al.*, 2012). Yet, our understanding of the impacts of these so-called 'matrix habitats' on beta diversity is limited.

The effect of matrix habitats on fragment beta diversity may be a function of fragment versus matrix habitat contrast (Kupfer *et al.*, 2006; Driscoll *et al.*, 2013). For instance, low contrast matrices may provide supplementary resources and may therefore boost beta diversity within remaining habitat fragments through species spillover (see Tscharntke *et al.*, 2012 and references therein). In such instances, the influence of habitat fragmentation as a driver of landscape wide biodiversity losses can be overestimated which may have ecological implications for conservation planning (Tscharntke *et al.*, 2012). High contrast matrices, on the other hand, may result in the invasion of fragments by generalist species, thereby homogenizing fragment communities and lowering beta diversity (e.g. Chabrerie *et al.*, 2013; Maron *et al.*, 2013). For instance, a study on Costa Rican birds found that intensive agriculture decreased bird beta diversity at large spatial scales, thereby disrupting ecological processes critical for maintaining biological diversity (Karp *et al.*, 2012).

If beta diversity patterns vary in response to matrix habitat types, we may also expect the processes inferred from these patterns to vary. By decomposing beta diversity into estimates of nestedness and spatial turnover, we may make some inferences about the processes that drive these patterns (e.g. Baselga, 2010). 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). High levels of nestedness may therefore suggest selective extinctions and colonisations among sites due to differences in area, isolation or matrix habitat types (Wang *et al.*, 2010). Conversely, spatial turnover indicate the replacement of species at one site in response to changing environmental conditions or spatially constrained dispersal (Gaston & Blackburn, 2000). The correlation between spatial turnover and environmental or geographical distance are in many instances used to infer the relative contributions of niche- and dispersal-based community assembly processes in structuring communities (e.g. Tuomisto *et al.*, 2003; Chase & Myers, 2011). However, habitat fragmentation may alter the relative importance of niche- and dispersal-based assembly processes and the spatial scales at which they act (Jamoneau *et al.*, 2012). Finding out whether niche- or dispersal-based assembly processes control community composition is important because if these processes differ across taxa and landscapes, conservation efforts that focus on maintaining them will also have to differ (Olivier & van Aarde, 2014).

In this study, we investigate the influence of high and low contrast matrix habitats on forest bird and tree beta diversity and inferred community assembly processes within a coastal forest landscape mosaic in South Africa. We focused on tree and bird communities because they represent two taxa with distinctly different life history and dispersal strategies. As a result, we may expect different responses to matrix habitat transformation. Furthermore, trees and birds within forest fragments are also likely to interact to some degree (e.g. Lenz *et al.*, 2011; Neuschulz *et al.*, 2011). By studying trees and birds, we were therefore also able to asses if the structure of the surrounding matrix influences such interactions. Studies investigating matrix effects typically sample across forest edges using transects running perpendicular to the border. However, such an approach may not be suitable when studying beta diversity, simply because there may be an almost complete species turnover across the forest edge as the community of the matrix replace the community of the forest (Marsh, 2013). We therefore surveyed transects that ran parallel to the forest edge and at different distances from the edge within the forest and matrix interiors. Coastal forests in South Africa are well suited to such as sampling design because they are limited to a narrow, linear strip of ancient sand dunes almost perfectly aligned to the Indian Ocean coastline (Eeley *et al.*, 1999). Inferences from beta diversity are furthermore dependent on sampling grain (Olivier & van Aarde, 2014). Whether one infer niche- or dispersal-based assembly as the main process structuring communities may therefore be a function of sampling scale, rather than ecological reality.We therefore used a fractal sampling design (see Marsh & Ewers, 2013), which allowed us to sample at more than one spatial scale. As a result, we could test whether inferences about assembly processes are robust to alternative scale choices.

To estimate beta diversity we modelled changes in the dissimilarity-distance decay relationship within bird and tree communities. When habitats that adjoin coastal forests are natural (low contrast matrices), spillover of matrix species may increase beta diversity. However, if transformed habitats (high contrast matrices) adjoin coastal forests, the prevalence of disturbance-adapted species may homogenize forest communities and lower beta diversity. We therefore hypothesize that beta diversity will be higher when forest fragments are adjoined by natural habitats, but lower when forests are adjoined by transformed habitats (H1). The transformation of matrix habitats may also lead to the loss of forest specialist species (e.g. Deikumah *et al.*, 2014), thereby possibly causing assemblages to become more nested. We therefore hypothesize that the contribution of nestedness to overall beta diversity will be greater when forests are adjoined by transformed habitats than when they are adjoined by natural habitats (H2). Habitat transformation may furthermore disrupt niche processes and make species assemblages more random than expected (e.g. Jamoneau *et al.*, 2012). As a result, we hypothesized that niche-based assembly mechanisms will explain most of the variation in beta diversity in forests adjacent to natural habitats, while dispersal-based assembly mechanisms will explain most of the variation in forests adjacent to transformed habitats (H3). Finally, we used an indicator species analysis to determine species-specific responses to habitat transformation and conclude with recommendations to protect species diversity in coastal forests and the surrounding habitats.

METHODS

Study region

Coastal forests occur within the Maputaland-Pondoland-Albany biodiversity hotspot (Küper *et al.*, 2004) as well as the Maputaland Centre of Plant Endemism (van Wyk & Smith, 2000). They also form part of two critically endangered eco-regions, the Maputaland Coastal Forest Mosaic and the KwaZulu-Cape Coastal Forest Mosaic (Burgess *et al.*, 2004), which highlight their importance in supporting regional diversity (also see van Aarde *et al.*, 2014). However, as much as 82% of forests may have been lost through land-use changes driven by humans, thereby causing coastal forests to harbour an extinction debt (Olivier *et al.*, 2013).

Coastal forests are limited in extent and occur mainly on calcareous sand dunes formed by deposits left by the regression of the Indian Ocean after the last glacial maximum (18 000 BP) (Eeley *et al.*, 1999). Fragments are therefore long (range = 3.7 – 82 km) and narrow (range = 0.3 – 2.1 km) and resemble a peninsula stretching down from the mainland tropics surrounded by an ‘ocean’ of mixed habitat and land-use types (Visser *et al.*, 2014). At the time of the study, these included sugarcane and agroforestry plantations, rural and urban settlements and/or natural grasslands and woodlands. Our survey sites were located within and adjacent to nine of these forests fragments (range = 2.1 – 87.3 km^2) situated along approximately 300 kilometres of coastline between the Tugela river mouth in the south (S -

29.2268°; E 32.8578°) and Lake Kosi in the north (S -27.0019°; E 32.8578°) (Fig. 1). We surveyed sites during the summers (November-March) of 2011, 2012 and 2013.

Sampling design

We sampled tree and bird communities using a sampling pattern based upon a fractal series of equilateral triangles created explicitly for investigating beta diversity (Marsh & Ewers, 2013). Our sampling hierarchy consisted of two sampling grains (fine and coarse) that each comprised a number of aggregated sampling units. Three tree-sampling plots were located on the apices of an equilateral triangle with sides 564m. Given that coastal forest fragments are particularly narrow, this resulted in one tree plot near the forest edge, one plot in the forest interior and one plot along the forest-ocean edge. We then surveyed three bird points around each tree plot. These bird points were arranged as an equilateral triangle with sides 178m. For our analysis, we summed these three bird points and linked them to each tree survey plot. We replicated this survey design within the matrix habitat directly adjacent to each forest fragment, i.e. we arranged bird survey points as equilateral triangles with sides 178m and with a survey point located on each apex. However, we did not survey any tree plots in the adjacent matrix. Based on this survey design we had six bird, and three tree transects that ran parallel to the forest edge and the Indian Ocean. For birds we had three transects in the matrix (matrix hinterland (MH), matrix interior (MI) and matrix edge (ME)) and three transects in the forest (forest edge (FE), forest interior (FI) and forest-ocean edge (FOE)). For trees we only had three transects in the forest (forest edge (FE), forest interior (FI) and forest-ocean edge (FOE)) and none in the adjacent matrix. Transects were located within coastal forests adjoined by transformed matrices (high contrast - sugarcane and agroforestry plantations, rural settlements) and natural matrices (low contrast - grasslands and woodlands). These tree plots and bird points represented the fine sampling scale. The sum of the three tree plots and the sum of the nine bird survey points (arranged as three equilateral triangles) represented the coarse sampling scale. We therefore had two transects for birds (matrix and forests) and one transect for trees (forest) at the coarse sampling scale within forests adjoined by transformed and natural habitat matrices (Fig. 4.1).

Tree censuses and bird surveys

We recorded trees in 103 16m x 16m plots while birds were surveyed using point counts at 342 points (Bibby *et al.*, 2000). We surveyed bird points between 04.00 h and 09.00 h. Each observer surveyed 4-9 points per day depending on habitat type. To reduce potential observer bias, observers 'shared' transect fractals, in other words, observes rotated among surveying the edge, interior and forest-ocean fractals. We allowed for a two-minute period for birds that may have been disturbed on arrival at the survey point to resettle and thereafter recorded birds for 10 minutes. For each encounter, we estimated distances from the observer to the bird using a digital rangefinder (Nikon Laser 550As, Tokyo, Japan). We recorded all birds seen and heard, but excluded largely aerial species such as swifts and swallows as well as birds that flew above the forest canopy. We also did not survey points during rain or windy conditions. For trees, we measured the diameter at breast height (DBH) for every individual tree ≥30cm tall, and identified the individual to species level. Surveyors were trained in, and had prior experience of, local tree and bird identification.

Data analysis

Beta diversity

We used the Sørensen dissimilarity index (β_{sor}) to test if beta diversity is higher when natural matrices, as opposed to transformed matrices, adjoined forest fragments. We calculated pair-wise dissimilarities for each transect and evaluated how the slopes and intercepts of the distance decay relationship for β_{sor} varied from the matrix to the forest interiors at fine and coarse sampling scales. This method is equivalent to the distance-decay of similarity proposed by Nekola & White (1999) where regressions of compositional dissimilarities against geographical distance estimate rates of distance decay. We measured geographic distances as the minimum straight-line distance between sampling units of each transect using the Haversine formula. This formula takes into account the spherical shape of the earth when calculating the distance between two points (Sinnott, 1984). To account for the inherent dependence of the dissimilarity values, we computed the significance of the Pearson correlations by means of Mantel permutation tests (999 permutations). To test for differences in intercepts and slopes among transects located in forests adjoined by transformed matrices and forests adjoined by natural matrices we compared the linear and quadratic terms of the regression lines between β_{sor} using an analysis of covariance (ANCOVA) (Zar, 1984) in the software program Graphpad Prism 5.00 (GraphPad Software, San Diego California USA, www.graphpad.com).

To determine the contribution of nestedness and spatial turnover to overall beta diversity we partitioned β_{sor} into contributions by turnover (Simpson dissimilarity, β_{sim}; Lennon *et al.*, 2001) and nestedness-driven dissimilarity (β_{nes}) following the approach suggested by Baselga (2010). This approach relies on the fact that Sørensen and Simpson dissimilarities are equal in the absence of nestedness, so their difference is a measure of the nestedness component of beta diversity (Baselga, 2010). We recognise that the most appropriate way to decompose beta diversity is currently debated (see Podani & Schmera, 2011; Baselga, 2012; Carvalho *et al.*, 2013; Legendre, 2014), but this issue was beyond the scope of our analyses. We performed an analysis of biotic dissimilarity with geographic distances (as described above and following Nekola & White, 1999) using β_{sim} and β_{nes} as measures of dissimilarity. We used a Mantel test with 999 permutations to assess the significance of the relationship between dissimilarity (β_{sim} and β_{nes}) and distance. We then used ANCOVA’s to test for significant differences in the intercepts and slopes of β_{sim} and β_{nes} among transects in forests adjoined by natural matrix habitats and those adjoined by transformed matrix habitats. We also used ANCOVA’s to test if the relative contribution of β_{sim} and β_{nes} to β_{sor} differed significantly between transects located in transformed matrices and adjacent forests compared to those located in natural matrices and adjacent forests. We repeated the same analytical procedures at each sampling scale.

Niche- and dispersal-based community assembly

We used partial Mantel tests to model the individual effects of variables representing niche- and dispersal-based assembly processes on bird and tree species composition. We did this for each transect (e.g. forest edge, forest interior and forest-ocean edge) when forests were adjoined by natural and transformed matrices and at each sampling scale. For birds, tree community composition was the only environmental variable and represented niche-based community assembly. For trees, a habitat suitability modelling exercise showed that median rainfall in winter, minimum relative humidity in winter, annual mean plant available water and elevation explained 90% of the probability of coastal forest occurrence (for details on the methodology see Olivier *et al.*, 2013). We therefore assembled digital maps of these four variables (Schulze, 2006), and used these as environmental variables associated with tree community composition. Maps were 200m x 200m raster (grid cell) layers and covered the distribution of coastal forests in the study area. We extracted the mean raster value of each variable for each fragment in ArcGIS 10.0 (ESRI, 2011). Because sampling scales overlapped with more than one grid cell at the coarse sampling scale, we calculated the mean value of the overlapping grid cells. To reduce the dimensionality and avoid likely problems of colinearity between these potentially correlated variables we used principal components analysis (PCA). The first two components accounted for 98% and 86% of environmental variation at fine and coarse sampling scales respectively and were retained for analysis.

Elevation explained most of the variability of principal component axis one (PCA1) , while median rainfall in winter, minimum relative humidity in winter and mean annual plant available water explained most of the variability of principal component axis two (PCA2). For both trees and birds, geographic distances among sampling points represented the spatial component of beta diversity i.e. the variation explained by the geographic distance between sites was taken as evidence of dispersal-based community assembly.

To evaluate the relative importance of environmental predictors and spatial factors in explaining variation in beta diversity components we used hierarchical partitioning (Chevan & Sutherland, 1991). This method decomposes the R^2 of the regressions between β_{sor} and the environmental and spatial variables for birds and trees along each transect. The analysis then splits the variation explained by each variable into a joint effect together with the other explanatory variables and into an independent effect not shared with any other variable. The estimated relative importance of each variable is represented by the size of its pure effect.

Species and functional groups

We conducted a compositional indicator species analysis to identify which species characterize each bird and tree transect in natural and transformed matrices at fine and coarse sampling scales. Indicator species analysis permits statistically rigorous assessments of which species characterize a given ecosystem (Bakker, 2008). Unless stated otherwise, all analysis were done in R (R Development Core Team, 2012) using the packages vegan 2.0-4 (Oksanen *et al.*, 2007), betapart version 1.2 (Baselga & Orme, 2012), hier.part version 1.0-4 (Walsh & Mac Nally, 2007) and indispecies version 1.7.1 (De Caceres & Jansen, 2013).

RESULTS

Within coastal forests, we identified 74 bird species from 2584 records and 171-point counts. The adjacent matrix habitats yielded 121 bird species from 1694 records and 171-point counts. For trees we collected 10 548 records of 140 species from 57 survey plots.

Patterns of beta diversity

Levels of bird beta diversity were similar within forest fragments adjoined by natural or transformed matrices at fine and coarse sampling scales (Fig. 4.2). Slopes of the distance decay relationship in forests adjoined by transformed matrices were also similar to those adjoined by natural matrices. For instance, we only recorded significant differences at fine scales for β_{sim} and β_{nes} at the ocean-forest edge and none at coarse scales (Fig. 4.2). This suggests that matrix transformation did not influence patterns of bird beta diversity within coastal forests. Estimates of bird β_{sor} were, however, lower within forests than matrix habitats, irrespective of whether matrices were natural or transformed (Fig. 4.3). This was particularly true for forest edges, where beta diversity was low along the forest edge but high along the matrix-forest edge.

Levels of tree beta diversity were also similar within forest fragments adjoined by natural or transformed matrices at fine and coarse sampling scales (Fig. 4.2). However, differences among the slopes of the distance decay relationships suggest that matrix habitat type may influence patterns of tree beta diversity. We recorded significant differences between the slopes of the distance decay relationship for β_{sor} and β_{sim} in forests adjoined by transformed matrices compared to forests adjoined by natural matrices at fine and coarse sampling scales (Fig. 4.2). Estimates of β_{sor} and β_{sim} increased significantly with geographic distance when matrices were transformed, but less so when they were natural (Fig. 4.2). The slopes of the distance decay relationship for β_{nes} only differed between transformed and natural matrices along forest edges (Fig. 4.2).

Nestedness and species turnover

Species turnover (β_{sim}) drove the observed patterns in bird β_{sor} at fine and coarse scales. Estimates of β_{sim} were high within matrix habitats, but lower within forests, especially at the forest edge (Fig. 4.3). Although the contribution of nestedness (β_{nes}) to β_{sor} remained consistently small, it did increase when matrix habitats were transformed (Fig. 4.3) (range % β_{nes} natural habitats = 7.6% - 15.8%; range % β_{nes} transformed habitats = 9.1% - 25.0%).

For trees, we recorded similar patterns with β_{sim} dominating estimates of β_{sor}. However, the contribution β_{nes} increased markedly towards the forest edge when forests were adjoined by transformed matrices (range % β_{nes}= 16 - 33%) but less so when forests were adjoined by natural matrices (range % β_{nes}= 8 - 19%). The contribution of β_{nes} made up a third (33%) of β_{sor} along transformed forest edges.

Niche- and dispersal-based assembly

Partial Mantel tests revealed contrasting results among transects located within forests adjacent to natural matrices compared to those located adjacent to transformed matrices. At coarse scales, bird species composition was significantly associated with tree species composition in forests adjacent natural matrices. However, when matrix habitats were transformed this association was disrupted, and bird species composition was not associated with tree species composition. At fine scales, we recorded a similar effect along forest edges (Table 4.1).

Trees had a significant positive association with PCA1 and PCA2 when natural and transformed matrices adjoined forest fragments. However, when we controlled for geographic distance, the significance of this relationship disappeared. At fine scales, trees had a significant association with geographic distance at the forest edge, forest interior and forest-ocean edge only when matrices were transformed.

Variance partitioning indicated that when natural matrices surround forest fragments, tree species composition explain most of the variation in the bird community. However, when transformed matrices adjoin forest fragments, geographic distance explained a greater proportion of the variance i.e. bird community assembly became more random (Table 4.2). This was the case at fine and coarse sampling scales. A similar pattern emerged for the factors underlying tree community assembly. At the coarse sampling scale, the environmental variables PCA1 and PCA2 explained most of the variation in the tree community when natural matrices forests adjoined forests. However, when transformed matrices adjoined forests, geographic distance explained most of the variation. We recorded the same effect at fine sampling scales, with the exception of the forest interior. Here geographic distance explained most of the variation in tree community composition irrespective of whether natural or transformed matrices adjoined forests. We present a summary of all our results in Appendix S4.1 of the Supporting Information.

Indicator species

Four bird species had significant indicator values for forests adjacent to natural matrix habitats. Woodward’s batis *Batis fratrum*, Livingstone’s turaco *Tauraco livingstonii*, and the brown scrub-robin *Erythropygia signata* are forest dependent specialists, while the eastern nicator *Nicator gularis* is an insectivore closely associated with forests and woodlands in the region. None of these species had significant indicator values along transformed matrices. Along transformed matrices only two forest-associated species, the olive sunbird *Nectarinia olivacea* and purple-crested turaco *Gallirex porphyreolophus* had significant indicator values.

A similar pattern emerged at fine scales where six bird species were associated with natural forest edges but none along transformed forest edges. These also included forest-dependent species such as Woodward's batis, terrestrial brownbul *Phyllastrephus terrestris*, Livingstone's turaco and the endemic Rudd's apalis *Apalis ruddi*.

Within matrix habitats, three and two bird species had significant indicator values in natural and transformed matrices respectively. These were all habitat generalists. However, one forest-dependent specialist, the yellow-bellied greenbul *Chlorocichla flaviventris*, and three forest-associated generalists (black-backed puffback *Dryoscopus cubla*, southern boubou *Laniarius ferrugineus* and the red-eyed dove *Streptopelia semitorquata*) were significantly associated with matrix forest edges when the matrix was natural. The only significant indicator species along matrix edges in transformed habitats was the yellow-fronted canary *Crithagra mozambicus*, a matrix generalist.

For trees, indicator species when matrix habitats were natural mostly included large forest canopy trees such as *Euclea natalensis*, *Diospyros natalensis*, *Diospyros inhacaensis*, *Dovalis longispina* and *Tricalysia sonderiana* as well as large canopy trees such as *Strychnos gerrardii* normally associated with the savannahs of the hinterland. Indicator species of forests adjacent to transformed habitats included forest pioneers such as *Celtis africana*, *Allophylus natalensis* and *Cordia caffra* as well as climbers such as *Rhoicissus rhomboidea* and *Grewia caffra*. Differences in indicator species among forests adjacent natural habitats versus forests adjacent transformed habitats were most pronounced along forest edges. We present a list of the bird and tree species characteristic of each habitat transect in Appendix S4.2 of the Supporting Information.

DISCUSSION

The relentless transformation of natural habitats globally makes it increasingly important to understand how transformed habitats influences diversity within remaining habitat fragments. Our results suggest that although forest beta diversity did not decrease significantly when matrix habitats were transformed, matrix habitat transformation did disrupt community assembly processes within forest bird and tree communities. We recorded this effect at coarse and fine sampling scales. At fine sampling scales, however, this effect was strongest along forest edges. These findings suggest that the effect of landscape change on coastal forest tree and bird species may stretch well beyond habitat loss and elicit an adaptive response of assemblages to changing living conditions that may benefit habitat generalists, but impair specialists.

The similar, low levels of beta diversity within forests adjoined by transformed or natural matrices suggest that matrix species do not spillover into forests, irrespective of whether the matrix is transformed or natural. However, the high levels of beta diversity in the matrix, especially along forest matrix edges, indicate spillover of forests species into the adjacent matrix habitats. Such spillover of forest habitat opportunists may boost bird diversity within adjacent matrix habitats and contribute to ecological functions (Blitzer *et al.*, 2013). For instance, Lenz *et al.*, (2011) showed that trumpeter hornbills *Bycanistes bucinator*, the largest frugivores in our study area, regularly move between forest fragments and large fruiting trees in agricultural areas, thereby dispersing seeds over large distances and among patches of suitable habitat. Forest fragments may therefore function as species rich sources that spread forest species into the surrounding habitat types. By doing so, these forests may play an important role in maintaining regional diversity and ecological function across the landscape mosaic. However, our results also suggest that when matrix habitats are transformed spillover may become infrequent and sporadic. For instance, bird communities along natural matrix forest edges shifted from one dominated by forest-associated frugivores to one dominated by matrix generalists along transformed edges. The transformation of matrix habitats may therefore disrupt spillover and dispersal among fragments, thereby essentially isolating forest fragments. Such isolation could have implications for metapopulation and metacommunity dynamics (e.g. Vandermeer & Carvajal, 2001), functional richness (e.g. Barbaro *et al.*, 2014) and the persistence of forest communities (e.g. Boscolo & Metzger, 2011).

Although our results suggest that matrix species do not spillover into forests, the altered biotic and abiotic environmental conditions associated with transformed matrices may influence tree community composition by limiting seed dispersal, seedling recruitment, growth and survival in adjacent forest fragments (Lawes *et al.*, 2007; Lôbo *et al.*, 2011; Tabarelli *et al.*, 2012; Arroyo-Rodríguez *et al.*, 2013). The transformation of the matrix exposes the coastal forest edge to altered microclimatic fluxes (e.g. light, heat, moisture and wind), which could lead to hotter drier conditions than previously experienced (e.g. Mesquita *et al.*, 1999; Weathers *et al.*, 2001). This may cause an increase in invasive plant species, disturbance-favouring early successional trees and climbers, coupled with a correlated decline of old-growth trees (e.g. Laurance *et al.*, 2006). The disappearance of species with large seeds that are shade tolerant could explain why we recorded high levels of nestedness in forests that adjoined transformed matrices, specifically at the forest edge. Changes in environmental conditions that cause an increase in generalists at the expense of forest specialists may furthermore cause tree community assembly to become more random or ‘hyperdynamic’ (e.g. Laurance, 2002), as indicated by our finding that spatial factors (i.e. dispersal-based assembly) seem to structure tree communities’ adjacent transformed matrices. Conversely, environmental factors (i.e. niche-based assembly) seem to structure tree community assembly along natural matrices. This may be because natural matrix habitats such as grasslands and woodlands buffer forest tree communities from altered environmental conditions near the forest edge by forming a natural ecotone. Such an ecotone may protect forest species from the deleterious effects associated with high contrast habitat edges and may be the reason why large forest trees persist, even along forest edges.

