Biodiversity in Human-Modified Landscapes: Case Studies, the State of Research, and Implications for Conservation

by

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Declaration

I, **Morgan Jayne Trimble**, declare that the 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:

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Disclaimer

This thesis includes several manuscripts that were prepared for submission to different scientific, peer-reviewed journals. Referencing has been standardized, but styles differ somewhat according to journal specifications.

Morgan J. Trimble

“The last word in ignorance is the man who says of an animal or plant, "What good is it?" If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering.”

― Aldo Leopold*, Round River: From the Journals of Aldo Leopold*

Dedication

To my parents, Bruce and Renee Trimble.

Biodiversity in Human-Modified Landscapes: Case Studies, the State of Research, and Implications for Conservation

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Abstract

Protected areas (PAs) cover 12.9% of Earth's land, while just 5.8% has strict protection for biodiversity (Earth's variety of ecosystems, species, and genetic variation). Constraints of size and configuration, mismanagement, anthropogenic pressure, and climate change hamstring the capacity of PAs to conserve biodiversity. Increasingly, studies of biodiversity in human-modified landscapes provide an evidence base to support policies to make land outside of PAs as amenable as possible for biodiversity persistence.

I reviewed research on biodiversity in sub-Saharan Africa's human-modified landscapes within four ecosystem categorizations: rangelands, tropical forest, Cape

Floristic Region, and urban and rural built environment. I found potential for human-modified landscapes to contribute to conservation across ecosystems. Available research could guide policy-making; nonetheless, several issues require further investment, e.g. research deficiencies, implementation strategies, and conflict with biodiversity.

I also conducted case studies that could support land-use planning in South Africa's coastal forest, part of a biodiversity hotspot. By comparing herpetofaunal communities over a land-use gradient, I found old-growth forest harbored the highest richness and abundance. Richness was low in sugar cane cultivation and degraded forest but substantial in acacia woodland and eucalyptus plantation. Composition differed between natural and anthropogenic vegetation types. Functional group richness decreased monotonically along the gradient, driven by sensitivity of fossorial herpetofauna and vegetation-dwelling frogs. Environmental variables were good predictors of frog abundance, but less so for reptiles. Maintaining forest and preventing degradation is important for herpetofaunal conservation while restoration and plantations have more value than cultivation.

Old-growth remnants and post-disturbance regenerating vegetation also provide habitat for birds. However, occurrence does not ensure persistence. I calculated population trends for 37 bird species and general trends in overall bird density in different vegetation types. Seventy-six percent of species assessed have declined, 57% significantly so at an average rate of 13.9% per year. Overall, bird density fell at 12.2% per year across vegetation types. Changes in rainfall, habitat area, and survey coverage may partly explain trends. However, species with larger range extents declined more sharply than others and may be responding to environmental changes on a broad scale. These results cast doubt on the future persistence of birds in this human-modified landscape and justify further study.

Such studies can support sensible land-use management; however, biases in study topics should not lead to gaps in the evidence base. By reviewing the global literature, I demonstrated clear geographical bias among biomes and geopolitical regions and taxonomic bias among species groups. Furthermore, distribution of published papers did not generally reflect threats of low PA coverage, high land conversion, and high human population density. Forests were the subject of 87% of papers, and 75% focused on the Americas and Europe, while Africa and Asia were critically understudied.

This thesis highlights that managing human-modified landscapes for biodiversity could contribute to conservation. However, responses to land uses are complex, location- and species-specific, and often poorly understood, hindering integration of information into policy recommendations. Further research is needed to elucidate what, where, and how biodiversity persists alongside humans to enhance conservation efficacy, especially in understudied regions.

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This work is the result of three years' worth of ideas, sweat, blood, and coffee. I'm grateful for the support from the colleagues, friends, family, and organizations that allowed me to create this thesis—for the most part with aplomb, punctuated only occasionally by panic and despair (or so I would like to remember it).

Much credit is due to my supervisor, Professor Rudi van Aarde. Without his inspiring dedication to his work and contagious passion for conservation biology, I would not have pursued this project or, very likely, a PhD at all. Thank you for setting such an example, and for the support, opportunities, expectations, trust, encouragement, and, most of all, wisdom.

Thanks also to my family, especially my parents, Bruce and Renee, who are unbelievably supportive. I'm grateful for a family that values learning, exploration, experiences, and fulfillment beyond more traditional metrics of success. Nevertheless, making you proud means a lot to me.

The Conservation Ecology Research Unit (CERU) has been a family away from home since I moved to South Africa seven years ago. Thanks especially to Lilian Scholtz for taking care of me so kindheartedly. Many CERU colleagues, current and former, helped me on my academic journey, via mentoring, commiserating, or most commonly, a combination of the two. Dr Sam Ferreira, Jo Fourie, Dr Rob Guldemond, and Dr Tim Jackson provided valuable guidance, and my time as a student was greatly enriched by Shaun D'Araujo, Alida de Flamingh, Dr. Matt Grainger, Jessi Junker, Tamara Lee, Oscar Mohale, Michael Mole, Dr Cornelio Ntumi, Pieter Olivier, Laura Owens, Andrew Purdon, Ashley Robson, Natasha Visser, Dr Kim Young, and the other students who have been a part of CERU. I am also grateful for many friends, both old and new, for providing encouragement, perspective, and frequent laughs.

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Chapter 1. General Introduction

Conservation biology has flourished as a discipline over the past four decades in step with the threat humanity's activities pose to biodiversity, the variety of genetic material, species, and ecosystems on Earth. The so-called biodiversity crisis has ethical, aesthetic, and utilitarian consequences, the relative importance of which, if any, can be argued ad infinitum. Beyond question, however, is the unprecedented scale of human influence on nature and dominance over other species. Humanity has commandeered more than 40% of Earth's land surface for crops and pastures alone, and demand will grow (Millennium Ecosystem Assessment 2005). Already by 1995, 83% of land on Earth was directly influenced by humans as indicated by significant human population density, conversion to agriculture, proximity to transport networks, and nighttime light visible to satellites (Sanderson et al. 2002, Kareiva et al. 2007). This pervasive human footprint "suggests that human beings are stewards of nature, whether we like it or not" (Sanderson et al. 2002).

The declaration of protected areas to maintain slices of the wild has been the backbone of the conservation movement. Formally, a protected area is: "a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" (Dudley 2008). Often, conservation of biodiversity within protected areas is achieved by strict control over human access (Dudley 2008). However, a persistent undercurrent encouraging a greater integration of conservation efforts *within* landscapes dominated by humans has long inspired many conservation biologists. Perhaps Aldo Leopold's "Land Ethic" from *A Sand County Almanac* is the most famous early example

(Leopold 1949), but the sentiment of managing landscapes where humans live, work, and extract resources in a manner that attempts to cater for biodiversity persistence has been repeated with urgency (for the foundational literature of this renewal, see Daily 1999, Daily et al. 2001, Rosenzweig 2003) in more recent publications (e.g. Ranganathan et al. 2008, DeClerck et al. 2010, Koh and Gardner 2010).

Scientific interest in the biodiversity of human-modified landscapes has recently escalated for two predominant reasons. First, there is increasing recognition that protected areas alone are far from sufficient to conserve much of the world's biodiversity in the long term (Mora and Sale 2011). At the species level of biodiversity, species–area relationships indicate that as people make increasing areas of land inhospitable to other species, they inflict a linear reduction on the number of species Earth can support (Rosenzweig 2003). That is, if we protect some benchmark percentage of land for nature, e.g. 10% of Earth's terrestrial surface (see Brooks et al. 2004), and species cannot persist in the unprotected 90%, we can expect global species loss of 90% of the original steady-state diversity (Rosenzweig 2003). Richness above the predicted levels maintained in protected areas would be temporary, representative of an unpaid extinction debt (Kuussaari et al. 2009). Mismatches between priority areas in need of conservation and the actual configuration of the world's protected areas create problems (Joppa and Pfaff 2009, Jenkins et al. 2013); moreover, protected areas might not even conserve the meager percentage of species we expect them to given their area. Ill-conceived management interventions (e.g. Konvicka et al. 2008), inadequate protection from outside influences (Joppa et al. 2008, Newmark 2008), and climate change (Loarie et al. 2009) could all result in extinctions, even within protected areas (see Newmark 2008).

Second, evidence suggests that encouraging the persistence of biodiversity beyond protected areas will be important for maintaining ecosystem function, and thus, ecosystem services valuable to society (Balvanera et al. 2006, Cardinale et al. 2012). Pollination, pest control, decomposition, and nutrient cycling are examples of ecosystem services which are important in production landscapes and contribute to economic value yet depend to varying degrees on biodiversity maintenance (Tscharntke et al. 2005). Globally, too, humanity depends on important services provided by nature including waste treatment, and water and climate regulation (Turner et al. 2007).

Research on what, why, and how different components of biodiversity are able to persist in different human land uses, under different management regimes, and in various ecosystem types could support land-use planners and land managers that seek to make the best possible decisions in support of biodiversity in a framework of evidence-based conservation (Sutherland 2004). This is especially relevant in rapidly developing landscapes where human activities are both extensifying and intensifying to support growing populations and economies and could have dramatic consequences for biodiversity. Such is the case in Africa, and thus, in Chapter 2, I aim to qualitatively discuss the current state of research on biodiversity of human-modified landscapes in sub-Saharan Africa in relation to predominant land uses in four major ecosystem types: the extensive rangelands, the relatively well researched tropical forests, the biologically rich Cape Floristic Region, and the rapidly developing urban and rural built environment. This review paper presents the available research and discusses opportunities and constraints for further research and implementation.

In Chapter 3 (currently under review for publication), I present a case study detailing patterns of herpetofauna occurrence over a land-use intensification gradient from relatively undisturbed, old-growth coastal forest to degraded forest, regenerating forest (i.e. acacia woodlands), eucalyptus plantations, and sugar cane cultivation. Besides traditional metrics (i.e. abundance, richness, diversity, and community composition), I also categorize frog and reptile species into trait-based functional groups to better understand community responses to land use.

However, species occurrence in human-modified landscapes is not necessarily indicative of persistence. For example, research suggests that “ecological traps”, highly attractive habitats that are of low quality, may be relatively common in human-modified landscapes (Battin 2004). Although they result in low fecundity and survival, they attract individuals from surrounding high quality habitats through mismatched environmental cues with the predicted consequence of near certain population extinction (Battin 2004). Therefore, simply recording a species in a given land-use type may lead to the incorrect assumption that the human-modified land provides suitable habitat for the species. It is important, then, to assess species’ likelihood for persistence through more thorough assessment of reproduction and survival, or their consequence, population trend. Therefore, in Chapter 4 (published in January 2011 in the journal *PLoS ONE*) I aim to provide a case study that assesses trends for bird populations in a human-modified coastal dune forest landscape in South Africa. I assess population trends for 37 bird species and general trends in overall bird density in different vegetation types based on a 13-year monitoring database. I also assess species’ characteristics as potential covariates for population trends.

These two case studies are examples of the type of research that can support evidence-based conservation by indicating the consequences of particular land uses within a given ecosystem for specific components of biodiversity. On a global scale, conservation efforts beyond protected areas could benefit from a reliable, relevant evidence base, so in Chapter 5 (published in December 2012 in the journal *Ecosphere*), I present a systematic review of the global literature on biodiversity in human-modified landscapes. The intent of this assessment is to illustrate whether the evidence base is biased geographically among biomes or geopolitical regions and taxonomically among species groups. Furthermore, I assess how biases relate to geographic characteristics (i.e. area, biome type, species richness, human population density, proportion of transformed land, and an index of conservation importance) and, taxonomically, to the number of described species per group. Chapter 6 presents a general discussion of the thesis and its outcomes and, along with Chapter 5, includes ideas for future work.

As a PhD student at the University of Pretoria, I have had the opportunity to work on several projects beyond my formal thesis chapters. In part, my interest in the topic of conservation beyond protected areas was sparked by a controversial article published in *BioScience* (Licht et al. 2010) promoting the use of South African predator conservation tactics to protect wolves *Canis lupus* in the United States. The journal published my response, which encouraged greater consideration for the ecological consequences of fencing (Trimble and Aarde 2010); fencing continues to be a controversial topic within the conservation community (Creel et al. 2013, Packer et al. 2013). Given the relevance, I include this response here as Appendix 1. In conducting the field research for Chapter 3, I carried out a preliminary investigation into the use of polyvinyl chloride pipes for trapping

African vegetation-dwelling frogs and showed for the first time on the continent that it could be successful, although capture rate was low. A note on the study is included as Appendix 2 and was published in the *African Journal of Ecology* (Trimble and van Aarde 2013). I was also first author on a paper that adapted age assessment techniques for Africa elephants *Loxodonta africana* to aerial based surveys; it was published in October 2011in *PLoS ONE* (Trimble et al. 2011). With coauthors Robert Guldemond and Matthew Grainger, I published a response article in *Restoration Ecology* discussing the evidence base for ecological restoration projects in South Africa (Guldemond et al. 2011). I also coauthored a paper with Kim Young and Professor van Aarde on density dependence in elephant populations, which is currently under review.

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Chapter 2. Supporting Conservation with Biodiversity Research in Sub-Saharan Africa's Human-Modified Landscapes

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Abstract

Protected areas cover 12% of terrestrial sub-Saharan Africa. However, given the inherent inadequacies of these protected areas to cater for all species in conjunction with the effects of climate change and human pressures on protected areas, the future of biodiversity depends heavily on the 88% of land that is unprotected. The study of biodiversity patterns and the processes that maintain them in human-modified landscapes can provide a valuable evidence base to support science-based policy-making that seeks to make land outside of protected areas as amenable as possible for biodiversity persistence. I discuss the literature on biodiversity in sub-Saharan Africa's human-modified landscapes as it relates to four broad ecosystem categorizations (i.e. rangelands, tropical forest, the Cape Floristic Region, and the urban and rural built environment) within which I expect similar patterns of biodiversity persistence in relation to specific human land uses and land management

actions. Available research demonstrates the potential contribution (and potential failures) of biodiversity conservation in human-modified landscapes within all four ecosystem types and goes some way towards providing general conclusions that could support policy-making. Nonetheless, conservation success in human-modified landscapes is hampered by constraints requiring further scientific investment, e.g. deficiencies in the available research, uncertainties regarding implementation strategies, and difficulties of coexisting with biodiversity. However, information currently available can and should support efforts at individual, community, provincial, national, and international levels to support biodiversity conservation in human-modified landscapes.

Introduction

Conservation of biodiversity in Africa, like elsewhere, has historically focused on the fortress model, whereby most protected areas (PAs) were declared to the exclusion of people (see Adams and Hulme 2001, Siurua 2006, Carruthers 2009). Though PAs are essential for conservation success, they are unlikely to be sufficient (Rosenzweig 2003). For example, large mammal populations have been reduced by half in some African PAs since 1970 (Craigie et al. 2010), probably due, in part, to increasing isolation of PAs (Newmark 2008). Weak enforcement and ineffective management plague many of Africa's current PAs (Kiringe et al. 2007, Metzger et al. 2010, Pare et al. 2010), and many also fail to cater to species with extensive spatial requirements, e.g. migratory animals (Thirgood et al. 2004, Kirby et al. 2008, Western et al. 2009, Holdo et al. 2010) and elephants *Loxodonta africana* (van Aarde and Jackson 2007). Even small-bodied species are not necessarily safe-guarded (Pauw 2007). Additionally, the configuration of PAs within the continent neglects key areas for biodiversity (Chown et al. 2003, Fjeldsa et al. 2004, Fjeldsa and Burgess 2008, Eardley et al. 2009, Beresford et al. 2011), a problem that may escalate if climate change makes PAs inhospitable to species they once protected (Loarie et al. 2009). If species' ranges shift with shifting climate, the areas crucial for their persistence will be transient (Hole et al. 2011). Furthermore, the scale of beta-diversity and habitat heterogeneity often extends far beyond that of individual PAs (Gardner et al. 2007), and human activities beyond PAs influence biodiversity within them (Hansen and DeFries 2007).

Therefore, there are calls for an increased focus on biodiversity beyond African PAs (e.g. Eardley et al. 2009) on two fronts. First, conservation of some biodiversity elements depends on how well the matrices outside of PAs cater for persistence. At the species level, for example, the Blue Crane *Anthropoides paradiseus* in South Africa (McCann et al. 2007), Ethiopia's critically endangered Sidamo lark *Heteromirafra sidamoensis* (Spottiswoode et al. 2009, Donald et al. 2010), and the last giraffes *Giraffa camelopardalis peralta* in West Africa (Ciofolo 1995) all depend on human-modified landscapes. At the ecosystem level, three biomes fall below the threshold 10% protection status within the Afrotropic realm, i.e. tropical and subtropical dry broadleaf forests (6%), montane grasslands and shrublands (8%), and deserts and xeric shrublands (9%), while several ecoregions are < 5% protected, especially when limited to the IUCN I-IV categories, e.g. Southern Congolian forest-savanna mosaic (0%), Angolan montane forest-grassland mosaic (0%), and highveld grasslands (<1%) (Jenkins and Joppa 2009). Second, there are important links between biodiversity and ecosystem function, ecosystem services, and human livelihoods in working landscapes (Daily et al. 2001, Rosenzweig 2003). For example, maintaining natural habitat in and around farms can enhance pollination and, thus, has an economic value to production landscapes (Carvalheiro et al. 2010, Munyuli 2012), and natural systems in Africa provide economic and nutritional benefits to both rural and urban dwellers (Schreckenberg 1999, Vanderpost 2006, Tabuti et al. 2009).

Even though, globally, scientists have neglected the biogeography of human-modified landscapes in sub-Saharan Africa, ecologists are increasingly studying the capacity of such landscapes to support biodiversity (Trimble and van Aarde 2012). Such studies are required in order for policy-makers to make defensible decisions regarding land use in relation to biodiversity conservation in the face of rapid economic development in Africa. Agriculture in Africa has been characterized by traditional, labor-intensive, smallholder enterprise; production has been low and has remained relatively stagnant (Abate et al. 2000, Deininger et al. 2011). However, economic development and population growth are driving change in African landscapes; several Africa nations sit among the world's fastest growing economies (IMF 2013). In 2009, the population reached 1 billion and is predicted to double by 2050 (UN-HABITAT 2010). Urbanization is a strong force in Africa; 40% of the current population is city-dwelling, and by 2050, 60% will be urban (UN-HABITAT 2010). Even so, the rural population will also grow substantially, predicted to increase by nearly 50% by mid-century (UN Population Division 2012), while growing urban centers will depend heavily on rural resources. To meet this demand, and in the interest of improving food security, there are calls for both intensifying smallholder agriculture (Muriuki et al. 2005, Baiphethi and Jacobs 2009, Snapp et al. 2010, Baudron et al. 2011) and extensifying production (Muriuki et al. 2005).

Therefore, the interest in biodiversity in human-modified lands is timely. Although Africa's natural ecosystems are more intact than many other regions', a proactive approach to biodiversity conservation that strives for the most prudent management of the unprotected matrices between PAs is clearly preferable to trying to reconnect and restore already degraded ecosystems (Gardner et al. 2010). Thus, as policy-makers chart the future course of development in Africa, they should consider the effects of different choices on biodiversity in human-modified lands, what steps can be taken to prevent biodiversity loss, and the benefits and costs of biodiversity persistence to people. Studies of biodiversity patterns and the processes that maintain them in human-modified landscapes provide an evidence base to support defensible management decisions that meet the needs of people and biodiversity simultaneously. The evidence base should, furthermore, provide for relevant ecological contexts. For example, management standards for timber plantations aim to minimize impact on biodiversity in surrounding natural forests. Yet, the same standards have been applied in plantations embedded in grasslands with dubious efficacy for minimizing impacts on grassland biodiversity (Pryke and Samways 2003, Lipsey and Hockey 2010).

This scientific focus on biodiversity in human-modified landscapes is distinct from Africa's thirty-some-year experiment in community-based conservation (CBC, but also known as Integrated Conservation and Development Projects, Community-Based Natural Resource Management, and others), but these two fields can and should be amalgamated. Promoters of CBC claim that it increases the chance of conservation success and simultaneously reduces rural poverty by allowing community involvement in management and profit from natural resources, especially large mammals (see Hackel 1999). The philosophy of linking wildlife conservation and rural economic development and the practical successes and failures therein have been discussed in a large body of literature (e.g. Hackel 1999, Songorwa et al. 2000, Torquebiau and Taylor 2009). However, the discussion has focused on socioeconomics and politics with fleeting consideration for assessing actual biodiversity persistence under different CBC models, a problem pointed out by Caro (1999) and subsequently largely ignored.

In this review, I aimed to elucidate the current state of knowledge regarding biodiversity in sub-Saharan Africa's human-modified landscapes. I separate the discussion into four major ecosystem types (see Fig. 2.1) within which I expect similar patterns to emerge. 1) Rangelands attract the bulk of the attention as Africa's biggest ecosystem type, and rangeland biodiversity is perhaps the most compatible with human land-uses, so biodiversity-conscious land-use planning in rangelands could yield huge benefits. 2) Tropical forests are discussed briefly with a focus on Central and East African forests, and I refer readers to an excellent review of the abundant literature from West Africa (Norris et al. 2010). 3) The Cape Floristic Region, though small, is extremely rich in species yet threatened by extensive commercial development, and I discuss a growing body of literature on land-use management in the region. Finally, 4) the urban and rural built environment will become an increasingly important concern for biodiversity conservation in Africa where the increase of urban land cover is predicted to be the highest in the world at nearly 600% in the first three decades of the 21st century (Seto et al. 2012); proper management and infrastructure development could attenuate the consequences for biodiversity. Furthermore, I discuss the constraints and opportunities for future progress of biodiversity conservation in human-modified landscapes of Africa.

Methods

Literature search

I searched the ISI Web of Knowledge (up to 2012) with keywords “Africa” and “biodiversity or conservation” and each of the following terms: “agricultur*”, “agroforestry”, “communal”, “farm*”, “game farm”, “game ranch”, “human-modified”, “multiple-use management”, “peri$urban”, “private nature reserve”, “range$land”, “rural”, “suburban”, and “urban”. I also searched for the terms “countryside biography”, “reconciliation ecology”, “off-reserve conservation” (see Daily et al. 2001, Rosenzweig 2003). Additionally, I included relevant papers found coincidentally or in reference lists.

Biodiversity in Human-Modified Landscapes of African Ecosystems

Rangelands

Two-thirds of sub-Saharan Africa is composed of rangelands (Fig. 2.1), consisting of arid and semi-arid grasslands, woodlands, savannas, shrublands, and deserts. The rural people inhabiting rangelands are typically agropastoralists, combining small-scale farming and livestock keeping, or specializing in either farming or herding. Some agricultural practices in rangelands may be harmful to biodiversity, e.g. overcultivation, overgrazing (Kerley et al. 1995), bush fires, cultivation of marginal and easily eroded land, and widespread use of chemicals and pesticides (Darkoh 2003). Many people in rangelands also depend heavily on wild resources, e.g. via hunting and gathering or by profiting from wildlife tourism

(Homewood 2004). Game ranching is an increasingly popular land-use option across African rangelands (McGranahan 2008), and so are "eco-estates" (Grey-Ross et al. 2009a) as people choose to live amongst the natural beauty of African rangelands and their considerable species diversity, especially charismatic large mammals.

The ecological mechanisms that maintain different rangeland types in different locations, e.g. grassland versus woodland, are not fully understood though interactions between soils, climate, fire, herbivory, and human disturbance are thought to be important (see Bond and Parr 2010) . The biggest threats to grasslands include afforestation or bush encroachment and clearing for agriculture (Bond and Parr 2010), while threats to the woodlands include woodcutting, clearing for agriculture, and over-use (Schreckenberg 1999, Tabuti 2007). Many perceive that biodiversity is declining in rangeland systems; they blame poor agricultural practices, land conversion, and over-utilization of wild resources by rural people and worry that these patterns will increase with population growth (e.g. Darkoh 2003, Thiollay 2006). However, documented evidence of biodiversity loss in rural rangelands is sparse. Of course, many areas have likely lost some species, but surprisingly, long-inhabited regions lacking formal PAs, e.g. Kenya's Laikipia district, maintain abundant wildlife including large carnivores and elephants (Gadd 2005, Kinnaird and O'Brien 2012) that might seem at odds with human occupation (Woodroffe et al. 2007). Rangeland systems are often characterized by disturbances such as fire, unpredictable rainfall, grazing and browsing pressure, and physical disturbance. Therefore, rangeland biodiversity may be relatively resilient to anthropogenic disturbance due to the ability to disperse, colonize, and persist in patchy and fluctuating environments (Homewood 2004).

Thus, human-modified landscapes have the potential to maintain a relatively large portion of rangeland biodiversity (see Scholes and Biggs 2005).

Nonetheless, conservation in rangelands has traditionally excluded people from designated PAs. In South Africa, for example, conservation planning often dichotomizes "human land-use" and conservation with little consideration for different land-use options that may be variably amenable to biodiversity (e.g. Chown et al. 2003, Wessels et al. 2003). On the other hand, some authors have called to "mainstream" conservation into human-modified lands (e.g. Soderstrom et al. 2003, Pote et al. 2006). O'Connor and Kuyler (2009) used expert opinion to rank the impact of land uses in moist grasslands on overall biodiversity integrity (in order from least to most impact: conservation, game farming, livestock, tourism, crops, rural, dairy, timber, and urban). Empirical studies are amassing to assess such assertions, which could support land-use planning for conservation. Here I discuss emerging research on biodiversity in several of the most common rangeland land uses.

Grazing

Grazing is important to the maintenance of grassland and savanna habitats, economic development, and management for biodiversity. However, plant responses to grazing are idiosyncratic and incompletely understood (see Watkinson and Ormerod 2001, Rutherford et al. 2012). Overgrazing can lead to degradation and bush encroachment (the slow proliferation of woody plants at the expense of grasses), while too little grazing can result in succession to woodland (Watkinson and Ormerod 2001). Of course, grazing effects on vegetation can affect higher trophic levels as well, so it is important to understand vegetation responses to grazing, not only for livestock production, but also because vegetation dynamics affect many other species. However, not all grazing landscapes are alike; unique vegetation dynamics in different ecosystems mean that different landscapes respond differently to grazing pressure (Todd and Hoffman 2009).

Research is emerging that investigates aspects of grazing management and biodiversity in Africa; I summarize 30 such studies in Table S.2.1. Generally, these studies look at grazing intensity, or proxies such as bush encroachment, and show that many wild species may be maintained depending on management and location. For example, traditional pastoral practices, i.e. burning and boma creation, may even be necessary to maintain avian diversity in some East African savanna areas (Gregory et al. 2010). Contrastingly, bush encroachment due to overgrazing in Ethiopia may provoke Africa's first avian extinction (Spottiswoode et al. 2009, Donald et al. 2010).

Table S.2.1 shows that only about a third of studies compared biodiversity of livestock grazing landscapes to controls with indigenous grazers such as PAs. Most studies came from South Africa (67%) and most assessed grazing effects on plants (43%) or insects (27%). Many areas of investigation remain open, such as the role of vegetation structure including keystone, isolated trees in maintaining biodiversity in human land-use areas; such trees are important for maintaining diversity in natural systems (Dean et al. 1999). A common conclusion with regards to plant diversity is that spatial heterogeneity in grazing management that includes PAs will enhance gamma diversity because different species thrive at different grazing intensities (e.g. Fabricius et al. 2003).

Agricultural mosaic

While extensive grazing is common in arid-savannas and xeric shrublands, an agricultural land-use mosaic of grazing and cropping interspersed with settlements is common in more mesic savannas and grasslands. This mosaic effect may have important consequences for the maintenance of biodiversity, and studies of biodiversity in agricultural mosaics (24 studies summarized in Table S.2.2) identify some common themes. Compared to strict PAs, agricultural mosaics may actually be beneficial to some species groups. For example, Caro (2001) illustrated greater diversity and abundance of the small mammal assemblage in the agricultural matrix outside Katavi National Park, Tanzania than inside, a pattern that also holds for Niokolo Koba National Park, Senegal (Konecny et al. 2010). Richness of birds, amphibians, small mammals, butterflies, and trees is similar at 41 sites across a land-use gradient from Katavi National Park to non-intensive agricultural land; however, composition changes along the gradient, and although the PA holds some unique species, some species found outside the PA are absent within (Gardner et al. 2007). Thus, agricultural mosaics may contribute to greater gamma diversity at the landscape scale; nonetheless understanding the conservation implications of higher gamma diversity may require a regional or global perspective on species rarity and commonness.

It is a common finding that agricultural intensification (e.g. mechanization of agriculture, shortening fallows, destruction of remnant habitat patches, and introduction of cash crops) can have detrimental effects on the biodiversity value of agricultural mosaics. The mosaic effect of traditionally managed farms in KwaZulu-Natal, South Africa may support, and even enhance, bird diversity (Ratcliffe and Crowe 2001), but intensification results in species declines due to loss of "edge" habitats. In Burkina Faso, common butterfly species occur in cultivated areas, while specialists are more common in old fallows and grazed areas, probably because grazing maintains host plants and, thus, diversity (Gardiner et al. 2005). In this case, an agricultural mosaic of shifting fallows could support butterfly meta-populations that allow species persistence, while intensification could be detrimental (Gardiner et al. 2005). In Ethiopian grasslands, low-intensity agriculture supports moderate plant diversity, while larger-scale, mechanized farms reduce tree cover and diversity (Reid et al. 1997). Similarly, In the Serengeti-Mara ecosystem, commercial mechanized agriculture is associated with declining wildlife populations (Homewood et al. 2001, Homewood 2004).

Cropping

Cropping is perhaps more at odds with biodiversity than grazing is because cropping involves the direct removal of indigenous vegetation and planting of, generally, non-indigenous species. Nonetheless, crops can still harbor or support wild species, and their conservation value may depend on the crops planted, the farming methods employed, and the arrangement of fields with respect to natural habitat. I found relatively few studies that assessed biodiversity in cultivated areas only (10 studies summarized in Table S.2.3), as opposed to agricultural mosaics (Table S.2.2). This perhaps reflects the current state of African agriculture, where most farms are smallholder or subsistence based rather than expansive, commercial cultivation; although there are exceptions, average farm size is just 2 to 3 ha (Deininger et al. 2011). Where commercial cultivation does occur, loss of biodiversity may be seen as a foregone conclusion not worth investigating (see Thiollay 2006). Many of the studies of biodiversity in cultivation were concerned primarily with the benefits of that diversity for production via pest control, fertility enhancement, or pollination services, rather than for its value to conservation (e.g. Midega et al. 2008, Tchabi et al. 2008, Carvalheiro et al. 2010).

Agroforestry

Agroforestry, the integration of trees into agriculturally productive landscapes, has garnered much attention in the global conservation community because it has been shown to provide habitat for relatively high levels of forest species diversity (see Bhagwat et al. 2008). In African rangelands, agroforestry can be divided into two types: technological and traditional. Technological agroforestry deals with the expertise to plant and maintain tree species that will increase productivity in agricultural production systems. Kenyan farmers, for example, plant crops of fodder trees, which raise milk yields of cows and goats (Pye-Smith 2010a). Government programs in Niger, Zambia, Malawi, and Burkina Faso support large-scale "evergreen agriculture" projects to plant indigenous trees such as *Faidherbia albida* among crops, which maintain green cover year-round, increase yields by improving soil fertility, and provide fodder and firewood (Garrity et al. 2010). Evergreen agriculture and other technological agroforestry projects are touted by proponents as having greater biodiversity value than do monoculture crops (see Garrity et al. 2010, Kalaba et al. 2010, Pye-Smith 2010a, b). Yet, evidence to support these claims remains mostly anecdotal, warranting further research because plans are underway to expand technological agroforestry projects throughout Africa (Garrity et al. 2010).

Traditional agroforestry, on the other hand, is a millennia-old practice, particularly evident in the parkland savannas of West Africa, of people maintaining savanna tree species in pastures, fields, and villages. These trees provide shade, food, wood, and even cash when commercially traded (e.g. shea, baobab), and traditional agroforestry may contribute to the maintenance of tree species in addition to species for which trees provide habitat. Many studies have enumerated tree diversity in farmlands (Table S.2.4). Even so, the conservation value of agroforestry varies. Augusseau et al. (2006) report that in Burkina Faso, on a farm scale, few indigenous species are important to farmers and none are planted. Even where tree richness is maintained at a relatively high level, the persistence of trees in traditional agroforestry can be compromised if the economic value of totally clearing the land, e.g. for mechanized, intensive agriculture or firewood, outpaces the value of non-timber products (Tabuti et al. 2009). Additionally, based on demographic profiles of tree species, tree regeneration appears to be problematic in many human-modified landscapes (e.g. Fandohan et al. 2010, Schumann et al. 2010, Venter and Witkowski 2010). For example, a study in Benin shows that the largest shea trees are often in villages or fields, but seedling survival is low compared to nearby PAs (Djossa et al. 2008). Regeneration potential can also be diminished when harvesting tree products affects recruitment, as is the case for *Khaya senegalensis* in Benin (Gaoue and Ticktin 2008). Where natural regeneration potential is compromised, intervention may be required to ensure rejuvenation (Kindt et al. 2008, Ouinsavi and Sokpon 2008), especially if traditional rotational land-use systems such as long fallow, where trees are often most capable of regenerating, are abandoned (Schreckenberg 1999, Raebild et al. 2007).

Fortunately, agroforestry management in rangeland ecosystems is an active area of research with regards to developing strategies to encourage tree persistence (Augusseau et al. 2006, Kindt et al. 2008, Tabuti et al. 2009). Yet, there is a surprising lack of research to assess the value of savanna agroforests for faunal diversity or even non-tree plant diversity (Table S.2.4), aspects that have been more thoroughly studied in the tropical forest context (Bhagwat et al. 2008), and this dearth should be remedied.

Game ranching and private nature reserves

The wildlife industry, including game ranching, game farming, and private nature reserves, has become big business, especially in southern and East African rangelands. These land-use options involve profiting from consumptive (e.g. trophy hunting, live animal sales, meat) or non-consumptive (e.g. tourism, aesthetic value) use of wildlife on communal or private land. South Africa alone has an estimated 9,000 private game ranches, covering 20.5 million ha, many of which were converted from traditional livestock ranches (NAMC 2006). Ranching game rather than domestic livestock may ameliorate effects of overgrazing because indigenous species have coevolved with indigenous vegetation (Kerley et al. 1995), and indigenous browsers may help control bush encroachment (Taylor and Walker 1978, McGranahan 2008). Thus, the wildlife industry may be a boon to biodiversity conservation; however, very few studies have actually assessed impacts on biodiversity, which may be positive or negative and likely depend on management actions (Cousins et al. 2008).

Occurrence and abundance of mammal species on private land has increased due to game ranching (Lindsey et al. 2009). Nonetheless, some aspects of the wildlife industry are worrying. Privatization of wildlife (and sometimes legislative requirements) begets ubiquitous game fencing (McGranahan 2008, Lindsey et al. 2009) with substantial ecological consequences including the interruption of natural movements, inbreeding, and overstocking (Hayward and Kerley 2009, Lindsey et al. 2009). Ranches are often quite small (South African provincial averages range from 8.2 to 49.2 km^2), and smaller ranches necessitate more intensive management interventions (Bothma 2002, Lindsey et al. 2009). Additionally, the industry's focus on trophies may skew natural communities in favor of valuable species and induce semi-domestication (Mysterud 2010), and it has resulted in extra-limital introductions, questionable breeding practices, and persecution of predators (Lindsey et al. 2009). Even within the mammal community, generally the focus of game ranching, the full complement of species of a given ecosystem may not be maintained on ranches despite deliberate re-introductions (Grey-Ross et al. 2009b).

Thus, much more research is needed on the biodiversity value of the wildlife industry and what measures, e.g. promoting conservancies over single game ranches (Lindsey et al. 2009), can improve this value. Best-practice management in terms of grazing pressure, fire regimes, bush encroachment, wildlife ownership policies, and fencing needs more attention (McGranahan 2008). Furthermore, surprisingly little is known about the impacts of game ranching on species other than large mammals. Even so, game ranches are likely more amenable to most indigenous biodiversity than are many other commercial land-use options. For example, large eagles in South Africa's Karoo shrublands are much more common in areas stocking indigenous mammals than in areas with domestic livestock and cultivation (Machange et al. 2005).

Tropical forests

Though rangelands cover the majority of Africa, tropical forests also make up a considerable portion (~20% (Brink and Eva 2009)) (Fig. 2.1), particularly rich in biodiversity. Research on biodiversity in human-modified landscapes is biased towards tropical forests (Trimble and van Aarde 2012). Nonetheless, biodiversity in human-modified tropical forest landscapes in Africa has received much less scientific attention than in other regions, especially South and Central America (Gardner et al. 2010). African tropical forests tend to be in less conflict with high human population densities than elsewhere (e.g. Southeast Asia and Brazilian Atlantic forests) (Gardner et al. 2010), although in West Africa 80% of the original forest extent is now an agricultural-forest mosaic home to 200 million people (Norris et al. 2010).

I do not attempt a comprehensive review of African tropical forest biodiversity in human-modified landscapes and refer readers to Norris et al. (2010) for an excellent treatment of the West African scenario. They lament the lack of data regarding biodiversity in African agricultural-forest mosaics but are able to reach some general conclusions. Land uses that maintain tree cover are more amendable to forest biodiversity than those that do not. Species richness increases in some modified habitats, such as logged and secondary forest, for some species groups, but endemic forest species are often lost. Additionally, relatively high species richness in modified habitats comprises, in part, species not present in the baseline forest comparison, so species richness alone likely overestimates the value of modified habitats for forest species. Furthermore, habitat modification seems to affect richness of forest plant species more negatively than of some animal groups.

Although logically, it seems more difficult to encourage the persistence of biodiversity in human-modified landscapes embedded in tropical forests than in rangelands, research can indicate best practices for land-use planning. In contrast to West Africa, Central Africa still maintains large tracts of relatively undisturbed forest that are becoming increasingly threatened by development, and lessons learned from studying African forest biodiversity in human-modified landscapes should be incorporated into development policy for the region (Norris et al. 2010).

The tropical forest biome extends to East and southern Africa where forests are less extensive; they are confined largely to high altitudes inland and a linear belt along the coast. These geographic constraints present unique challenges for conservation and heighten the importance of maintaining endemic species and retaining connectivity in fragmented forests. Fewer studies consider East and southern African tropical forests than West African forests, but work is emerging to support land-use planning in the region, and results largely conform to those found for West Africa. Agroforestry in Ethiopian and Tanzania supports less diversity than forests but more than other land uses (Hemp 2006, Gove et al. 2008, Hall et al. 2011, Negash et al. 2012). While Schmitt et al. (2010) found higher overall plant richness in Ethiopian coffee agroforests than natural forests, richness of typical forest species was lower. In Kenya, connectivity of coastal forest fragments for primates may be influenced by matrix structure (Anderson et al. 2007). Farmland outside tropical forest remnants, especially structurally complex subsistence farms, support higher bird richness than forests; however, many forest species are lost, highlighting the importance of maintaining the forest remnants but also supporting traditional farming techniques over commercial monocultures (Laube et al. 2008, Mulwa et al. 2012). Furthermore, structurally diverse farmland surrounding forest remnants may enhance forest pollinator communities (Hagen and Kraemer 2010). Similarly, South African forest remnants embedded in various matrix types have similar bird species richness, but abundance is highest in fragments in agricultural matrices due to the presence of forest generalists and open-habitat species, while forest specialists are rare (Neuschulz et al. 2011). Forest fragments and grasslands in the agricultural mosaic outside a PA in southern Mozambique have more beetle species and higher abundance, while endemic beetle species are better represented inside the PA (Jacobs et al. 2010).

Cape Floristic Region

While small in area (approximately 90,000 km^2, see Fig. 2.1), the Cape Floristic Region (CFR) of South Africa is a biodiversity hotspot of global significance (Myers et al. 2000) consisting of a Mediterranean-type ecosystem with high species turnover across the landscape and high endemicity. In-depth conservation assessments and systematic planning have been conducted for the region and generally focused on pristine habitat that could be formally protected (see Cowling and Pressey 2003). Because spatial turnover of species is so high, however, successful conservation will depend heavily on efforts in human-modified landscapes beyond PAs (Cox and Underwood 2011). Based on species-area curves for plants and vertebrates in the CFR, practicing biodiversity friendly management on just 25% of the land that is beyond PAs, but still in a natural or semi-natural state, might add an additional 541 species to the 7,340 estimated to occur in PAs (Cox and Underwood 2011).

However, in contrast to many areas of Africa dominated by subsistence agriculture, the CFR is characterized by large areas of intensively managed agricultural monocultures with low biodiversity value (Giliomee 2006). Overall, only 26% of the CFR has been transformed, but the CFR is made up of different habitat types, and some, especially in the fertile lowlands, have lost much more of their area to cultivation, urbanization, and heavy invasion of exotic plants; for example, coast renosterveld is more than 80% transformed (Rouget et al. 2003a). Transformation threatens not only the CFR's plants but also endemic and vulnerable animals such as the Black Harrier *Circus Maurus*, which has been displaced from the inland plains by cereal agriculture and now breeds, less successfully, in the coastal strip and inland mountain habitats (Curtis et al. 2004). Though the Black Harrier can forage in cultivated areas, it relies on intact vegetation to breed (Curtis et al. 2004).

PAs within the CFR are concentrated in areas of low agricultural value (e.g. mountains and coastlines), so biodiversity in fertile areas depends on conservation on privately owned land (Rouget et al. 2003b, Giliomee 2006). To increase the biodiversity value of agricultural areas, the primary focus should be on conserving remnants of natural vegetation on farms (Giliomee 2006). This is being attempted with some success though incentive-driven stewardship agreements that protected almost 70,000 ha of vegetation on private land between 2003 and 2007 (Von Hase et al. 2010). Additionally, farm management practices may be variably amenable to biodiversity. For example, though vineyards have very different arthropod communities than those in natural vegetation, organic vineyards support greater diversity than do more intensively managed vineyards (Gaigher and Samways 2010). However, these effects may be taxon dependent; for instance, organic vineyard management benefits richness of monkey beetles (crucial pollinators), but not bees (Kehinde and Samways 2012). Similarly, apple orchards support less arthropod diversity than natural vegetation does, but orchards that are not sprayed with pesticides have a higher diversity than sprayed sites (Witt and Samways 2004). On the other hand, farms with a mixture of different crops and remnants of natural vegetation maintain most fynbos bird species and attract several additional species, while single crop sites without remnant vegetation have much less bird diversity and lose many fynbos species (Mangnall and Crowe 2003). Clearly, maintaining remnant vegetation and connectivity in agricultural areas of the CFR is crucial, but more research is needed to tailor agricultural practices to better conserve CFR species in production landscapes.