The disappearance of large fruiting trees and the dominance of forest pioneers on edges may also have direct impacts on the bird community, leading to less specialized and more robust plant-bird networks (e.g. Menke *et al.,* 2012). Our results suggest that the transformation of matrix habitats disrupts the natural association between forest bird and tree communities. This is probably because of an increase of generalist bird species and the concurrent decline of forest specialists in response to compositional changes in the tree community. As the tree community shifts from one dominated by large canopy trees (e.g. *Diospyros inhacensis*, *Diospyros natalensis*) to one dominated by pioneers (e.g. *Acacia karroo*, *Celtis africana*) forest specialists such as Livingstone's turaco disappear while generalist species such as purple-crested turaco's flourish. Because of this cascade effect, the structure of the bird community becomes more random and less dependent on environmental factors, similar to what we recorded for trees. This may lead to an unstable bird community that are prone to invasions and eventual collapse. For instance, Mac Nally *et al.*, (2014) suggest that land-use changes across northeastern Australia result in the proliferation of a despotic native species, the yellow-throated miner *Manorina flavigula*, which may cause the collapse of bird assemblages in remaining forests. The transformation of matrix habitats may therefore have a profound influence on forest communities – so much so that deterministic extinctions predicted by conventional species-area relationships may well be underestimates in severely transformed landscapes (see also Koh & Ghazoul, 2010 and Jamoneau *et al.*, 2012).

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). Such an approach might not be successful in preventing the extinctions we predicted in a previous contribution (Olivier *et al.*, 2013), specifically because forest species seem to utilize the ever changing array of grasslands, bush-lands and woodlands that surround coastal forest fragments. Here multi-habitat dependency may have evolved in response to these forests being fragmented for a considerable time, shaped by thousands of years of climate change, fire and human activities (Bond *et al.,* 2003). We therefore suggest that a landscape complementation approach (e.g. Dunning *et al.*, 1992), which includes matrix habitats adjacent forest fragments, may be our best bet to prevent predicted extinctions in the coastal forest landscape mosaic. Furthermore, by including matrix habitats within restoration plans that focus on these forests the risk of restoration failure may be reduced (e.g. Grainger *et al.*, 2011). Matrix habitats such as grasslands and/or woodlands may buffer forest communities from impacts associated with a high contrast matrix forest boundary (e.g. Kennedy *et al.,* 2010), and provide important linkages between forest fragments which may lessen the effects of forest fragmentation (e.g. Guldemond & van Aarde, 2010). Such an approach may also encourage spillover of bird species across forest and matrix boundaries. Spillover could enhance natural plant regeneration, contribute to a rapid re-establishment of coastal forest communities in degraded forests and adjacent matrix habitats, boost regional diversity and allow coastal forests to track environmental change under changing climatic conditions.

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TABLES

Table 4.1. Results from Mantel (white cells) and partial Mantel (grey cells) tests between bird β_{sor} and distance matrices of geographic distance and tree species dissimilarity (β_{sor}). Also shown are the results of tree β_{sor} and distance matrices of geographic distance, PCA1 and PCA2. PCA1 and PCA2 represent the two axes of a principal component analysis that included four environmental variables: median rainfall in winter, minimum relative humidity in winter, mean annual plant available water and elevation.

	Fine scale						Coarse scale	
	Forest edge		Forest interior		Forest ocean edge		Forest fragment	
	Natural	Transformed	Natural	Transformed	Natural	Transformed	Natural	Transformed
Birds								
Geographic distance	-0.10	0.23	0.02	0. 39*	0.10	0.49*	0.04	0.25
Tree community	0.55**	0.21	0.10	0.31	-0.12	0.55*	0.35*	0.31
Tree community /Geographic distance	0.56**	0.10	0.10	0.11	-0.15	0.34*	0.36*	0.19
Trees								
Geographic distance	0.07	0.61*	0.12	0.62*	0.23*	0.70*	0.35*	0.80*
PCA1	0.09	-0.13	-0.02	-0.17	0.19	-0.13	0.33*	0.45
PCA2	0.19	-0.55	0.04	-0.58	0.43**	-0.43	0.37*	0.41
Geographic distance /PCA1/PCA2	0.11	0.11	-0.20	-0.02	0.12	0.10	0.24	0.26

Table 4.2. Results from the hierarchical partitioning of variation for forest trees and birds at fine and coarse sampling scales along natural and transformed matrices. The proportion of variance in beta diversity explained by each variable were categorised as representing either niche-based or dispersal-based assembly processes. Geographic distance represented dispersal-based assembly for birds and trees respectively. Niche-based assembly is represented by tree community composition for birds and principal component axis one (PCA1) and principal component axis two (PCA2) for trees.

	Fine scale						Coarse scale	
	Forest edge		Forest interior		Forest ocean edge		Forest fragment	
	Natural	Transformed	Natural	Transformed	Natural	Transformed	Natural	Transformed
Birds								
Geographic distance – dispersal-based assembly	3.98	59.49	0.12	81.50	24.24	53.80	3.65	32.55
Tree community – niche-based assembly	96.02	40.51	99.88	18.50	75.75	46.20	96.35	67.55
Trees								
Geographic distance – dispersal-based assembly	7.13	52.61	84.68	54.39	12.55	63.35	26.65	56.73
PCA1 – niche-based assembly	19.16	4.47	7.12	10.19	0.54	7.84	24.98	21.27
PCA2 – niche-based assembly	73.71	42.92	8.20	35.42	86.90	28.80	48.36	22.00

FIGURES

Figure 4.1 - The study area along the north-east coast of South Africa showing our survey sites (black triangles) located within nine coastal forest fragments along approximately 300km of coastline. b) A schematic representation of our sampling design. Black circles represent bird survey points, which were located on the vertices of equilateral triangles with sides of length 178m. White squares represent tree survey plots that were located on the vertices of equilateral triangles with sides of length 564m. c) A schematic representation of our survey design that included six bird and three tree transects that ran parallel to the forest edge and the Indian Ocean at fine scales: MH (Matrix hinterland), MI (Matrix interior), ME (Matrix edge), FE (Forest edge), FI (Forest interior) and FOE (Forest ocean-edge). At coarse sampling scales one bird and one tree transect was located within forest habitats, as well as an additional bird transect within the adjacent matrix habitat.

Figure 4.2 – Relationship between bird and tree dissimilarity and geographic distance. B_{sor}, β_{sim}, and β_{nes} were used as measures of dissimilarity. A Mantel test with 999 permutations was applied to assess the significance of the Pearson correlation coefficient (r): *$P<0.05$. P-values refer to the results of an ANCOVA, which tested for significant differences among the slopes of transects located within forests adjoined by transformed and natural matrices. Grey lines represent forests adjoined by natural matrices and black lines represent forests adjoined by transformed matrices. Solid lines represent trees and broken lines represent birds. ns. = not significant.

Figure 4.3 – Estimates of tree and bird beta diversity for forests adjoined by natural and transformed matrices at fine and coarse sampling scales. Also shown is estimates bird beta diversity within natural and transformed matrices. The contribution of turnover (β_{sim}) and nestedness (β_{nes}) to overall beta diversity is reported for each transect. Grey bars represent

forests adjoined by natural matrices and black bars represent forests adjoined by transformed matrices.

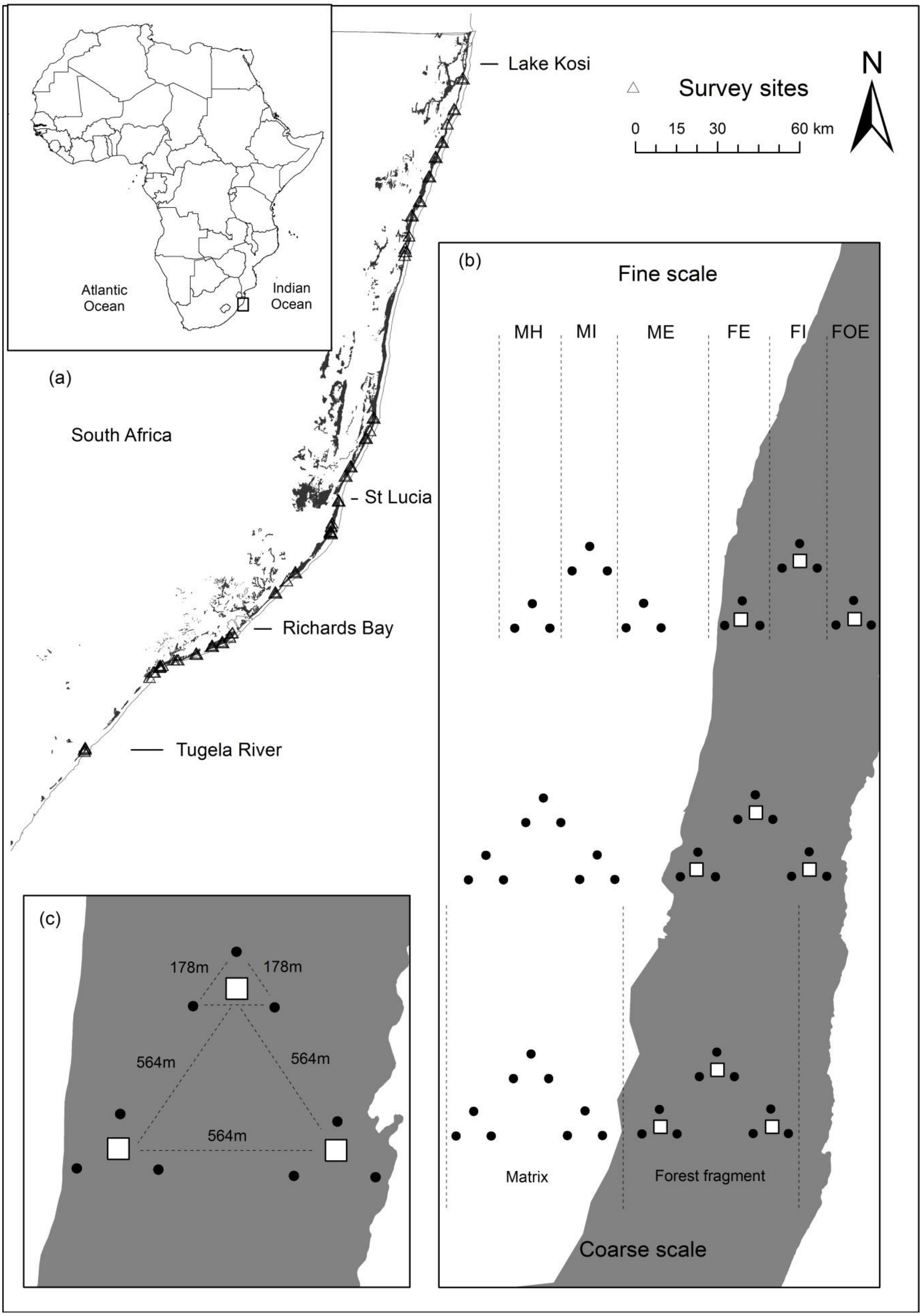
Atlantic
Ocean
Indian
Ocean
(a)
South Africa
Lake Kosi
Survey sites
0 15 30 60 km
N
St Lucia
Richards Bay
Tugela River
(b)
Fine scale
MH
MI
ME
FE
FI
FOE
Matrix
Forest fragment
Coarse scale
(c)
178m
178m
564m
564m
564m

Figure 4.1.

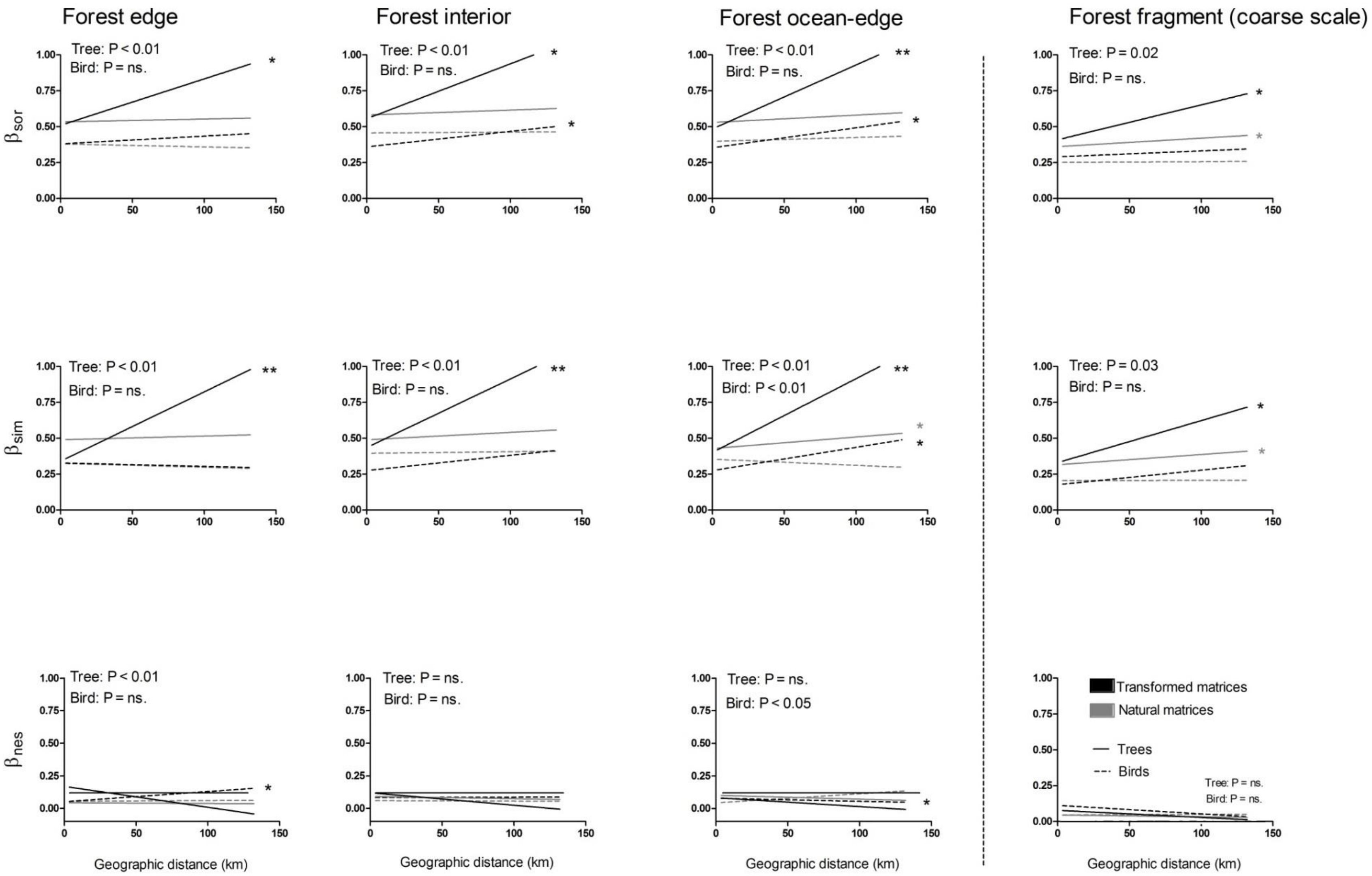
Forest edge
Forest interior
Forest ocean-edge
Forest fragment (coarse scale)
βsor
Tree: P < 0.01
Bird: P = ns.
*
Tree: P < 0.01
Bird: P = ns.
*
*
Tree: P < 0.01
Bird: P = ns.
**
*
Tree: P = 0.02
Bird: P = ns.
*
*
βsim
Tree: P < 0.01
Bird: P = ns.
**
Tree: P < 0.01
Bird: P = ns.
**
Tree: P < 0.01
Bird: P < 0.01
**
*
*
Tree: P = 0.03
Bird: P = ns.
*
*
βnes
Tree: P < 0.01
Bird: P = ns.
*
Tree: P = ns.
Bird: P = ns.
Tree: P = ns.
Bird: P < 0.05
*
Tree: P = ns.
Bird: P = ns.
Transformed matrices
Natural matrices
Trees
Birds
0.00
0.25
0.50
0.75
1.00
0
50
100
150
Geographic distance (km)

Figure 4.2.

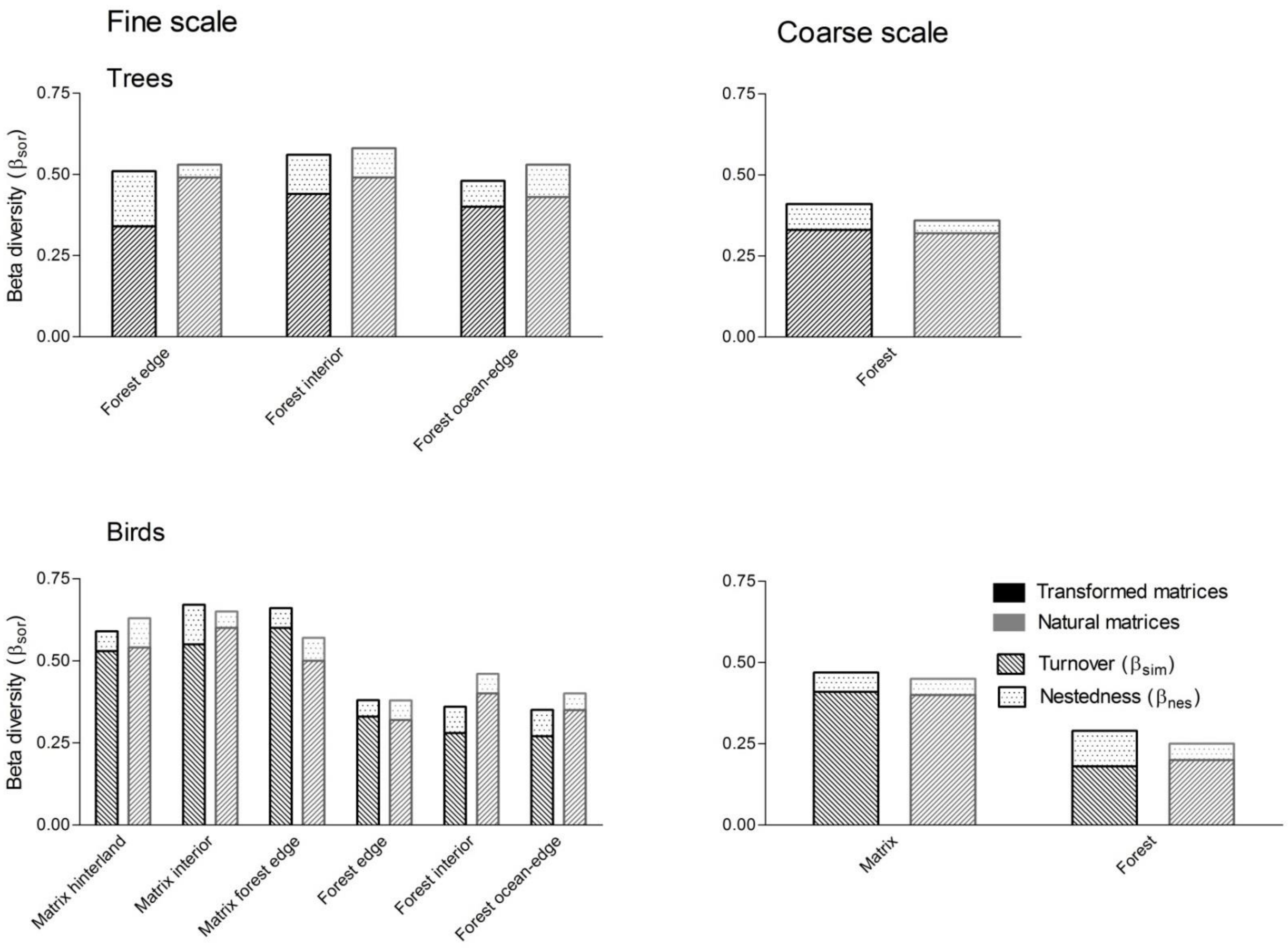
Fine scale
Trees
Coarse scale
Beta diversity (β_{sor})
0.75
0.50
0.25
0.00
Forest edge
Forest interior
Forest ocean-edge
Forest
Birds
Matrix hinterland
Matrix interior
Matrix forest edge
Matrix
Transformed matrices
Natural matrices
Turnover (β_{sim})
Nestedness (β_{nes})

Figure 4.3.

SUPPORTING INFORMATION

Appendix S4.1 - A summary of our results showing the three hypotheses tested in the study and the support, or lack thereof, recorded for each.

Appendix S4.2 – Indicator species characterizing bird and tree communities at different distances from the forest edge at fine and coarse sampling scales.

Appendix S4.1.

Table S4.1. A summary of our results showing the three hypotheses tested in the study and the support, or lack thereof, recorded for each. (Int. = Forest interior transect, Ocean = Forest ocean-edge transect).

		Birds							Trees						
		Natural			Transformed			Support	Natural			Transformed			Support
H1: Beta diversity will be higher when forest fragments are adjoined by natural habitats, but lower when forests are adjoined by transformed habitats	Coarse scale	$B_{sor} = 0.25$ $B_{sim} = 0.20$ $B_{nes} = 0.05$			$B_{sor} = 0.29$ $B_{sim} = 0.18$ $B_{nes} = 0.11$			No	$B_{sor} = 0.36$ $B_{sim} = 0.32$ $B_{nes} = 0.04$			$B_{sor} = 0.41$ $B_{sim} = 0.33$ $B_{nes} = 0.08$			No
	Fine scale	Edge	Int.	Ocean	Edge	Int.	Ocean		Edge	Int.	Ocean	Edge	Int.	Ocean	
		$B_{sor}=0.38$ $B_{sim}=0.32$ $B_{nes}=0.06$	$B_{sor}=0.46$ $B_{sim}=0.40$ $B_{nes}=0.06$	$B_{sor}=0.40$ $B_{sim}=0.35$ $B_{nes}=0.05$	$B_{sor}=0.38$ $B_{sim}=0.33$ $B_{nes}=0.05$	$B_{sor}=0.36$ $B_{sim}=0.28$ $B_{nes}=0.08$	$B_{sor}=0.35$ $B_{sim}=0.27$ $B_{nes}=0.08$	Yes	$B_{sor}=0.53$ $B_{sim}=0.49$ $B_{nes}=0.04$	$B_{sor}=0.58$ $B_{sim}=0.49$ $B_{nes}=0.09$	$B_{sor}=0.53$ $B_{sim}=0.43$ $B_{nes}=0.10$	$B_{sor}=0.51$ $B_{sim}=0.34$ $B_{nes}=0.17$	$B_{sor}=0.56$ $B_{sim}=0.44$ $B_{nes}=0.12$	$B_{sor}=0.48$ $B_{sim}=0.40$ $B_{nes}=0.08$	Yes
H2: The contribution of nestedness to overall beta diversity will be greater when forests are adjoined by transformed habitats than when they are adjoined by natural habitats	Coarse scale	$\%B_{nes}=20$			$\%B_{nes}=38$			Yes	$\%B_{nes}=11$			$\%B_{nes}=20$			Yes
	Fine scale	Edge	Int.	Ocean	Edge	Int.	Ocean		Edge	Int.	Ocean	Edge	Int.	Ocean	
		$\%B_{nes}=16$	$\%B_{nes}=13$	$\%B_{nes}=13$	$\%B_{nes}=13$	$\%B_{nes}=22$	$\%B_{nes}=23$	Yes, but not along edges	$\%B_{nes}=8.0$	$\%B_{nes}=16$	$\%B_{nes}=19$	$\%B_{nes}=33$	$\%B_{nes}=21$	$\%B_{nes}=17$	Yes, but not along the ocean
H3: Niche-based assembly mechanisms will explain most of the variation in beta diversity in forests adjacent to natural habitats, while dispersal-based assembly mechanisms will explain most of the variation in forests adjacent to transformed habitats	Coarse scale	Niche = 96.39% Dispersal = 3.61%			Niche = 67.45% Dispersal = 32.54%			Yes	Niche=73.94% Dispersal=26.65%			Niche=43.26% Dispersal= 56.73%			
	Fine scale	Edge	Int.	Ocean	Edge	Int.	Ocean		Edge	Int.	Ocean	Edge	Int.	Ocean	
		Niche =96.1% Dispersal =3.9%	Niche =99.8% Dispersal =0.2%	Niche =75.8% Dispersal =24.2%	Niche =40.5% Dispersal =59.5%	Niche =18.5% Dispersal =81.5%	Niche =46.2% Dispersal =53.8%	Yes	Niche =92.8% Dispersal =7.2%	Niche =15.4% Dispersal =84.6%	Niche =86.9% Dispersal =13.1%	Niche =47.3% Dispersal =52.7%	Niche =45.6% Dispersal =54.4%	Niche =36.7% Dispersal =63.3%	Yes, except natural interior

Appendix S4.2.2

Table S4.1a, b, and c. Indicator bird species characterizing forest and matrix birds communities at coarse sampling scales. Stat refers to the indicator value, a quantitative index of species alliance to a classification of sites, which ranges between 0 and 1. ***P<0.001; **P<0.01; *P<0.05.

Table S4.1a. Indicator bird species at coarse sampling scales.