Urban and rural built environment

Plant and vertebrate species richness and endemism are correlated with human population density and human infrastructure in sub-Saharan Africa (Balmford et al. 2001, Burgess et al. 2007, Fjeldsa and Burgess 2008), which is substantial in many regions (see Fig. 2.1). That the pattern endures in relatively developed South Africa means either that species persist to some degree with humans in disturbed habitats at current levels, that human-disturbed habitats actually attract more species, or that a major extinction debt is yet to be paid (Chown et al. 2003, Fairbanks 2004). Regardless, areas with high human density, which in Africa, are predicted to increase dramatically, outpacing growth in all other regions in the coming decades (Seto et al. 2012), require appropriate regulations to ensure they remain as amenable as possible to biodiversity conservation. This will be especially important in some of Africa's most biologically rich yet rapidly urbanizing regions; by 2030 for example, the urban area within the Eastern Afromontane and Guinean Forests of West Africa hotspots is forecasted to be 1,900% and 920% of 2000 levels respectively (Seto et al. 2012).

Some obvious steps include discouraging urban sprawl; providing appropriate housing for low income populations while controlling illegal settlements in biodiversity sensitive areas; designing relevant green spaces that include aquatic habitats and indigenous plants; and managing invasive species, waste, and pollutants (Muriuki et al. 2011, Puppim de Oliveira et al. 2011). Research on managing Africa's urban and rural built environments for biodiversity is in its infancy and is mostly constrained to South Africa. Clearly, more research is needed, yet several studies provide pertinent information for planners.

While urban environments might not seem particularly hospitable to biodiversity, even small home gardens in African cities can harbor a remarkable number of species, especially in the tropics, both intentionally cultivated and otherwise (Cumming and Wesolowska 2004, Lubbe et al. 2010, Bigirimana et al. 2012). In South Africa, socioeconomics, urbanicity, and ecological factors influence plant diversity and the proportion of invasive species in home gardens (Lubbe et al. 2010, Molebatsi et al. 2010). Gardens with a high number of non-indigenous species contribute to biotic homogenization and pose the risk of new introductions that could prove detrimental to indigenous ecosystems. Therefore, invasive species in the urban landscape need to be controlled through regulation and removal, especially in threatened and fragile ecosystems (Alston and Richardson 2006, Cilliers et al. 2008, Dures and Cumming 2010, Bigirimana et al. 2012).

Green spaces such as city parks, tree-lined streets, and even golf courses in urban environments can support certain species. Dures and Cumming (2010) show that bird diversity in sand fynbos in an urban gradient in Cape Town is more affected by habitat quality than by patch metrics such as area. Thus, controlling invasive species even in high-density housing areas may be more beneficial for birds than expanding the low quality network of urban reserves. Alien pine tree removal helps restore invertebrate species diversity in Cape Town, and fragments of natural vegetation and gardens with indigenous plants help maintain it (Pryke and Samways 2009). In the Durban Metropolitan Open Space System, complex habitats (i.e. with trees and shrubs) support higher invertebrate diversity than simplified habitats (i.e. mown lawns); however, simple habitats might cater for certain rare species (Whitmore et al. 2002). Green spaces in urban Pretoria contribute to butterfly and moth diversity (McGeoch and Chown 1997) and also support indigenous birds (van Rensburg et al. 2009), while maintaining urban riparian vegetation is necessary for dragonfly conservation in Pietermaritzburg (Samways and Steytler 1996). Better ecological planning for developments such as golf courses or estates could increase the likelihood for biodiversity persistence and minimize negative consequences, even in the CFR (Fox and Hockey 2007). Additionally, habitat engineering, e.g. creating biotopes for dragonflies (Steytler and Samways 1995), might be a useful tool in the urban context to promote biodiversity, although continual management of these habitats may be necessary to ensure persistence of species (Suh and Samways 2005).

When species are range-restricted such that a single metropolitan area may affect most of their range, special attention is required. For example, two small forest parks in Durban suburbs are home to the last remnant populations of the rare tree *Oxyanthus pyriformis* whose specialist pollinators, the long-tongued hawkmoths, appear unable to tolerate suburban living. Hand pollination and planting of seedlings will be necessary to maintain the species (Johnson et al. 2004). Similarly, conservation of plants in Cape Town is hampered by apparent sensitivity of specialist pollinator birds to urbanization, which is concerning given the increasing urbanization in the CFR (Seto et al. 2012). Durban covers a large portion of the range of the black-headed dwarf chameleon *Bradypodion* *melanocephalum,* and translocations from sites demarcated for development to sites reserved for conservation have proven somewhat successful, dependent on adequate alien-plant-control and restoration of indigenous habitat (Armstrong 2008). Unique landscape features within urban areas may also require special attention. For example, Table Mountain in Cape Town harbors endemic species whose conservation depends not only on the PA of Table Mountain but also on management of lower elevation suburban woodlands (Pryke and Samways 2010).

On the rural end of the settlement spectrum, less attention has been given to biodiversity persistence. Some agricultural mosaic studies consider rural settlements, but a few studies treat it explicitly. For example, similar to shifting cultivation, some cultures practice shifting settlement, and abandoned settlements have been shown to provide valuable seasonal resources, e.g. fruit trees, to chimpanzees *Pan troglodytes* in Mali (Duvall 2008). Even road verges may provide for some species. For example, verges in the Karoo support some plant species not found in adjacent grazing lands, though many species from pastures are not found in verges (O'Farrell and Milton 2006). Verges also support invertebrates and could prove valuable to conservation because verges are public spaces that can be managed for biodiversity (Tshiguvho et al. 1999).

Understanding more about urban settlement and biodiversity may even benefit conservation in once remote PAs where rural sprawl and infrastructure for wildlife tourism can be dramatic (Wittemyer et al. 2008). For example, recent decades have seen substantial increases in rural sprawl along with the construction of 60 tourist lodges, 1,200 boreholes, and 540 km of roads in the Okavango Delta, one of Botswana's premiere conservation areas (Vanderpost 2006).

Constraints and Opportunities

The science of biodiversity in human-modified landscapes

As others have pointed out, understanding the value of human-modified landscapes for biodiversity, especially in Africa, is hampered by data constraints (Norris et al. 2010, Pettorelli et al. 2010, Waltert et al. 2011, Trimble and van Aarde 2012). Many studies are limited in temporal and spatial scale, and poor study design may result in insufficient sampling of habitats. The focus on species richness of certain habitat types while failing to account for the importance of species from other habitats in assigning conservation value to different land-use options may neglect the bigger picture; Bond and Parr (2010), for example, call for more collaboration between forest conservationists and others. More consideration for the value of different species in terms of commonness and rarity also needs to be developed because this review, like others highlights that human-modified landscapes often fail to cater for endemic and specialist species (Waltert et al. 2011), and a better understanding of beta and gamma diversity at a landscape scale is necessary.

Additionally, further investigation into the relationship between occurrence and persistence is required, as are more studies that delve beyond species richness into the processes that support the observed patterns of biodiversity. For example, studies of demographic processes (e.g. Djossa et al. 2008, Schumann et al. 2010, Venter and Witkowski 2010) and population trends (e.g. Stoner et al. 2007, Trimble and van Aarde 2011) for species inhabiting human-modified landscapes can provide insight beyond mere patterns of occurrence. Furthermore, umbrella species are not necessarily informative for other taxa. As elsewhere (Gardner et al. 2010), studies of biodiversity in African human-modified landscapes is biased towards certain taxa—and the patterns exhibited by these species might not apply to others (Caro 2001). Also, genetic diversity, has not generally been considered though it may be important in terms of traits valuable to humans and valuable for conservation (Ashley et al. 2006). Conservation in human-modified landscapes may be particularly important in conserving genetic diversity because the traditional fortress PA model may encompass relatively little, especially for plants (Atta-Krah et al. 2004).

Many authors lament erosion of ecological knowledge to maintain species, especially trees, medicinal plants, and wild food plants, and urge more effort towards domestication, cultivation, and marketing to provide farmers with the means to conserve species while easing pressure on wild stock and improving food security and economic stability (Leakey and Tchoundjeu 2001, Dold and Cocks 2002, Dovie et al. 2007, Kindt et al. 2008, Ntupanyama et al. 2008, Tabuti et al. 2009, Khumalo et al. 2012). However, care must be taken to ensure that genetic diversity is maintained in the process (Lengkeek et al. 2006, Muchugi et al. 2008). Development of domestication and cultivation methods could promote the use of native species in human-dominated lands, and these native plants may contribute to conservation of other taxa (Dovie et al. 2007), but more research is clearly required.

Implementing policies

Given the limitations of the available science, it is difficult to develop strategies to encourage land uses that are of the highest conservation value. The effect of policy on biodiversity conservation in human-modified landscapes under different land tenure systems and different settlement patterns needs more research because decisions are largely opinion driven and not evidence based (Homewood 2004, Duvall 2008). Perhaps the community-based conservation literature, which has focused heavily on implementation and policy, could lend some insight. A review of this literature stresses that better implementation results are achieved when there is quality governance, resilient local institutions with local power and accountability, consideration for local context, integration across social and ecological systems, and mutual learning involving communities and other involved parties, e.g. outside experts (Balint and Mashinya 2008). NGO's and foreign aid are more likely to encourage successful conservation when projects are flexible, small-scale, and targeted at local interests, and when they prioritize innovation, learning, and experimentation (Nelson 2009). Conservationists must also take cognizance of perspectives and needs of local communities in both rural and urban settings in order to better engage them in conservation management (Ferketic et al. 2010). CBC projects that are independent of PAs are excellent opportunities to maintain biodiversity on human-modified land of marginal use for agriculture; and expert opinion, monitoring, and ecological modeling tools can help communities manage their natural resources (Du Toit 2002).

I have indicated several gaps in the literature on biodiversity in African human-modified landscapes, and while much more work is required to create sensible policies that meet conservation needs and those of governments and people (Ashley et al. 2006), as it stands, current research can go some way towards supporting policy-making. Studies of biodiversity persistence in different land-use options for a given region can be incorporated into scenario modeling for future development. For example, Turpie et al. (2007)

amalgamated studies of plants, invertebrates, birds, and mammals in human-modified landscapes to predict how varying levels of afforestation or dairy production in the Drakensberg grasslands of South Africa would influence alpha diversity.

Some generalities emerge from the literature that may be helpful in working towards sensible policies. Generally, diversifying human-modified landscapes at all levels, e.g. polyculture cropping, diverse agroforestry, and maintaining farmlands with high heterogeneity in terms of both crops and vegetation structure, is likely to support more species than do more homogenous land uses, while potentially also providing economic stability against a background of fluctuating markets for specific crops (Franzen and Mulder 2007). It is apparent that, often, endemic and specialist species cannot persist in human-modified landscapes; thus, protected area expansion and development should be focused within areas rich in such species (see Jenkins et al. 2013). Past and present implementation strategies are beyond the scope of this review, yet there is literature dealing with such strategies in Africa that may be of use, e.g. certification of sustainable and biodiversity friendly products (Lilieholm and Weatherly 2010).

Living with nature

Maintaining biodiversity in landscapes where humans live, work, and extract resources implies that humans will have to coexist with other species. While the consequences of living without nature may be worse than the difficulties of living with it, certain issues present considerable obstacles for promoting conservation beyond PAs, especially for mammals. Human-wildlife conflict is particularly troublesome for conservation of large mammals in human-dominated landscapes, e.g. carnivores threaten livelihoods by predating livestock and, occasionally, people. However, specific and practical actions can greatly reduce the probability of carnivore attacks. For example, in Kenyan communal lands, having a domestic dog accompany herds can reduce the risk of a carnivore attack by 63%; conversely each additional boma gate increases the risk of attack by 40% (Woodroffe et al. 2007). However, carnivores are not the only concern. Other animals, such as baboons and bush pigs, can damage structures and destroy crops while larger herbivores, such as elephants, also threaten human lives. Knowledge of attitudes of people employing different land uses can help land-use planners develop strategies to reduce conflict and negative attitudes towards conservation. For example, crop agriculture should not be encouraged in predominantly pastoral areas where elephants and people coexist relatively peacefully (Gadd 2005). Furthermore, land-use planning that incorporates knowledge of which crops are most likely to generate conflict could allow creation of buffer zones in areas with high potential for conflict (Hockings and McLennan 2012).

The risk of disease transmission poses an additional difficulty. Diseases of domestic animals threaten wildlife. For example, domestic dogs are carriers of canid diseases transmissible to wild carnivores (Butler et al. 2004) and were partly responsible for extinction of the African wild dog *Lycaon pictus* and decimation of lions *Panthera leo* in areas of the Serengeti (see Woodroffe 1999). Additionally, livestock can transmit animal diseases (e.g. bovine tuberculosis) to wildlife with negative conservation outcomes, while wildlife can also transmit diseases (e.g. foot and mouth) to livestock with immense economic consequences (Michel et al. 2006, Thomson 2009).

Fencing has been heavily used in Africa to assist people in their ability to coexist with nature—to reduce direct conflict and disease transmission. Laws regarding fencing differ by country; for example, Zambia requires game fences while Namibia encourages large-scale cooperation between game-farmers to discourage fencing (McGranahan 2008). Obviously, fencing has serious ecological consequences (Hayward and Kerley 2009, Trimble and van Aarde 2010) and is anathema in many ways to the goals of conservation, especially conservation beyond PAs (Trimble and van Aarde 2010). However, non-traditional fencing technologies (see Hayward and Kerley 2009), such as fences targeted at particular problem species (e.g. elephant fences that allow other species to pass), virtual barriers, or fencing wildlife out of villages and fields instead of into PAs, may be acceptable compromises. The effect of fences on the persistence of species in human-modified landscapes certainly deserves more investigation.

Economically, wild animals provide an important resource for many people in Africa (Bharucha and Pretty 2010), which may threaten species persistence. "Sustainable use" is frequently discussed with relation to bushmeat hunting, but food scarcity and population growth dictate that it will likely be impossible to enforce rules for sustainable use unless food security issues are addressed (Fa et al. 2003). Sustainable harvesting is also an issue for plants (Sambou et al. 2002). Community forests must be carefully managed, e.g. by restricting harvesting of pole-sized stems to certain species, to ensure that species are not used to extinction (Obiri et al. 2002). Additionally, rules must be assessed to ensure that they achieve the desired goals; for example, in the Republic of Guinea, tax to the forestry administration for harvesting palm wine counterproductively encourages harvesters to employ lethal yet profitable methods of harvesting to compensate for the initial investment (Sambou et al. 2002).

Conclusion

There is clearly both necessity and great potential for human-modified land in sub-Saharan Africa to contribute to the conservation of the continent's biodiversity. While PAs will remain essential, and are especially important for protecting species sensitive to human disturbance (Devineau et al. 2009), a greater focus on biodiversity conservation beyond their boundaries could be complementary to overall conservation goals. The information gleaned from studies of biodiversity in human-modified landscapes in Africa discussed in this review goes some way toward providing policy-makers with evidence to support defensible decisions for land-use planning and conservation management beyond PAs. Improving the amenity of human-modified landscapes for biodiversity can be encouraged at all levels from individuals' choices to plant indigenous home gardens, to grass roots endeavors to manage communal resources, to communities deciding to share their land with wildlife, to commercial farms going organic and maintaining patches of natural habitat. Governmental intervention at the level of the city (e.g. green space planning), region (e.g. extension agencies demonstrating biodiversity friendly agricultural practices), nation (e.g. policy-setting for control of invasive species, pesticide or poison usage, and land-use zoning), or even internationally (e.g. cooperative removal of boundary fences) are also warranted.

Although several factors including lack of knowledge, implementation challenges, and problems of coexistence with wildlife may constrain successful implementation of biodiversity conservation in human-modified landscapes, given each constraint, opportunity exists for progress. On the bright side, scientific interest in the topic is increasing (Trimble and van Aarde 2012), and as research accumulates, it will allow for systematic reviews useful for policy decisions. Additionally, many issues associated with human-wildlife coexistence are primarily related to large mammals and efforts to solve these problems should continue. Meanwhile, the barriers to implementing strategies to conserve other species groups in human-modified landscapes are far from insurmountable and such strategies should be prioritized.

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Figures

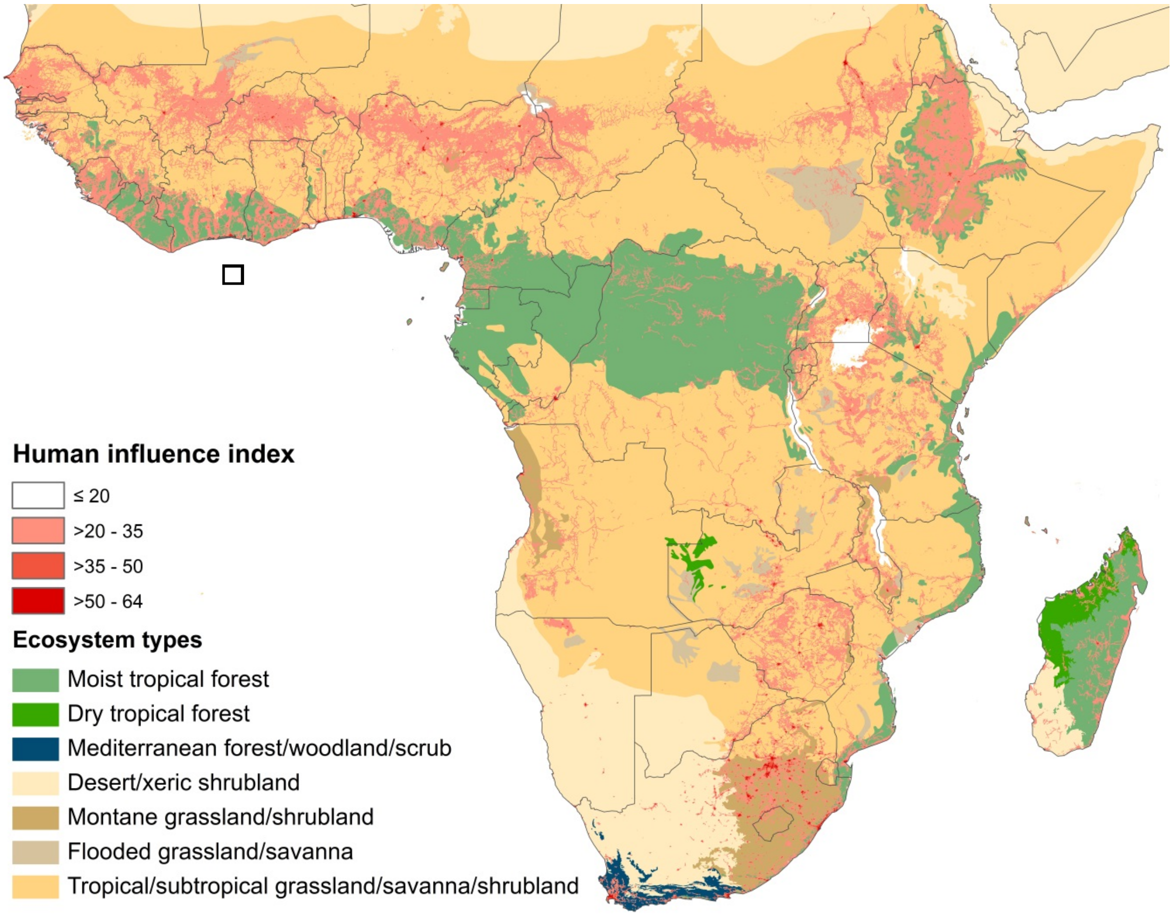

Fig. 2.1. Map of sub-Saharan Africa showing ecosystem types adapted from Olson et al. (2001): rangelands (desert and xeric shrubland, montane grassland/shrubland, flooded grassland/savanna, and tropical/subtropical grassland/savanna/shrubland), tropical forests (moist and dry tropical forest), the Cape Floristic Region (Mediterranean forest/woodland/scrub), and the urban and rural built environment represented by the human influence index (Wildlife Conservation Society and Center for International Earth Science Information Network 2005), a dataset comprising nine data layers incorporating population pressure (population density), human land use and infrastructure (built-up areas, nighttime lights, land use, land cover), and human access (coastlines, roads, railroads, navigable rivers).

Supplementary Tables

Table S.2.1. Summary of studies investigating biodiversity of grazing landscapes in sub-Saharan African rangelands.

Reference	Country	Habitat	Taxa	Land-use variable	Control [a]	Biodiversity variable	Finding	Conclusion
Bergström and Skarpe (1999)	Botswana	xeric shrubland	large herbivores	gradient of cattle density with distance to village	NA	abundance	large herbivores not found near villages; some species more sensitive than others	heavy cattle and goat grazing near villages probably excludes wild herbivores
Blaum et al. (2007a)	South Africa	semiarid savanna	5 rodent species	increasing levels of shrub encroachment as proxy for grazing intensity	NA	abundance, diversity, community composition	increasing shrub cover affects rodents differently	overall species richness decreased with increasing shrub cover
Blaum et al. (2007b)	South Africa	semiarid savanna	10 mammalian carnivores	increasing levels of shrub encroachment as proxy for grazing intensity	NA	abundance	species react disparately	intermediate shrub cover is best
Blaum et al. (2009a)	South Africa	semiarid savanna	ground-dwelling arthropods	increasing levels of shrub encroachment as proxy for grazing intensity	NA	abundance, diversity, community composition	mixed results for different groups: abundance trends were mixed; richness showed bell-shaped pattern; composition definitely changes	can use some species for indicators of bush encroachment
Blaum et al. (2009b)	South Africa	semiarid savanna	12 small and medium mammalian carnivores	gradient of stocking rates with and without predator control	NA	abundance	abundance of all species lowest on farms with high stocking rate; predator control affected species differently	need to expand research and monitoring

Colville et al. (2002)	South Africa	Succulent Karoo	monkey beetles	contrasting grazing histories	NA	abundance, richness, composition, plant turnover	higher abundance in disturbed sites generally but higher richness in undisturbed sites, with distinct assemblages at each site	monkey beetles useful indicators of overgrazing
Davis et al. (2012)	South Africa	savanna	dung beetles	communal grazing	Kruger National Park	abundance, richness, biomass, structure	higher richness, abundance, and biomass in PA than communal grazing and different structure	higher mammal diversity in the PA allow for a more complex beetle community despite higher mammal density in the communal land
Fabricius et al. (2003)	South Africa	xeric succulent thicket	terrestrial arthropods, reptiles	commercial and subsistence rangeland with varying grazing intensity	Great Fish River Reserve Complex	richness, community similarity	greater richness generally in nature reserve; snakes and lizards twice as abundant in communal grazing; locations generally housed 2/3's of total diversity	nature reserves important, but mixed land-use mosaic supports greater gamma diversity
Georgiadis et al. (2007)	Kenya	savanna	large herbivores	commercial ranches, communal ranches, transitional properties	NA	density, trends	many herbivores can thrive when sharing with moderate livestock densities, but only few when livestock densities are high	maintaining high wild species diversity at landscape scale depends on network of unfenced areas with low or zero livestock densities
Gregory et al. (2010)	Kenya	savanna	birds	traditional pastoral practices (i.e. burn patches, abandoned bomas)	undisturbed matrix	species richness, abundance, community composition	greater density of birds and unique species assemblages on burn and boma patches than undisturbed control	disturbances caused by traditional pastoralism may be critical to maintaining avian diversity
Haarmeyer et al. (2010)	South Africa	Succulent Karoo	plants	different grazing intensities	farm with no grazing	abundance, species richness, composition, dynamics	endemic richness and abundance decreased with grazing, but grazed and ungrazed plots harbor unique species	no or moderate grazing necessary to preserve plant diversity and vegetation patterns

Hejcmanová et al. (2010)	Senegal	savanna	plants	grazing and wood collection, 15 year fenced, 5 year fenced	NA	abundance, richness, % cover, functional diversity	shift towards woody species with time in sites where grazers excluded	enclosures may prove useful management strategy in degraded rangelands
Hendricks et al. (2005)	South Africa	Succulent Karoo	plants	gradient of grazing intensity	little-grazed areas of Richtersveld National Park	species richness, cover	species richness and cover lowest at high intensity grazing	livestock in conservation areas may not be compatible with conservation goals
Kinnaird and O'Brien (2012)	Kenya	savanna	large mammals	livestock management gradient	wildlife sanctuary with no livestock	occupancy, abundance, richness	fenced and group ranches had lower richness and occupancy than sanctuaries and conservancies	landowners need to be provided with incentives for tolerating wildlife
Mayer et al. (2006)	South Africa	Succulent Karoo	monkey beetles	livestock grazing intensity (communal versus commercial)	NA	abundance, richness, composition	grazing intensity does not determine abundance and richness; composition varies	changes in vegetation affects composition of beetle assemblages; thus, grazing affects pollinator diversity
Mohammed and Bekele (2010)	Ethiopia	savanna	plants	open hay-fields and grazed woodlands	NA	diversity, biomass production, range condition	higher diversity in wooded grazing land than open grassland, biomass production follows quadratic relationship with range condition	management of hay-fields may reduce diversity
Morris et al. (2009)	Kenya	savanna	game birds	heavy grazing, seasonal grazing, abandoned grazing	wildlife sanctuary	abundance, richness, composition	doves most abundant in moderate grazing; francolin, spurfowl, and quail in sanctuary; abandoned landscape has highest richness	maintaining a mosaic of wildlife and livestock grazing with patches of ungrazed habitat will support diverse population of game birds

Monadjem and Garcelon (2005)	Swaziland	savanna	3 vulture species	government cattle ranches (no wildlife protection), cattle ranches (with protection for wildlife)	conservation areas	nest densities	nest densities highest in conservation areas, less on cattle ranches, and negligible on gov't ranches	vultures do not breed on intensive ranches although vegetation appears similar structurally
O'Connor et al. (2011)	South Africa	grassland	plants	grazing management (stocking rate, cattle-to-sheep ratio)	NA	abundance, richness, composition	mixed results for different trials and groups; increaser and decreaser species identified	trials suffer from lack of baseline data and limited replication
Reid and Ellis (1995)	Kenya	arid savanna	1 tree species	livestock corrals	non-corral sites	abundance of seeds and seedlings, size class of older trees	seedling emergence, growth, and survival better in corrals; older tree survival not significantly different outside corrals	contrary to popular belief, pastoralism may enhance recruitment of trees
Rutherford and Powrie (2010)	South Africa	Succulent Karoo	plants	low and high grazing intensity	NA	% cover, richness, abundance	total number of species declines with heavy grazing while annuals and geophytes increase	beta diversity across disturbance regimes increases gamma diversity at a landscape level
Rutherford and Powrie (2011)	South Africa	grassland	plants	heavy grazing	Tsolwana Nature Reserve	richness, diversity, composition	grazing led to higher richness at plot scale, but plots were more similar to each other	overall richness was similar between grazed and ungrazed
Rutherford et al. (2012)	South Africa	savanna	plants, termites	grazing gradient	NA	abundance, richness, composition, cover	cover was reduced in high grazing but no difference in richness or diversity of plants or termites although composition changed	increased grazing in mopane savanna would result in different species assemblages and physiognomy
Savadogo et al. (2008)	Burkina Faso	savanna-woodlands	herbaceous plants	grazing, fire, and selective tree cutting	undisturbed sites	abundance, richness	different groups respond differently	site- and group-specific responses require landscape approach
Seymour and Dean (1999)	South Africa	Succulent Karoo	invertebrates	moderate and high intensity grazing	NA	abundance, richness, composition	abundance higher with high grazing but richness greater at moderately grazed sites	high abundances at severely degraded areas may compound effects of overgrazing

Shackleton (2000)	South Africa	savanna	plants	communal grazing areas	PAs	abundance, richness, beta diversity	fewer plant species in PAs	communal land maintains high diversity, but more work should be done to ensure persistence
Smart et al. (2005)	South Africa	savanna	lizards	communal rangelands	PAs	abundance, richness, vegetation	communal lands have different vegetation; lizard richness higher in communal lands, but different assemblage than in PAs	Species used by people may not persist beyond PAs
Todd and Hoffman (2009)	South Africa	Succulent Karoo	plants	commercial and communal rangelands	NA	% cover, richness, community composition, dynamics	divergence of communities maintained despite vegetation changes in both land uses	longevity of shrub species prevent quick recovery from overgrazing in contrast to shorter lived grassland species
Vaudo et al. (2012)	South Africa	Thicket /savanna	bees	livestock grazing	game farms	colony density, colony strength	land with indigenous herbivores may have greater colony density but are not healthier	more research is needed to confirm patterns
Wasiolka and Blaum (2011)	South Africa	xeric shrubland	plants, reptiles	livestock grazing	Kgalagadi Transfrontier Park	abundance, richness, composition, plant cover	plant and reptile richness and abundance higher in PA than farmland	livestock farming leads to significant changes in vegetation composition and resources for the reptile community

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[a] NA indicates no control; PA stands for protected area.

Table S.2.2. Summary of studies investigating biodiversity of agricultural mosaic landscapes in sub-Saharan African rangelands.

Reference	**Country**	**Habitat**	**Taxa**	**Land-use variable**	**Control** [a]	**Biodiversity variable**	**Finding**	**Conclusion**
Anadón et al. (2010)	Mauritania, Mali	savanna	raptors	settlement gradient, cultivation	grassland	abundance, richness, composition	richness relates positively to cultivation, but resident species relate negatively to human population	resident species may be negatively affected by habitat degradation
Caro (1999)	Tanzania	savanna	large and medium mammals	gradient of human presence from seasonal pastoralism to permanent settlements and cultivation	Katavi National Park	densities, composition	densities higher in low intensity use; some mammals still occur seasonally in high intensity use	illegal hunting is the main cause of lower mammal densities
Caro (2001)	Tanzania	savanna	small mammals	cultivation, pastures, settlements, little used areas	Katavi National Park	abundance, diversity, community composition	diversity and abundance greater outside than inside park	large mammals may not be effective umbrellas for small mammals
Devineau et al. (2009)	Burkina Faso	savanna	plants	agricultural mosaic	PAs	abundance, richness, composition, species traits	effect depends on land type and plant group but generally favors widespread species outside PAs	plants are not sufficiently protected in the agricultural landscape, so PAs are necessary
Eilu (2003)	Uganda	savanna	plants	cultivation, fallow, plantation	natural woodland/ grassland	abundance, richness, composition	natural habitats support highest diversity; banana crops and some annual crops supported substantial diversity	farmers should be advised how to maintain plant diversity in agricultural landscapes
Fritz et al. (2003)	Zimbabwe	savanna	mammals	river segments bordered by fields of various sizes, settlements, and grazing	uninhabited river segments	abundance, richness	field area affects abundance and occurrence of species	agricultural mosaics affect most species but especially when fields are larger than 3.2 ha

Gardiner et al. (2005)	Burkina Faso	savanna	butterflies	cultivation, fallow, grazing	30-year fallow	abundance, richness, composition	no difference in richness; abundance highest in cultivation yet more even in fallow	changes in species groups relate to vegetation changes
Gardner et al. (2007a)	Tanzania	savanna	small mammals, frogs, birds, butterflies, trees	gradient of human presence from seasonal pastoralism to permanent settlements and cultivation	Katavi National Park	abundance, richness, composition	richness does not decline with land-use gradient but composition in different management areas is distinct	PAs are crucial but human-modified landscapes can have vital and complementary conservation value
Happold and Happold (1997)	Malawi	savanna	mammals	tobacco farm with mix of intense cultivation, remnant vegetation, plantations, fallow	NA	abundance, richness	66% of species known to occur in region occur on the farm; large remnants are especially important	farms that contain remnants of natural vegetation can play an important role in mammal conservation
Hoare and Du Toit (1999)	Zimbabwe	savanna	elephants	gradient of settlement and cultivation coverage	NA	density	elephant density declines with increasing human transformation	elephants coexist in human agricultural matrix up to a threshold of transformation
Konecny et al. (2010)	Senegal	savanna	small mammals	cultivation, pastures, fallow	Niokolo Koba National Park	abundance, richness, composition	diversity and abundance greater outside than inside the park	traditional agriculture may support species not found in less disturbed locations
Mapinduzi et al. (2003)	Tanzania	savanna	plants	pastoral settlement, agro-pastoral settlement	NA	richness, erosion risk	greater diversity and less erosion risk in pastoral than agro-pastoral settlements	traditional ecological knowledge provides a valuable basis for assessing rangeland biodiversity
Moreira (2004)	South Africa	grassland	4 bird species	cultivation, grazing, plantation, fallow	NA	occurrence	relationship between occurrence and land use differs by species	afforestation and agricultural intensification threaten bustard species
Mworia et al. (2008)	Kenya	savanna	large mammals	small-scale ranches, small-scale farms, communal grazing	PAs	abundance, richness, composition	wildlife density peaks at intermediate cattle grazing; small-scale agriculture not an important factor	management must maintain heterogeneous landscape and maintain access to water

Nacoulma et al. (2011)	Burkina Faso	savanna	plants	communal cultivation, fallows, remnants	W National Park	abundance, composition, structure, traits	elevation and soil determine vegetation type; traditional land use does not necessarily lead to loss of species	combination of communal management and PAs best for conservation
O'Connor (2005)	South Africa	grassland	plants	plantation, commercial and communal cultivation/pastures	protected grasslands	abundance, richness, composition	plantations have more indigenous species than other land uses; no effect of grazing intensity on richness, only composition	conservation should focus on species only found on unprotected rangelands
Ratcliffe and Crowe (2001)	South Africa	grassland	birds	farms with various compositions of cultivation and pastures	NA	abundance, richness	species characteristic of variegated landscapes are lost with intensive farming	population declines due to intensification of agriculture so re-creation of a habitat mosaic with lots of edge habitat necessary
Reid et al. (1997)	Ethiopia	grassland/ woodlands	trees	small- and large-holder fields and pastures	riparian woodlands, wooded grasslands	abundance, diversity, cover	cover and diversity high in riparian woodlands, moderate in small-holder and wooded grasslands, and low in large-holder farms	small-holder farms may be compatible with conservation, but riparian woodlands are key
Russell and Downs (2012)	South Africa	grassland	frogs	plantations, sugar cane	PAs	richness, diversity, composition	lower richness in plantations and cultivation	Land use should be considered for frog conservation
Soderstrom et al. (2003)	Burkina Faso	savanna	birds	cultivation, fallow, grazing	NA	abundance, richness, composition	richness highest on actively disturbed land and decreases with fallow age; many species only found on cultivated land	woody vegetation should include many different species, and large trees should be maintained
Stoner et al. (2007)	Tanzania	savanna	larger mammals	gradient of resource use restrictions	PAs	population trends	declines common in all land-use categories, but least common in strict PAs; species commonly fared poorly in unprotected landscapes	PAs may fail some species and more monitoring is necessary

Tabuti (2007)	Uganda	savanna	16 tree species	cultivation, fallow, homestead, seasonally flooded, bush	NA	abundance, occurrence, population structure	most species rare, but few widespread; some not able to persist in some land uses	growing human population threatens species persistence
Thiollay (2006)	Burkina Faso	savanna	non-passerine birds	traditional cultivation and fallow	PAs	abundance, composition	some bird groups maintain substantial populations in cultivated areas, but raptors and large game birds mostly absent	hunting, habitat degradation, and grazing cause extinctions and declines of large birds
Wessels et al. (2011)	South Africa	savanna	trees	communal pastures, cultivation	Kruger National Park	cover, height	more large trees in the communal areas but few small trees	large trees are probably protected by people, but regeneration may be problematic

[a] NA indicates no control; PA stands for protected area.

Table S.2.3. Summary of studies investigating biodiversity of cropping landscapes in sub-Saharan African rangelands.

Reference	Country	Habitat	Taxa	Land-use variable	Control [a]	Biodiversity variable	Finding	Conclusion
Ayuke et al. (2011)	Malawi, Burkina Faso	savanna	termites & earthworms	management leading to high- and low-carbon soils	fallow	abundance, diversity	higher richness and abundance under field management that results in high-carbon; higher worm richness but not termite in fallow	management that increases soil carbon supports diversity
Carvalheiro et al. (2010)	South Africa	savanna	pollinators	orchard	distance to natural habitat	abundance, richness	pollinators decline in abundance and richness with distance to natural habitat	need to make farmland more suitable for pollinators by maintaining remnants of natural habitat throughout
Carvalheiro et al. (2011)	South Africa	savanna	plants & pollinators	sunflower fields differing in weed occurrence	distance to natural habitat	abundance, richness, composition	weed diversity increased pollinator diversity	natural habitat patches should be conserved and flowering plants maintained within fields to maximize productivity and conservation
Fitzherbert et al. (2006)	Tanzania	savanna	butterflies	cultivation	areas with little human impact, e.g. Katavi National Park	abundance, richness, composition	abundance and richness low in cultivation	increased cultivation could reduce butterfly diversity
Gardner et al. (2007b)	Tanzania	savanna	amphibians	cultivation	Katavi National Park	abundance, richness, composition	cultivation decreases diversity	transformation of miombo could threaten amphibian species
Midega et al. (2008)	Kenya, South Africa	savanna	ground-dwelling spiders	monoculture maize, maize intercropped with "push-pull" crops	NA	abundance, richness, composition	abundance higher in the intercrop; diversity not generally greater	"push-pull" intercropping may provide valuable pest control in maize agro-ecosystems

Mponela et al. (2010)	Malawi	savanna	plants	marginal land within cultivated landscape	marginal land in uncultivated landscape	abundance, richness, composition	fallow areas in cultivated landscapes were rich in disturbance tolerant species; uncultivated areas had high conservation value species	marginal land in uncultivated areas should be spared for conservation
Pryke and Samways (2012)	South Africa	grassland	arthropods	plantations, grassland remnants	PAs	abundance, richness, composition	Interior of grassland remnant networks similar in arthropod assemblage to PAs	provided they are wide enough, grassland remnant ecological networks have conservation value in human-dominated landscapes
Sinclair et al. (2002)	Tanzania	savanna	birds, insects	cultivation	PAs	abundance, richness, composition	bird abundance in agriculture much reduced; half of insectivorous and granivorous species not recorded in cultivation; consistent with drop in insect abundance	many species will become relegated to PAs unless restoration of cultivation is achieved
Tchabi et al. (2008)	Benin	savanna	abuscular mycorrhizal fungi	cultivation	natural savanna, long fallow	density, richness, composition	spore density and species richness higher in natural savanna and yam cultivation, intermediate in fallow, and low in cotton	agricultural practices decrease richness; it is not quickly restored by fallow which could harm soil fertility

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[a] NA indicates no control; PA stands for protected area.

Table S.2.4. Summary of studies investigating biodiversity of agroforestry landscapes in sub-Saharan African rangelands.

Reference	Country	Habitat	Taxa	Land-use variable	Control [a]	Biodiversity variable	Finding	Conclusion
Augusseau et al. (2006)	Burkina Faso	savanna	trees	fallows, cultivation	NA	density, size, richness, composition	farmers modify species diversity towards dominance of a few useful species	new techniques in agroforestry management are needed to encourage tree conservation
Bayala et al. (2011)	Burkina Faso	savanna	trees	home, village, and bush parklands	NA	abundance, richness, size, composition	diversity was related to farming system and many species were rare	domestication and conservation strategy are key to maintaining parklands and threatened species
Djossa et al. (2008)	Benin	savanna	1 tree species	fallow, cropland, villages	W National Park	abundance, size	regeneration problem in crops, villages, and fallows	baobabs can withstand harvesting of NTFPs, but future intensification may lead to problems
Fandohan et al. (2010)	Benin	savanna	1 tree species	farmlands, fallow	gallery forest	abundance, size	trees less common in farmland and fallow and more vulnerable	introduction of seedlings to farmlands may be necessary
Fifanou et al. (2011)	Benin	savanna	trees	farms of different size	NA	abundance, richness, composition	small land holdings had higher richness; people plant trees for food and medicine	traditional agroforestry supports tree species richness
Kindt et al. (2008)	Burkina Faso, Mali, Niger, Senegal	savanna	trees	village fields, bush fields, sylvo-pastoral zone	forest reserves	abundance, size, richness, composition	low richness in village fields, intermediate in bush fields and sylvo-pastoral zone, highest in forest reserves	projects to encourage farmer assisted maintenance and regeneration of trees may be necessary
Ouinsavi and Sokpon (2008)	Benin	savanna	trees	farms	NA	richness, abundance, regeneration	density and composition depend on socioeconomic and environmental factors	more evenness should be promoted in farmlands by encouraging management of rarer species

Pote et al. (2006)	South Africa	savanna	1 tree species	fields, villages	plains and rock outcrops	abundance, size	villages and fields have low recruitment	population is stable due to low mortality, but seedlings are not well protected in human-modified areas
Raebild et al. (2007)	Burkina Faso	savanna	trees	fallows, cultivation, plantations	gallery forest	density, size, richness, composition	richness highest in fallow; regeneration low in parklands	fallow important for keeping tree diversity
Schreckenberg (1999)	Benin	savanna	trees	cultivation, fallow, bush	gallery forest	abundance, size, composition	many trees valuable to people are maintained in fields and fallows	changes in the agricultural system may result in declining importance of valuable species and incentive to maintain them
Schumann et al. (2011)	Burkina Faso	savanna	1 tree species	fallows, crops	W National Park	harvest intensity, abundance, sprouting	healthy stands in fallows and park but no saplings in croplands	stands are well preserved despite harvest due to life history traits
Venter and Witkowski (2010)	Benin	savanna	1 tree species	farmland	NA	abundance, size	largest individuals found in farmed land but juvenile recruitment low	sporadic recruitment probably enough to maintain population due to low mortality

[a] NA indicates no control; PA stands for protected area.

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Chapter 3. Frog and Reptile Communities and Functional Groups Over a Land-Use Gradient in a Coastal Tropical Forest Landscape of High Richness and Endemicity

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Abstract

Information on the response of herpetofauna to different land uses is limited though important for land-use planning to support conservation in human-modified landscapes. Though transformation is dogmatically associated with extinction, species respond idiosyncratically to land-use change, and persistence of species in habitat fragments may depend on careful management of the human-modified matrix. I sampled herpetofauna over a vegetation-type gradient representative of regional land uses (old-growth forest, degraded forest, acacia woodland (i.e. new-growth forest), eucalyptus plantation, and sugar cane cultivation) in the forest belt skirting the southeastern coast of Africa, part of a biodiversity hotspot hosting many endemic herpetofaunal species in a highly transformed landscape. I categorized species into trait-derived functional groups, and assessed abundance and richness of groups and compared community metrics along the gradient. I further assessed the capacity of environmental variables to predict richness and abundance. Overall, old-growth forest harbored the highest richness and abundance, and frogs and reptiles responded similarly to the gradient. Richness was low in cultivation and, surprisingly, in degraded forest but substantial in acacia woodland and plantation. Composition differed between natural vegetation types (forest, degraded forest) and anthropogenic types (plantation, cultivation), while acacia woodland grouped with the latter for frogs and the former for reptiles. Functional group richness eroded along the gradient, a pattern driven by sensitivity of fossorial/ground-dependent frogs (F2) and reptiles (R2) and vegetation-dwelling frogs (F4) to habitat change. Environmental variables were good predictors of frog abundance, particularly abundance of functional groups, but less so for reptiles. Conserving forest and preventing degradation is essential, restoration and plantations have intermediate conservation value, and cultivation is least amenable to forest herpetofauna. My study demonstrates the utility of function-related assessments, beyond traditional metrics alone, for understanding community responses to transformation. Particularly, fossorial/ground-dependent frogs and reptiles and vegetation-dwelling frogs should be closely monitored.