Matrix				Forest			
Natural	Stat	Transformed	Stat	Natural	Stat	Transformed	Stat
Spectacled Weaver	0.86*	Yellow-fronted Canary	0.84*	Livingstone's Turaco	0.91***	Olive Sunbird	0.88*
Black-collard Barbet	0.84*	Fan-tailed Widowbird	0.80	Woodwards Batis	0.91**	Purple crested Turaco	0.84*
Croaking Cisticola	0.84*	Red Bishop	0.78*	Brown Scrub Robin	0.89**	Burcell's Coucal	0.73
Emerald-spotted Wood-dove	0.71	Pin-tailed Whydah	0.72	Eastern Nicator	0.86*	Trumpeter Hornbill	0.67
Eastern Nicator	0.63	Brown-hooded Kingfisher	0.67	Rudd's Apalis	0.80	Klaas's Cuckoo	0.63
Little Bee-eater	0.63	Red-capped Robin Chat	0.67	Brown-hooded Kingfisher	0.63	Lemon Dove	0.63
Rudd's Apalis	0.63	Bronze Mannikin	0.63	Crowned Hornbill	0.63	White-eared Barbet	0.63
Terrestrial Brownbul	0.63	Diederick Cuckoo	0.63	African Crowned Eagle	0.45	Cape White-eye	0.57
Gorgeous Bush-shrike	0.55	Purple-banded Sunbird	0.63	Crested Guineafowl	0.45	African Paradise Flycatcher	0.45
Purple-crested Turaco	0.55	White-eared Barbet	0.57	Emerald-spotted Wood-dove	0.45	Amethyst Sunbird	0.45

Table S4.1b – Indicator bird species at fine scales: matrix transects.

Matrix hinterland				Matrix interior				Matrix edge			
Natural	Stat	Transformed	Stat	Natural	Stat	Transformed	Stat	Natural	Stat	Transformed	Stat
Sombre Greenbul	0.73	Yellow-fronted Canary	0.60	Croaking Cisticola	0.71	Blue-cheeked Bee-eater	0.60	Yellow-bellied Greenbul	0.79*	Yellow-fronted Canary	0.82**
Croaking Cisticola	0.71	Fork-tailed Drongo	0.58	Black-backed Puffback	0.64	Fan-tailed Widowbird	0.60	Black-backed Puffback	0.78*	Red-collard Widowbird	0.58
Black-backed Puffback	0.56	Black-bellied Starling	0.47	Black-collard Barbet	0.64	Rufous-naped Lark	0.51	Red-eyed Dove	0.71*	Rufous-naped Lark	0.58
Terrestrial Brownbul	0.55	House Sparrow	0.47	Zitting Cisticola	0.64	Yellow-breasted Apalis	0.51	Southern Boubou	0.71*	Yellow-throated Longclaw	0.58
Cape Longclaw	0.45	Purple-banded Sunbird	0.47	Black-crowned Tchagra	0.55	Common Fiscal	0.47	Yellow-rumped Tinkerbird	0.66	Natal Francolin	0.51
Emerald-spotted Wood-dove	0.45	Red-collard Widowbird	0.47	Emerald-spotted Wood-dove	0.55	House Sparrow	0.47	Croaking Cisticola	0.64	Cape White-eye	0.47
European Bee-eater	0.45	African Stonechat	0.33	Southern Boubou	0.47	Amethyst Sunbird	0.33	Eastern Nicator	0.63	Crested Barbet	0.47
Gorgeous Bush-shrike	0.45	Amethyst Sunbird	0.33	Blue-mantled Crested-flycatcher	0.45	Cape White-eye	0.33	Livingstone's Turaco	0.63	Little Bee-eater	0.47
Purple-creasted Turaco	0.45	Bronze Mannikin	0.33	Cape Longclaw	0.45	Fork-tailed Drongo	0.33	Terrestrial Brownbul	0.63	White-eared Barbet	0.47
Rudd's Apalis	0.45	Cape Wagtail	0.33	Dark-backed Weaver	0.45	Indian Myna	0.33	Gorgeous Bush-shrike	0.56	African Hoopoe	0.33

Table S4.1c – Indicator bird species at fine scales: forest transects.

Forest edge				Forest interior				Forest ocean			
Natural	Stat	Transformed	Stat	Natural	Stat	Transformed	Stat	Natural	Stat	Transformed	Stat
Terrestrial Brownbul	0.84**	Purple-crested Turaco	0.69	Woodward's Batis	0.84**	Southern Boubou	0.79*	Woodward's Batis	0.78*	Purple-crested Turaco	0.75*
Woodward's Batis	0.84**	Black-bellied Starling	0.51	Rudd's Apalis	0.84**	Collard Sunbird	0.69	Terrestrial Brownbul	0.73	Burchell's Coucal	0.58
Eastern Nicator	0.79*	Cape White-eye	0.47	Eastern Nicator	0.62	Dark-capped Bulbul	0.64	Eastern Nicator	0.71	Cape White-eye	0.51
Livingstone's Turaco	0.79*	Klaas's Cuckoo	0.47	Livingstone's Turaco	0.62	Olive Sunbird	0.60	Livingstone's Turaco	0.66	Olive Sunbird	0.51
Blue-mantled Crested-flycatcher	0.78*	Lemon Dove	0.47	Terrestrial Brownbul	0.64	Purple-crested Turaco	0.58	Blue-mantled Crested Flycatcher	0.64	Gorgeous Bush-shrike	0.47
Rudd's Apalis	0.78**	Ashy Flycatcher	0.33	Brown Scrub-robin	0.55	White-eared Barbet	0.58	Brown Scrub-robin	0.63	African Emerald Cuckoo	0.33
Brown Scrub-robin	0.63	Bar-throated Apalis	0.33	Crowned Hornbill	0.55	African Emerald Cuckoo	0.33	Brown-hooded Kingfisher	0.55	African Dusky Flycatcher	0.33
Green Malkoha	0.56	Long-crested Eagle	0.33	Emerald-spotted Wood-dove	0.48	African Paradise Flycatcher	0.33	Rudd's Apalis	0.55	Amethyst Sunbird	0.33
Crested Guineafowl	0.48	Orange-breasted Bush-shrike	0.33	African Yellow White-eye	0.32	Bar-throated Apalis	0.33	Crowned Hornbill	0.45	Bar-throated Apalis	0.33
Crowned Hornbill	0.48	-		African Crowned Eagle	0.32	Black-headed Oriole	0.33	African Crowned Eagle	0.32	Black-headed Oriole	0.33

Table S4.2a and b. Indicator tree species characterizing forest and matrix bird communities at coarse sampling scales. Stat refers to the indicator value, a quantitative index of species alliance to a classification of sites, which ranges between 0 and 1. FD ***P<0.001; **P<0.01; *P<0.05.

Table S4.2a. Indicator tree species at coarse sampling scales.

Forest			
Natural	Stat	Transformed	Stat
Euclea racemosa	1.0***	Rhoicissus rhomboidea	0.89**
Mystroxylon aethiopicum	1.0***	Trichilia sp.	0.88*
Diospyros inhacaensis	0.95**	Cordia caffra	0.84*
Pavetta gerstneri	0.89**	Turraea floribunda	0.84*
Grewia caffra	0.80	Acacia karroo	0.78*
Strychnos gerrardii	0.80	Clerodendrum glabrum	0.72
Searsia natalensis	0.78	Dovyalis rhamnoides	0.72
Synaptolepis kirkii	0.78	Ekebergia capensis	0.72
Tricalysia delagoensis	0.78	Zanthoxylum capense	0.72
Xylotheca kraussiana	0.78	Chaetachme aristata	0.63

Table S4.2b. Indicator tree species at fine scales: forest transects.

Forest edge				Forest interior				Forest ocean			
Natural	Stat	Transformed	Stat	Natural	Stat	Transformed	Stat	Natural	Stat	Transformed	Stat
Euclea natalensis	0.91**	Celtis africana	0.85**	Drypetes natalensis	0.85**	Allophylus natalensis	0.83**	Diospyros natalensis	0.95***	Rhoicissus rhomboidea	0.82***
Diospyros natalensis	0.84**	Cordia caffra	0.75**	Dovalis longispina	0.81*	Dovyalis rhamnoides	0.68*	Drypetes natalensis	0.95***	Allophylus natalensis	0.75
Euclea racemosa	0.84**	Trichilia spp.	0.69*	Diospyros inhacaensis	0.78*	Acacia karroo	0.58	Euclea racemosa	0.90***	Cordia caffra	0.75*
Mystroxylon aethiopicum	0.84**	Dovyalis rhamnoides	0.68*	Euclea racemosa	0.78*	Rhoicissus revoilii	0.58	Diospyros inhacaensis	0.89***	Brachylaena discolor	0.69
Dovyalis longispina	0.79*	Rhoicissus rhomboidea	0.68*	Grewia caffra	0.78**	Vepris lanceolata	0.51	Tricalysia sonderiana	0.79*	Psychotria capensis	0.64
Diospyros inhacaensis	0.78*	Acacia karroo	0.58	Monanthotaxis caffra	0.71*	Albizia adianthifolia	0.47	Monanthostaxis caffra	0.78*	Dovyalis rhamnoides	0.60
Monanthostaxis caffra	0.78*	Gymnosporia nemerosa	0.58	Teclea gerrardii	0.73	Clerodendrum glabrum	0.47	Pavetta gerstneri	0.78*	Clerodendrum glabrum	0.58
Strychnos gerrardii	0.78*	Zanthoxylum capense	0.58	Mystroxylon aethiopicum	0.71*	Rhoicissus rhomboidea	0.47	Teclea gerrardii	0.73	Ekebergia capensis	0.58
Landolphia kirkii	0.71*	Clerodendrum glabrum	0.51	Ochna natalitia	0.71	Elaeodendron croceum	0.33	Ochna natalitia	0.71	Turraea floribunda	0.58
Synaptolepis kirkii	0.71*	Pavetta capensis	0.47	Tarenna junodii	0.71*	Acridocarpus natalitius	0.33	Catunaregam obovata	0.71*	Zanthoxylum capense	0.58

Chapter 5. Different life-history traits cause bird species to respond to different habitat fragmentation parameters, but do not influence extinction risk in South African coastal forests

Publication Details

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ABSTRACT

Aim To determine if bird species with different life-history traits respond differently to different habitat fragmentation parameters (i.e. area, connectivity and matrix habitats) and if these responses influence extinction risk.

Location Fragmented coastal forests in South Africa

Methods I surveyed birds and trees within nine forest fragments and adjacent matrix habitats and grouped bird species into five functional groups based on intrinsic species traits. I then used structural equation models (SEMs) to examine how functional group diversity is affected by fragmentation parameters after accounting for biotic and abiotic patch characteristics. Afterwards I performed an independent assessment based on relative abundance distributions, habitat specialization, range size, and proportion of range comprised of forest habitats to test if extinction risk is related to intrinsic species traits and the fragmentation parameter that species respond to.

Results Functional groups did not respond in the same way to different fragmentation parameters. Rather, the extent and form of species responses to each fragmentation parameter depended on species' intrinsic traits. Extinction risk was nearly uniformly distributed among functional groups and was not related to species intrinsic traits or the fragmentation parameter that species responded to.

Main conclusions Predictions of how species respond to fragmentation that does not consider the composite nature of fragmentation and/or the influence of intrinsic species traits may not provide a true reflection of the effects of landscape change on biodiversity. By using SEM's researchers can include the basic tenets of island biogeography theory as well as aspects of landscape ecology to develop testable predictions of biodiversity change across landscapes with differing land-use histories and species with differing traits. The extinction debt of coastal forests may be best addressed through a landscape complementation conservation approach that includes matrix habitats adjacent to coastal forest fragments in conservation plans.

Keywords: Extinction debt; island biogeography; functional groups; landscape ecology; structural equation models; IUCN Red List; landscape complementation; matrix habitats.

INTRODUCTION

Habitat loss and fragmentation apparently drives the current extinction crisis (Gibson *et al.*, 2011; Rybicki & Hanski, 2013). Extinction, however, often does not immediately follow on habitat loss. Instead, community characteristics such as species richness or evenness may be decoupled from prevailing landscape conditions and be reflected as an extinction debt (Kuussaari *et al.*, 2009; Krauss *et al.*, 2010). Predicting extinction debts has important implications for conservation, simply because the associated time lag provides opportunities to apply conservation measures to mitigate potential species losses (Kuussaari *et al.*, 2009; Wearn *et al.*, 2012). However, not all species, guilds, or communities are equally susceptible to extinction (Purvis *et al.*, 2000). For instance, large bodied species tend to have low population densities, slow life histories and are more likely to be targeted by human hunters (McKinney, 1997; Fa *et al.*, 2005). Consequently such species may face a higher risk of extinction than their smaller-bodied counterparts (Cardillo *et al.*, 2005). One may therefore infer that an extinction debt will likely be made up of these vulnerable species. Identifying these species then becomes particularly important from a conservation perspective because it may allow the development of targeted conservation initiatives that could reduce extinction debts and risks.

Extinction risk is in many instances correlated with an organism's life-history and ecological traits (Cardillo *et al.*, 2008; Davidson *et al.*, 2009; Murray *et al.*, 2011). For example, for birds extinction risk correlates with body and range size, habitat and diet specialization, migratory status and generation length (Owens & Bennet, 2000). As a result, a species' risk of extinction can be reflected by general categories such as International Union for Conservation of Nature (IUCN) Red List status (www.iucnredlist.org). The IUCN assesses threat for species globally, and is widely regarded as the most authoritative list of threatened species (Rodrigues *et al.*, 2006). Indeed, a number of studies have assumed that species listed as threatened by the IUCN face the highest risk of extinction and therefore represent the extinction debt (e.g. Brooks *et al.*, 1997; Olivier *et al.*, 2013).

However, despite particular traits predisposing species or groups of species to extinction, external factors such as climate change, invasive species or habitat fragmentation also influences a species' vulnerability to extinction (Lee & Jetz, 2010; Collen *et al.*, 2011). For example, Murray *et al.*, (2011) showed that extrinsic threats are equally important and interact with intrinsic traits to create guild-specific pathways to extinction. The IUCN Red List does not, however, provide information on the extrinsic drivers that make species vulnerable to extinction (González-Suárez *et al.*, 2013). As a result there may be omissions (species that should be on the list given historic declines but are not picked up by the rules) or commissions (naturally rare species that are included on the list although their population statuses have nothing to do with habitat loss or overexploitation). Species categorised as threatened with extinction may therefore not be, while species not categorised as threatened with extinction may well be (Mace *et al.*, 2008). Considering both intrinsic traits and extrinsic threats simultaneously are therefore important if we want to unravel the complete picture of extinction risk (Cardillo *et al.*, 2008; Tingley *et al.*, 2013).

Habitat fragmentation probably interacts with species traits to endanger some species but not others (Ewers & Didham, 2006; Laurance *et al.*, 2011). However, although habitat fragmentation is often marked as the overlaying driver of extinctions, it is in fact a landscape-scale process that involves both habitat loss and the breaking apart of habitat (Fahrig, 2003). It therefore might a) reduce habitat area, b) reduce habitat connectivity, c) increase the amount of habitat exposed to edge effects and d) alter matrix habitats that adjoin remaining habitat fragments (Fahrig, 2003; Ewers *et al.*, 2010). Each of these four processes (i.e. fragmentation parameters) may therefore be considered as a separate extrinsic threatening process. Because unique suites of intrinsic traits of species respond differently to different threatening processes (e.g. Norris *et al.*, 2004), we may expect each fragmentation parameter to interact in a different way with different intrinsic species traits. For instance, habitat specialists with large body sizes and poor dispersal abilities may be impacted upon disproportionally by a decrease in habitat area compared to small bodied generalists with high rates of dispersal (Ewers & Didham, 2006). In addition, species at higher trophic levels, such as predators, could be more heavily affected by isolation than those at lower trophic levels (e.g. Ryall & Fahrig, 2006). The transformation of matrix habitats may also have a major impact on generalist species that depend on these habitats for food and/or nesting materials, but less so on forest specialists restricted to forest habitats (e.g. Kennedy *et al.*, 2010).

Identifying how each fragmentation parameter interacts with intrinsic species traits may be useful from both a theoretical and practical perspective. Within fragmented landscapes, managers are faced with four broad management options to reduce the impact of fragmentation. They may opt to 1) increase habitat area, 2) increase habitat connectivity, 3) decrease the amount of habitat exposed to edge effects and 4) maintain natural matrix habitats among habitat fragments. However, given the budgetary and logistical constraints associated with conservation measures (Bradshaw *et al.*, 2009), it is unlikely, yet preferable, that all of these measures will be realised. Therefore if we can identify the fragmentation parameter that drives extinction risk we can focus scarce conservation resources to restore that specific parameter.

In this study I test if intrinsic species traits cause bird species to respond to different fragmentation parameters and if these responses influence extinction risk. To do this, I surveyed birds within coastal forest fragments and matrix habitats that adjoin forest fragments within a fragmented coastal forest along the tropical north-east coast of South Africa. Coastal forests here are situated within the Maputaland-Pondoland-Albany biodiversity hotspot (Küper *et al.*, 2004), but have been subjected to more than two centuries of escalating human disturbances and now likely harbour an extinction debt (Olivier *et al.*, 2013). I first test if intrinsic traits cause bird species to respond to different fragmentation parameters (area, connectivity and matrix habitats). I hypothesise that functional groups would respond differently to fragmentation parameters. For instance, functional groups dominated by forest-dependent species will be strongly influenced by area and isolation, while groups that are dominated by forest-associated species will be strongly influenced by the adjacent matrix habitats. Based on studies conducted elsewhere (e.g. Newbold *et al.*, 2012; Bregman *et al.*, 2014) I also expect forest-dependent insectivorous and frugivores to respond to changes in area, while large-bodied carnivores may be more susceptible to isolation. Second, I test if extinction risk is related to intrinsic species traits and the fragmentation parameter that species respond to. I performed an independent assessment based on relative abundance distributions, habitat specialization, range size and proportion of range comprised of forest habitats to identify species most likely to be threatened with extinction. Given the amount of historical forest loss in the study area, I hypothesise that species at risk of extinction will be restricted to functional groups that are strongly affected by area and isolation.

METHODS

Study area

Coastal forests and its associated biotas have a complex biogeographical origin (see Lawes, 1990; Eeley, 1999; Lawes *et al.*, 2007) and are considered as threatened (Berliner, 2009). In South Africa these forests represent the southernmost outlier of East African Tropical Coastal Forest which extends from tropical central Africa along the east African coast (Burgess & Clarke, 2000) (Fig. 5.1). Presently coastal forests form part of two critically endangered eco-regions: the Maputaland Coastal Forest Mosaic and the KwaZulu-Cape Coastal Forest Mosaic (Burgess *et al.*, 2004). These eco-regions support high levels of floristic endemism as well as a number of narrowly endemic species, including relict species. Coastal forests are also situated within the Maputaland-Pondoland-Albany biodiversity hotspot (Küper *et al.*, 2004) as well as the Maputaland Centre of Plant Endemism (van Wyk & Smith, 2000).

Coastal forests have been plagued by a series of anthropogenic disturbances that probably started with the arrival of Iron Age farmers in the early 1300's. Since then subsistence farming, cattle grazing, unregulated burning, commercial logging, agricultural plantations, urban developments and dune mining all contributed to an estimated forest loss of 82% (see Olivier *et al.*, 2013 and references therein). The remaining forests are now fragmented and imbedded within a matrix of human modified land use activities that include agroforestry and sugarcane plantations, rural and urban settlements, as well as natural grasslands and woodlands (van Aarde *et al.* 2014). My survey sites were located within and adjacent to nine of these fragments (range = 2.1 – 87.3 km^2) situated along approximately 300 kilometres of coastline between the Tugela river mouth in the south (S -29.2268°; E 32.8578°) and Lake Kosi in the north (S -27.0019°; E 32.8578°) (Fig. 5.1). Survey sites were located at random positions within forest fragments and surveys were conducted during the summers (November to March) of 2011, 2012 and 2013.

Data collection

Bird species diversity

My bird survey comprised of 293 point counts (Bibby *et al.*, 2000) within coastal forest fragments. The number of survey points per fragment ranged from 9 to 18 for fragments < 5km^2, 18 to 27 for fragments between 5 and 20km^2 and 27 to 54 for fragments > 20km^2. I also conducted 357 point counts within matrix habitats that surrounded these forest fragments. Matrix habitats included sugarcane (33 points) and agroforestry plantations (63 points), rural settlements (90 points), natural woodlands (93 points) and grasslands (78 points).

Point counts were conducted between 04:00 h and 10:00 h by the same three observers. Each observer surveyed 4 to 9 points per day depending on habitat type. Observers were trained in, and had prior experience of local bird identification. Points were at least 178m apart and were located using handheld GPSs. An observer allowed for a 2min period for birds that may have been disturbed upon arrival at the survey point to resettle and thereafter recorded birds for 10min. For each encounter, estimated distances from the observer to the bird were recorded by a digital rangefinder (Nikon Laser 550As). Only birds seen or judged to be calling within a 60m radius based on the rangefinder distances, were recorded. We excluded birds that flew above the canopy in forest fragments and also birds that did not settle within a 60m radius in the various matrix habitats. Surveys did not take place during rainy or windy days. I evaluated sampling effort for each fragment by generating species accumulation curves using the software program EstimateS (Colwell, 2006).

Functional groups

All species recorded within forest fragments during our surveys were assigned to a functional group based on functional traits sourced from Hockey *et al.* (2005). I then used InfoStat software (http://www.infostat.com.ar Di Rienzo *et al.*, 2010) to define functional groups following the procedures recommended by Pla *et al.*, (2012). I selected i) habitat specialization (forest-dependent or forest-associated), ii) diet, and iii) body size as functional traits to be included in the analysis. A species diet was ranked from 1 (if the dietary item made up a large proportion of overall diet) to 3 (if the dietary item made up a small proportion of overall diet) (see Supporting Information Appendix S5.1). I transformed categorical variables to dummy variables and then performed a cluster analysis using the Gower coefficient as a measure of similarity and the Ward linkage algorithm to create a dendogram for bird species. I retained five functional groups (clusters) and used MANOVA with Hotelling post-test and Bonferroni adjustment to assess grouping significance. I then calculated the Shannon diversity index, defined as: $H = -\sum p_i \log(p_i)$, where p_i is the proportion of all individuals comprised by species i (Magurran & McGill, 2011), for each functional group.

Structural equation models

Environmental variables

Biotic patch variable

Trees were recorded in 113 16m x 16m plots located in nine coastal forest fragments along 300km of coastline. The number of survey points per fragment ranged from 4 to 6 for fragments < 5km^2, 6 to 9 for fragments between 5 and 20km^2 and 9 to 15 for fragments > 20km^2. Every tree taller than 30cm was identified and measured. The Shannon diversity index was then calculated for each forest fragment.

Abiotic patch variables

A habitat suitability modelling exercise showed that median rainfall in winter, minimum relative humidity in winter, annual mean plant available water and elevation explained 90% of the probability of coastal forest occurrence (for details on the methodology see Olivier *et al.*, 2013). I assembled digital maps of these four variables (Schulze, 2006), and used these as predictors of bird and tree diversity in our models. Maps were 200m x 200m raster (grid cell) layers and covered the distribution of coastal forests in the study area. I extracted the mean raster value of each variable for each fragment in ArcGIS 10 (Environmental Systems Research Institute, Redlands, California, www.esri.com). A principal components analysis (PCA) was then used to reduce these potentially correlated variables into orthogonal principal components. The first two components accounted for 99% of environmental variation and were retained for analysis. Principal component axis one (PCA1) represented elevation, while median rainfall in winter, humidity and plant available water were represented by principal component axis two (PCA2).

The latitudinal position of each forest fragment was also included as a model variable. This was done for two reasons. First, my study fragments were distributed linearly along the coastline (Fig. 5.1). I therefore wanted to account for the possible indirect effects of a latitudinal gradient on diversity (see Bruton & Cooper, 1980). Secondly, by including latitude as a model variable I also accounted for the possible effects of spatial autocorrelation that violates the assumption of independently distributed errors in regression models and inflate Type I errors (see Legendre, 1993).

Fragmentation parameters

Fragment area was calculated from a digital map (LandSAT, 2010) that covered the distribution of coastal forests in South Africa. Fragment connectivity was calculated by using the incidence function model of Hanski (1994):

$$I_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j^b$$

,where I is the connectivity index, i is the stand in question, j each of the other forest fragments, d_{ij} is the distance from i to j, and A the area of the fragment j. A value of 0.5 was used for the exponent b following the recommendation of Moilanen & Nieminen (2002). Lenz *et al.* (2012) showed that trumpeter hornbills (*Bycanistes bucinator*), the largest frugivores in our study area, have a maximum potential seed-dispersal distance of 14.5km. I therefore opted to calculate fragment connectivity by taking into account all forest fragments within a radius of 14.5km.

To determine the influence of adjacent matrix habitats on bird species diversity within forest fragments I calculated the dissimilarity in community composition among the matrix bird community and the adjacent forest bird community by using the Sørensen dissimilarity index (β_{SOR}). Dissimilarities were generally higher among anthropogenically transformed matrix habitats (sugarcane, rural settlements, and agroforestry plantations) and forest fragments than among natural matrix habitats (grasslands and woodlands) and forest fragments (Fig. 5.2). I reasoned that high levels of dissimilarity will lower diversity within forest fragments, while low levels of dissimilarity will increase fragment diversity.