Introduction

Scientists are increasingly studying biodiversity in human-modified landscapes to augment conservation efforts in protected areas with appropriate landscape management beyond them (Daily 1999, Trimble and van Aarde 2012). This is a salient issue in the biologically rich and unique coastal forest belt skirting the southeastern coastline of Africa, which spans the Maputaland Center of endemism (van Wyk 1996) and the Maputaland-Pondoland-Albany biodiversity hotspot (Küper et al. 2004, Perera et al. 2011). However, mining, tourism, agriculture, and subsistence communities have contributed to substantial forest loss and degradation (Kyle 2004). An estimated 82% of coastal forest in KwaZulu-Natal has been destroyed, which jeopardizes ecological integrity and threatens species persistence, even within forest fragments (Trimble and van Aarde 2011, Olivier et al. 2013). Appropriate land-use planning could support the persistence, or at least occurrence, of forest biodiversity in the matrix surrounding fragments and may ameliorate the impacts of fragmentation and isolation. However, amenability of the matrix to forest species likely depends on land use and the species in question, so teasing out which land uses are amenable to which species could contribute to evidence-based land-use policy (see Sutherland 2004, O'Connor and Kuyler 2009).

Herpetofauna are specialized in habitat requirements (Kanowski et al. 2006, Botts et al. 2013), are sensitive to habitat modification, and face global extinction crises (Gibbons et al. 2000, Stuart et al. 2008, Böhm et al. 2013). Forest conservation is particularly important for African frogs; forests harbor two-thirds of Afrotropical Realm species, 32% of which are threatened (Stuart et al. 2008), and range declines over the past century for endemic frogs have been recorded in the coastal forest region (Botts et al. 2013). While herpetofauna are important components of ecosystems as both predators and prey and can influence whole-ecosystem processes (e.g. Beard et al. 2002, Whiles et al. 2006), they are little studied (Trimble and van Aarde 2010), particularly in human-modified landscapes (Trimble and van Aarde 2012), and especially in Africa (Gardner et al. 2007a). Additionally, because habitat modification is a non-random filter for species, identifying characteristics of species that are sensitive to land-use change (see Suazo-Ortuno et al. 2008) can provide insight into taxonomic and functional homogenization and inform broadly applicable conservation strategies (Smart et al. 2006, Cadotte et al. 2011, Mouillot et al. 2013). However, function-related responses to habitat change are particularly poorly understood for herpetofauna (Gardner et al. 2007a).

Nonetheless, frogs and reptiles do occur in human-modified landscapes, and encouraging appropriate matrix land uses can contribute to their conservation (Anand et al. 2010, Sodhi et al. 2010). To clarify the effects of forest transformation and inform land-use planning, I sought to document the response of herpetofaunal communities to a gradient of land uses characteristic of the coastal forest region, which is rich in herpetofauna and harbors many endemic and threatened species (Branch 1998, Armstrong 2001, Stuart et al. 2008, du Preez and Carruthers 2009, Measey 2011, Perera et al. 2011, IUCN 2012). I sampled terrestrial herpetofaunal communities of five vegetation types, subjectively ranked by structural similarity to old-growth forest: forest, degraded forest, acacia woodland (a seral stage of forest regeneration (van Aarde et al. 1996)), eucalyptus plantation, and sugar cane cultivation. I focused on three aims: 1) to test how abundance, richness, diversity, and composition of frog and reptile communities change along the gradient, 2) to assign species to functional groups, sets of species with similar ecological roles, and assess changes in relative and proportional abundance of groups and group richness along the gradient, and 3) to quantify potential ecological drivers of community change by relating environmental variables to overall richness and abundance of frogs and reptiles and to abundance of functional groups.

Methods

Study area

I sampled terrestrial herpetofauna along a 25 km section of coastline across a land-use gradient southwest of Richards Bay, KwaZulu-Natal, South Africa, from 4 km north of the Umlalazi River mouth to just south of the Richards Bay harbor, up to 2.3 km inland (Fig. 3.1). The region falls within the southern terminus of the East African Tropical Coastal Forest (see van Aarde et al. 2013).

Sampling methods

I used a stratified random sample design of 30 trap arrays divided evenly among 5 vegetation types: forest, degraded forest (determined by presence of invasive plants *Lantana camara* and/or *Chromolaena odorata*), acacia woodland (new-growth forest dominated by *Acacia karroo*), eucalyptus plantation, and sugar cane cultivation. Trap arrays were installed in three periods, two arrays per vegetation type per period, between February 19 and March 13, 2012. I checked arrays daily for five days, identified species captured, and released them ≥ 50 m away. Each array was operational for 120 ± 1 hrs. Arrays were separated from each other by ≥ 500 m and from known water bodies by ≥ 300 m (Fig. 3.1).

Each array employed seven complementary sampling techniques, detailed in Appendix S1,to represent as many species as possible (Ribeiro-Júnior et al. 2008). Arrays consisted of three 15 m arms of 0.5-m-tall black plastic drift fence, dug 0.1 m into the ground, spaced at 120°, and connected at a central pitfall bucket. Arms featured pitfall buckets at 7.5 and 15 m from the center bucket, and a funnel trap on either side between the outer two pitfalls. The fence guided frogs and reptiles into pitfalls and funnel traps. Four polyvinyl chloride (PVC) pipe traps (see Trimble and van Aarde 2013) and four wooden cover boards were installed 10 m beyond the northern-pointing fence arm and checked on days two, four, and five. An active search was performed and audio recordings were made in the vicinity of each array, and species found when installing or removing traps were recorded. I measured eight environmental variables at each array and assessed the distribution of array points along southwest—northeast and coastal distance geographic gradients, see Appendix S1.

Analyses

I assessed sampling saturation overall and per vegetation type, separately for amphibians and reptiles, with sample-based accumulation curves calculated in EstimateS 8.2.0 (Gotelli and Colwell 2001, Colwell 2009). I assessed whether vegetation type affected observed richness (species per array) and abundance (individuals per array) with Poisson generalized linear modeling (GLM) and X^2 analysis of deviance (or quasi-Poisson GLM and *F*-tests to account for overdispersion) (Zuur et al. 2009).

I estimated richness of frogs and reptiles per vegetation type with non-parametric richness estimators calculated in EstimateS: four abundance-based (Chao1, ACE, Jack1, and Jack2) and two incidence-based that included frog species identified from audio recordings (Chao2 and ICE). I calculated the range of the proportion of estimated richness that I actually observed based on the lowest and highest of the six estimators. I used the asymmetrical 95% CI of Chao1 and Chao2 to assess whether richness differed between vegetation types (Colwell 2009).

I calculated Shannon diversity overall and per vegetation type based on abundance data for frogs and reptiles and explored differences in evenness and diversity with Rényi diversity profiles calculated in BiodiversityR (Kindt and Coe 2005).

To assess composition, I calculated pairwise Bray-Curtis similarity on raw frog and reptile abundance, square-root-transformed abundance (to decrease the influence of abundant species), and frog incidence data including species identified in audio recordings (here, Bray-Curtis simplified to Sorenson similarity) (Clarke and Gorley 2006, Anderson et al. 2011). I used Primer 6's (Clarke and Gorley 2006) analysis of similarity (ANOSIM) to compare community composition among vegetation types and visualized differences with non-metric multidimensional scaling (NMDS).

I assigned species to functional groups based on functional traits from published information (Branch 1998, du Preez and Carruthers 2009, Pla et al. 2012). Frogs traits comprised maximum snout-urostyle length, primary stratum of activity (fossorial, on ground, or in vegetation), where eggs are laid (ground, water, or vegetation), and where tadpoles develop (water or underground). Reptiles traits comprised maximum snout-ventral length, mean clutch size, active stratum (allowing multiple options of burrowing/fossorial, ground-active, or climbing on vegetation/rocks), reproductive strategy (viviparous or egg-laying), locomotion (legs or legless), and feeding style (venomous, constrictor, or ambush). I defined functional groups in InfoStat (Di Rienzo et al. 2011); following Pla et al. (2012), I transformed categorical variables into a set of quantitative principal coordinates with multidimensional scaling and retained a set of axes that explained ≥ 85% of variation, then used Euclidian distances and the Ward linkage algorithm to create dendrograms for frogs and reptiles separately. I retained four functional groups each for frogs and reptiles and used MANOVA with Hotelling post-test and Bonferroni adjustment to assess grouping significance.

I modeled abundance of functional groups on vegetation type with Poisson GLM and compared to the null model with X^2 analysis of deviance (or quasi-Poisson GLM and *F*-tests to account for overdispersion) (Zuur et al. 2009). Similarly I compared proportional abundance of each functional group across vegetation types with binomial GLM (or quasi-binomial to account for overdispersion) (Zuur et al. 2009). I also tallied the number of functional groups represented per vegetation type.

I compared environmental variables among vegetation types with ANOVA. I dropped canopy cover and height from further analyses because they were significantly collinear with each other and temperature range, herb cover, and litter depth with correlation coefficient magnitude ≥ 0.6 (Zuur et al. 2009); I retained the latter variables plus litter cover, soil pH, and mean temperature. I used Poisson GLM to assess the relationships between environmental variables and frog and reptile richness and abundance and the abundance of functional groups. For each case, I parameterized the model set of single-order combinations of six environmental variables and a null model. I used AICc to compare models and performed multi-model averaging across models with AICc differences (Δ_i) < 4 (Grueber et al. 2011). Where overdispersion was present, I used quasi-Poisson GLMs and quasi-AICc (QAICc) (Zuur et al. 2009).

Results

I captured 436 individuals representing 17 frog and 20 reptile species (Table 3.1). Nine frog species were recorded with audio recorders (three that were not captured in arrays), bringing the number of species recorded to 40. Many calls carried further than the 50m estimated by Hilje and Mitchell Aide (2012); thus, I excluded five species recorded in audio recordings that are only known to call from water bodies (Channing 2001, du Preez and Carruthers 2009), resulting in 38 species considered in further analyses (Table 3.1). Only *Amietophrynus gutturalis* (Table 3.1 provides common names) was recorded in every vegetation type.

Richness, abundance, and diversity

Sampling approached but did not reach an asymptote for frogs or reptiles overall or any vegetation type, and 95% CI for frog and reptile abundances overlapped (Fig. S.3.1). The proportion of expected species that I observed was 71-93% for frogs and 63-84% for reptiles and differed by vegetation type (Table 3.2). Richness estimators varied but were similar within groups, except for reptiles in forest (Table 3.2). Incidence-based estimators were higher than abundance-based estimators for frogs because they included auditory records (Table 3.2).

While species and individuals recorded per array did not differ significantly between vegetation types (Fig. 3.2), 95% CI indicated Chao1 for frogs was significantly higher in forest, acacia woodland, and plantation than in degraded forest or cultivation. Chao2 for frogs did not differ significantly among vegetation types. Other estimators ranked vegetation types variably but suggested higher richness in forest, acacia woodland, and plantation and lower richness in degraded forest and cultivation (Table 3.2). Reptile Chao1 was significantly higher in forest, acacia woodland, and plantation than in cultivation, while Chao2 was significantly higher in forest than degraded forest and cultivation (Table 3.2). Other estimators consistently ranked reptile richness highest in forest; intermediate in acacia woodland and plantation; and lowest in degraded forest and cultivation.

For both frogs and reptiles, Shannon diversity was highest in plantation and lowest in cultivation and degraded forest (Table 3.2). Rényi profiles confirmed these rankings and showed diversity rankings of other vegetation types depended on the influence of evenness, i.e. Rényi profiles intersected (Kindt and Coe 2005) (Fig. S.3.2).

Composition

ANOSIM of square-root-transformed data indicated significant difference in composition among vegetation types (Table 3.3). Frog community structure in forest differed significantly from that in acacia woodland, plantation, and cultivation, while degraded forest differed from cultivation. Reptile community structure differed significantly between natural vegetation types (forest, degraded forest, or acacia woodland) and anthropogenic types (cultivation or plantation), except degraded forest did not differ significantly from plantation. NMDS ordination illustrated these patterns (Fig. S.3.3). Results based on raw abundance and frog incidence data were similar (Fig. S.3.3, Table S.3.1).

Functional groups

Group size was similar, and group descriptions were ecologically sensible (Tables 3.1 & 3.4). Traits differed between functional groups for frogs (Wilks' $\lambda = 1.6\text{x}10^{-4}$, $F_{12,29}$ =

64.82, $p < 0.001$) and reptiles (Wilks' $\lambda = 2.4 \times 10^{-5}$, $F_{24,27} = 42.63$, $p < 0.001$), and Hotelling post-tests indicated significant differences among all functional groups.

Vegetation type was a significant predictor of abundance for functional groups F2 and R2 and of proportional abundance for F1, F2, F3, and R2 (Table 3.4). Proportional abundance of several functional groups changed directionally along the gradient from forest to cultivation, while number of groups represented decreased (Fig. 3.3).

Environmental predictors

Environmental variables differed significantly among vegetation types (Fig. 3.4). They were variably effective at predicting frog and reptile richness and abundance; proportion of deviance explained by the global model ranged from 0.06 for reptile richness to 0.67 for abundance of functional group F2 (Table S.3.2). Generally, models performed better for frogs than reptiles and for functional group abundance than overall richness and abundance (Table S.3.2, S.3.3). The importance and effect of environmental variables differed among dependent variables (Table S.3.3).

Discussion

I assessed how a rich herpetofaunal community responded to a land-use gradient to elucidate the consequences of forest transformation and inform land-use planning. One-quarter of the species I encountered are endemic or near-endemic to Maputaland, a third to southern Africa, and all but one to Africa (Branch 1998, du Preez and Carruthers 2009). My study falls at the juncture of three global conservation concerns: tropical forest loss

(Wright and Muller-Landau 2006), immense pressure on coastal habitat (Arthurton et al. 2006), and frog and reptile extinction crises (Stuart et al. 2008, Böhm et al. 2013).

Richness, diversity, composition

The number of species and individuals observed was highest in forest. Richness estimators for both frogs and reptiles indicated higher richness in forest, acacia woodland, and plantation and lower richness in degraded forest and cultivation. Thus, richness did not monotonically decrease along the gradient with subjective decrease in forest similarity. Diversity was generally highest in plantation and lowest in degraded forest and cultivation. Community composition in forest and degraded forest differed from anthropogenic land-uses, i.e. plantation and cultivation, while the acacia woodland community grouped with the former for reptiles and the latter for frogs.

Degraded forest hosted an impoverished version of the forest assemblage for both frogs and reptiles. This was unexpected based on studies of herpetofaunal response to selective logging, which may be analogous to the processes that degrade forests in the study area, e.g. physical disturbance by humans and livestock and effects from neighboring transformed land. A recent review found no evidence for loss of herpetofaunal richness in selectively logged areas (Gardner et al. 2007a). However, in West African forests, Hillers et al. (2008) found that degradation, represented by structural measures, was associated with reduced richness and altered community composition of leaf-litter frogs, possibly via changes in microclimate. In my study, degraded forest had lower mean canopy cover and height but higher ranges of these and of herb cover and litter depth than did forest. Thus, altered microclimate may drive the low abundance, richness, and diversity observed in degraded forest.

Acacia woodland represents a seral stage of forest succession (van Aarde et al. 1996), expected to support lower richness than old-growth forest (Wassenaar et al. 2005). My results are similar to other studies' (Gardner et al. 2007a, Wanger et al. 2010, Hilje and Mitchell Aide 2012) that report lower richness in new-growth but a substantial representation of old-growth species. However, that community structure in acacia woodland was similar to that of forest for reptiles but not for frogs hints at barriers to frog recolonization of new-growth forest.

Plantations of exotic trees hosted structurally distinct frog and reptile communities compared to forest but a high richness and diversity, in agreement with other studies (Vonesh 2001, Gardner et al. 2007a). Plantation communities likely combine species typical of forest with species characteristic of open habitats and are not necessarily biodiversity deserts as is often assumed (see Armstrong et al. 1998). Nonetheless, some studies have found plantations to be depauperate in amphibians (e.g. Kudavidanage et al. 2011). Inland from my study area, Russell and Downs (2012) found few frog species in large-scale eucalyptus plantations. The plantations in my study were small-scale with small, coppiced trees and had vegetated understories. Thus, the effects of plantation variables, e.g. size, age, and management, require further study.

Consistent with other studies (e.g. Russell and Downs 2012), sugar cane cultivation had few species, few individuals, and low diversity. However, cultivation harbored species absent or rare in other vegetation types, e.g. *Psammophis brevirostris*, but they were wide-ranging, open habitat species (Branch 1998, du Preez and Carruthers 2009).

Functional groups

A trait- rather than species-based approach is expected to better quantify and predict the effects of disturbance on communities and the consequences for ecosystem functionality (Mouillot et al. 2013). Functional groups are known to be differentially susceptible to disturbance; e.g. small-bodied frogs and those that lay eggs in soil are thought to be more disturbance-sensitive than large-bodied frogs and those that lay eggs in water (Suazo-Ortuno et al. 2008). In my study, fossorial/ground-dependent frogs (F2) and reptiles (R3) decreased along the gradient from forest to cultivation in abundance and proportional abundance. Vegetation-dwelling frogs (F4) were not found in plantation or cultivation. These groups appear to be particularly challenged in human-modified habitats, likely because of changes in soil and vegetation properties, a hypothesis supported by the results of modeling functional group abundance on environmental variables.

The number of functional groups per vegetation type declined along the gradient from all eight recorded in forest to just five in cultivation, in line with the suggestion that functional diversity declines monotonically along a disturbance gradient in contrast to species richness (Mouillot et al. 2013). Few studies have investigated functional aspects of herpetofaunal response to land-use change (Gardner et al. 2007a). Pineda et al. (2005) found reduced frog guild richness in coffee plantations compared to forest. My results agree with, and extend to plantations and cultivation, the observation that frog functional diversity is lower in degraded forest than in primary forest (Ernst et al. 2006). Loss of functional groups implies increased overlap among species' trait profiles and, thus, functional homogenization (Braiser and Lockwood 2011), and has consequences for ecosystem function (e.g. Tilman et al. 2001, O'Connor and Crowe 2005, Cardinale et al. 2012). Therefore, measures of functional diversity should complement those of species richness (Ernst et al. 2006), and the effects of functional diversity loss in herpetofaunal communities warrant further investigation.

Environmental predictors

Environmental variables were good predictors of abundance of frog functional groups, probably because functional groups combine species with similar roles in the ecosystem, which are likely similarly dependent on particular conditions. F1, F2, and F3 all showed a significant negative relationship with herb cover and mean temperature, while soil pH and litter cover had positive effects. Abundance of F4 was positively related to litter depth, which conceivably reflects dependence of vegetation-dwelling frogs on increased canopy cover or vegetation density rather than litter depth per se.

The relationship between frog abundance and environmental variables suggests that frogs respond to the vegetation-type gradient due to changes in microhabitat conditions. Thus, environmental variables have potential for predicting frog community responses to land uses not assessed here. Land uses resulting in soil acidification, reduced litter cover, or increased herb cover or mean temperature appear to be generally negative for frogs (Wyman 1988, Suazo-Ortuno et al. 2008).

Environmental variables were less effective predictors of reptile functional group abundance. However, R1, ambush-hunting and constricting snakes, was positively associated with litter cover as was R2, fossorial reptiles, which was also negatively associated with mean temperature. For these species, litter cover may offer concealment and could be associated with prey availability; however, abundance of R3, ground-active and climbing lizards, was negatively associated with litter cover.

Un-modeled factors or a lesser dependence on specific microhabitat may explain the weaker relationship between reptile abundance and environmental variables. Compared to reptiles, frogs and frog eggs have more stringent moisture and temperature requirements and are sensitive to solar radiation (Gibbons et al. 2000, Suazo-Ortuno et al. 2008). Furthermore, reptiles often move greater lifetime distances than do frogs (Gibbons et al. 2000), so their occurrence may more often reflect mere transience.

Constraints and future research

Interpreting herpetofaunal studies requires caution due to sampling constraints, low capture success, and limited spatial extent common in many studies, and sampling efficacy is species- and habitat-dependent (Gardner et al. 2007a, Ribeiro-Júnior et al. 2008). Thus, I used a combination of methods emphasizing passive techniques to reduce observer bias, while maintaining standardized effort across vegetation types. Still, the samples are unlikely to represent the complete community due to true rarity and furtive habits of many species. Nonetheless, the standardized nature of my sampling enables future work to build on my capture data by increasing the coverage extent or investigating other vegetation types or seasons.

I experienced low capture success, a common challenge in the tropics where high richness and rarity is expected (Gardner et al. 2007a). Concerns over cost (~32 person-hours per array), introduction of seasonal effects (e.g. Gardner et al. 2007b), and the impracticality of increasing the study area (coastal forest gives way to grassland and savanna inland) prohibited additional trapping arrays. Nonetheless, the percentage of species observed to estimated richness was comparable to other studies (e.g. Bell and Donnelly 2006, Gardner et al. 2007c, Suazo-Ortuno et al. 2008), although many species were recorded infrequently. Clearly, failure to detect a species does not imply absence, nor does presence imply persistence solely within that habitat (Gardner et al. 2007a). Persistence and the potential for ecological traps (Battin 2004) should be further investigated.

Future research on species-specific responses to land-use change would be useful because species respond idiosyncratically (Gardner et al. 2007a). The functional group approach goes some way towards assessing differential responses of components of the community. However, broadly defined functional groups overestimate redundancy (Cadotte et al. 2011). Thus, loss of functional groups across the gradient likely underestimated true functional diversity loss (Petchey and Gaston 2002).