SEM model construction

I used path analysis and structural equation models (SEMs) (Shipley, 2000; Grace, 2006) to examine the relationship between functional group species diversity, fragmentation parameters and environmental variables. SEM allows the partitioning of the correlations between predictor and response variables into direct and indirect effects and thus enables the evaluation of hypothesized causal relationships in data sets with more than one dependent variable (Grace, 2006). This is done by fitting a series of equations that represent a hypothesis about the relationship between variables, where the response variable in one equation can be a predictor in another equation (Grace, 2006). The overall model can then be tested, along with significant tests for the individual parameters of the model (McCune & Grace, 2002). Furthermore, apart from significant tests, standardized regression coefficients indicate the strength and direction of the relationship among variables. As a result I could evaluate the direct or indirect effect of each predictor variable (exogenous variables) on each response variable (endogenous variables).The strength of SEM, however, lies in the *a priori model*, which is based on purely theoretical knowledge of the study system (Grace & Bollen, 2005).

I developed six *a priori* theoretical SEMs based on the hypothesis that the diversity within bird functional groups would be affected by fragmentation parameters such as forest fragment area, fragment connectivity and matrix habitat composition. I did not include edge length as a model variable as it was highly correlated with area (Pearson correlation 0.94). I also expected bird diversity to be impacted by local habitat conditions (e.g. van Rensburg *et al.*, 2000). I therefore included tree species diversity as a covariate in our models. I reasoned that, similar to birds, tree diversity within fragments would also be affected by fragment area and connectivity, but also by abiotic environmental variables such as elevation, rainfall, humidity and plant available water (represented in our models by PCA1 and PCA2). I also expected latitude to influence bird and tree diversity given the temperate-tropical latitudinal gradient present in our study area. These *a priori* models included all the hypothesised potential links between variables (Fig. 5.3). The structures of the six a priori SEMs remained the same except for the bird diversity variable which was substituted in each model. For example, in the first model overall bird diversity was the response variable, in the second model the diversity of forest-dependent insectivores was the response variable and so on. This was carried out to specifically test the influence of fragmentation parameters on the diversity of different functional groups. These theoretical models were then converted into testable SEM models following the recommendations of Grace *et al.*, (2010) (Table 5.1).

To develop the final SEMs, I started with the initial *a priori* SEMs and then evaluated their residual correlations, modification indices and model fits when implementing them for a specific functional group. I used the chi-square test, the root mean square error of approximation (RMSEA), and the comparative fit index (CFI) as measures of model fit. As recommended by Grace (2006) I used the following criteria to indicate SEMs with a satisfactory fit: 1) P-values of chi-square tests >0.05; 2) lower 90% confidence intervals of RMSEA <0.05, and 3) CFIs > 0.90. In a final step, I deleted non-significant paths (with P > 0.05) in SEMs with satisfactory model fit and reassessed model fits. I did not, however, remove non-significant pathways when interpreting the output from the final models because

I was interested in the strength of individual path coefficients. To take into account the possible effect of small sample size, I bootstrapped each model 2000 times and also calculated the Bollen Stine P-value to evaluate model fit. Individual path coefficients were then evaluated using z tests and by testing the consequences for model chi-square by omitting them from the model. All variables included in my models were observed variables and exogenous variables were allowed to correlate freely. SEM analyses were carried out in R version 2.15.1 (R Development Core Team 2012) using the LAVAAN package (Rossel, 2012). Moran's I values were calculated using the R package spdep (available at http://cran.r-project.org/web/packages/spdep). All model variables were tested for normality using a Shapiro-Wilks test, and transformed to conform to normality when necessary. Transformations used were: $\log(x)$ for area and $\sqrt{x}$ for connectivity. After transformation bivariate plots showed homoscedasticity and linearity. Variables were then scaled to have a mean of 0 and a standard deviation of 1 by transforming them to a z score (Kline, 2005).

Extinction risk

To determine extinction risk I first constructed two rank abundance distributions: one for all the individuals recorded during my survey and one for all the individuals recorded during a survey of coastal forests in southern Mozambique and that followed survey protocols similar to mine (see Guldemond & van Aarde, 2010). Species ranked under the 25th percentile were classified as very rare, 25th to 50th as rare, 50th to 75th as relatively common and greater then 75th as common (see Mace & Kershaw, 1997). Second, I used digital maps provided by BirdLife International (available at http://www.birdife.org/datazone/info/spcdownload) to calculate the global and local (range size within South Africa) range of each bird species. I classified local ranges under the 25th percentile as very small, 25th to 50th as small, 50th to 75th as medium and greater than 75th as large. Third, I calculated the percentage of local range that was made up of coastal forests for each species. I again used percentiles to classify the percentage of local range made up of coastal forests as very small, small, medium or large. I reasoned that species that were 1) dependent on forested habitats, 2) very rare, 3) had very small local ranges and 4) had a large proportion of their ranges made up by forest habitats were the species most likely to be threatened with extinction through habitat loss and fragmentation.

RESULTS

Within old growth coastal forest fragments I identified 66 bird species from 2584 records and 293 point counts. Surveys in the adjacent matrix habitats yielded twice as many (121) bird species from 1694 records and 357 point counts. For trees I collected 22 542 records of 195 tree species from 113 survey plots. The average number of tree species per plot was 27.6 (range = 12 to 50), and the average number of bird species per plot was 8.5 (range = 1 to 17). Bird species richness of forest points was four times higher than points surveyed in the adjacent matrix that yielded an average of 2.0 (range = 0 to 7) species per survey point.

Functional groups

Cluster analyses identified five functional groups: 1) forest-dependent generalists (n=24), 2) forest-dependent insectivores (n=8), 3) forest-associated generalists (n=17), 4) forest-associated insectivores (n=16), and 5) carnivores and nectar feeders (n=12). Carnivores and nectar feeders included forest-associated and forest-dependent species. Diversity among forest survey points for forest-associated insectivores was significantly auto-correlated in space up to 10km (Moran's I test, $P < 0.05$). The same was true for forest-dependent insectivores.

Functional group responses to fragmentation parameters

All final SEMs had P-values of chi-square tests > 0.05, lower 90% confidence intervals of RMSEA equal to 0 and CFI's >0.90. SEMs explained 86% (adjusted R^2=0.86) of variation in tree diversity with fragment connectivity having the strongest significant effect (path weight = 0.82). Tree diversity also increased as latitude decreased (path weight = -0.28). The model that reflected on overall bird diversity explained 61% (adjusted R^2=0.61) of variation in bird diversity within coastal forest fragments. For this model, area had the strongest effect on bird diversity (path weight = 0.67), followed by tree species diversity (path weight = 0.44) and matrix habitat (path weight = 0.31) (Fig. 5.3). The variables included in our models explained nearly half of the variation in functional group diversity for all of the functional groups in our analysis (R^2=0.48 for forest-associated generalists to R^2=0.97 for forest-associated insectivores).

Tree diversity never had a significant effect on diversity for any bird functional group. However, it had a strong effect on forest-associated generalists (path weight = 0.64), carnivores and nectar feeders (path weight = 0.36) and forest associated insectivores (path weight = 0.27), even though these effects were not statistically significant. Tree diversity had an unexpectedly weak effect on forest-dependent insectivores (path weight = 0.19) and forest-dependent generalists (path weight = -0.09). For these forest dependent functional groups, latitude had a strong effect on diversity. As latitude decreased, diversity increased which suggest that as conditions become more tropical to the north of the study area, functional groups that are dependent on coastal forests become more diverse.

Functional groups as independent response variables responded differentially to different fragmentation parameters (Fig. 5.4). Area had the strongest effect on forest-dependent insectivores (path weight = 0.54). Connectivity had the strongest effect on carnivores and nectar feeders (path weight = 0.40) as well as on forest-associated insectivores (path weight = 0.32). Forest-associated generalists benefitted from natural matrix habitats (path weight = -0.24) which, indicates that it may play an important role in driving diversity. However, the opposite was true for forest-dependent generalists that benefitted from transformed matrix habitats (path weight = 0.90).

Extinction risk

I identified five species, African broadbill (*Smithornis capensis),* black-throated wattle-eye (*Platysteira peltata),* grey waxbill (*Estrilda perreinie)*, Neergaard's sunbird (*Nectarinia neergardi),* and the southern banded snake eagle (*Circaetus fasciolatus)* that were forest dependent, very rare, had very small local ranges and which included coastal forests in a large part of their range. The pink-throated twinspot (*Hypargos margaritatus)* was the only forest-associated species that met these requirements. A further six species, African yellow white-eye (*Zosterops senegalensis),* bearded scrub-robin (*Erythropygia quadrivirgata),* crested guineafowl (*Guttera pucherani),* eastern bronze naped pigeon (*Columba delegorguei),* narina trogon (*Apaloderma narina)* and the white-eared barbet (*Stactolaema leucotis)* were rare or very rare and had either a restricted local distribution or a large part of their range made up by coastal forests. Four of these species were more common in Mozambique than South Africa: African broadbill, bearded scrub robin, narina trogon and Neergaard's sunbird.

Forest-dependent insectivores had the highest proportion of species at risk of extinction (3 out of 7), followed by carnivores and nectar feeders (2 out of 11), forest-dependent generalists (4 out of 25) and forest-associated generalists (2 out of 18) (see Supporting Information Appendix S5.3). There was no significant difference in the proportion of species at risk of extinction among functional groups (χ^2=7.43; P=0.11).

DISCUSSION

Habitat fragmentation is a landscape scale process that includes changes in habitat amount, patch size, patch isolation and exposure of patch edges to a novel matrix habitat (Ewers *et al.*, 2010). Yet, these diverse aspects of altered habitat quality and quantity are in many instances still viewed under the single banner of habitat fragmentation (Didham *et al.*, 2012 but see Haila, 2002 and Lindenmayer & Fisher 2007). In this study, I show that different species respond to different fragmentation parameters. Their responses largely depended on intrinsic traits such as body size, feeding guild and habitat specialization. Predictions of how species respond to fragmentation that does not consider the composite nature of fragmentation and/or the influence of intrinsic species traits may therefore not reflect on the effects of landscape change on species.

As expected, habitat area had the strongest effect on forest-dependent insectivore diversity, connectivity on carnivores and nectar feeders and matrix habitats on forest-associated generalists. However, contrary to my expectations, forest-dependent generalists did not respond strongly to area or isolation, while connectivity, and not matrix habitats, had the strongest effect on forest-associated insectivores. These widely varying functional responses highlight the caveats of using models that do not consider the composite nature of fragmentation and/or the influence of intrinsic species traits to predict species responses to landscape change. For instance, the equilibrium theory of island biogeography (IBT: MacArthur & Wilson, 1967) is widely regarded as the dominant ‘fragmentation model’ in the literature as well as one of the backbones of conservation science (e.g. Simberloff & Abele, 1976). Yet, IBT assumes that all species perceive the matrix as hostile and respond to landscape structure in the same way. However, within anthropogenically-modified landscapes strong external influences on patches are paramount and there is a blurring of the boundaries between what constitutes the ‘patch’ and the ‘matrix’ from the niche perspective of an organism (Kupfer *et al.*, 2006). Consequently, IBT may be a poor predictor of how species respond to habitat change in real landscapes where land-uses surrounding habitat fragments are not necessarily inhospitable to fragment-dwelling organisms (Fisher & Lindenmayer, 2007; Laurance, 2008). This has led to landscap ecology, and its recent incarnation countryside biogeography, being proposed as an alternative framework to IBT because it recognises the potential opportunities that matrix habitats, and specifically human made habitats, can afford too many species (Daily *et al.*, 2003; Mendenhall *et al.*, 2014; Trimble & van Aarde, 2014). However, given the variability in species responses to land-use change across different landscape types (e.g. Gardner *et al.*, 2009), formulating testable predictions based on landscape ecology remains challenging. My results suggest that a SEM can be based on the basic tenets of IBA (e.g. area and isolation), but can also include aspects of landscape ecology (e.g. matrix habitats) and patch variables (e.g. elevation). Such an approach may then allow researchers to determine the relative importance of direct versus indirect casual relationships between landscape (IBA and landscape ecology) and patch variables and may lead to testable predictions of biodiversity change across landscapes with differing land-use histories and species with differing traits.

It therefore follows that conservation actions based only on IBT may not have the desired effect of halting extinctions, especially if extinction risk is not a function of habitat loss or increased isolation. To date I relied on the IUCN Red List and a modelled estimates of forest loss to show that coastal forests harbour an extinction debt of 14 bird species (Olivier *et al.*, 2013). However, I did not identify which species constitute the extinction debt, although I assumed it were those listed as threatened in South Africa (Barnes, 2000). My independent assessment identified 13 species that likely comprise the extinction debt (six of these species were also considered threatened based on the South African Red List). These 13 species were part of functional groups that were strongly influenced by area, connectivity and matrix habitats, and thus did not support my hypothesis that extinction risk is restricted only to functional groups that are strongly affected by area and isolation. This may be because the coastal forest landscape mosaic is naturally fragmented, consisting of woodlands, grasslands, and regenerating forests whose extent vary in response to fire, climate and levels of CO2 in the atmosphere (Bond et al., 2003). In such a naturally fragmented landscape, multi-habitat dependency may be common as species rely on more than one habitat type for food and nesting resources (Neuschulz *et al.*, 2012). Fragmentation effects may therefore only appear when the landscape, and not only coastal forest, becomes fragmented. In other words, all natural habitat types (e.g. forests, grasslands and woodlands) represent habitat 'islands' surrounded by an inhospitable 'ocean' of sugarcane and Eucalyptus and Pinus plantations as well as urban and rural settlements.

The prevention of predicted extinctions in coastal forests may therefore not depend only on increasing forest area and reducing forest isolation. For instance, grasslands abutting forests typically have more species of invertebrates than forests (e.g. Bond & Parr, 2010) and could therefore boost diversity within some functional groups. An increase in forest area may therefore be advantageous to threatened forest-dependent insectivores such as the African broadbill and the black-throated wattle-eye. These species have specialized feeding requirements and limited dispersal abilities and therefore often require large home ranges – requirements that an increase in forest area will conceivably provide (Şekercioḡlu *et al.*, 2002). However, increasing forest area indiscriminately could have cascading negative consequences for threatened forest-associated generalists such as the pink-throated twinspot and yellow white-eye that rely on natural matrix habitats and further worsen the existing extinction debt instead of addressing it.

Given the interdependence of extinction risk, fragmentation parameters and species traits what course of conservation action may then be most effective in preventing predicted extinctions in coastal forests? My findings suggest that conservation incentives should not ignore the natural heterogeneity of the coastal forest mosaic. This can be achieved by implementing a landscape complementation approach (e.g. Dunning *et al.*, 1992) where conservation efforts do not only focus on forest fragments but also on the matrix habitats directly adjacent forest fragments. A landscape complementation approach will allow for retractions or expansions of forest margins in response to changes in fire, rainfall or climate and, in doing so, facilitate metapopulation dynamics within a heterogeneous landscape (Hanski & Ovaskainen, 2000). Intact matrix habitats may furthermore buffer fragments from the expected effects of habitat fragmentation (e.g. Guldemond & van Aarde, 2010) while still providing alternative or supplementary resources for species that occur here. Such an approach may also be particularly important in the light of climate change predictions, as Eeley *et al.*, (1999) predict that coastal forest distribution will increase as global climate change. By focusing on habitats that adjoin coastal forest fragments, the radiation potential as well as the ability of these forests to track environmental change may be boosted.

Before concluding, I must also consider the potential caveats associated with my approach. First, the results of analyses like this one can be biased by sampling artefacts and issues of detectability (Thornton *et al.*, 2012). I did not fit *a posteriori* detectability models because I was interested in all of the species recorded during my survey. Obtaining p-adjusted estimates of occurrence for a few generalist species in a few sites would have nullified the study questions and is unlikely to guide the development of effective policies in species rich environments (see Banks-Leite *et al.*, 2014). Rather, I gave particular care during sampling design to control for covariates that could influence detection probability by controlling for time of day, season, extreme weather, vegetation structure, proximity to edge, matrix type and observer (also see Olivier & van Aarde (2014) for a detailed description of the sampling design). However, detection probability could have influenced my estimates of extinction risk. For instance, forest-dependent species considered threatened in South Africa such as the spotted ground thrush (*Zoothera guttata*) and Pel's fishing owl (*Scotopelia peli*) were not recorded during my survey. If I assume that these species were recorded once, they would also have a high risk of extinction based on my analysis of rank abundance, local range size, and proportion of range made up of coastal forests. For the purpose of this analysis, however, I was only interested in determining extinction risk for species recorded during the extensive surveys of coastal forests in South Africa and Mozambique. Second, in my analysis I assume that extinction risk is only a function of range size, available habitat and species intrinsic traits. In reality extinction is a complex process dependent on species interactions the presence or absence of invaders or overexploitation by humans (e.g. Brook *et al.*, 2008). For instance, transformed matrix habitats had a positive effect on forest-dependent generalists. This may suggest that indirect effects mediated by unmeasured latent factors such as competition for food sources or nesting sites, nest predation and/or parasitism could play an important role in structuring coastal forest bird communities (e.g. Chalfoun *et al.*, 2002; Benson *et al.*, 2013; Robertson *et al.*, 2013). An increase in mortality rates in transformed matrices may furthermore reverse the outcome of competitive interactions, thereby allowing inferior species to supplant dominant ones within fragments (e.g. Cantrell *et al.*, 1998). Such possible species interactions and the role of the surrounding matrix will require further investigation as our dataset only allow us to speculate on their causes. Nevertheless, from our current findings we infer that much of the diversity recorded within coastal forests may be a function of matrix habitats that surround forest fragments.

CONCLUSION

A core activity for conservation science is to identify species that need protection and then devise measures of how to provide it (Manne & Pimm, 2001). In this study, I show that a broad 'what works for one will work for all' approach to conservation might not prevent predicted extinctions in coastal forests, but may instead aggravate the extinction debt. This is because bird species did not respond in the same way to different fragmentation parameters (area, isolation and matrix habitats). Rather, the extent and form of species responses to each fragmentation parameter depended on species' intrinsic traits. The best chance of preventing predicted extinctions may be through a landscape complementation conservation approach that includes matrix habitats adjacent to coastal forests. Models based only on IBT that do not consider the composite nature of fragmentation and/or the influence of intrinsic species traits may not provide a true reflection of the effects of landscape change on biodiversity. By using SEM's researchers can include the basic tenets of IBA and landscape ecology to develop testable predictions of biodiversity change across landscapes with differing land-use histories and species with differing traits.

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TABLES

Table 5.1 - The fragmentation parameters and biotic and abiotic environmental variables included in structural equation models to predict diversity within bird functional groups.

Predictor variable	Abbreviation	Calculated	Range
Fragmentation parameter			
Area	AREA	LandSAT 2010 image	2.1 – 87.3 km^2
Connectivity	ISO	Incidence function model of Hanski (1994)	2.9 – 49.3
Matrix dissimilarity	MTX	Sørensen dissimilarity index (β_{SOR}) between the bird community of each forest fragment and the bird community of the adjacent matrix habitat	0.32 – 0.86
Biotic variable			
Tree species diversity	TREE	Shannon diversity index	2.3 – 3.6
Abiotic variables			
Elevation	PCA1	First principal component from a principal component analysis	-33.4 – 31.6
Minimum relative humidity in winter; Median rainfall in winter; Mean annual plant available water	PCA2	Second principal component from a principal component analysis	-11.5 – 10.5
Latitude	LAT	Latitudinal position of each forest fragment	S 29.2268° - S 27.0019°

FIGURES

Figure 5.1 - The study area along the north-east coast of South Africa. Triangles represent survey sites that were located within nine coastal forest fragments along approximately 300 km of coastline. Different shades of green represent different forest types: coastal lowland, dune and swamp forests that occur throughout the study area.

Figure 5.2 - Bird community dissimilarity among coastal forest fragments and matrix habitat types that adjoin forest fragments. (a) Sugarcane plantations, (b) agroforestry plantations, (c) rural settlements and (d) natural grasslands and woodlands. Dissimilarity generally decreased as the adjacent matrix became natural and structurally more similar to forest fragments.

Figure 5.3 - Structural equation models (SEMs) examining the influence of fragmentation parameters and environmental variables on bird diversity within five functional groups in coastal forest fragments. Illustrated are standardized partial regression coefficients showing the strength of effects of variables on each other (‘direct effects’). Significant pathways are indicated by a bold arrow and R^2-values are given next to the two endogenous variables. I also report the χ^2-value, degrees of freedom (d.f.), Bollen Stein *P*-value (*P*) and the Comparative Fit Index (CFI) for each model. Abbreviations used in the models include: CONNECT = connectivity, LAT = latitude, MATRIX = matrix community dissimilarity when compared to the forest community of the adjacent fragment, PCA1 = principal component axis 1 representing elevation, PCA2 = principal component axis 2 representing median rainfall in winter, minimum relative humidity in winter, and mean annual plant-available water.

Figure 5.4 - Direct effects of area, isolation and matrix habitats on bird diversity within five functional groups as derived from structural equation models (SEMs, Fig. 5.3). Mean and

95% confidence intervals is shown for each fragmentation parameter and for each functional group.

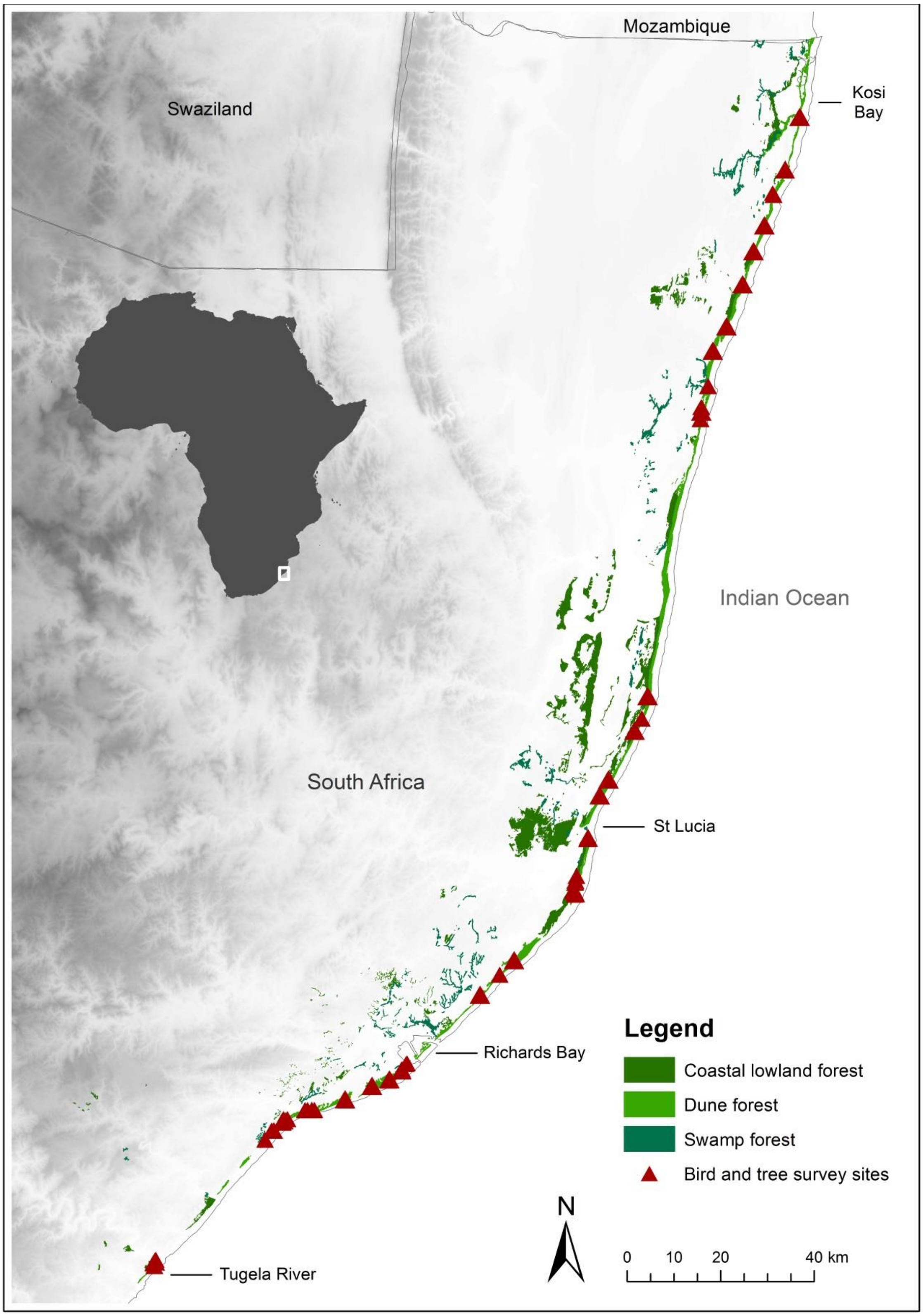

Mozambique
Swaziland
Kosi Bay
Indian Ocean
South Africa
St Lucia
Richards Bay
Tugela River
Legend
Coastal lowland forest
Dune forest
Swamp forest
Bird and tree survey sites
N
0
10
20
40 km

Figure 5.1.