Conservation implications

Two species in this study are of explicit conservation concern (*Afrixalus spinifrons* and *Hemisus guttatus* (IUCN 2012)), and Botts et al. (2013) demonstrated that habitat specialist frogs in the region have undergone range contractions, likely due to habitat loss. Therefore, small-range, endemic species are of concern even if not formally threatened, while most reptile species observed in this study have not even been evaluated (IUCN 2012).

My results highlight the sensitivity of fossorial/ground-dependent herpetofauna to forest transformation. Unfortunately, this group includes many small-range species, e.g. *Leptopelis natalensis* and *Acontias plumbeus*. Thus, although they are difficult to study

(Maritz and Alexander 2008), fossorial species warrant monitoring, especially because they are poorly known (Böhm et al. 2013). Vegetation-dwelling frogs should also be monitored.

Maintaining old-growth forest is important for conserving herpetofauna. However, other vegetation types did support occurrence of some species, which should be considered in land-use planning, especially given the conservation challenges imposed by the linear nature of the coastal forest system (Olivier et al. 2013, van Aarde et al. 2013). Degraded forest harbored particularly low richness and diversity, so degradation must be prevented, a concern even within protected areas because many allow access to local people for wood collection and grazing or lack management altogether (Kyle 2004). Restoration projects that generate acacia woodland could provide habitat and increase connectivity of forest fragments. Plantations may hold some value for connecting not only forest fragments, but perhaps also savanna and grassland fragments due to their diverse combination of forest and open-habitat species including species of conservation concern, e.g. *Hemisus guttatus*. However, caution is required in extrapolating my results from small- to large-scale plantations, and hydrological impacts may negatively offset conservation value (Armstrong et al. 1998). Finally, sugar cane cultivation was of little value for forest associated herpetofauna.

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Figures

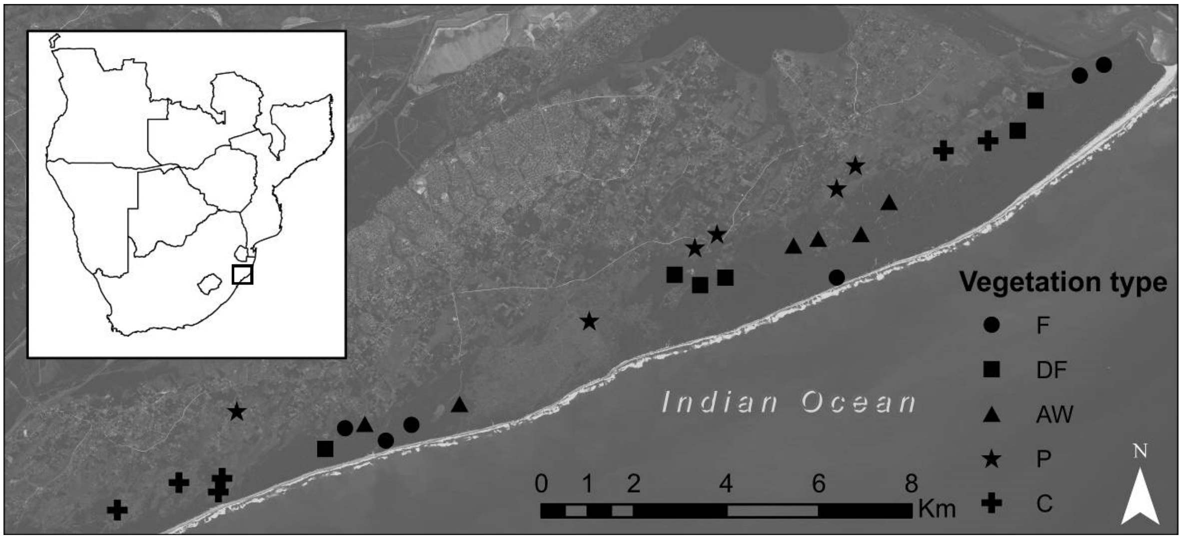

Fig. 3.1. Study area map indicating location of trapping arrays in five vegetation types (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation); inset shows study area location in southern Africa.

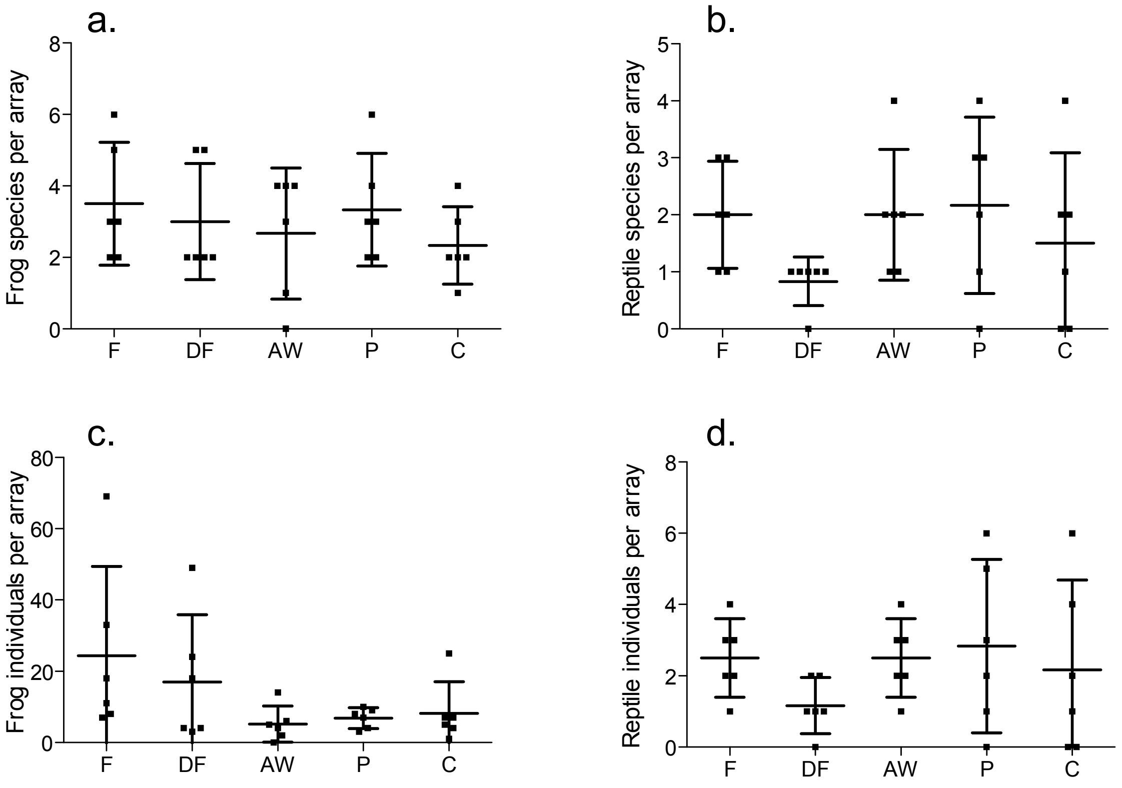

Fig. 3.2. Vegetation type (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation) was not a significant predictor in Poisson or quasi-Poisson GLM for species observed per array for (a) frogs (X^2 = 1.87, df = 4, p = 0.76) and (b) reptiles (X^2 = 4.73, df = 4, p = 0.32) or individuals recorded per array for (c) frogs (Φ = 11.40, $F_{4,25}$ = 2.70, p = 0.05) and (d) reptiles (Φ = 1.18, $F_{4,25}$ = 1.05, p = 0.40). Graphs illustrate mean and 95% CI.

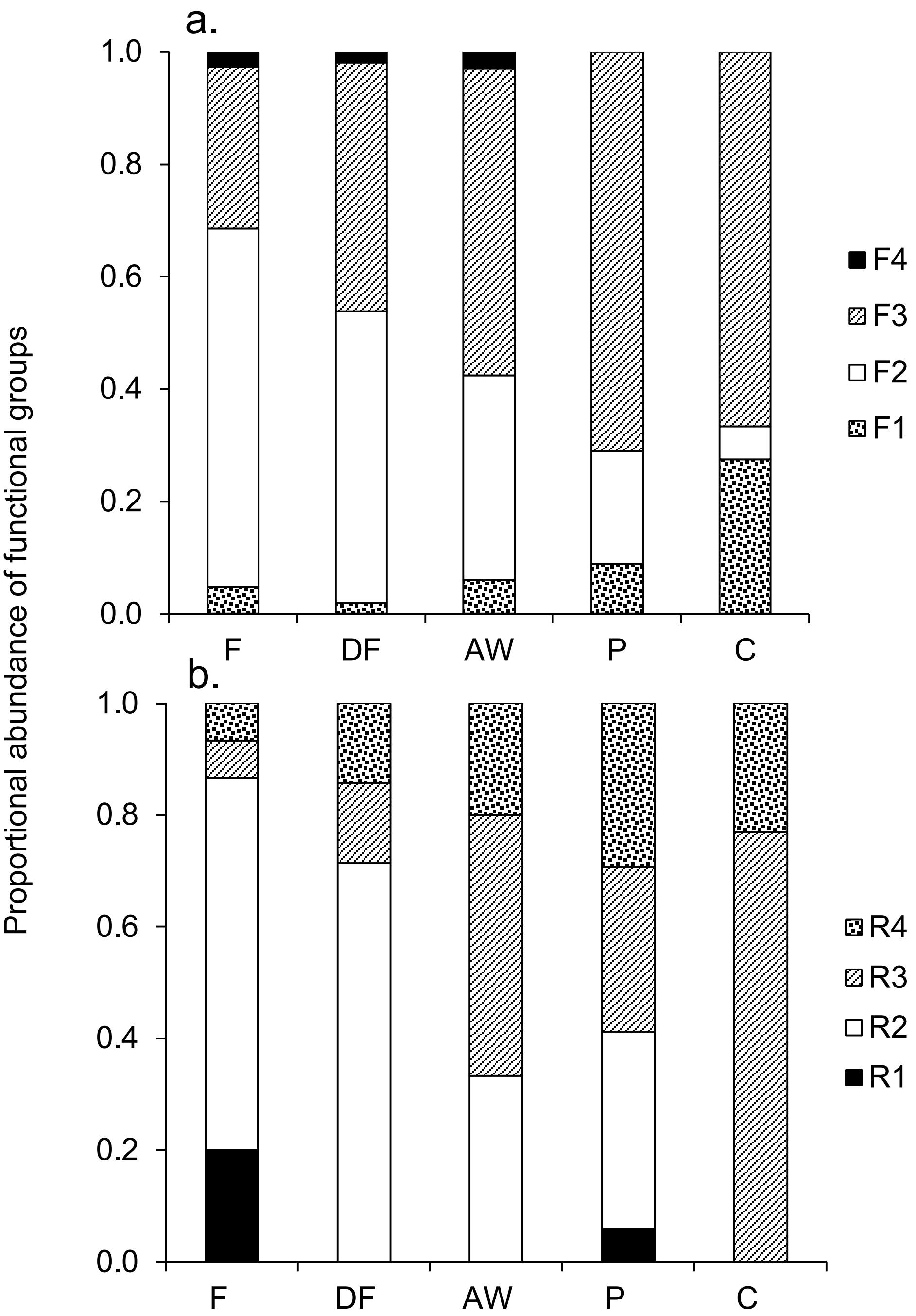

Fig. 3.3. Proportional abundance of functional groups for (a) frogs and (b) reptiles for each vegetation type (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation).

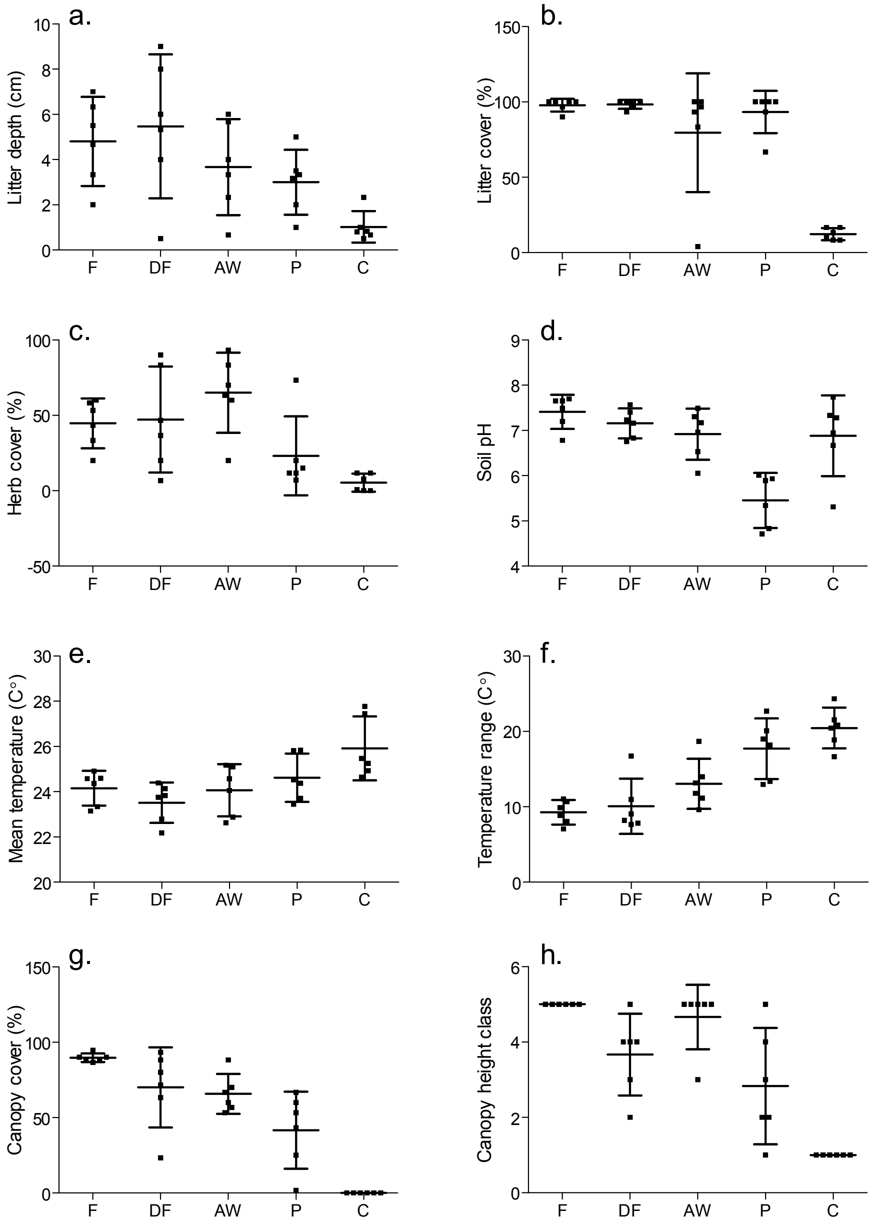

Fig. 3.4. Environmental variables differed significantly among vegetation types (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation) for (a) litter depth ($F_{4,25} = 4.69$, $p < 0.01$), (b) litter cover ($F_{4,25} = 24.70$, $p < 0.001$), (c) herb cover ($F_{4,25} = 6.02$, $p < 0.01$), (d) soil pH ($F_{4,25} = 11.08$, $p < 0.001$), (e) mean temperature ($F_{4,25} = 4.66$, $p < 0.01$), (f) temperature range ($F_{4,25} = 15.38$, $p < 0.001$), (g) canopy cover ($F_{4,25} = 25.29$, $p < 0.001$), and (h) canopy height (in classes: 1 = 0–2 m, 2 = > 2–4 m, 3 = > 4–6 m, 4 = > 6–8 m, and 5 = > 8 m) ($F_{4,25} = 19.83$, $p < 0.001$). I illustrate means and 95% CI.

Tables

Table 3.1. Abundance of frog and reptile species captured in trapping arrays (where * indicates confirmation of frog species by audio recording [a]) across vegetation types (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation), and functional group to which species are assigned based on functional traits.

Scientific name, common name [b]	**F**	**DF**	**AW**	**P**	**C**	**Total**	**Functional group**
Frogs							
Amietophrynus gutturalis, guttural toad	41	44	16	27	33	161	F3
Arthroleptis wahlbergi, bush squeaker	89	51	10	5	0	155	F2
Phrynobatrachus natalensis, snoring puddle frog	0	0*	0*	0	10	10*	F1
Breviceps sopranus, whistling rain frog [c]	3	2	2	0	2	9	F2
Phrynobatrachus mababiensis, dwarf puddle frog	6	0	0	2	0	8	F1
Afrixalus spinifrons (spinifrons), Natal leaf-folding frog	2	2	0	0	0	4	F4
Amietophrynus rangeri, raucous toad	1	2	0	1	0	4	F3
Breviceps mossambicus, Mozambique rain frog [c]	0	0	0	3	0	3	F2
Phrynobatrachus acridoides, East African puddle frog	0	0	0	0	3	3	F1
Afrixalus fornasinii, greater leaf-folding frog	2	0	0	0	0	2	F4
Hyperolius pusillus, water lily frog	0	0	1	0	1	2	F1
Kassina senegalensis, bubbling kassina	1*	0	0	1*	0	2*	F1
Leptopelis natalensis, Natal tree frog	1	1*	0	0	0*	2*	F2
Amietophrynus garmani, eastern olive toad	0	0	1	0	0	1	F3
Hemisus guttatus, spotted shovel-nosed frog	0	0	0	1	0	1	F2
Hyperolius tuberilinguis, tinker reed frog	0	0	1	0	0	1	F4
Strongylopus fasciatus, striped stream frog	0	0	0	1	0	1	F2
Ptychadena oxyrhynchus, sharp-nosed grass frog	0	0*	0*	0*	0*	0*	F3
Reptiles							
Scelotes mossambicus, Mozambique dwarf burrowing skink	6	5	2	0	0	13	R2
Panaspis wahlbergii, Wahlberg's snake-eyed skink	0	0	1	3	3	7	R3
Mabuya varia, variable skink	0	1	6	0	0	7	R3
Lygodactylus capensis (capensis), Cape dwarf gecko	0	0	0	1	3	4	R3
Zygaspis vandami (arenicola), Van Dam's round-	1	0	3	0	0	4	R2

headed worm lizard							
Mabuya striata (striata), striped skink	0	0	0	0	3	3	R3
Hemidactylus mabouia, Moreau's tropical house gecko	1	0	0	1	0	2	R3
Acontias plumbeus, giant legless skink	2	0	0	0	0	2	R2
Gerrhosaurus flavigularis, yellow-throated plated lizard	0	0	0	0	1	1	R3
Psammophis brevirostris (brevirostris), short-snouted grass snake	0	0	0	1	3	4	R4
Leptotyphlops sp., thread snakes [d]	0	0	0	4	0	4	R2
Crotaphopeltis hotamboeia, herald snake	0	1	0	2	0	3	R4
Psammophis mossambicus, olive grass snake	0	0	1	2	0	3	R4
Aparallactus capensis, Cape centipede eater	1	0	0	2	0	3	R2
Causus rhombeatus, rhombic night adder	1	0	1	0	0	2	R4
Lamprophis fuliginosus, brown house snake	0	0	0	1	0	1	R1
Philothamnus natalensis (natalensis), eastern green snake	1	0	0	0	0	1	R1
Mehelya nyassae, black file snake	1	0	0	0	0	1	R1
Thelotornis capensis (capensis), vine snake	0	0	1	0	0	1	R4
Philothamnus hoplogaster, green water snake	1	0	0	0	0	1	R1
Total individuals observed	161	109	46	58	62	436	
Total species observed (including audio recordings)	18	9(11)	13(15)	17(18)	10(12)	37(38)	

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[a] Audio records of guttural toad *Amietophrynu gutturalis*, water lily frog *Hyperolius pusillus*, tinker reed frog *Hyperolius tuberilinguis*, painted reed frog *Hyperolius marmoratus*, and red-legged kassina *Kassina maculata* were excluded because they only call from water bodies.

[b] Scientific and common names follow nomenclature in du Preez and Carruthers (2009) and Branch (1998).

[c] These *Breviceps* species are cryptic (Minter 2003), and while species identification was confirmed by expert examination of photographs, only genetic identification would provide certainty; these results should be interpreted with caution.

[d] I did not identify *leptotyphlops* to species level because they are cryptic, and the complex is under further revision. Currently, four species are known from the region of the study (Branch 1998).

Table 3.2. Observed species richness and abundance, abundance- and incidence-based richness estimators, percent of predicted richness actually observed, and Shannon diversity of frogs and reptiles across five vegetation types (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation).

	Species obs.	**Ind. obs.**	**Abundance-based estimators**				**Incidence-based estimators**		**Percent observed (range)**	**Shannon diversity**
			Chao 1 (95% CI)	**ACE**	**Jack 1**	**Jack 2**	**Chao 2 (95% CI)**	**ICE**		
Frogs										
Total	17 (18)	369	18.2 (17.1–27.4)	20.6	22.8	23.9	22.8 (18.9–46.9)	22.9	71–93%	1.35
F	9	146	10.0 (9.1–19.7)	12.2	12.3	13.4	10.3 (9.1–19.8)	14.6	62–90%	1.09
DF	6 (8)	102	6.0 (6.0–6.0)	6.7	8.5	10.0	9.7 (8.2–21.7)	14.2	56–100%	0.99
AW	6 (8)	31	7.5 (6.2–21.1)	12.0	8.5	10.0	12.2 (8.6–35.2)	18.4	43–80%	1.22
P	8 (9)	41	11.0 (8.4–31.0)	10.8	12.2	14.4	10.3 (9.1–19.8)	13.7	56–87%	1.23
C	5 (7)	49	5.0 (5.0–5.0)	5.6	6.7	6.9	8.7 (7.2–20.7)	15.6	45–100%	0.97
Reptiles										
Total	20	67	23.8 (20.6–42.0)	23.8	27.7	31.6	25.4 (21.1–46.3)	28.5	63–84%	2.71
F	9	15	19.5 (11.0–63.2)	37.5	15.7	21.0	32.3 (15.2–96.6)	67.8	13–57%	1.9
DF	3	7	4.0 (3.1–15.9)	7.0	4.7	6.0	3.8 (3.06–14)	6.7	43–79%	0.8
AW	7	15	10.0 (7.4–30.0)	13.5	10.3	12.5	9.5 (7.3–26.6)	11.9	52–74%	1.68
P	9	17	10.5 (9.2–21.5)	12.0	13.2	14.4	10.7 (9.2–21.1)	14.6	62–86%	2.07
C	5	13	5.0 (5.0–6.6)	5.4	6.7	6.9	5.3 (5.0–10.2)	6.6	72–100%	1.55

Table 3.3. Analysis of similarity (ANOSIM) results comparing frog and reptile community composition among vegetation types based on Bray–Curtis similarity of square-root-transformed abundance data.