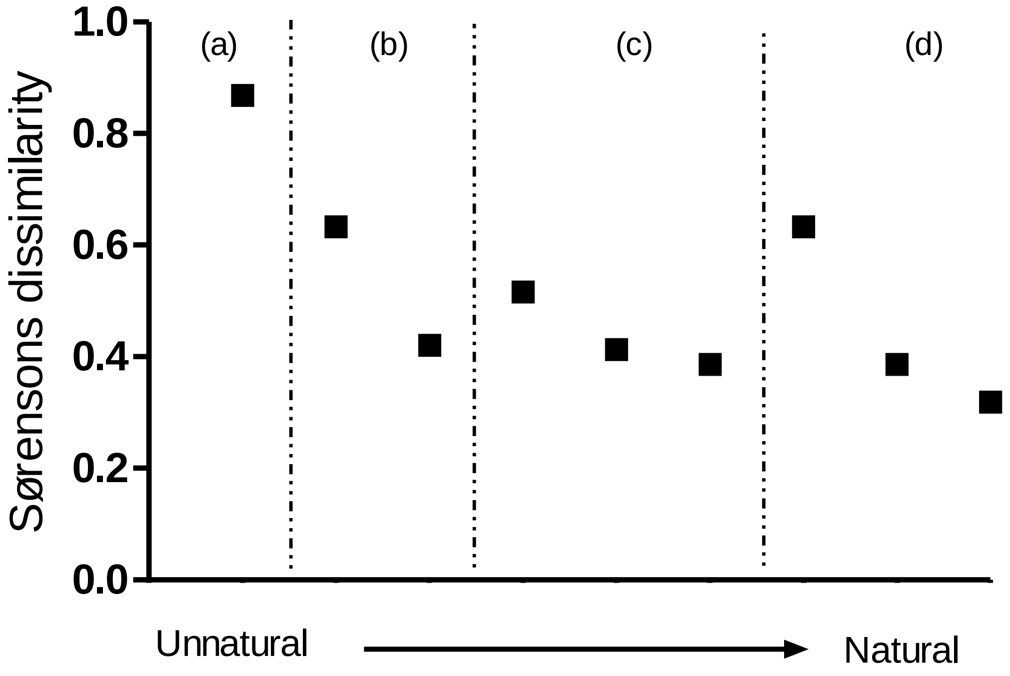
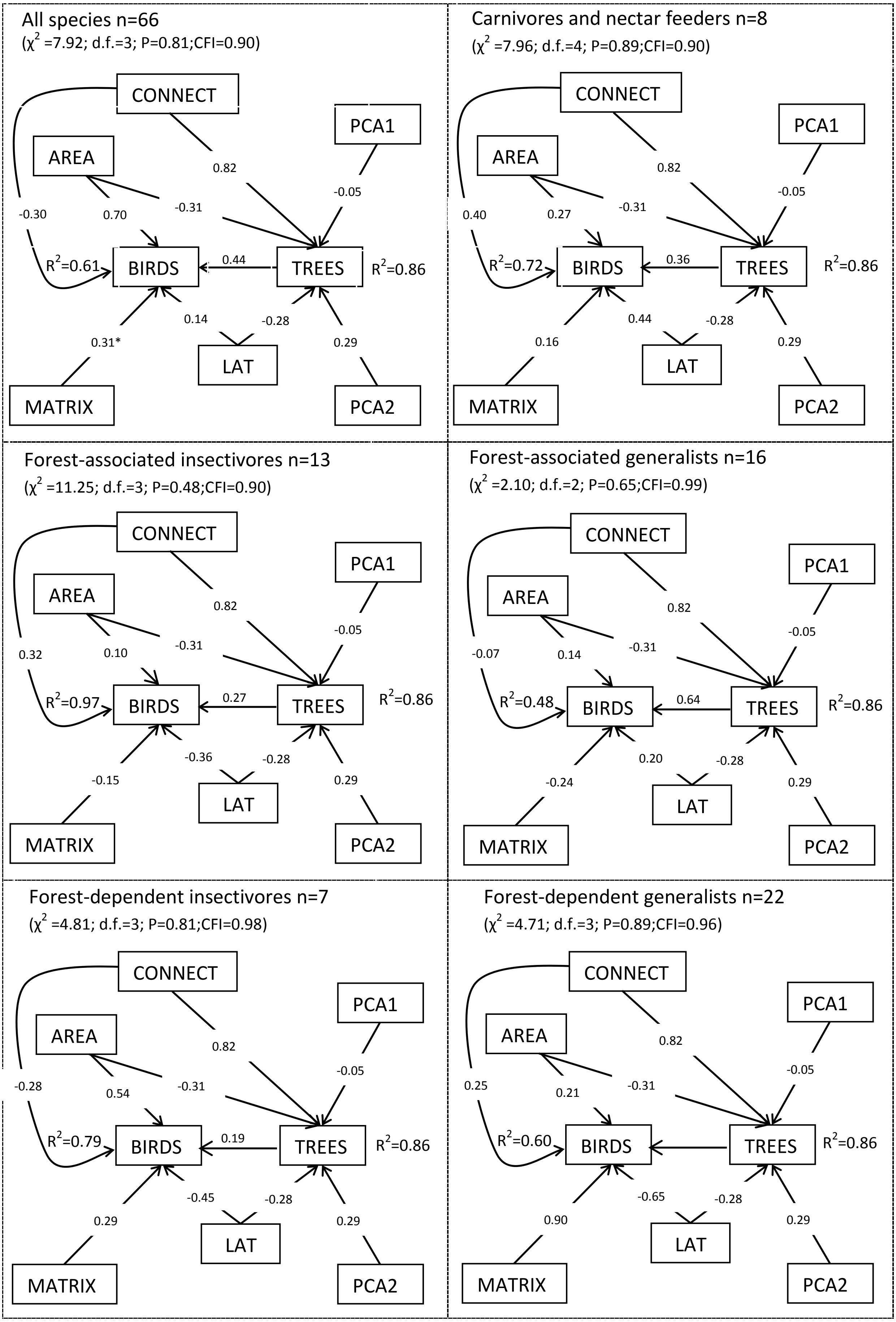

Sørensons dissimilarity
1.0
0.8
0.6
0.4
0.2
0.0
(a)
(b)
(c)
(d)
Unnatural
Natural

Figure 5.2.



All species n=66
(χ^2 =7.92; d.f.=3; P=0.81;CFI=0.90)

Carnivores and nectar feeders n=8
(χ^2 =7.96; d.f.=4; P=0.89;CFI=0.90)

Forest-associated insectivores n=13
(χ^2 =11.25; d.f.=3; P=0.48;CFI=0.90)

Forest-associated generalists n=16
(χ^2 =2.10; d.f.=2; P=0.65;CFI=0.99)

Forest-dependent insectivores n=7
(χ^2 =4.81; d.f.=3; P=0.81;CFI=0.98)

Forest-dependent generalists n=22
(χ^2 =4.71; d.f.=3; P=0.89;CFI=0.96)

Figure 5.3.

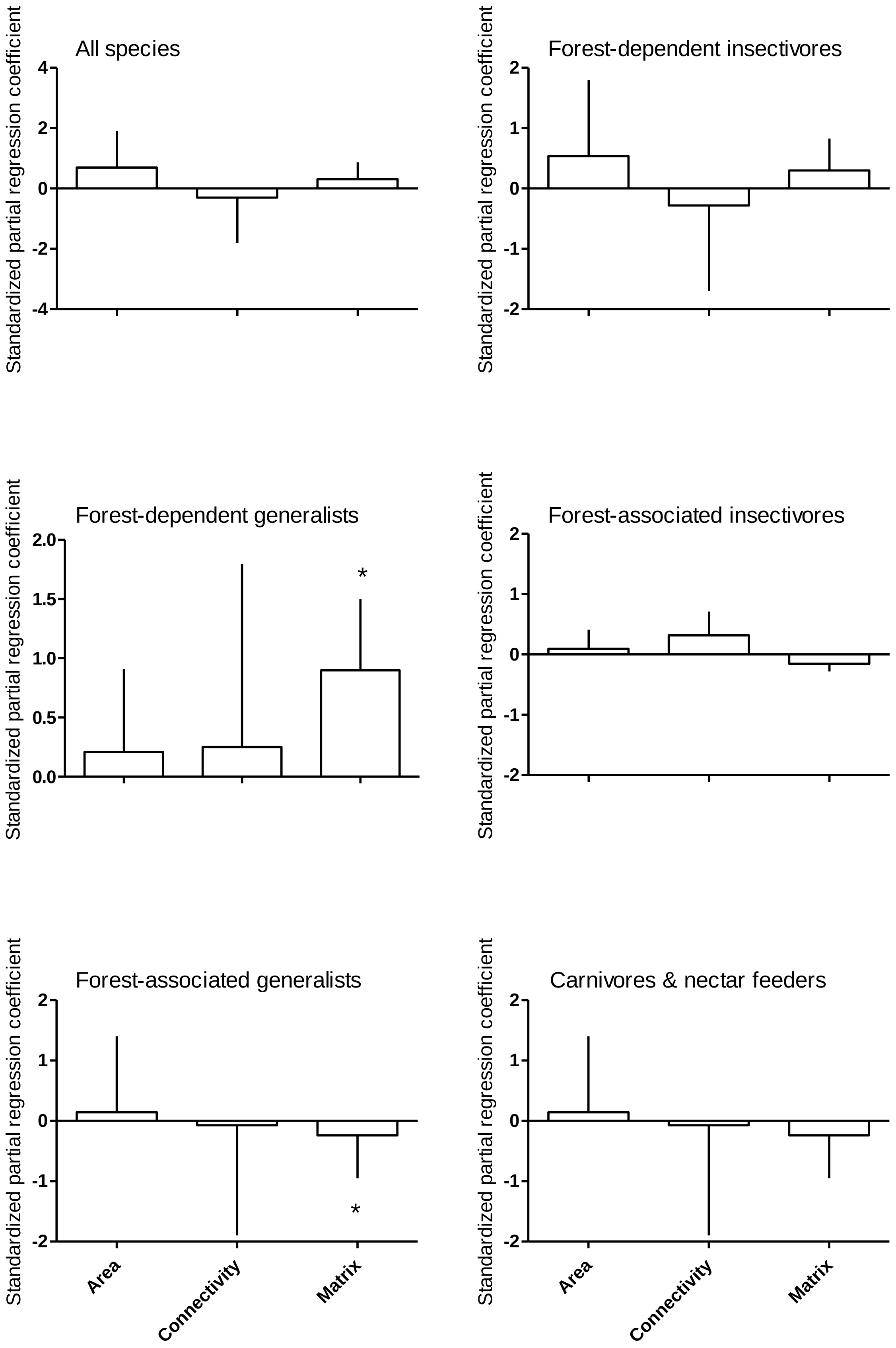

All species
Forest-dependent insectivores
Forest-dependent generalists
Forest-associated insectivores
Forest-associated generalists
Carnivores & nectar feeders
Standardized partial regression coefficient
4
2
0
-2
-4
1
-1
2.0
1.5
1.0
0.5
0.0
*
Area
Connectivity
Matrix

Figure 5.4.

SUPPORTING INFORMATION

Appendix S5.1 Functional traits of bird species recorded in coastal forests.

Appendix S5.2 List of bird species assigned to each functional group. Functional groups also include species that were only recorded in southern Mozambique by Guldemond & van Aarde (2010).

Appendix S5.3 Variables used to determine extinction risk of bird species recorded during my surveys of coastal forests in South Africa and those recorded during a 2007 survey in southern Mozambique (Guldemond & van Aarde, 2010).

Appendix 1 Table S5.1 – Functional traits of bird species recorded in coastal forests in South Africa and southern Mozambique. The diet of the bird species was ranked from 3 to 1. A value of 3 indicates the main diet of the bird species, while a value of 1 were assigned when the feeding strategy contributed only a minor part of the species' overall diet. Information sourced from Hockey *et al.*, (2005).

Common name	Scientific name	Forest associated/dependent	Body weight (g)	Feeding guild				
				Insectivores	Frugivores	Granivores	Nectarivores	Carnivores
African Emerald Cuckoo	*Chrysococcyx cupreus*	Dependent	35	3	0	0	0	0
African Broadbill	*Smithornis capensis*	Dependent	25	3	0	0	0	0
African Crowned Eagle	*Stephanoaetus coronatus*	Dependent	3600	0	0	0	0	3
African Dusky Flycatcher	*Muscicapa adusta*	Associated	11	3	2	0	0	0
African Paradise-Flycatcher	*Terpsiphone viridis*	Associated	14	3	2	0	0	0
African Yellow White-eye	*Zosterops senegalensis*	Dependent	10	3	2	0	1	0
Ashy Flycatcher	*Muscicapa caerulescens*	Associated	16.5	3	2	0	0	0
Bar-throated Apalis	*Apalis thoracica*	Dependent	10.5	3	2	0	0	0
Bearded Scrub-Robin	*Erythropygia quadrivirgata*	Dependent	26.7	3	0	0	0	0
Black-backed Puffback	*Dryoscopus cubla*	Associated	27	3	2	0	0	0
Black-bellied Starling	*Lamprotornis corruscus*	Dependent	50	2	3	0	0	0
Black-collard Barbet	*Lybius torquatus*	Associated	54	2	3	0	1	0
Black-headed Oriole	*Oriolus larvatus*	Associated	65	3	2	0	1	0
Black-throated Wattle-eye	*Platysteira peltata*	Dependent	13.4	3	0	0	0	0

Common name	Scientific name	Forest associated/dependent	Body weight (g)	Feeding guild				
				Insectivores	Frugivores	Granivores	Nectarivores	Carnivores
Blue-mantled Crested-Flycatcher	*Trochocercus cyanomelas*	Dependent	10	3	0	0	0	0
Brown-hooded Kingfisher	*Halcyon albiventris*	Associated	60	3	0	0	0	1
Brown Scrub-Robin	*Erythropygia signata*	Dependent	35	3	2	1	0	0
Buff-spotted Flufftail	*Sarothrura elegans*	Dependent	45	3	0	2	0	0
Burchell's Coucal	*Centropus burchellii*	Associated	180	0	0	0	0	3
Cape White-eye	*Zosterops virens*	Associated	13.5	3	2	0	1	0
Collared Sunbird	*Hedydipna collaris*	Dependent	8	2	1	0	3	0
Crested Guineafowl	*Guttera edouardi*	Dependent	1500	1	2	3	0	0
Crowned Hornbill	*Tockus alboterminatus*	Associated	245	3	2	0	0	0
Dark-backed Weaver	*Ploceus bicolour*	Dependent	35	3	2	0	1	0
Dark-capped Bulbul	*Pycnonotus tricolour*	Associated	40	2	3	0	1	0
Emerald-spotted Wood-dove	*Turtur chalcospilos*	Associated	65	1	2	3	0	0
Eastern Bronze-naped Pigeon	*Columba delegorguei*	Dependent	153	0	3	2	0	0
Eastern Nicator	*Nicator gularis*	Associated	56	3	0	0	0	0
Golden-tailed Woodpecker	*Campethera abingoni*	Associated	70	3	0	0	0	0
Gorgeous Bush-shrike	*Telophorus viridis*	Associated	37	3	0	0	0	0
Green Malkoha	*Ceuthmochares aereus*	Dependent	67	3	2	0	0	0
Green Pigeon	*Treron calvus*	Associated	240	0	3	0	0	0
Green Twinspot	*Mandingoa nitidula*	Dependent	10	0	0	3	0	0

Common name	Scientific name	Forest associated/dependent	Body weight (g)	Feeding guild				
				Insectivores	Frugivores	Granivores	Nectarivores	Carnivores
Green-backed Camaroptera	*Camaroptera brachyuran*	Associated	11	3	0	0	0	0
Grey Sunbird	*Cyanomitra veroxii*	Dependent	12	2	0	0	3	0
Grey Waxbill	*Estrilda perreini*	Dependent	7.6	2	0	3	1	0
Hadeda Ibis	*Bostrychia hagedash*	Associated	1225	3	0	0	0	0
Klaas's Cuckoo	*Chrysococcyx klaas*	Associated	26	3	0	0	0	0
Lemon Dove	*Aplopelia larvata*	Dependent	150	0	2	3	0	0
Lesser Honeyguide	*Indicator minor*	Associated	28	3	0	0	0	0
Livingstone's Turaco	*Tauraco livingstonii*	Dependent	300	0	3	0	0	0
Neergaard's Sunbird	*Cinnyris neergaardi*	Dependent	6.5	1	2	0	3	0
Narina Trogon	*Apaloderma narina*	Dependent	67	3	0	0	0	0
Olive Bush-shrike	*Telophorus olivaceus*	Dependent	34.5	3	2	0	0	0
Olive Sunbird	*Cyanomitra olivacea*	Dependent	12	2	1	0	3	0
Orange-breasted Bush-shrike	*Telophorus sulfureopectus*	Associated	27	3	0	0	0	0
Pale Flycatcher	*Melaenornis pallidus*	Associated	22.6	3	2	0	1	0
Pink-throated Twinspot	*Hypargos margaritatus*	Associated	13.5	2	0	3	0	0
Purple-banded Sunbird	*Cinnyris bifasciatus*	Associated	7.5	2	0	0	3	0
Purple-crested Turaco	*Purple-crested turaco*	Associated	300	0	3	0	0	0
Red-capped Robin-Chat	*Cossypha natalensis*	Associated	32	3	0	0	0	0
Red-chested Cuckoo	*Cuculus solitaries*	Associated	75	3	0	0	0	0
Red-eyed Dove	*Streptopelia semitorquata*	Associated	250	0	2	3	0	0
Rudd's Apalis	*Apalis ruddi*	Associated	10	3	2	0	0	0

Common name	Scientific name	Forest associated/dependent	Body weight (g)	Feeding guild				
				Insectivores	Frugivores	Granivores	Nectarivores	Carnivores
Scaly-throated Honeyguide	*Indicator variegates*	Dependent	48	3	2	0	0	0
Scarlet-chested Sunbird	*Chalcomitra senegalensis*	Associated	14.5	2	0	0	3	0
Southern Banded Snake Eagle	*Circaetus fasciolatus*	Dependent	1000	0	0	0	0	3
Sombre Greenbul	*Andropadus importunes*	Associated	34	2	3	0	1	0
Southern Boubou	*Laniarius ferrugineus*	Associated	60	3	2	0	1	0
Spectacled Weaver	*Ploceus ocularis*	Associated	30	3	2	1	0	0
Square-tailed Drongo	*Dicrurus ludwigii*	Dependent	30	3	0	0	0	0
Tambourine Dove	*Turtur tympanistria*	Dependent	72	2	1	3	0	0
Tawny-flanked Prinia	*Prinia subflava*	Associated	9.5	3	0	0	2	0
Terrestrial Brownbul	*Phyllastrephus terrestris*	Dependent	34	3	2	1	0	0
Trumpeter Hornbill	*Bycanistes bucinator*	Dependent	720	2	3	0	0	0
White-browed Scrub-Robin	*Cercotrichas leucophrys*	Associated	20	3	0	0	0	0
White-eared Barbet	*Stactolaema leucotis*	Dependent	54	2	3	0	0	0
Woodward's Batis	*Batis fratrum*	Dependent	12	3	0	0	0	0
Yellow-bellied Greenbul	*Chlorocichla flaviventris*	Dependent	40	2	3	1	0	0
Yellow-breasted Apalis	*Apalis flavida*	Associated	8	3	2	0	1	0
Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*	Dependent	14.5	0	3	0	0	0

Appendix 2 Table S5.2 – List of bird species assigned to each functional group. The conservation status of species considered threatened in South Africa by Barnes (2000) is indicated in brackets. Barnes (2000) based his assessment of the IUCN Red List criteria. NT – Near Threatened, VU – Vulnerable, and EN- Endangered. Asterisks (*) indicate the species that my analysis identified as at risk of extinction.

Forest-dependent insectivores	Forest-associated insectivores	Carnivores and nectar feeders	Forest-associated generalists	Forest dependent generalists
African Emerald Cuckoo	Brown-hooded Kingfisher	African Crowned Eagle (NT)	African Dusky Flycatcher	Bar-throated Apalis
African Broadbill (NT)*	Eastern Nicator	Burchell's Coucal	African Paradise-Flycatcher	Black-bellied Starling
Blue-mantled Crested-Flycatcher	Golden-tailed Woodpecker	Collared Sunbird	African Yellow White-eye	Brown Scrub Robin
Narina Trogon*	Gorgeous Bush-shrike	Grey Sunbird	Ashy Flycatcher	Buff-spotted Flufftail
Square-tailed Drongo	Green-backed Camaroptera		Black-backed Puffback	Crested Guineafowl*
Woodward's Batis (NT)	Hadeda Ibis	Olive Sunbird	Black-collard Barbet	Dark-backed Weaver
Black-throated Wattle-eye (NT)*	Klaas's Cuckoo	Purple-banded Sunbird	Black-headed Oriole	Eastern Bronze-naped Pigeon (VU)*
Bearded Scrub Robin*	Lesser Honeyguide	Scarlet-chested Sunbird	Cape White-eye	Emerald-spotted Wood-dove
Olive Bush-shrike	Orange-breasted Bush-shrike	Neergaard's Sunbird (NT)*	Crowned Hornbill	Green Malkoha
	Pale Flycatcher	Southern Banded Snake Eagle (VU)*	Dark-capped Bulbul	African Green Pigeon
	Red-capped Robin-Chat		Pink-throated Twinspot (NT)*	Green Twinspot
	Red-chested Cuckoo		Rudd's Apalis (NT)	Grey Waxbill*
	Tawny-flanked Prinia		Sombre Greenbul	Lemon Dove
	White-browed Scrub-Robin		Southern Boubou	Livingstone's Turaco

Forest-dependent insectivores	Forest-associated insectivores	Carnivores and nectar feeders	Forest-associated generalists	Forest dependent generalists
			Spectacled Weaver	Purple-crested Turaco
			Yellow-breasted Apalis	Red-eyed Dove
				Scaly-throated Honeyguide
				Tambourine Dove
				Terrestrial Brownbul
				Trumpeter Hornbill
				White-eared Barbet*
				Yellow-bellied Greenbul
				Yellow-rumped Tinkerbird

Appendix 3 Table S5.3 – Variables used to determine extinction risk of bird species recorded during my surveys of coastal forests in South Africa and those recorded during a 2007 survey in southern Mozambique (Guldemond & van Aarde, 2010).

Species	% contribution to community (SA)	% contribution to community (MZ)	SA range (km^2)	% of SA range in coastal forest	Global range (km^2)	Endemic	Forest associated/dependent
African Broadbill	0.04589	0.31617	33121	1.82664	3010000	No	Dependent
African Crowned Eagle	0.13768	0	244200	0.27027	6610000	No	Dependent
African Dusky Flycatcher	0.09179	0.04517	354596	0.18613	2390000	No	Associated
African Emerald Cuckoo	0.22946	0	294845	0.22385	11400000	No	Dependent
African Green-Pigeon	0.04589	0.09033	201339	0.32781	11400000	No	Associated
African Paradise-Flycatcher	0.04589	0.09033	627576	0.10517	14500000	No	Associated
African Yellow White-eye	0.32125	0.4065	20878	2.25596	8340000	No	Dependent
Ashy Flycatcher	0.09179	0.1355	354596	0.16328	7510000	No	Associated
Bar-throated Apalis	0.96374	0	548053	0.06915	1230000	No	Dependent
Bearded Scrub-Robin	0.04589	0.49684	79200	0.67929	1620000	No	Dependent
Black-backed Puffback	4.68105	3.97471	487223	0.13546	5720000	No	Associated
Black-bellied Starling	1.00964	1.71635	67069	0.9781	496000	No	Dependent
Black-collared Barbet	0.13768	0.81301	437387	0.1509	4660000	No	Associated
Black-headed Oriole	0.13768	0.54201	481664	0.13702	6080000	No	Associated
Black-throated Wattle-eye	0	0.04517	51005	1.23909	3620000	No	Dependent
Blue-mantled Crested Flycatcher	1.69803	0.85818	169795	0.3887	1240000	No	Dependent

Species	% contribution to community (SA)	% contribution to community (MZ)	SA range (km^2)	% of SA range in coastal forest	Global range (km^2)	Endemic	Forest associated/dependent
Brown Scrub-Robin	0.6425	2.43902	130459	0.50591	200000	Yes	Dependent
Brown-hooded Kingfisher	0.45893	2.03252	373804	0.17656	3770000	No	Associated
Buff-spotted Fluftail	0.04589	0	193619	0.34088	7050000	No	Dependent
Burchell's Coucal	1.14732	1.26468	364102	0.18127	6970000	No	Associated
Cape White-eye	0.96374	0.1355	1087679	0.05461	1310000	Yes	Associated
Collared Sunbird	2.43231	1.12918	266104	0.24802	9200000	No	Dependent
Crested Guineafowl	0.32125	0.22584	45083	1.24659	3810000	No	Dependent
Crowned Hornbill	0.45893	0.1355	119680	0.55147	3000000	No	Associated
Dark-backed Weaver	4.08444	3.11653	96830	0.68161	1380000	No	Dependent
Dark-capped Bulbul	3.30427	2.80036	477617	0.03873	19600000	No	Associated
Eastern Bronze Naped Pigeon	0.04589	0	38861	0.50436	232000	No	Dependent
Eastern Nicator	2.79945	2.98103	62617	0.6947	923000	No	Associated
Olive Sunbird	1.74392	1.53568	71026	0.92924	5390000	No	Dependent
Emerald-spotted Wood-Dove	0.27536	4.01987	364117	0.18126	5840000	No	Associated
Golden-tailed Woodpecker	1.37678	0.94851	577080	0.11246	6440000	No	Associated
Gorgeous Bush-Shrike	1.14732	1.67118	107230	0.60711	450000	No	Associated
Green Malkoha	1.19321	0.31617	84222	0.66016	5170000	No	Dependent
Green Twinspot	0.27536	0.09033	126953	0.51988	1540000	No	Dependent
Green-backed Camaroptera	7.80174	4.83288	272358	0.24233	15700000	No	Associated
Grey Sunbird	2.61588	1.89702	52042	1.26052	155000	No	Dependent

Species	% contribution to community (SA)	% contribution to community (MZ)	SA range (km^2)	% of SA range in coastal forest	Global range (km^2)	Endemic	Forest associated/dependent
Grey Waxbill	0	0.04517	33043	1.9974	1040000	No	Dependent
Hadeda Ibis	0.32125	0.72267	1172799	0.05628	16200000	No	Associated
Klaas's Cuckoo	0.82607	0.22584	479465	0.1364	14000000	No	Associated
Lemon Dove	0.18357	0.04517	232657	0.28368	2070000	No	Dependent
Lesser Honeyguide	0.13768	0.22584	945672	0.06979	9850000	No	Associated
Livingstone's Turaco	2.34052	4.20054	21351	2.65093	974000	No	Dependent
Narina Trogon	0.13768	0.90334	160354	0.41159	10200000	No	Dependent
Neergaard's Sunbird	0	0.4065	12977	3.35208	144000	Yes	Dependent
Olive Bush-Shrike	0	0.58717	262988	0.25096	332000	No	Dependent
Orange-breasted Bush-Shrike	0.13768	0.36134	328838	0.20071	8780000	No	Associated
Pale Flycatcher	0	0.04517	236066	0.24527	9110000	No	Associated
Pink-throated Twinspot	0.04589	0.1355	34414	1.39478	156000	Yes	Associated
Purple-banded Sunbird	0.45893	0.58717	44824	1.47243	2020000	No	Associated
Purple-crested Turaco	2.29463	2.16802	119236	0.54011	2170000	No	Associated
Red-capped Robin-Chat	5.04819	4.38121	131186	0.5031	3640000	No	Associated
Red-chested Cuckoo	0.82607	1.67118	694030	0.0951	12100000	No	Associated
Red-eyed Dove	0.78017	2.39386	1140543	0.05787	13800000	No	Associated
Rudd's Apalis	1.46856	0.4065	18647	2.90127	159000	Yes	Associated
Scaly-throated Honeyguide	0.5966	0.1355	181819	0.363	3470000	No	Dependent

Species	% contribution to community (SA)	% contribution to community (MZ)	SA range (km^2)	% of SA range in coastal forest	Global range (km^2)	Endemic	Forest associated/dependent
Scarlet-chested Sunbird	0.27536	0.18067	164025	0.40238	9420000	No	Associated
Sombre Greenbul	5.64479	5.05872	283584	0.23274	1250000	No	Associated
Southern Boubou	2.98302	2.12285	494807	0.13339	721000	Yes	Associated
Southern Banded Snake Eagle	0.04589	0	19118	2.90825	601000	No	Dependent
Spectacled Weaver	0.82607	0.271	252890	0.26098	3000000	No	Associated
Square-tailed Drongo	3.39605	4.20054	83563	0.78982	4590000	No	Dependent
Tambourine Dove	2.93713	2.61969	245596	0.26873	8130000	No	Dependent
Tawny-flanked Prinia	0.32125	0	466873	0.14137	14600000	No	Associated
Terrestrial Brownbul	2.01927	2.80036	324645	0.2033	2430000	No	Dependent
Trumpeter Hornbill	0.68839	2.12285	104942	0.62892	4070000	No	Dependent
White-browed Robin-Chat	0.04589	1.26468	167893	0.33355	6370000	No	Associated
White-eared Barbet	0.36714	0.1355	79751	0.82758	923000	No	Dependent
Woodwards' Batis	2.15695	0.99368	10493	4.73649	296000	Yes	Dependent
Yellow-bellied Greenbul	8.81138	5.55556	138826	0.46389	3990000	No	Dependent
Yellow-breasted Apalis	4.08444	3.88437	281526	0.23444	5650000	No	Associated
Yellow-rumped Tinkerbird	6.97568	8.03975	24048	2.66966	7150000	No	Dependent

Chapter 6. Multi-scale sampling boosts inferences from beta diversity patterns in coastal forests of South Africa

Publication details

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ABSTRACT

Aim We used a hierarchical fractal-based sampling design to test how sampling grain influences (1) beta diversity of and (2) inferences from the modelled contribution of niche- versus dispersal-based assembly processes in structuring tree and bird assemblages.

Location Coastal forest fragments, South Africa.

Methods We surveyed 103 tree plots and 267 bird points within eight forest fragments and partitioned beta diversity (β_{sor}) into its turnover (β_{sim}) and nestedness (β_{nes}) components. We evaluated how sampling at fine, intermediate and coarse scales influenced beta diversity components, and compared how tree and bird beta diversity responded to sampling grain variation. We then explored the relative contributions of niche- and dispersal-based assembly processes in explaining spatial turnover as a function of sampling grain and/or study taxon, by using multiple regression modelling on distance matrices and variance partitioning.

Results The β_{sor} of trees and birds was mainly explained by β_{sim} at all sampling scales. For both taxonomic groups, β_{sor} and β_{sim} decreased as sampling scale increased. Beta diversity differed among trees and birds at fine, but not at coarse, sampling scales. Dispersal-based assembly processes were the best predictors of community assembly at fine scales, whereas niche-based assembly processes were the best predictors at coarse scales. However, most of the variation in tree community composition was explained at fine scales (by dispersal-based assembly processes), while most of the variation in bird community composition was explained at coarse scales (by niche-based assembly processes).

Main conclusions Our study shows that inferences from beta diversity are scale dependent. By matching the grain of the data with the grain at which predictor variables and associated processes are likely to operate, multi-scale sampling approaches can help improve planning for biodiversity conservation and should be part of initiatives aimed at ecological conservation plans.

Keywords: Conservation, dispersal-based assembly, dispersal limitation, fractal sampling, fragmentation, nestedness, niche-based assembly, sampling scale, Sørensen dissimilarity, spatial turnover.

INTRODUCTION

Studies of the variation in species composition among sites (beta diversity) allow inferences about the processes that generate and maintain diversity (Anderson *et al*., 2011). However, estimates of beta diversity are influenced by both spatial grain (the size of the sampling unit) and spatial extent (the total area encompassed) (e.g. Mac Nally *et al*., 2004; Barton *et al*., 2013). Processes inferred from beta diversity estimates might therefore, in many instances, also be a function of the scale at which the studies were conducted.

Inferred processes are often derived from the deconstruction of beta diversity estimates into nestedness and spatial turnover components (e.g. Baselga, 2010). Nestedness reflects differences in the number of species that occur among sites; species present in one site are a subset of the species occurring at another more species-rich site (Ulrich *et al.*, 2009). Spatial turnover, in contrast, involves the replacement of species present at one site by different species at another site (Gaston & Blackburn, 2000). The correlation between spatial turnover and environmental or geographical distance is often used to infer the relative contributions of niche- and dispersal-based community assembly processes in structuring communities (e.g. Nekola & White, 1999; Tuomisto *et al.*, 2003). Whether community composition is controlled by niche- or dispersal-based assembly processes continues to fuel contemporary debates in ecology (see Chase & Meyers, 2011, and references therein), yet one may expect that, because estimates of spatial turnover are influenced by spatial scale, inferences on the relative contribution of niche- and dispersal-based assembly processes may also be a function of scale (e.g. Freestone & Inouye, 2006). Indeed, Weiher *et al.* (2011) noted that the scaling of community assembly deserves increased research attention; however, such studies remain rare.

Assembly processes inferred from beta diversity estimates may not only be a function of spatial scale, but also of the life-history traits of the study organism (Barton *et al.*, 2013). For instance, dispersal-based assembly processes, such as dispersal limitation, may play a greater role in shaping community assembly in taxa that are poorer dispersers compared with taxa that are more mobile (Weiher *et al.*, 2011). Furthermore, species traits associated with different trophic levels may also determine the relative contribution of community assembly processes. For example, niche-based assembly processes may play a greater role in shaping the community composition of birds than plants (e.g. Driscoll & Lindenmayer, 2009; Özkan *et al.*, 2013). Unravelling the relative contribution of assembly processes in shaping community composition is not only important from a theoretical perspective but also from a practical one, because if these processes vary across taxa and spatial scales, conservation efforts that focus on maintaining them will also have to differ. For instance, communities that are assembled by mostly niche-based processes may be more susceptible to habitat loss and may thus benefit from site-scale conservation initiatives. Conversely, communities that are driven by dispersal-based assembly processes may benefit more from a coarser landscape-scale perspective to conservation.

Most studies so far on the influence of spatial scale on beta diversity and assembly processes have considered these factors as separate entities and in isolation (e.g. Mac Nally *et al*., 2004) and have focused either on single taxa (e.g. Kristiansen *et al*., 2013) or more than one taxa within the same taxonomic group (e.g. Josefson & Göke, 2013; but see Gossner *et al*., 2013). These limitations may be because of the constraints associated with simultaneously sampling at different scales and across taxonomic groups. To address the limitations imposed by scale, Marsh & Ewers (2013) proposed a sampling design based on fractal geometry that explicitly addresses questions about beta diversity and spatial scale. Such a design provides the opportunity to aggregate data on different ecological groups at different spatial grains, and could enable investigators to match the grain of the data with the grain at which predictor variables and associated processes are likely to operate (Ewers *et al*., 2011).

In this study, we used fractal sampling to assess how beta diversity and associated contributions of niche- and dispersal-based assembly processes change across multiple sampling scales and taxa within a fragmented, subtropical coastal forest along the east coast of South Africa. Unravelling the processes that drive community assembly is of particular importance for conservation here, as these forests form part of two critically endangered ecoregions (Burgess *et al*., 2004) and may also harbour an unpaid extinction debt (Olivier *et al*., 2013).

We defined changes in sampling scale as changes in sampling grain. We sampled tree and bird communities that occurred within the coastal forests, and built on previous findings that metrics of beta diversity may be influenced by spatial grain and extent (e.g. Mac Nally *et al*., 2004; Martiny *et al*., 2011; Steinbauer *et al*., 2012), to hypothesize that beta diversity will decrease as sampling scale increases (i.e. plot size increases) for both taxonomic groups (H1). We focused on tree and bird communities because they represent two taxa with distinctly different dispersal strategies, and they also occupy different trophic levels. Because assemblages of less mobile species are expected to differ more between sites than those of more mobile species (Kessler *et al*., 2009), we hypothesized that tree beta diversity will be significantly higher than bird beta diversity at all sampling scales (H2). Lastly, we hypothesized that the relative contribution of niche- and dispersal-based assembly processes in shaping community assembly will differ as a function of sampling scale and study taxon (H3). Dispersal-based processes will play a greater role in tree community assembly, while niche-based assembly processes will play a greater role in bird community assembly.

MATERIALS AND METHODS

Study region

In addition to forming part of two critically endangered ecoregions, the Maputaland Coastal Forest Mosaic and the KwaZulu–Cape Coastal Forest Mosaic, the east coast forests of South Africa are also situated within the Maputaland–Pondoland–Albany biodiversity hotspot (Küper *et al*., 2004) as well as the Maputaland Centre of Plant Endemism (van Wyk & Smith, 2000). These coastal forests are limited in extent and occur mainly on calcareous sand dunes formed by deposits left by the regression of the Indian Ocean during the last glacial period (8000–10,000 BP) (Eeley *et al*., 1999). Niche-based assembly processes play important roles in structuring coastal forest communities (e.g. Griffiths & Lawes, 2006; Tsvuura *et al*., 2012). However, coastal forests may also be a meeting ground for species that are typical of hinterland habitats or distant coastal areas, most notably, in the study area, the tropical coastal forests to the north and the temperate forests to the south (van Aarde *et al*., 2014). Dispersal-based assembly processes may therefore also be of relevance in structuring coastal forest communities. We therefore considered these dunes to be an appropriate testing ground to quantify the influence of sampling scale on inferred assembly processes.

Our survey sites were located within and adjacent to eight coastal forests fragments (range 2.1–87.3 km^2) situated along approximately 300 km of coastline between the Tugela river mouth in the south (–29.2268° S, 32.8578° E) and Lake Kosi in the north (–27.0019° S, 32.8578° E; Fig. 6.1). These fragments were embedded in a matrix of either sugarcane or agroforestry plantations, rural homesteads and urban settlements. Some fragments were also adjoined by natural grasslands and woodlands. Survey sites were positioned randomly within the forest fragments and surveys were conducted during the summers (November–March) of 2011, 2012 and 2013.

Sampling design

A fractal-based sampling design provides a clearly defined structure for aggregating data on ecological phenomena that vary over different spatial scales (Ewers *et al*., 2011; Marsh & Ewers, 2013). We therefore used a fractal sampling procedure to develop a sampling hierarchy that consisted of three sampling grains for trees (fine, intermediate and coarse) and four sampling grains for birds (fine, intermediate, intermediate-coarse, and coarse). Each sampling grain comprised a number of aggregated sampling units. Survey plots and points represented the finest sampling scale for trees and birds, respectively (sample sizes *n* = 103 and *n* = 267, respectively). These plots/points were then arranged as equilateral triangles with sides of 564 m for trees and 178 m for birds. These first-order fractals represented the intermediate sampling scale for trees and birds (n = 20 and n = 55, respectively). Each tree plot was placed in the middle of a first-order bird fractal. The sampling design therefore also allowed us to have a second-order bird fractal that comprised nine survey points. We defined this sampling scale as intermediate-coarse (n = 16; Fig. 6.1) and was only applicable to birds, not to trees. Second-order fractals were at least 564 m apart. The sum of tree plots and bird survey points within a forest fragment represented our coarsest sampling scale (n = 8). Within the forest fragments we also surveyed extra points in order to achieve sampling saturation at coarse sampling scales. Bird survey points were always added as equilateral triangles around a single tree survey point. We evaluated sampling effort for each fragment by generating species accumulation curves using the software program ESTIMATES version 8 (Colwell, 2006).

To determine whether the adjacent matrix habitat influenced bird community composition within forest fragments, we paired each second-order forest fractal with another second-order fractal placed in the matrix habitat directly adjacent to the focal forest fragment. By doing so we were able to include matrix species composition as a covariate in our models. These second-order matrix fractals comprised nine bird survey points and were located in agricultural plantations, rural settlements, woodlands and grasslands. The forest and matrix second-order fractals were positioned on the same longitude and were a minimum of 500 m and a maximum of 1000 m apart, respectively (Fig. 6.1).

Tree censuses and bird surveys

Trees were recorded in 103 16 m × 16 m plots, while birds were surveyed using point counts (Bibby *et al.*, 2000). We surveyed 267 and 162 bird points within forest and matrix habitats. The number of survey points per fragment ranged from 12 to 48 for birds and from 4 to 18 for trees. For birds we also conducted point counts in adjacent matrix habitats: sugarcane and agroforestry plantations, rural subsistence areas, grasslands and woodlands. Point counts were conducted between 04:00 h and 09:00 h by the same two observers. Each observer surveyed four to nine points per day, depending on habitat type. To reduce potential observer bias, observers 'shared' fractal points, in other words a first- or second-order fractal was never surveyed by only one observer. We allowed a 2-min period for birds that may have been disturbed on arrival at the survey point to resettle, and thereafter recorded birds for 10 min. For each encounter, estimated distances from the observer to the bird were recorded with a digital rangefinder (Nikon Laser 550As; Nikon, Tokyo, Japan). All birds seen and heard were recorded, but we excluded largely aerial species, such as swifts and swallows, and birds that flew above the forest canopy. Point counts were not surveyed during rainy or windy conditions. For every individual tree ≥ 30 cm tall, diameter at breast height (d.b.h.) was measured and the individual was identified to species level. Surveyors were trained in, and had prior experience of, local tree and bird identification.

Data analyses

Beta diversity

The most appropriate way to decompose beta diversity is an ongoing debate (Podani & Schmera, 2011; Baselga, 2012; Carvalho *et al.*, 2013) and beyond the scope of our analyses. We disentangled the relative contributions of nestedness and spatial turnover to overall beta diversity at each sampling scale by partitioning total diversity (Sørensen dissimilarity, β_{sor}) into contributions by turnover (Simpson dissimilarity, β_{sim}; Lennon *et al.*, 2001) and nestedness-driven dissimilarity (β_{nes}) following Baselga (2010). This approach relies on the fact that Sørensen and Simpson dissimilarities are equal in the absence of nestedness, so their difference is a measure of the nestedness component of beta diversity (Baselga, 2010).

First, we calculated multiple-site dissimilarities (Baselga, 2013) for trees and birds and evaluated how sampling scale influenced β_{SOR}, β_{SIM} and β_{NES}. Second, we calculated pairwise dissimilarities and evaluated how sampling scale influenced the slopes of the distance decay curves for β_{sor}, β_{sim} and β_{nes}. This method is equivalent to the distance–decay of similarity proposed by Nekola & White (1999), where rates of distance decay are estimated through regression of compositional dissimilarities against geographical distance. We measured geographical distances as the minimum straight line distance between sampling units at each sampling scale using the Haversine formula, which takes into account the spherical shape of the earth when calculating the distance between two points (Sinnott, 1984). Euclidean distances between first- and second-order fractals were calculated from the longitudinal and latitudinal coordinates in the centre of each equilateral triangle. For forest fragments, we first calculated the centroid of each fragment and then used the straight line distances between the longitudinal and latitudinal coordinates of the centroids to construct a dissimilarity matrix. To account for the inherent dependence of the dissimilarity values, the significance of the Pearson correlations was computed by means of Mantel permutation tests (999 permutations). To test for differences in intercepts and slopes, we compared the linear and quadratic terms of the regression lines between β_{sim} and β_{nes} using an analysis of covariance (ANCOVA; Zar, 1984) in the software program GRAPHPAD PRISM 5.00 (GraphPad Software, San Diego, CA, USA; http://www.graphpad.com/). We used the same procedure to see whether the intercepts and slope of the distance–decay relationship for β_{sor}, β_{sim} and β_{nes} varied with sampling scale and among taxa. All other analyses were performed in R (R Core Team, 2012) using the packages ‘betapart’ version 1.1 (Baselga & Orme, 2012) and ‘vegan’ version 1.8-5 (Oksanen *et al*., 2007).

Niche- versus dispersal-based assembly processes

A habitat suitability modelling exercise that also included variables such as soil type, clay content, aspect, slope and temperature showed that median rainfall in winter, minimum relative humidity in winter, annual mean plant-available water and elevation explained 90%

of the probability of coastal forest occurrence (Olivier *et al.*, 2013). We assembled digital maps of these four variables (Schulze, 2006) and used these as predictors of tree species community assembly in further analyses. The maps comprised 200 m × 200 m raster (grid cell) layers and covered the distributional range of coastal forests in the study area. We extracted the raster value of each variable at each sampling scale in ARCGIS 10 (ESRI, Redlands, CA, USA). Where sampling scales overlapped with more than one grid cell (e.g. intermediate and coarse scales), we calculated the mean value of the overlapping grid cells. We used a principal components analysis (PCA) to reduce potentially correlated variables into orthogonal principal components. The first two components accounted for 97%, 95% and 99% of environmental variation for fine, intermediate and coarse sampling scales, respectively, and were retained for analysis. Principal component axis 1 (PCA1) represented elevation and accounted for 89%, 74% and 88% of environmental variance at fine, intermediate and coarse scales respectively. Median rainfall in winter, minimum relative humidity in winter and mean annual plant-available water were represented by principal component axis 2 (PCA2) and accounted for 8%, 21% and 11% of environmental variation at fine, intermediate and coarse scales respectively . We then constructed Euclidean dissimilarity matrices of each principal component axis at fine, intermediate and coarse sampling scales.

For birds, we considered three sampling scales in our models: fine scale (first-order fractal), intermediate scale (second-order fractal) and coarse scale (forest fragment). This was because each tree plot was associated with a first-order bird fractal at the finest sampling scale. We focused on two environmental variables that might explain dissimilarity in species composition: (1) tree species composition and (2) the density of individual trees per sampling plot. We also included matrix bird species composition as a covariate in our model, to determine whether differences in the bird community that inhabit the adjacent matrix influence the community composition of birds within forest fragments. We calculated the mean density of tree stems in each tree survey plot and constructed a Euclidean distance matrix for fine, intermediate and coarse sampling scales.

For both trees and birds we included geographical distances among sampling points (fine, intermediate and coarse scales) as a model variable. The variation explained by the geographical distance between sites was taken as evidence of dispersal-based community assembly.

Modelling approach and variation partitioning

We used multiple regressions on distance matrices (MRM; Lichstein, 2007) to examine how niche and dispersal assembly processes explained the variability in community composition at different sampling scales. Each explanatory matrix contained distances or dissimilarities between all pairwise combinations of *n* environmental or spatial factors. Each model used all the combinations of explanatory variables at each sampling scale. Tests of statistical significance were then performed with 999 random permutations (Legendre *et al*., 1994). The response variables in our models were the dissimilarity matrices of species turnover (β_{sim}) for birds and trees. For trees, our predictor variables were geographical distance (representing dispersal-based community assembly) as well as PCA1 and PCA2 (representing niche-based community assembly). For birds, our predictor variables were geographical distance (representing dispersal-based community assembly), turnover in tree species composition ($\beta_{sim\text{-}tree}$), tree stem densities (representing niche-based community assembly), and turnover in matrix bird species composition ($\beta_{sim\text{-}matrix\ birds}$). We interpreted variance fractions on the assumption that a relatively large R^2 value provides evidence that the processes modelled by the corresponding explanatory variables are important in shaping community structure, whereas a relatively small R^2 value provides evidence that they are not (Tuomisto *et al*., 2012).

To determine the relative contribution of each predictor variable in explaining model variation, we used hierarchical partitioning. This method assesses the independent, joint and total contribution of each predictor variable by averaging a measure of goodness-of-fit (R^2 in multiple linear regressions) over all possible models that include the predictor variable (Chevan & Sutherland, 1991). The estimated relative importance of each variable is then represented by the size of its pure effect. To determine the likelihood that the independent contributions of each predictor variable were significant and not a chance event, we performed a randomization test and assessed z scores at the 95% level. All analyses were conducted in R using packages 'ecodist' (Goslee & Urban, 2007) and 'hier.part' (Walsh & Mac Nally, 2007).

RESULTS

Our surveys of coastal forests returned 20,548 records of 189 tree species in 103 survey plots. We identified 74 bird species among 2584 records at 267 sampling points. Within the adjacent matrix habitats, we identified 121 bird species from 1694 records and 162 sampling points. The average number of tree species per plot was 26.6 (range 12–50, SD = 7.7) and the average number of bird species per plot was 8.5 (range 1–17, SD = 3.1). The bird species richness of forest points was four times higher than for points surveyed in the adjacent matrix, which had an average of 2.0 (range 0–7, SD = 1.2) species per survey point. The number of bird species recorded within forest fragments ranged from 28 to 40 (SD = 5.9), while the number of tree species ranged from 45 to 94 (SD = 19.0).

Beta diversity

The β_{sor} of trees and birds in coastal forests was mainly explained by β_{sim}, with a small explanatory contribution β_{nes} (Table 6.1). This pattern held at all sampling scales for both multi-site and pairwise dissimilarity measures (Tables 6.1 & 6.2).

The absolute values of β_{SOR} and β_{SIM} decreased with increasing sampling scale for both trees and birds (Table 6.1). The intercepts of the distance–decay relationship of β_{sor} for trees and birds were significantly higher at the finest compared with the coarsest sampling scale (trees $P < 0.04$; birds $P < 0.0001$; Table 6.2). We recorded the same trend (i.e. intercepts of the distance–decay relationship were significantly higher at the finest compared with the coarsest sampling scale) in trees for both β_{sim} ($P = 0.001$) and β_{nes} ($P = 0.0004$). However, for birds this trend held only for β_{sim} ($P < 0.0001$) and not for β_{nes} ($P < 0.98$).