Vegetation type comparison	**Frogs (Global R = 0.174, p < 0.01)**		**Reptiles (Global R = 0.194, p < 0.001)**	
	R statistic [a]	**p [b]**	**R statistic [a]**	**p [b]**
Forest–degraded forest	−0.02	0.52	−0.05	1.00
Forest–acacia woodland	0.22	< 0.05*	0.15	0.08
Forest–plantation	0.24	< 0.05*	0.25	< 0.05*
Forest–cultivation	0.79	< 0.01**	0.38	< 0.001***
Degraded forest–acacia woodland	0.00	0.40	0.09	0.2
Degraded forest–plantation	−0.01	0.47	0.18	0.06
Degraded forest–cultivation	0.27	< 0.05*	0.28	< 0.05*
Acacia woodland–plantation	0.05	0.20	0.30	< 0.01**
Acacia woodland–cultivation	0.16	0.07	0.35	< 0.01**
Plantation–cultivation	0.11	0.10	0.09	0.17

[a] ANOSIM generates an R statistic ranging from −1 (where similarities across different vegetation types are higher than within types) to 1 (where similarities within types are higher than between types) (Clarke and Gorley 2001).

[b] Significance of each comparison is indicated by $*p \leq 0.05$, $** p \leq 0.01$, $*** p \leq 0.001$.

Table 3.4. Functional group descriptions (F*x* are frog groups, R*x* are reptile groups), number of species per group, and statistics describing significance of vegetation type as a predictor of abundance and proportional abundance of each functional group in Poisson (or quasi-Poisson) and binomial (or quasi-binomial) GLMs respectively (see Table 3.1 for species composition of groups).

Functional Group	Description	Number of species	Vegetation type as predictor of abundance	Vegetation type as predictor of proportional abundance
F1	Small, ground-dwelling frogs (except water lily frog) that lay eggs in water	5	$\Phi = 2.05$, $F_{4,25} = 1.93$, $p = 0.14$	$X^2 = 27.05$, df = 4, $p < 0.001$
F2	Fossorial or ground-dwelling species (except Natal tree frog) that lay eggs in the ground, i.e. ground dependent. Tadpoles of three species develop in the ground	6	$\Phi = 7.32$, $F_{4,25} = 5.89$, $p < 0.01$	$\Phi = 1.62$, $F_{4,24} = 11.60$, $p < 0.001$
F3	Large, ground-dwelling frogs that lay eggs in water	4	$\Phi = 4.82$, $F_{4,25} = 0.79$, $p = 0.54$	$\Phi = 1.25$, $F_{4,24} = 7.93$, $p < 0.001$
F4	Small, vegetation-dwelling frogs that lay eggs in vegetation	3	$X^2 = 9.15$, df = 4, $p = 0.06$	$\Phi = 3.78$, $F_{4,24} = 0.29$, $p = 0.88$
R1	Snakes that attack by constricting or ambush, tend to be shorter than R4	4	$X^2 = 8.38$, df = 4, $p = 0.08$	$X^2 = 7.69$, df = 4, $p = 0.10$
R2	Legless, burrowing species, tend towards small clutch size	5	$X^2 = 14.01$, df =4, $p < 0.01$	$\Phi = 1.69$, $F_{4,21} = 3.09$, $p < 0.05$
R3	Ground-active and climbing lizards, locomotion with legs, hunt by ambush	6	$\Phi = 1.64$, $F_{4,25} = 2.15$, $p = 0.10$	$\Phi = 1.84$, $F_{4,21} = 2.56$, $p = 0.07$
R4	Venomous snakes, tend to be longer than R1	5	$\Phi = 1.03$, $F_{4,25} = 1.07$, $p = 0.39$	$\Phi = 1.17$, $F_{4,21} = 0.68$, $p = 0.61$

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Supplementary Material

Appendix S1

Pitfall traps:

Pitfall traps were dark plastic 20 liter buckets dug into the ground such that the rim of the bucket was flush with ground level. Several small drainage holes (0.5 cm) were drilled in the bottom of each bucket. Each trap array contained seven pitfall buckets, one at the central point, and two along each arm. Bucket lids, to protect buckets from sun, rain, and predators, were suspended 10 cm over buckets using wire stands. 3 cm of soil and leaf litter were placed inside buckets along with a wet sponge to maintain a suitable environment for trapped organisms. Sampling effort in pitfall traps was 35 trap nights per array, 210 trap nights per vegetation type, and 1050 trap nights in the overall study.

Funnel traps:

I constructed funnel traps out of 0.5 cm wire mesh following Fisher et al. (2008). Funnel traps were cylinders 90 cm long and 14 cm in diameter with inverted cone funnels with 4 cm openings inserted in each end. Funnel traps were installed along each side of each drift fence arm with soil built up around the bottom to guide amphibians and reptiles moving along the fence into the funnel. Funnels were covered with leaves and vegetation to provide shade for trapped organisms. Sampling effort in funnel traps was 30 trap nights per array, 180 trap nights per vegetation type, and 900 trap nights in the overall study.

Cover boards:

Four cover boards were placed on the ground in an array 10 meters beyond the final pitfall bucket of the northern most pointing drift fence arm. The boards were 60 cm square sheets of 2 cm plywood.

PVC pipe traps:

Pipe trap were mounted on a tree nearest the cover boards at each array point. Each pipe trap array consisted of four, 60 cm long, opaque white PVC pipes. I inserted two pipes, one of 16 mm internal diameter and one of 44 mm internal diameter, into the ground near the base of a tree. I capped one end of another two pipes, one of each of the two diameters, fixed them together with cable ties, and hung them vertically from the tree trunk such that the open end was at a height of 2 m. The caps allowed retention of standing water in the bottom of the hanging pipes, and I drilled a hole in the pipes 15 cm from the bottom to prevent the pipes from totally filling with water (following recomendations in Boughton et al. 2000). I installed pipes on a variety of tree species with circumference at breast height ranging from 10 cm to 200 cm (mean 53.7 cm, standard deviation 41.2 cm). In forest and degraded forest, I commonly hung pipes on White Stinkwood *Celtis africana* and Horsewood *Clausena anisata* trees. In acacia woodland, pipes were hung on Sweet Thorn *Acacia karroo* while I used eucalyptus trees in woodlots. At five of the six sugar cane cultivation array sites, there were no trees nearby, so all four pipes were inserted into the ground. I hung pipes in a dead tree of unknown species at one cultivation site.

Acoustic sampling:

Automated acoustic recordings were made at each site with Song Meter SM2+ Terrestrial Acoustic Recorders (manufactured by Wildlife Acoustics, Concord, Massachusetts). Recorders were mounted to a tree 1 m off the ground, within a 15 m radius of the center bucket of the array, and set to record at a sample rate of 44,100 Hz for 5 minutes every hour, on the hour, for a 24-hour period. Acoustic detection depends on the power of each species' call, but estimates suggest that calling amphibians will be picked up by audio recorders over a 50 m radius (Hilje and Mitchell Aide 2012). I analyzed audio files with Raven Pro version 1.4 software (Bioacoustic Research Program, Cornell Lab of Ornithology, Ithaca, New York) to visualize spectrograms concurrently to listening to recordings. Calling amphibians were identified by comparison with species-specific spectrograms and audio recordings provided in du Preez and Carruthers (2009). Overall, I analyzed 720 5-min recordings, or 120 min per site.

Active search:

One active search was carried out per sampling array, and all searches were carried out by the same individual expert observer. Each search was performed during daylight hours and lasted 30 min, in which the observer searched an area extending roughly 50 m from the central pitfall bucket of each array. The observer searched the area at will, focusing on particular areas one might expect to encounter herpetofauna, e.g. under rocks, on trees, in fallen logs, and in leaf litter. All amphibian and reptile species identified visually by the observer were recorded.

Incidental recordings:

I recorded species found when installing or removing trap arrays, which was a relatively standardized effort. For the most part, species found included fossorial species caught when digging holes for the pitfalls or trenches for the drift fences.

Environmental variables:

I measured climatic and structural environmental variables to characterize study sites. At each sampling array, I used HOBO data loggers mounted on rods 20cm from the ground to record temperature every 10 minutes for the duration of the five days that each trapping array was active. I then calculated a mean temperature for each array and the range in degrees from the minimum and maximum temperature recorded on each data logger. I recorded structural variables including canopy cover, canopy height, litter depth, litter cover, and herb cover. Canopy cover was measured at three points, each 5 m away from the center bucket of the trapping array, by visually estimating coverage when looking through a 10 cm tube of 4 cm diameter. Canopy height was assigned to classes (0-2 m, > 2-4 m, > 4-6 m, > 6-8 m, and > 8 m). The other structural variables were measured in a 1 m x 1 m PVC pipe frame at each of the three sampling points. Litter depth was measured to the nearest cm with a ruler at the center of the frame, while litter cover (woody debris and leaves) and herb cover (herbaceous vegetation excluding grasses and trees) were visually estimated to the nearest 5%. For each array, I averaged the three values for each variable to achieve a single value. To calculate soil pH, a trowel-full of soil was collected from each of the three sampling points at each array and mixed in a bag. I oven-dried 50 g of each soil sample for 24 hours at 70℃. I combined 15 ml of each dried soil sample with 75 ml distilled water, shook for 1 min, let sit for 1 hour, shook again, and measured pH with a Consort c562 meter.

Geographic gradients

For each array point, I measured distance to the coast and distance along a southwest—northeast gradient according to distance from the most southwesterly array point. I assessed whether vegetation types differed significantly in coastal distance or southwest—northeast gradient with ANOVA. Vegetation types differed significantly in their distance from the coast ($F_{4,25} = 7.40$, $p < 0.01$), and Tukey's multiple comparison test indicated significant differences between plantation points and others. Besides plantations, the distance from the coast of other vegetation types did not differ significantly from each other. Contrastingly, there was no significant difference in southwest—northeast gradient among vegetation types ($F_{4,25} = 0.86$, $p = 0.50$). Thus, I assessed if coastal distance of array points effected observed richness (species per array) and abundance (individuals per array) with Poisson generalized linear modeling (GLM) (z-values) or quasi-Poisson GLM (t-values) to account for overdispersion (Zuur et al. 2009). Distance from coast was not a significant predictor for frog richness (z-value = 1.42, $p = 0.16$), frog abundance ($\Phi = 18.99$, t-value = 0.14, $p = 0.89$), reptile richness (z-value = 0.65, $p = 0.51$), or reptile abundance ($\Phi = 1.22$, t-value = 0.73, $p = 0.47$).

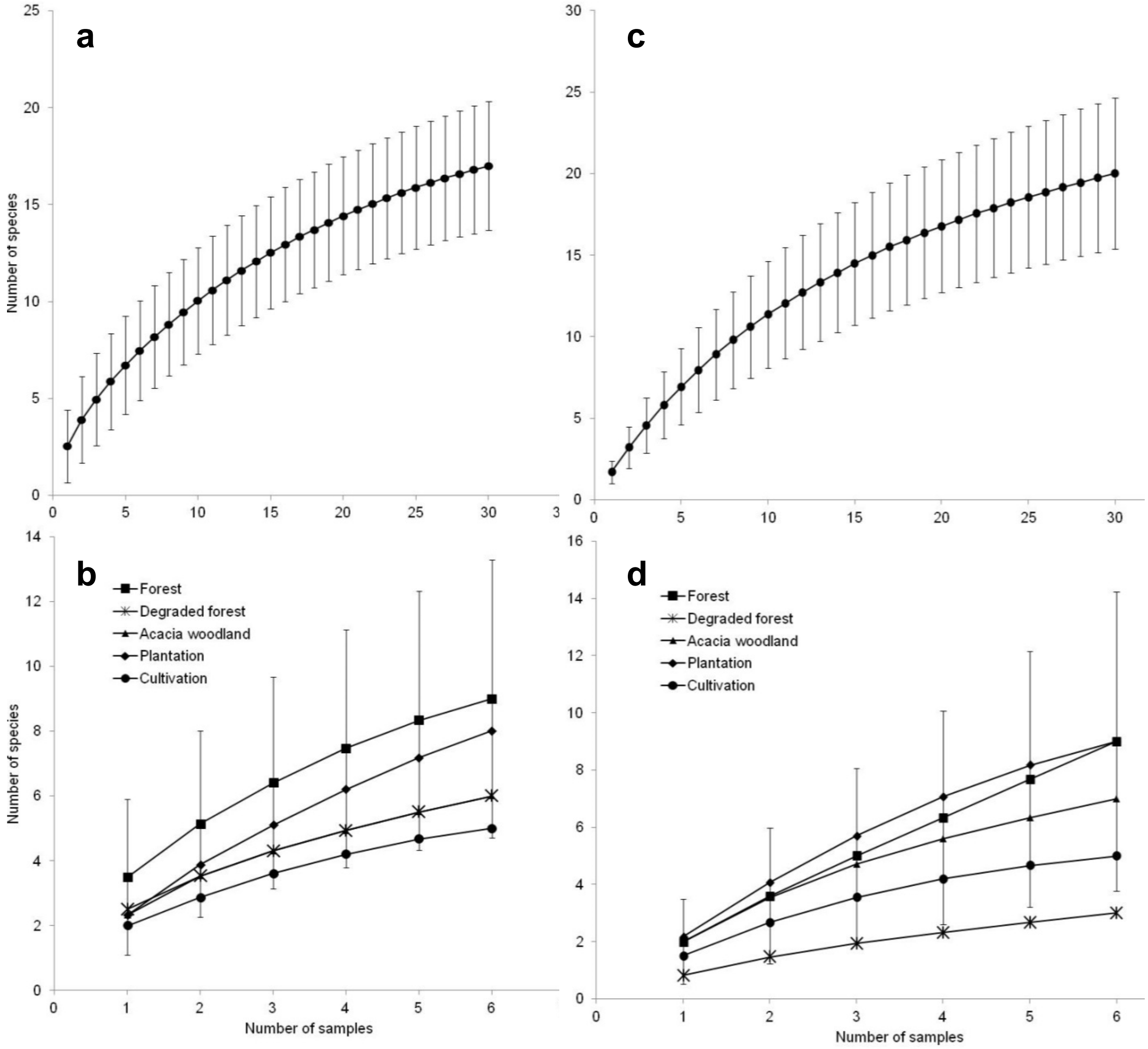

Fig. S.3.1. Species accumulation curves for (a) the total frog dataset, (b) frog samples grouped by vegetation type, (c) the total reptile dataset, and (d) reptile samples grouped by vegetation type. Error bars represent 95% CI and in (b) and (d) are shown only for forest.

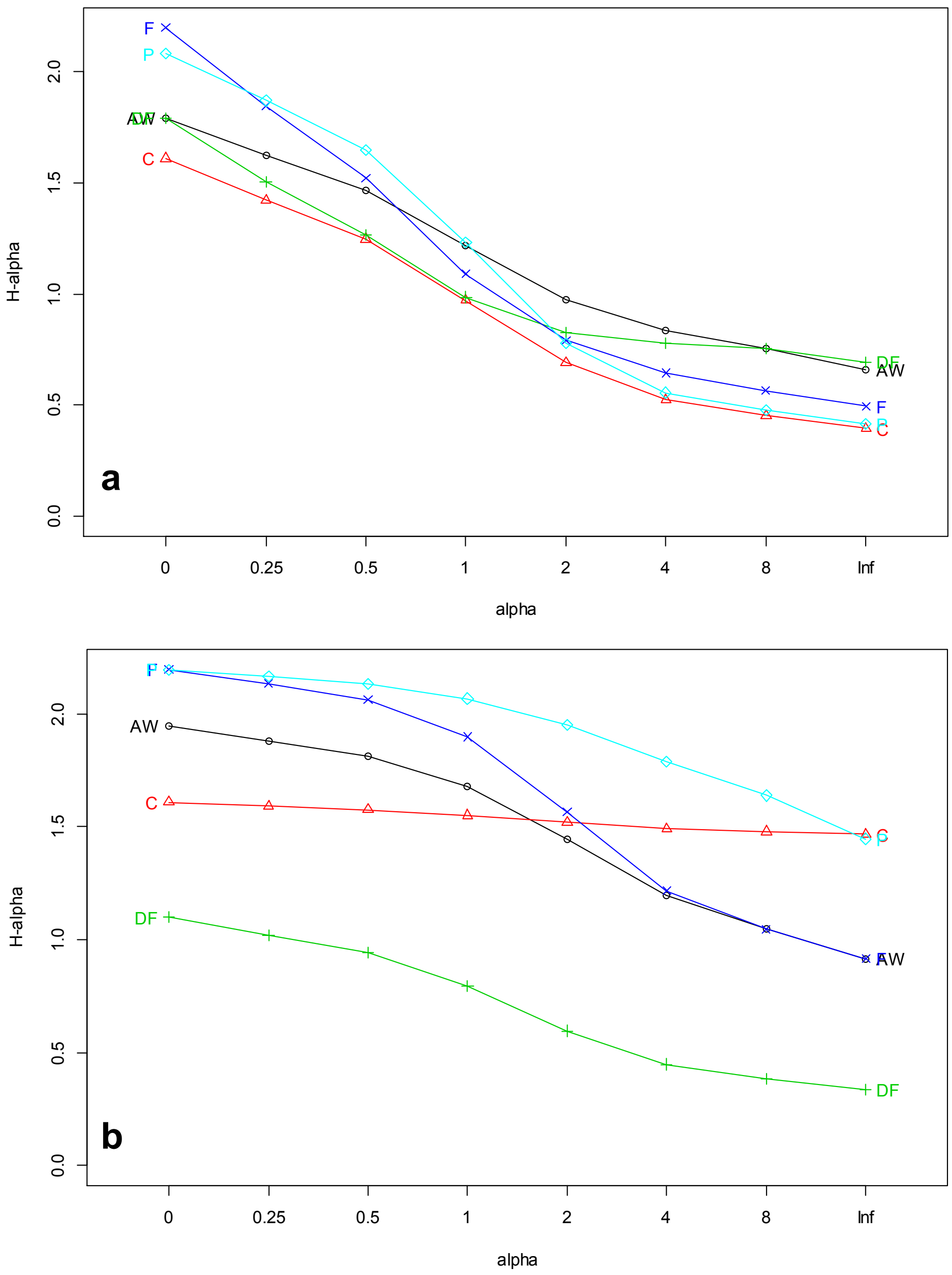

Fig. S.3.2. Rényi diversity profiles for (a) frogs and (b) reptiles in different vegetation types (dark blue is forest (F); green is degraded forest (DF); black is acacia woodland (AW), light blue is plantation (P), red is cultivation (C). Rényi diversity profiles are calculated with the formula $H_\alpha = \ln(\Sigma\, p_i^{\alpha}) / (1–\alpha)$, where H_α is the diversity value, p_i values are the proportions of each species (which are taken to the exponent α and summed for all species recorded), and α is a parameter taken from 0 to infinity to generate the profile (Kindt and Coe 2005). Values of H_α reflect species richness at $\alpha = 0$, are equivalent to the Shannon diversity index at $\alpha = 1$, and yield the logarithm of the reciprocal Simpson diversity index at $\alpha = 2$. Profiles indicate that frog diversity is lowest in cultivation, and reptile diversity is lowest in degraded forest and highest in plantation. The remaining vegetation types cannot be ranked definitively as their Rényi diversity profiles overlap.