The slopes and intercepts of the distance–decay relationships of β_{sor} and β_{sim} among trees and birds were not significantly different at coarse and intermediate sampling scales (first-order fractal β_{sor}, $P = 0.72$; first-order fractal β_{sim}, $P = 0.12$; fragment-scale β_{sor}, $P = 0.87$; fragment-scale β_{sim}, $P = 0.26$). However, the slopes of β_{sor} and β_{sim} of trees and birds differed significantly at the finest sampling scale (β_{sor}, $P < 0.0001$; β_{sim}, $P < 0.0001$). The slopes and intercepts of β_{sim} and β_{nes} differed significantly at each sampling scale for birds ($P < 0.0001$) but only at fine and coarse scales for trees ($P < 0.0001$).

Dissimilarity as a function of niche- and/or dispersal-based assembly processes

MRM models explained most of the variability in tree community dissimilarity at fine scales ($R^2 = 0.45$). However, explanatory powers decreased as sampling scale increased from intermediate ($R^2 = 0.40$) to coarse scales ($R^2 = 0.30$). Conversely, for birds, MRM models explained half of the variability in community dissimilarity at coarse scales ($R^2 = 0.50$) but little at fine scales ($R^2 = 0.15$).

There was a significant relationship between tree species turnover and geographical distance at fine ($P < 0.001$) and intermediate ($P = 0.001$), but not at coarse, sampling scales ($P = 0.77$) (Table 6.3). At coarse sampling scales PCA1 was the only variable that significantly increased with tree species turnover ($P = 0.02$). A similar pattern emerged for the factors underlying bird community dissimilarity. At fine and intermediate sampling scales, bird species turnover increased with geographical distance ($P < 0.001$ and $P = 0.004$, respectively). However, at coarse scales tree species turnover was the only variable that significantly increased with bird species turnover ($P = 0.04$).

The proportion of total variation that was explained by each predictor variable for each model varied with sampling scale (Fig. 6.2). For trees, the contribution of geographical distance consistently decreased as sampling scale increased (80% to 5%). Conversely, the contribution of PCA1 consistently increased with sampling scale (5% to 89%). For birds a similar pattern emerged. Geographical distance explained nearly 77% of the variation at the finest sampling scale but only 39% at the coarse sampling scales. For birds, tree species composition explained only 17% of the variation at fine scales but 49% at coarse scales. Matrix bird species composition and tree stem density never explained more than 18% and 6% of the variation, respectively. The individual contributions of all model variables were significantly greater than expected by chance based on *z* scores at the 95% level.

DISCUSSION

Although all aspects of diversity are scale dependent, they do not respond to changes in scale in the same way (Willis & Whittaker, 2002). Our detection of such responses should therefore be scale dependent, which may influence inferences about the processes that maintain diversity (e.g. Freestone & Inouye, 2006; Martiny *et al.*, 2011). Our assessment suggests that a multi-scale sampling approach can detect how sampling scale influences beta diversity patterns and affects inferences on community assembly processes, as well as identify the sampling grain at which predictor variables and associated processes are likely to operate for different taxa.

Our finding that beta diversity decreased with an increase in sampling grain is consistent with the results of others (e.g. Mac Nally *et al*., 2004; Martiny *et al*., 2011) and supports our first hypothesis. This apparent trend may simply be the result of a sampling effect, where the proportion of a community included in a sample increases with sampling scale because the focal unit size increases. As a result, the similarity of species composition between two sites increases (Mac Nally *et al*., 2004). This phenomenon may also be because of the well-known species–area relationship, where the number of species increases as a function of the focal area (see Schmera & Podani, 2013, and references therein). Community variables from coarse-scaled samples may therefore be more similar than those from fine-scaled samples.

Beta diversity decreased with sampling scale for both taxonomic groups, but the slope of the distance–decay relationship was higher for trees than for birds at each sampling scale. This finding provided support for our second hypothesis. However, contrary to our expectation, we only recorded significant differences between the slopes of the distance–decay relationship for tree and bird communities at fine sampling scales. At fine scales, niche structure, biological interactions and environmental characteristics may explain differences in turnover (e.g. McKinney & Drake, 2001). At coarse scales, however, species turnover may be similar among taxa because they respond in the same way to historical factors, as has previously been suggested by Lawes *et al.* (2007) for coastal forest assemblages. Here, geographical patterns of speciation, extinction filtering events and dispersal from areas of origin may have played an important role in shaping forest communities. The similarity between tree and bird beta diversity at coarse scales may also be ascribed to their similar responses to habitat loss and fragmentation. For instance, Arroyo-Rodríguez *et al*. (2013) found that beta diversity decreased within forest patches in landscapes with high deforestation levels, leading to floristic homogenization. They suggested that this homogenization is a result of the loss of rare species and a gain of disturbance-adapted species. This may also be the case for our study and may represent a response to the cumulative large-scale habitat loss incurred in recent times (Olivier *et al*., 2013).

Because species perceive and respond to the world at widely varying spatial scales, we hypothesized that different assembly processes will shape communities with different life-history strategies (Barton *et al*., 2013). Our results are consistent with this last hypothesis and highlight the importance of sampling at multiple spatial scales. We found that dispersal-based assembly processes probably drive tree community composition within coastal forests because geographical distance explained most of the variation (80%) in the model, with the largest R^2 value (0.45) being for trees. Conversely, the bird community is probably driven by niche-based assembly processes, because tree species composition explained most of the variation (49%) in the model, with the largest R^2 value (0.50) being for birds.

Had we only investigated one spatial scale, we may have concluded the opposite. For both taxonomic groups, niche-based assembly processes had the strongest influence on community composition at coarse sampling scales, while dispersal-based assembly processes had the strongest influence at fine sampling scales. This finding has two important implications. First, it supports that much of the ambiguity of niche- versus dispersal-based assembly in structuring communities may be a matter of the spatial scale at which studies are conducted (Chase & Myers, 2011; Weiher *et al*., 2011). Second, it emphasizes the importance of matching the grain of the data with the grain at which predictors and associated processes are likely to operate before drawing conclusions about the processes that maintain diversity.

Our results suggest that processes that drive tree community assembly are likely to operate at finer scales than processes that drive bird community assembly. For instance, based on the variables included in our models, we infer that dispersal limitation probably drives tree community assembly in coastal forests. Dispersal limitation allows for ecological drift, which is augmented by stochastic germination of seedlings and random tree deaths (Hubbell, 2001). Along with restricted seed dispersal, i.e. when seeds are more likely to fall close to the parent rather than far from it, these processes create 'patchiness' in community composition (Chave, 2008), therefore giving rise to fine-scale heterogeneity in tree community composition. In contrast to the tree community assembly, our models suggest that the processes that drive bird community assembly operate at coarse spatial scales, where the bird community of a forest fragment is a function of that fragment's tree community. This may be because of underlying functional relationships between bird and tree species (e.g. Kissling *et al.*, 2008) or because they respond to similar drivers that influence compositional changes across fragments. These drivers may include habitat fragmentation parameters (e.g. Polyakov *et al.*, 2013), historical factors (Lawes *et al.*, 2007) and/or the temperate–tropical latitudinal gradient within our study area (Bruton & Cooper, 1980). Similar trends in spatial turnover between trees and birds at coarse but not at fine scales might also be because of the influence of tree community variables on birds at coarse scales.

Before concluding, we need to consider the potential caveats associated with our approach. The variables included in our models only explained about half of the variability in bird and tree community composition. Variables related to species interactions (e.g. Siefert *et al.*, 2013), historical factors (Svenning *et al.*, 2011) and landscape effects (Arroyo-Rodríguez *et al.*, 2013) may also explain some of the variability in community composition. Furthermore, small sample sizes at coarse sampling grains and the length of the compositional gradient studied may introduce errors in beta diversity estimates (Crist *et al.*, 2003; Tuomisto *et al.*, 2012; Schmera & Podani, 2013). Our attempt to account for species interactions by including matrix bird species composition in our model did not contribute to the recorded variation in community structure at any sampling scale. Furthermore, because the four environmental variables we included in our models explained 90% of the probability of coastal forest distribution (Olivier *et al.*, 2013), we suggest that these variables are reasonably good proxies for the underlying environmental variability. However, our results suggest that factors driving tree community composition operate at fine spatial scales. Therefore, the scale of our environmental variables may have been too coarse to capture fine-scale environmental variation, such as light intensity, soil chemistry and hydrology. It is therefore possible that an unmeasured local environmental variable contributes in part to a local distance effect. If so, we may have overemphasized the role of dispersal-based assembly processes in shaping tree communities in these coastal forests.

What are the implications of our results for coastal forest conservation? The high level of turnover observed among forest fragments for both tree and bird communities suggests that every fragment contributed to regional diversity and should ideally be incorporated within conservation plans (as has been noted for coastal forests elsewhere, e.g. Guldemond & van Aarde, 2010). Species turnover here may be the result of the co-occurrence of Afromontane and tropical fauna and floras within coastal forests (Lawes *et al.*, 2007). As conditions become more tropical northwards along the South African coast, southern temperate forest species are gradually being replaced with northern tropical forest species. Our results suggest that the conservation of these communities may be achieved best with multi-scale conservation initiatives, such as site-specific case-by-case approaches to conserve forests, as well as landscape approaches that incorporate the role of historical and large-scale processes (e.g. Eeley *et al.*, 1999; Lawes *et al.*, 2007). For instance, our results imply that, in coastal forests, bird community composition depends on tree community composition. Disturbances that influence tree species composition, such as habitat loss, unsustainable harvesting or the invasion of alien plant species, may therefore also affect the community structure of birds that occur within fragments. However, we also found that the tree community is mostly driven by dispersal-based assembly processes, which could conceivably benefit from large-scale conservation initiatives. These could include stepping stones or corridors to enhance movement and functional connectivity, maintaining natural matrix habitats among forest fragments to facilitate dispersal, and restoration programmes to maintain or enhance the coastal forest corridor to enable north–south dispersal along the coastline.

CONCLUSIONS

We found that beta diversity and inferred assembly processes are a function of sampling scale. We therefore emphasize the importance of studying beta diversity at multiple spatial scales. In doing so, investigators can match the grain of the data with the grain at which predictor variables and associated processes are likely to operate. Based on this study, sampling only at fine scales could have failed to detect the importance of the fragmented tree community to the fragmented bird community. Conversely, had we only considered coarse sampling scales we could have overlooked the probable role played by dispersal limitation in shaping tree community composition. As a consequence, we could have proposed conservation initiatives that over-emphasized niche-based assembly processes (i.e. habitat based initiatives at a fine scale) to the detriment of dispersal-based assembly processes (i.e. landscape-based initiatives at a coarse scale) or vice versa. Our results therefore support the idea that conservation strategies need to focus more explicitly on the requirements of multiple taxa at multiple spatial scales to prevent the loss of species (Barton *et al*., 2013). To achieve this we propose the use of multi-scale sampling approaches, such as fractal sampling, as part of initiatives directed at ecological conservation plans.

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TABLES

Table 6.1. Comparison of multi-site dissimilarity values for overall dissimilarity (β_{SOR}), dissimilarity resulting from nestedness (β_{NES}) and turnover (β_{SIM}) for trees and birds in coastal forest fragments, South Africa, at four sampling scales. Tree beta diversity values at intermediate-coarse scales are not shown because the sampling design did not allow investigation at this scale for trees.

	Among points/plots (fine scale)		Among first-order fractals (intermediate scale)		Among-second order fractals (intermediate-coarse scale)		Among fragments (coarse scale)	
	Birds (*n*=267)	Trees (*n*=103)	Birds (*n*=55)	Trees (*n*=20)	Birds (*n*=16)	Trees	Birds (*n*=8)	Trees (*n*=8)
β_{SOR}	0.99	0.97	0.95	0.85	0.78	–	0.63	0.71
β_{NES}	0.01	0.01	0.02	0.05	0.05	–	0.07	0.12
β_{SIM}	0.98	0.96	0.93	0.80	0.73	–	0.56	0.59

Table 6.2. Results from ordinary least-square regression of overall dissimilarity (β_{sor}),dissimilarity resulting from nestedness (β_{nes}) and turnover (β_{sim}) as a function of geographical distance (distance–decay of similarity; Nekola & White, 1999) for trees and birds in coastal forest fragments, South Africa, between pairs of survey sites at four sampling scales. The sampling design allowed investigation of tree beta diversity at only three sampling scales, fine, intermediate and coarse. Regression models were applied separately for β_{sor}, β_{nes} and β_{sim} at each sampling scale. A Mantel test was applied to assess the significance of the Pearson correlation coefficient (*r*); *$P < 0.05$.

		Among points/plots (fine scale)		Among first-order fractals (intermediate scale)		Among-second order fractals (intermediate-coarse scale)		Among fragments (coarse scale)	
		Birds	Trees	Birds	Trees	Birds	Trees	Birds	Trees
β_{sor}	Intercept	0.61	0.56	0.40	0.46	0.27	–	0.25	0.40
	Slope	0.0004	0.001	0.001	0.001	0.001	–	0.001	0.001
	Mantel *r*	0.16	0.48	0.41	0.40	0.62	–	0.77	0.46
	P	0.001	0.001	0.001	0.001	0.001	–	0.001	0.02
β_{nes}	Intercept	0.11	0.07	0.08	0.07	0.06	–	0.05	0.07
	Slope	–0.00003	–0.00003	–0.00002	0.0002	–0.00003	–	0.0001	0.0004
	Mantel *r*	–0.02	–0.03	–0.02	0.19	–0.10	–	0.14	0.33
	P	0.816	0.73	0.76	0.03	0.75	–	0.20	0.06
β_{sim}	Intercept	0.5	0.49	0.32	0.39	0.21	–	0.20	0.33
	Slope	0.0004	0.001	0.001	0.001	0.0008	–	0.0001	0.0003
	Mantel *r*	0.13	0.44	0.37	0.36	0.61	–	0.58	0.19
	P	0.001	0.001	0.001	0.001	0.001	–	0.004	0.16

Table 6.3. Results of multiple regression modelling on distance matrices (MRM) by sampling scale for trees and birds in coastal forest fragments, South Africa. The response variables in our models were the dissimilarity matrices of species turnover (β_{sim}) for birds and trees. Explanatory variables were categorized as representing either niche- or dispersal-based assembly processes. For trees, the predictor variables were geographical distance, PCA1 and PCA2. PCA1 and PCA2 represented the two axes of a principal components analysis that included four environmental variables: median rainfall in winter, minimum relative humidity in winter, mean annual plant-available water and elevation. For birds, the predictor variables were geographical distance, turnover in tree species composition ($\beta_{\text{sim-tree}}$), tree stem densities and turnover in matrix bird species composition ($\beta_{\text{sim-matrix birds}}$). Sample size decreased as sampling scale increased from $n = 103$ to $n = 8$ for trees and from $n = 55$ to $n = 8$ for birds. The variation (R^2) explained by each model is shown. The significance of the slopes was evaluated by a permutation test ($n = 999$); *$P < 0.05$.

	Fine scale				Intermediate scale				Coarse scale			
	R^2	Intercept	Slope	P	R^2	Intercept	Slope	P	R^2	Intercept	Slope	P
Trees	0.45	0.31	–	< 0.01	0.40	0.19	–	<0.01	0.30	0.25	–	0.06
Dispersal-based assembly												
Geographical distance (km)	–		0.15	< 0.01	–		0.11	0.01	–		0.01	0.77
Niche-based assembly												
PCA1	–		0.001	< 0.01	–		0.001	0.04	–		0.003	0.02
PCA2	–		0.001	0.35	–		0.003	0.01	–		–0.001	0.73

	Fine scale				Intermediate scale				Coarse scale			
	R^2	Intercept	Slope	P	R^2	Intercept	Slope	P	R^2	Intercept	Slope	P
Birds	0.15	0.18	–	< 0.01	0.27	–0.01	–	0.01	0.50	–0.12	–	0.03
Dispersal-based assembly												
Geographical distance (km)	–		0.08	< 0.01	–		0.08	<0.01	–		0.12	0.07
Niche-based assembly												
Tree composition	–		0.06	0.25	–		0.16	0.29	–		0.43	0.04
Tree structure	–		0.04	0.10	–		0.014	0.79	–		–0.11	0.55
Adjacent matrix species												
Matrix species	–		–0.03	0.55	–		0.09	0.41	–		–0.04	0.81

FIGURES

Figure 6.1 (a) The study area along the north-east coast of South Africa. Triangles represent survey sites that were located within eight coastal forest fragments along approximately 300 km of coastline. (b) A schematic representation of the sampling design. Black circles represent bird survey points that were located on the vertices of equilateral triangles with sides of length 178 m. White squares represent tree survey plots that were located on the vertices of equilateral triangles with sides of length 564 m. Each tree plot was also located in the centre of a first-order bird fractal, which allowed a second-order bird fractal that comprised nine survey points. Each second-order fractal was paired with another second-order fractal placed in the matrix habitat directly adjacent to the focal forest fragment. These two second-order fractals (forest and matrix fractal) were located on the same longitude and were a minimum of 500 m and a maximum of 1000 m apart. Only bird points were surveyed in the adjacent matrix habitats, and were included as a covariate in the models. (c) A schematic representation of the sampling hierarchy. Black dots represent bird survey points and white squares represent tree survey plots. Each sampling grain comprised a number of aggregated sampling units. There were three defined sampling grains for trees (fine, intermediate and coarse) and four defined sampling grains for birds (fine, intermediate, intermediate-coarse and coarse).

Figure 6.2 Summary of the results of six separate hierarchical partitions showing the relative contribution of each predictor variable in explaining the model variation at fine, intermediate and coarse sampling scales. The predictor variables were categorized as representing either niche- or dispersal-based assembly processes. The dispersal-based assembly is represented by geographical distance (Distance) for birds and trees at each sampling scale. For trees, the niche-based assembly is represented by principal component axis 1 (PCA1) and principal component axis 2 (PCA2). PCA1 represents elevation, and PCA2 represents daily rainfall in winter, humidity and plant-available water. For birds, the niche-based assembly is represented by matrix habitat species composition (Matrix species), tree composition (Tree species) and tree density (Tree density). Shaded bars indicate independent effects, and white bars joint effects. The vertical axes correspond to the proportion of variance explained in each R^2 value. The sum of the independent effects equals 100% for each model.

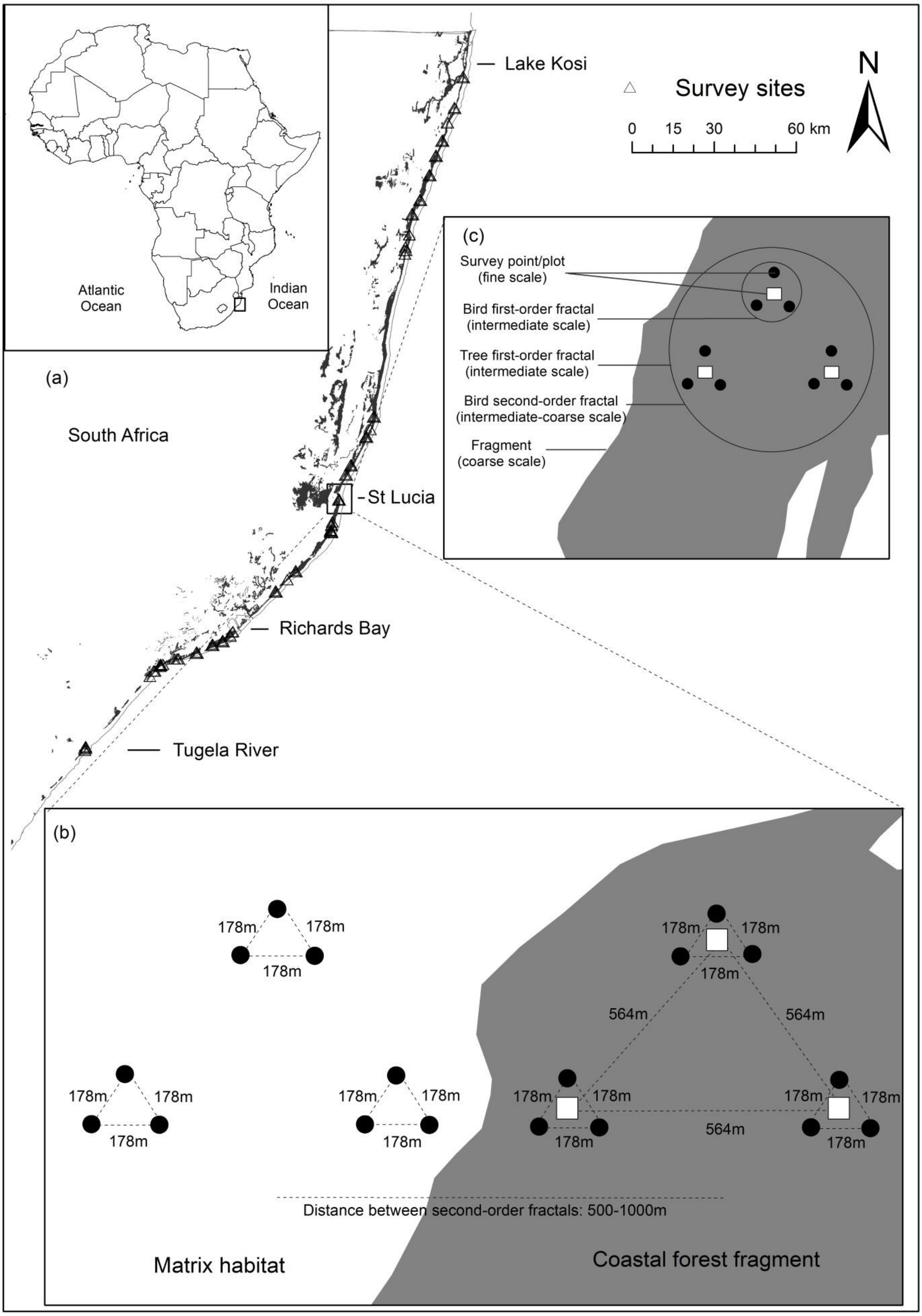
Lake Kosi
Survey sites
N
0 15 30 60 km
Atlantic Ocean
Indian Ocean
(a)
South Africa
St Lucia
Richards Bay
Tugela River
(c)
Survey point/plot (fine scale)
Bird first-order fractal (intermediate scale)
Tree first-order fractal (intermediate scale)
Bird second-order fractal (intermediate-coarse scale)
Fragment (coarse scale)
(b)
178m
564m
Distance between second-order fractals: 500-1000m
Matrix habitat
Coastal forest fragment

Figure 6.1

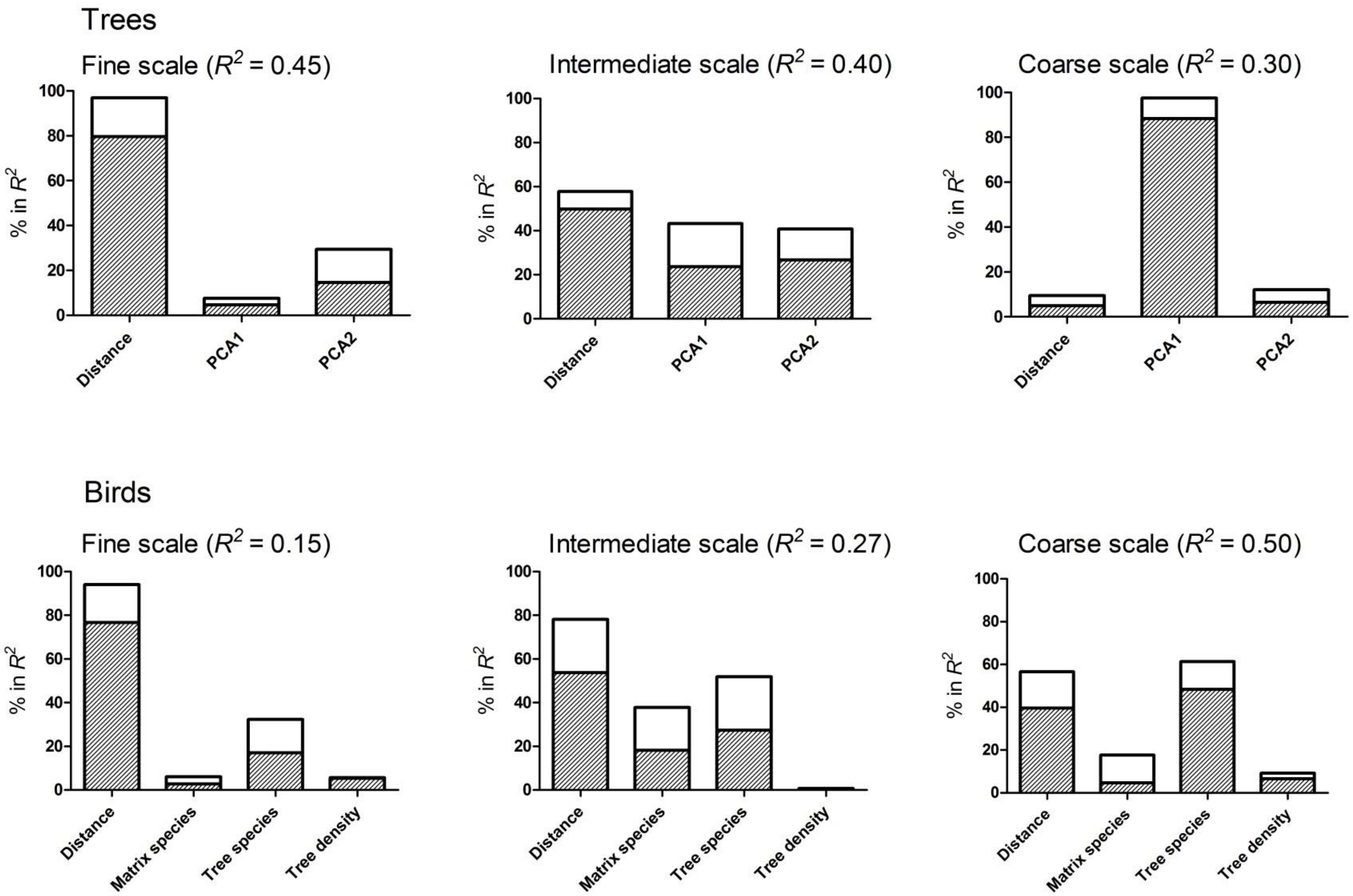
Trees
Fine scale (R^2 = 0.45)
Intermediate scale (R^2 = 0.40)
Coarse scale (R^2 = 0.30)
% in R^2
0
20
40
60
80
100
Distance
PCA1
PCA2
Birds
Fine scale (R^2 = 0.15)
Intermediate scale (R^2 = 0.27)
Coarse scale (R^2 = 0.50)
Matrix species
Tree species
Tree density

Figure 6.2

Chapter 7. General Conclusions

'*along the coast, as well as inland in the gorges between the mountains were wide forests with enormous trees. These forests could only be entered along the elephant paths but not safely without a gun in case one of these colossi happened to pass by…*' F. Krauss describing Durban Bay in 1839 (Skead, 2009).

Coastal forests in South Africa no longer fit the description of Mr Krauss in 1839. Presently some 20 million people (40% of the population) live within 100km of the South African coast (Department of Environmental Affairs, http://www.environment.gov.za/) and forests, woodlands and grasslands have given way to agricultural plantations, cultivations and urban settlements. Efforts to regain these losses and recover the 'unspoiled' past state may not make sense, especially given that the region's population are expected to increase in the coming decades and there are substantial pressures to accelerate economic development (UN, 2012). However, although it may be impossible to recover the forests of yesterday, we can try to conserve the processes that drive forest ecosystems for tomorrow. Conservation plans that focus on coastal forests should therefore be informed, but not controlled by past conditions, be flexible but goal orientated, and be futuristic but realistic.

My goal for this chapter is to provide a critical synthesis of the scientific insights obtained during my study and which can guide our conservation efforts along the coastal plains of South Africa. I base this synthesis on a modified version of the conceptual framework of Gardner *et al.*, (2009). This framework integrates a range of factors that define and contextualize the future of forest species that persist in human-modified landscapes (Fig. 7.1). In the first section, I address the influence of human activities on coastal forest biodiversity. I asses historical deforestation rates and demonstrate how landscape changes influence bird and tree communities. Second, I examine how different ecological and spatial contexts can determine our interpretation of biodiversity patterns. For instance, different species may respond differently to land-use change, and/or species responses may differ depending on the spatial scale at which they were studied. Finally, based on my findings I discuss the conservation opportunities in the human modified coastal forest mosaic. Throughout this chapter, I also draw upon my findings to identify additional research questions that may contribute towards exploiting such opportunities.

Understanding the problem: the influence of human activities on coastal forest biodiversity

Anecdotal accounts and historical reports suggest that South African coastal forests were once more widespread that they are today (e.g. Fourcade, 1884; Skead 2009). However, a reconstruction of historical trends in deforestation is hampered by the lack of relevant information. I therefore opted to use a habitat suitability modelling approach to determine the spatial distribution of coastal forests in the absence of anthropogenic disturbances (Chapter 3) and established that coastal forests could have been more widespread in the past than at present. Indeed, my models suggest that 82% of area suitable for the occurrence of coastal forests is not covered by forests, therefore implying extensive forest loss across the region. My modelling exercise also suggests that these forests have been fragmented for a considerable time, but are now smaller and more isolated than what may have been the case in the past. Furthermore, fragments are now in many instances surrounded by transformed habitats matrices such as sugarcane and agroforestry plantations instead of natural grasslands and woodlands (Chapter 3).

What are the implications of these landscape changes for coastal forest biodiversity? First, the extensive forest loss means that these forests may well harbour an extinction debt

(Chapter 3). Extinction debts are the expected future species losses in response to past habitat loss and can pose a significant, but often unrecognised challenge for biodiversity conservation (Kuussaari *et al.*, 2009). Yet, there are also a number of uncertainties associated with estimates of extinction debts. For instance, some authors have claimed that SARs overestimate extinction debts (He & Hubble, 2011), while others (Hanski *et al.*, 2013; Rybicki & Hanski, 2013) propose that SARs underestimates extinction rates because it assumes contiguous habitat when, in reality, habitat loss is typically accompanied by habitat fragmentation. Furthermore, estimates of extinction debts do not provide information on which species are threatened with extinction, although various studies have assumed that it is those listed as threatened on the IUCN Red List - I explore this issue further in Chapter 5. Given the natural fragmented nature of coastal forests, I suggest that it is unlikely that I have underestimated the magnitude of the extinction debt. However, the species-fragmented area relationship (SFAR) proposed by Hanski *et al.*, (2013) might be used to reduce the existing debt by identifying sites for forest restoration. For instance, in the SFAR modelling framework, the spatial arrangement of habitat fragments determines the magnitude of the extinction debt because it reflects on the metapopulation capacity of the landscape. One could therefore theoretically determine the spatial arrangement of fragments that minimize extinction debt and maximise species credit (e.g. Hanski, 2000). Forest conservation and restoration actions can then be targeted towards achieving such an arrangement of forest fragments. Such an approach may present a robust framework for implementing future restoration efforts, especially if it is combined with predictive models of forest occurrence. The relevance of SARs to predict extinctions is, however, still a contentious issue in ecology as indicated by the titles of recent publications that counter the argument that SARs overestimate extinctions – ‘Extinctions: consider all species’ (Brooks, 2011); ‘Species-area relationships underestimate extinction rates’ (Fattorini & Borges, 2012); ‘Geometry and scale in species-area relationships' (Pereira *et al.*, 2012); 'Conservation: forest fragments, facts, and fallacies' (Pimm & Brooks, 2013). These studies emphasise that the model of He & Hubbell (2011) only considers instantaneous extinctions and not the many more occurring over time as populations dwindle below a threshold where they could persist. The past and present loss of coastal forest habitats may therefore well lead to local extinctions of forest species in South Africa, as is evidenced by the disappearance of forest species such as the spotted ground-thrush (*Zoothera guttata*) and the eastern bronze-naped pigeon (*Columba delegorguei*) from forest fragments where they used to occur in the past (Barnes, 2000).

I did not investigate the influence of invasive species and altered disturbance regimes on coastal forest biodiversity. Yet, it remains an important avenue for future research (Fig. 7.1). For instance, although I found that matrix bird species do not spillover into forests, the altered biotic and abiotic environmental conditions associated with transformed matrices may influence tree community composition within forest fragments by favouring disturbance-favouring early successional trees and climbers as well as invasive plant species such as *Lantana camara* and *Chromolaena odorata* (Chapter 4). These species may homogenize fragment communities by colonizing canopy gaps in the fragment interior (P.I. Olivier, personal observation), disrupt community assembly processes and alter species interactions – however the extent, and under which conditions this may occur remain uncertain.

Understanding the challenge: spatial and temporal context of coastal forest biodiversity in a complex human modified landscape

Coastal forest communities may not only be influenced by the loss of forest extent, but also by the transformation of natural matrix habitats (e.g. grasslands and woodlands) into transformed matrix habitats (e.g. agricultural plantations and urban settlements). Such transformation of matrix habitats that surround coastal forest fragments may disrupt forest communities and influence ecological function (Chapter 4). The effect of landscape change on coastal forest tree and bird species may therefore stretch well beyond forest loss *per se* and the deterministic extinctions predicted by conventional species-area relationships. Natural matrix habitats may facilitate dispersal among forest fragments that maintain metapopulation and metacommunity dynamics, enable species spillover from forest fragments which may drive important ecological functions such as seed dispersal across the landscape, and buffer forest fragment interiors from changes in abiotic conditions associated with a high contrast matrix forest boundary (Chapter 4). As a result, the transformation of matrix habitats may intensify fragmentation impacts. For instance, when coastal forests were embedded within a natural matrix of grasslands and woodlands in southern Mozambique, Guldemond & van Aarde (2010) found no evidence for fragmentation effects or that fragments adhere to the predictions of island biogeography theory (IBT: MacArthur & Wilson, 1967). This finding suggests that when coastal forest fragments are embedded within a natural matrix (e.g. grasslands and woodlands), fragments may function as a continuous ‘forest habitat’. However, it may also indicate that ecological filters have stabilised community composition and that the whole landscape (forest and matrix habitats) is the scale at which species richness is determined. In other words, species found in forests may also be found in the matrix in a variegated landscape (Lawes *et al.*, 2000). Although I did not test these ideas in this study, the study area presents an opportunity for a future investigation where species-area relationships, nestedness, turnover and occupancy dynamics could be compared between fragments located within natural landscapes such as those found in southern Mozambique and fragments located within transformed landscapes such as those found in South Africa. One may expect that fragments located within transformed matrices will conform to island biogeographic predictions of species loss, while fragments embedded within natural matrices will have high richness and evenness across fragments irrespective of size and isolation (e.g.

Wethered & Lawes, 2003). Furthermore, in this thesis, I only considered the influence of two matrix types (natural and transformed) on coastal forest tree and bird communities. In reality, different matrix types may have different effects on forest fragment diversity (Wethered & Lawes, 2003). By examining the influence of different matrix types (e.g. sugarcane, agroforestry, urban and rural settlements) on coastal forest diversity may further enhance our understanding of how land-use changes affect ecological processes that structure communities in human-modified landscapes.

Matrix habitat transformation may also lead to biodiversity changes in coastal forests because generalists that are able to disperse and persist in modified matrices may replace forest specialist species (Chapter 4). However, the effect of such changes in community composition on ecosystem functioning is not clear. For instance, is the black-headed oriole (*Oriolus larvatus*) that persists in modified forests (e.g. Neuschulz *et al.*, 2011) a less effective seed disperser than the dark-backed weaver (*Ploceus bicolor*) that disappear when forests are modified? Empirical studies suggest that it may well be the case (e.g. Sekercioglu, 2006; Mouillot *et al.*, 2011); however, the extent to which such changes to the bird community will eventually affect the long-term sustainability and functionally of coastal forest fragments is yet to be understood. To answer questions such as these, future studies will need to focus on individual species and the proximate mechanisms associated with landscape modification (Fig. 7.1). For instance, does landscape modification influence food and breeding resources for some species but not others? Does landscape modification constrain dispersal for some species and not others? What are the physiological tolerance limits of forest dependent species and does landscape modification cause them to approach that limit?

The interpretation of biodiversity patterns are furthermore complicated by low congruence in species responses to habitat loss and fragmentation across landscapes and study regions (Gardner *et al.*, 2009). This is likely because species do not perceive human-modified landscapes as black and white mosaics of habitat and non-habitat (Haila, 2002). Rather, intrinsic species traits cause bird species to respond idiosyncratically to different habitat fragmentation parameters (i.e. area, connectivity and matrix habitats) (Chapter 5). This finding has at least two important implications. First, it supports the idea that a strict IBT model is a poor predictor of how species respond to habitat change in real landscapes simply because different species perceive habitat and non-habitat in different ways (Didham *et al.*, 2012). Therefore, IBT may accurately describe the responses of some species to habitat loss and fragmentation but not others. Species likely to adhere to strict IBT criteria are those that are forest-dependent, with specialised feeding requirements, small ranges and limited dispersal ability. These species may also face the highest risk of extinction and therefore likely comprise the extinction debt (Chapter 5). Conversely, species that are most likely not to adhere to predictions of IBT are those that are multi-habitat dependent generalists with large ranges and a low probability of extinction. However, it may be unrealistic to expect a single theory to explain diversity patterns across a range of taxa, species and habitats. Indeed, the founders of IBT, Robert MacArthur and Edward O. Wilson (1967) also noted that ‘A good theory points to possible factors and relationships in the real world that would otherwise remain hidden and thus stimulates new forms of empirical research…’ (MacArthur & Wilson, 1967, p.5). A functional approach may therefore well present a more refined and accurate way to enhance scientific understanding of biotic processes driving fragmentation effects in human-modified landscapes. Such an approach can be combined with landscape ecology and its recently recognised counterpart, countryside biogeography. These paradigms recognises the potential opportunities that matrix habitat can afford too many species, and may present a promising research avenue into how species respond to land-use change (e.g. Daily *et al.*, 2003). Second, because intrinsic traits cause species to respond to different fragmentation parameters (e.g. area, connectivity, matrix habitats) modelled estimates of the impact of habitat fragmentation on overall diversity and guild structure that considers habitat fragmentation as a single variable may not be accurate. For instance, a decrease in forest area may lead to a decline of species A, but to a simultaneous increase in species B that rely on non-forest habitats. Considering the different responses of functional groups to different fragmentation and/or land-use change parameters may therefore improve predictions about how communities will respond to global climate change and future land-use scenarios (e.g. Newbold *et al.*, 2014). My assessment of how functional groups respond to forest fragmentation can be further refined by employing a purely species-centred approach. For instance, species distribution models (SDMs) can be used to measure landscapes (e.g. patch size, isolation, matrix habitats) from the perspective of individual species which then offers an opportunity to test whether sensitivity to habitat loss and fragmentation is mediated by phylogenetic, ecological and life-history traits (see Bets *et al.*, 2014).

Our understanding of processes that structure and maintain diversity in human modified landscapes is also constrained by spatial scale (Wills & Whittaker, 2002). For instance, numerous studies have shown that the values of biodiversity metrics such as species richness or evenness are not constant but vary with spatial grain and extent (e.g. Rahbek, 2005; Field *et al.*, 2009). In Chapter 6, I illustrate that tree and bird beta diversity patterns and inferred assembly processes may be a function of the sampling grain at which studies were conducted. As a result, studies with similar sampling effort and temporal sampling protocol, but with different sampling grains are likely to report dissimilar ecological patterns, which may ultimately lead to inappropriate conservation strategies. Inferences from biodiversity patterns may therefore be scale dependent. Sampling scale may, however, not be the only factor influencing inferences from biodiversity patterns. Temporal sampling protocol as well as sampling intensity may affect the interpretation of ecological patterns (Banks-Leite *et al.*, 2012; Banks-Leite *et al.*, 2014). During my study, I employed a standardized fractal sampling design that minimized sampling artefacts and issues of detectability. However, an increase in sampling intensity could potentially lead to more informed inferences from recorded patterns (e.g. Gotelli & Colwell, 2001). This could be achieved by surveying each sampling point multiple times until sampling saturation is reached. The study design would thus remain the same, but sampling intensity will become significantly higher.

Another challenge associated with interpreting biodiversity patterns in coastal forests is the biogeographic complexity of the study area. The relative recent expansion of coastal forests along the east African coast, coupled with the close proximity of coastal scarp and Afrotemperate forest fragments in the hinterland may give rise to intricate patterns that cannot be unravelled by studying coastal forests in isolation from other habitats that make up the coastal plain. For instance, the high rates of bird and tree species turnover in these forests imply co-occurrence of temperate Afrotemperate species and tropical lowland species (Chapter 4 and 6). Furthermore, tree species diversity was strongly associated with latitude, which suggests that diversity increased when conditions became tropical. However, whether climate, local interactions, dispersal constraints, historical contingencies or combinations thereof dictate species distributions remains uncertain (but see Lawes, 1990 and Lawes *et al.*, 2007). Unravelling the ecological processes underlying community structure such as dispersal, speciation and extinction may therefore further contribute to the effective conservation of the biota that constitutes these communities.

Understanding the opportunity: the contribution of biodiversity conservation science in conserving biodiversity in the human modified coastal forest mosaic

The recognition of an extinction debt offers a window of conservation opportunity during which it is possible to restore habitat or implement alternative measures to safeguard the persistence of species otherwise committed to extinction (Wearn *et al.*, 2012). However, my findings suggest that a broad 'what works for one will work for all' approach to biodiversity conservation in coastal forests may not have the desired effect of halting predicted extinctions. This is because different species and taxa respond to different fragmentation parameters and are structured by different community assembly processes. For instance, niche-based assembly processes, that require a local conservation focus, may structure the bird community, while dispersal-based assembly processes, that require a regional conservation focus, may structure the tree community (Chapter 6). The high levels of turnover observed among forest fragments for both tree and bird communities furthermore suggest that every fragment contributed to regional diversity and should ideally be incorporated within conservation plans (Chapter 4 and Chapter 6). I therefore suggest that all large and small coastal forest fragments in the study area should be protected, especially those that are clustered together. This should ensure that networks of fragments that have strong biological connectivity are favoured around remaining forest fragments. Coastal forest conservation may furthermore benefit from a regional landscape complementation approach where conservation efforts do not only focus on forest fragments but also on the matrix habitats directly adjacent forest fragments. The conservation of natural matrix habitats such as grasslands, bushlands and woodlands around forest fragments may buffer forest communities from impacts associated with high contrast forest edges, enhance natural plant regeneration through species spillover, provide important linkages between forest fragments, boosts regional diversity and allow coastal forests to track environmental change. Such an approach may cater for species persistence rather than static biodiversity patterns because it takes into account the highly dynamic nature of the coastal forest landscape mosaic, with respect to both internal biodiversity processes and cross-scale human-ecological interactions. This is particularly important given the threat of ongoing climate change.

Although preventing forest loss and degradation should be our first priority, coastal forest restoration presents a valid and legal land-use option, which is ecologically attractive and sustainable (van Aarde *et al.*, 2014). The aim should be for local restoration actions to aggregate into a regional context that considers landscape connectivity. For instance, at the landscape level restoration can be used to complement the existing protected area network. Furthermore, because coastal forests are fragmented, actions to establish linkages between existing forest patches should be a priority. These linkages could consist of regenerating forests or natural grasslands or woodlands that may maintain natural processes such as dispersal and colonization across the region.

The benefit of restoring degraded forests, and conserving intact ones spreads wider than for coastal forests alone or for South African forests in general, or even beyond our boundaries (van Aarde *et al.*, 2014). The current rate of deforestation constitutes a major global biodiversity crisis that influence ecological services (such as biodiversity and coastline protection), the loss of many goods (such as timber and non-timber forest products) as well as the loss of means of existence for forest dwelling people (Lamb *et al.*, 2005). However, in this thesis I have shown that amid the challenges that face coastal forests, there are also opportunities for biodiversity conservation. By continuing to use science to unravel ecological drivers, and the influence of landscape change on forest diversity, we can plan and implement efficient conservation strategies to assure the persistence of forest species in human-modified landscape mosaics.

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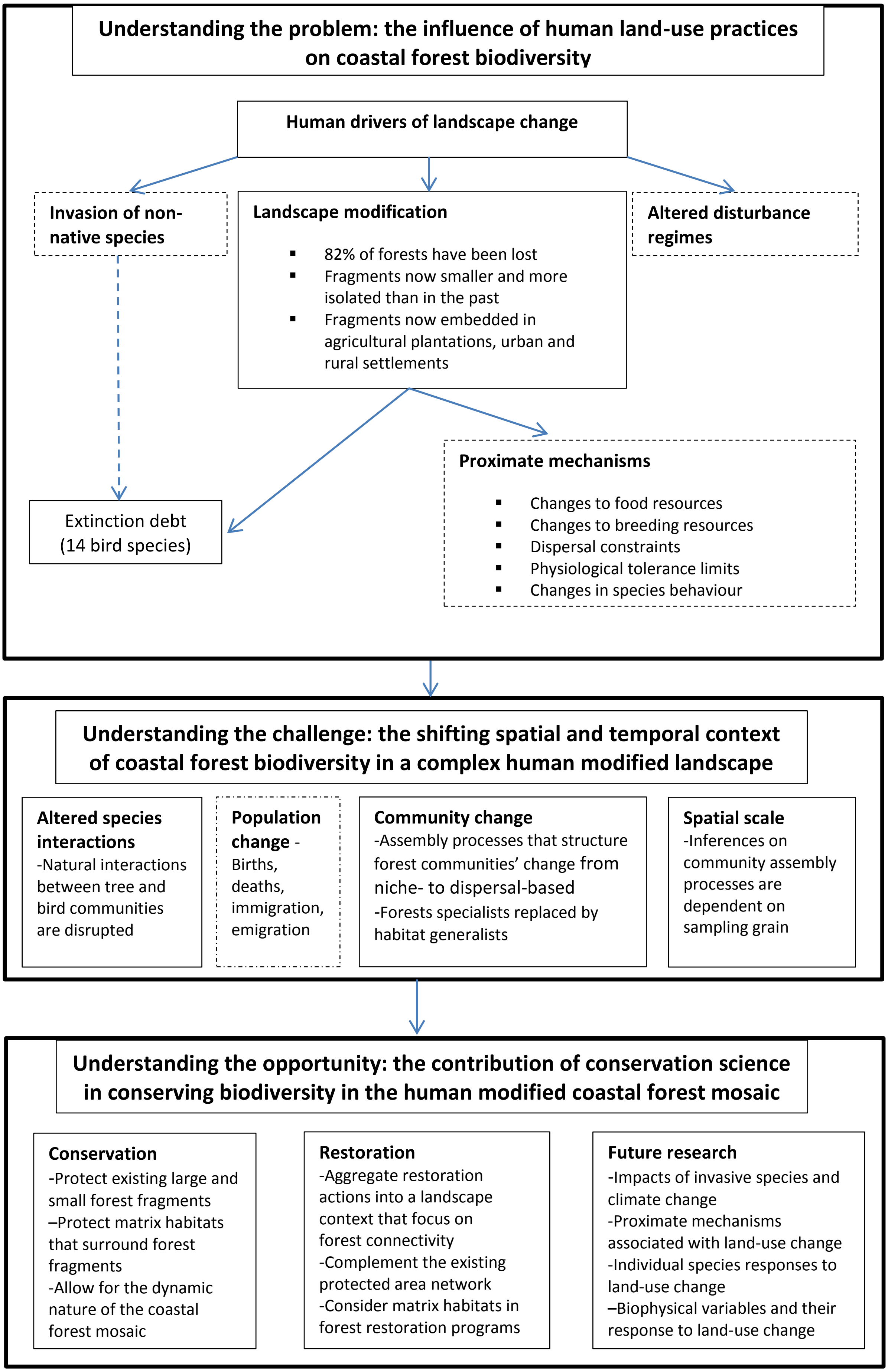

Understanding the problem: the influence of human land-use practices on coastal forest biodiversity

Human drivers of landscape change

Invasion of non-native species

Landscape modification

- 82% of forests have been lost
- Fragments now smaller and more isolated than in the past
- Fragments now embedded in agricultural plantations, urban and rural settlements

Altered disturbance regimes

Extinction debt (14 bird species)

Proximate mechanisms

- Changes to food resources
- Changes to breeding resources
- Dispersal constraints
- Physiological tolerance limits
- Changes in species behaviour

Understanding the challenge: the shifting spatial and temporal context of coastal forest biodiversity in a complex human modified landscape

Altered species interactions
-Natural interactions between tree and bird communities are disrupted

Population change - Births, deaths, immigration, emigration

Community change
-Assembly processes that structure forest communities' change from niche- to dispersal-based
-Forests specialists replaced by habitat generalists

Spatial scale
-Inferences on community assembly processes are dependent on sampling grain

Understanding the opportunity: the contribution of conservation science in conserving biodiversity in the human modified coastal forest mosaic

Conservation
-Protect existing large and small forest fragments
–Protect matrix habitats that surround forest fragments
-Allow for the dynamic nature of the coastal forest mosaic

Restoration
-Aggregate restoration actions into a landscape context that focus on forest connectivity
-Complement the existing protected area network
-Consider matrix habitats in forest restoration programs

Future research
-Impacts of invasive species and climate change
-Proximate mechanisms associated with land-use change
-Individual species responses to land-use change
–Biophysical variables and their response to land-use change

Figure 7.1. The conceptual framework of Gardner *et al.*, (2009) modified to reflect how the information presented in this thesis have contributed to our understanding of how landscape characteristics and disturbance history affect biodiversity patterns, ecological processes, and ultimately conservation actions in the coastal forest landscape mosaic. Solid squares display answers to the questions posed in Chapter 1 and elaborated upon in succeeding chapters. Dashed squares reveal research areas that still require further investigation.