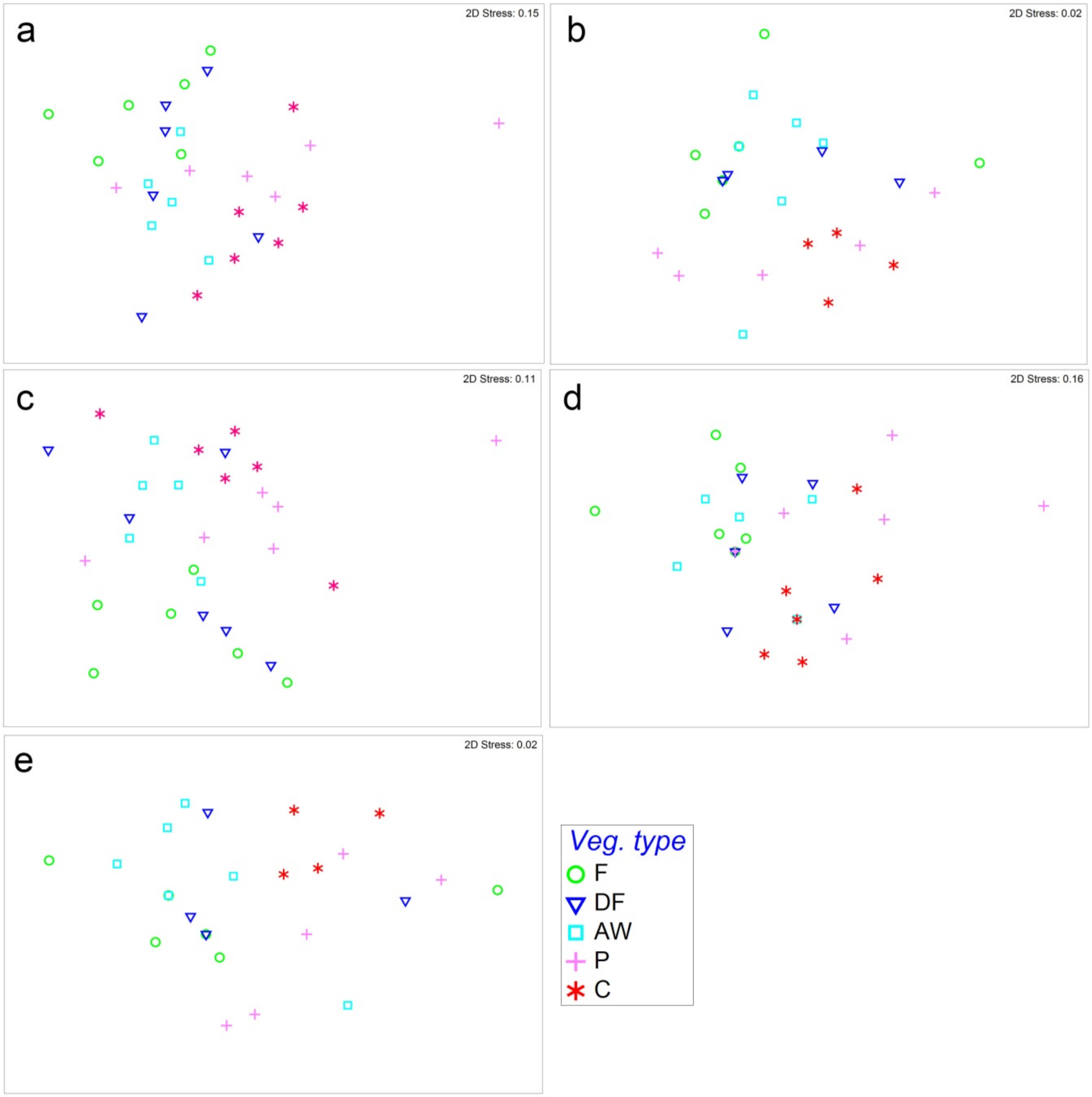

Fig. S.3.3. Non-metric multidimensional scaling ordination of Bray Curtis similarities based on square-root-transformed (a) frog and (b) reptile abundance data and (c) raw frog abundance, (d) frog incidence, and (e) raw reptile abundance data. Symbols represent samples taken at 30 trapping array sites across five vegetation types (F = forest, DF = degraded forest, AW = acacia woodland, P = plantation, C = cultivation), and clustering indicates similar community composition among sites. One array site for frogs and four array sites for reptiles were not plotted because they were outliers with zero captures.

Table S.3.1. Analysis of similarity (ANOSIM) results comparing frog and reptile community composition among vegetation types based on Bray Curtis similarity of raw abundance data for frogs and reptiles and incidence data for frogs including species identified from audio recordings.

Vegetation type comparison	**Frogs**				**Reptiles**	
	Abundance data (Global R = 0.158, p = 0.007)		**Incidence data (Global R = 0.146, p = 0.005)**		**Abundance data (Global R = 0.193, p = 0.001)**	
	R statistic [a]	**p** [b]	**R statistic** [a]	**p** [b]	**R statistic** [a]	**p** [b]
Forest–degraded forest	−0.01	0.45	0.01	0.44	−0.06	0.99
Forest–acacia woodland	0.30	0.01*	−0.03	0.61	0.14	0.11
Forest–plantation	0.28	< 0.05*	0.26	< 0.05*	0.24	< 0.05*
Forest–cultivation	0.66	< 0.01**	0.58	< 0.01**	0.38	< 0.01**
Degraded forest–acacia woodland	0.02	0.30	−0.07	0.80	0.09	0.20
Degraded forest–plantation	−0.03	0.55	0.17	0.09	0.18	0.05
Degraded forest–cultivation	0.14	0.10	0.21	0.07	0.28	< 0.05*
Acacia woodland–plantation	0.12	0.08	0.08	0.17	0.30	< 0.01**
Acacia woodland–cultivation	0.08	0.17	0.14	0.10	0.34	< 0.01**
Plantation–cultivation	0.11	0.09	0.22	< 0.05*	0.09	0.18

[a] ANOSIM generates an R statistic ranging from −1 (where similarities across different vegetation types are higher than within types) to 1 (where similarities within types are higher than between types) (Clarke and Gorley 2001).

[b] Significance of each comparison is indicated by * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Table S.3.2. Top selected models ($\Delta_i < 4$) relating environmental variables to (a) frog species richness, (b) frog abundance, (c) reptile species richness, (d) reptile abundance, and to abundance of functional groups (e) F1, (f) F2, (g) F3, (h) F4, (i) R1, (j) R2, (k) R3, and (l) R4 (D^2 = deviance explained by global models, VIF = variance inflation factor of global model, Par. = number of parameters in the model; LL = log-likelihood; AICc = Akaike's corrected information criterion; QAICc = Quasi-AICc; Δ_i = AICc or QAICc difference from best model; w_i = Akaike weights, the normalized relative likelihood of the model given the data).

a) Frog species richness including audio (D^2 = 0.32; VIF = 1)

Variables	**Par.**	**LL**	**AICc**	Δ_i	w_i
Litter cover	2	−51.62	107.69	0.00	0.16
Herb cover + Litter cover	3	−50.77	108.46	0.77	0.11
Null	1	−53.29	108.73	1.05	0.10
Litter cover + Range temp.	3	−51.20	109.32	1.63	0.07
Mean temp	2	−52.64	109.73	2.04	0.06
Litter cover + Litter depth	3	−51.49	109.90	2.21	0.05
Litter cover + Mean temp.	3	−51.56	110.05	2.37	0.05
Litter cover + Soil p H	3	−51.57	110.07	2.38	0.05
Herb cover + Litter cover + Mean temp.	4	−50.38	110.36	2.68	0.04
Herb cover + Mean temp.	3	−51.73	110.38	2.70	0.04
Herb cover	2	−53.13	110.71	3.03	0.04
Herb cover + Litter cover + Range temp.	4	−50.60	110.79	3.11	0.03
Litter depth	2	−53.18	110.81	3.12	0.03
Soil pH	2	−53.22	110.89	3.20	0.03
Range temp	2	−53.27	110.99	3.30	0.03
Herb cover + Litter cover + Litter depth	4	−50.76	111.12	3.43	0.03
Herb cover + Litter cover + Soil pH	4	−50.77	111.13	3.45	0.03
Litter cover + Mean temp. + Range temp.	4	−50.97	111.54	3.85	0.02

b) Frog abundance (D^2 = 0.64; VIF = 5.59)

Variables	**Par.**	**LL**	**QAICc**	Δ_i	w_i
Herb cover + Mean temp. + Soil pH	4	−128.24	58.36	0.00	0.54
Herb cover + Litter cover + Mean temp. + Soil pH	5	−125.19	60.42	2.06	0.19
Herb cover + Litter depth + Mean temp. + Soil pH	5	−127.40	61.21	2.85	0.13

Herb cover + Mean temp. + Range temp. + Soil pH	5	−127.41	61.21	2.86	0.13

c) Reptile richness (D^2 = 0.06; VIF = 1)

Variables	**Par.**	**LL**	**AICc**	Δ_i	w_i
Null	1	−46.18	94.51	0	0.31
Litter cover	2	−45.95	96.34	1.82	0.12
Range temp.	2	−46.04	96.53	2.01	0.11
Herb cover	2	−46.13	96.71	2.2	0.1
Soil pH	2	−46.14	96.73	2.22	0.1
Litter depth	2	−46.16	96.76	2.25	0.1
Mean temp.	2	−46.18	96.81	2.3	0.1
Litter cover + Litter depth	3	−45.69	98.31	3.8	0.05

d) Reptile abundance (D^2 = 0.10; VIF = 1.33)

Variables	**Par.**	**LL**	**QAICc**	Δ_i	w_i
Null	1	−55.15	87.08	0.00	0.32
Range temp.	2	−54.85	89.11	2.03	0.12
Litter cover	2	−54.91	89.20	2.12	0.11
Herb cover	2	−54.91	89.20	2.13	0.11
Soil pH	2	−54.96	89.28	2.20	0.11
Mean temp.	2	−55.11	89.49	2.41	0.10
Litter depth	2	−55.14	89.54	2.47	0.09
Range temp. + Soil pH	3	−54.30	90.96	3.88	0.05

e) Functional group F1 (D^2 = 0.40; VIF = 1.70)

Variables	**Par.**	**LL**	**QAICc**	Δ_i	w_i
Herb cover	2	−41.82	56.11	0.00	0.13
Herb cover + Mean temp.	3	−39.79	56.41	0.30	0.11
Herb cover + Litter cover + Mean temp.	4	−37.35	56.43	0.32	0.11
Herb cover + Soil pH	3	−40.06	56.73	0.61	0.10
Herb cover + Mean temp. + Soil pH	4	−37.65	56.78	0.67	0.09
Herb cover + Litter cover	3	−41.10	57.95	1.84	0.05
Herb cover + Mean temp. + Range temp. + Soil pH	5	−35.97	57.96	1.85	0.05
Herb cover + Litter cover + Mean temp. + Soil pH	5	−36.02	58.02	1.91	0.05
Herb cover + Range temp.	3	−41.81	58.78	2.67	0.03
Herb cover + Litter depth	3	−41.82	58.79	2.68	0.03

Herb cover + Litter depth + Mean temp.	4	−39.70	59.20	3.09	0.03
Herb cover + Mean temp. + Range temp.	4	−39.72	59.23	3.11	0.03
Herb cover + Litter cover + Soil pH	4	−39.72	59.23	3.11	0.03
Herb cover + Litter cover + Litter depth + Mean temp.	5	−37.13	59.33	3.22	0.03
Herb cover + Range temp. + Soil pH	4	−39.88	59.41	3.30	0.03
Litter cover	2	−44.66	59.46	3.35	0.02
Herb cover + Liter cover + Mean temp. + Range Temp.	5	−37.25	59.47	3.35	0.02
Herb cover + Litter depth + Soil pH	4	−40.04	59.60	3.49	0.02
Herb cover + Litter depth + Mean temp. Soil pH	5	−37.61	59.89	3.78	0.02

f) Functional group F2 ($D^2 = 0.67$; VIF = 5.15)

Variables	Par.	LL	QAICc	Δ_i	w_i
Litter cover + Mean temp. + Soil pH	4	−99.82	51.23	0.00	0.27
Herb cover + Litter cover + Mean temp. + Soil pH	5	−92.10	51.39	0.16	0.25
Litter cover + Litter depth + Mean temp. + Soil pH	5	−97.71	53.56	2.33	0.08
Mean temp. + Soil pH	3	−114.03	53.84	2.61	0.07
Herb cover + Mean temp. + Soil pH	4	−106.88	53.97	2.74	0.07
Litter cover + Mean temp. + Range temp. + Soil pH	5	−99.54	54.27	3.04	0.06
Mean temp. + Range temp. + Soil pH	4	−108.21	54.49	3.26	0.05
Herb cover + Mean temp. + Range temp. + Soil pH	5	−100.49	54.64	3.41	0.05
Herb cover + Litter cover + Litter depth + Mean temp. + Soil pH	6	−91.81	54.71	3.48	0.05
Herb cover + Litter cover + Mean temp. + Range temp. + Soil pH	6	−92.03	54.80	3.57	0.05

g) Functional group F3 ($D^2 = 0.56$; VIF = 2.35)

Variables	Par.	LL	QAICc	Δ_i	w_i
Herb cover + Mean temp. + Soil pH	4	−77.11	78.11	0.00	0.61
Herb cover + Litter cover + Mean temp. + Soil pH	5	−77.05	81.21	3.10	0.13
Herb cover + Litter depth + Mean temp. + Soil pH	5	−77.08	81.23	3.13	0.13
Herb cover + Mean temp. + Range temp. + Soil pH	5	−77.10	81.25	3.14	0.13

h) Functional group F4 ($D^2 = 0.34$; VIF = 1.59)

Variables	Par.	LL	QAICc	Δ_i	w_i
Litter depth	2	−15.88	36.20	0.00	0.20
Litter depth + Soil pH	3	−15.18	37.28	1.07	0.12
Litter cover + Litter depth	3	−15.36	37.65	1.44	0.10

Litter depth + Range temp.	3	−15.62	38.17	1.96	0.08
Herb cover + Litter depth	3	−15.75	38.42	2.21	0.07
Litter depth + Mean temp.	3	−15.85	38.61	2.41	0.06
Litter cover	2	−17.21	38.85	2.65	0.05
Litter cover + Litter depth + Soil pH	4	−14.72	39.04	2.83	0.05
Litter cover + Soil pH	3	−16.07	39.06	2.85	0.05
Range temp.	2	−17.60	39.65	3.45	0.04
Herb cover + Litter depth + Soil pH	4	−15.12	39.84	3.63	0.03
Litter depth + Range temp. + Soil pH	4	−15.16	39.91	3.71	0.03
Litter depth + Mean temp. + Soil pH	4	−15.17	39.95	3.74	0.03
Litter cover + Range temp.	3	−16.53	39.98	3.78	0.03
Litter cover + Litter depth + Range temp.	4	−15.22	40.05	3.84	0.03
Herb cover + Litter cover + Litter depth	4	−15.24	40.09	3.88	0.03

i) Functional group R1 (D^2 = 0.52; VIF = 1)

Variables	**Par.**	**LL**	**AICc**	Δ_i	w_i
Litter cover	2	−11.43	27.30	0.00	0.06
Litter cover + Mean temp.	3	−10.27	27.46	0.16	0.06
Herb cover + Litter cover	3	−10.35	27.62	0.32	0.05
Null	1	−12.75	27.65	0.35	0.05
Range temp.	2	−11.85	28.14	0.84	0.04
Litter depth	2	−11.87	28.18	0.88	0.04
Herb cover + Range temp.	3	−10.67	28.26	0.97	0.04
Litter cover + Mean temp. + Range temp.	4	−9.38	28.36	1.06	0.04
Herb cover + Litter depth	3	−10.80	28.52	1.22	0.03
Litter cover + Litter depth + Mean temp.	4	−9.46	28.53	1.23	0.03
Mean temp. + Range temp.	3	−11.00	28.92	1.62	0.03
Herb cover + Litter cover + Mean temp.	4	−9.72	29.03	1.74	0.03
Herb cover + Litter cover + Soil pH	4	−9.72	29.05	1.75	0.03
Herb cover + Litter cover + Litter depth	4	−9.80	29.20	1.90	0.02
Herb cover + Litter cover + Range temp.	4	−9.82	29.23	1.94	0.02
Herb cover	2	−12.40	29.23	1.94	0.02
Litter cover + Soil pH	3	−11.18	29.29	1.99	0.02
Litter cover + Range temp.	3	−11.19	29.31	2.01	0.02
Litter cover + Litter depth + Mean temp. + Range temp.	5	−8.41	29.32	2.02	0.02
Litter depth + Mean temp. + Range temp.	4	−9.86	29.33	2.03	0.02

Soil pH	2	−12.45	29.34	2.04	0.02
Litter cover + Litter depth	3	−11.22	29.36	2.06	0.02
Litter cover + Mean temp. + Soil pH	4	−9.96	29.52	2.22	0.02
Herb cover + Litter depth + Range temp.	4	−9.99	29.58	2.28	0.02
Litter depth + Mean temp.	3	−11.33	29.59	2.29	0.02
Mean temp.	2	−12.73	29.91	2.61	0.02
Litter depth + Range temp.	3	−11.55	30.03	2.73	0.02
Herb cover + Litter cover + Litter depth + Mean temp.	5	−8.80	30.09	2.80	0.02
Litter depth + Soil pH	3	−11.74	30.40	3.11	0.01
Herb cover + Litter depth + Soil pH	4	−10.42	30.43	3.14	0.01
Herb cover + Litter cover + Mean temp. + Range temp.	5	−9.00	30.50	3.20	0.01
Herb cover + Mean temp. + Range temp.	4	−10.46	30.52	3.22	0.01
Range temp. + Soil pH	3	−11.84	30.60	3.30	0.01
Herb cover + Litter cover + Mean temp. + Soil pH	5	−9.19	30.87	3.57	0.01
Litter cover + Litter depth + Mean temp. + Soil pH	5	−9.19	30.88	3.59	0.01
Herb cover + Soil pH	3	−11.99	30.91	3.61	0.01
Herb cover + Litter cover + Litter depth + Soil pH	5	−9.21	30.92	3.62	0.01
Herb cover + Range temp. + Soil pH	4	−10.67	30.94	3.64	0.01
Herb cover + Litter depth + Mean temp.	4	−10.72	31.03	3.74	0.01
Litter cover + Mean temp. + Range temp. + Soil pH	5	−9.36	31.22	3.93	0.01
Herb cover + Litter depth + Mean temp. + Range temp.	5	−9.40	31.29	3.99	0.01

j) Functional group R2 ($D^2 = 0.38$; VIF = 1.19)

Variables	**Par.**	**LL**	**QAICc**	Δ_i	w_i
Litter cover + Mean temp.	3	−32.74	64.67	0.00	0.18
Litter cover	2	−34.41	64.80	0.13	0.17
Mean temp.	2	−35.09	65.95	1.28	0.10
Herb cover + Litter cover + Mean temp.	4	−32.07	66.45	1.78	0.07
Litter cover + Soil pH	3	−34.05	66.88	2.21	0.06
Litter cover + Mean temp. + Soil pH	4	−32.51	67.20	2.52	0.05
Herb cover + Litter cover	3	−34.25	67.21	2.54	0.05
Litter cover + Litter depth + Mean temp.	4	−32.56	67.27	2.60	0.05
Litter cover + Range temp.	3	−34.32	67.33	2.66	0.05
Herb cover + Mean temp.	3	−34.37	67.42	2.75	0.05
Litter cover + Litter depth	3	−34.41	67.48	2.81	0.04
Litter cover + Mean temp. + Range temp.	4	−32.73	67.56	2.89	0.04

Mean temp. + Soil pH	3	−34.90	68.30	3.63	0.03
Mean temp. + Range temp.	3	−34.97	68.44	3.76	0.03
Litter depth + Mean temp.	3	−35.08	68.62	3.94	0.03

k) Functional group R3 (D^2 = 0.25; VIF = 1.83)

Variables	**Par.**	**LL**	**QAICc**	Δ_i	w_i
Litter cover	2	−36.04	46.33	0.00	0.34
Litter cover + Mean temp.	3	−35.86	48.81	2.48	0.10
Litter cover + Range temp.	3	−35.90	48.86	2.53	0.10
Herb cover + Litter cover	3	−35.96	48.92	2.59	0.09
Litter cover + Litter depth	3	−36.00	48.97	2.64	0.09
Litter cover + Soil pH	3	−36.03	49.00	2.67	0.09
Range temp.	2	−38.83	49.38	3.05	0.07
Null	1	−41.60	49.93	3.60	0.06
Litter depth	2	−39.35	49.96	3.62	0.06

l) Functional group R4 (D^2 = 0.18; VIF = 1.05)

Variables	**Par.**	**LL**	**QAICc**	Δ_i	w_i
Range temp.	2	−24.30	53.26	0.00	0.16
Mean temp.	2	−24.42	53.50	0.24	0.14
Null	1	−25.95	53.93	0.67	0.11
Mean temp. + Range temp.	3	−23.88	55.13	1.87	0.06
Litter depth + Range temp.	3	−23.99	55.34	2.08	0.06
Litter cover	2	−25.50	55.56	2.30	0.05
Mean temp. + Soil pH	3	−24.22	55.79	2.52	0.04
Litter depth + Mean temp.	3	−24.25	55.84	2.58	0.04
Herb cover + Range temp.	3	−24.26	55.86	2.59	0.04
Range temp. + Soil pH	3	−24.29	55.93	2.66	0.04
Litter cover + Range temp.	3	−24.30	55.94	2.67	0.04
Herb cover	2	−25.74	56.01	2.75	0.04
Soil pH	2	−25.75	56.03	2.77	0.04
Herb cover + Mean temp.	3	−24.36	56.06	2.80	0.04
Litter cover + Mean temp.	3	−24.42	56.18	2.91	0.04
Litter depth	2	−25.90	56.32	3.06	0.03
Litter depth + Mean temp. + Range temp.	4	−23.32	56.98	3.72	0.02

Table S.3.3. Multi-model averages (see Table S.3.2 for list of models with $\Delta_i < 4$ contributing to each average model) relating environmental variables to frog species richness, frog abundance, reptile species richness, reptile abundance, and to abundance of functional groups F1, F2, F3, F4, R1, R2, R3, and R4.

Variable [a]	**Parameter estimate**	**Unconditional SE**	**p**	**Relative importance** [b]
Frog species richness				
Intercept	1.2883	1.788	0.48	
Litter cover	0.0067	0.004	0.09	0.67
Herb cover	−0.0051	0.004	0.26	0.33
Mean temp.	−0.0965	0.113	0.41	0.22
Range temp.	0.0164	0.026	0.55	0.16
Litter depth	−0.0077	0.054	0.89	0.12
Soil pH	−0.0299	0.123	0.82	0.11
Frog abundance				
Intercept***	15.1130	1.744	< 0.001	
Herb cover***	−0.0197	0.003	< 0.001	1.00
Mean temp.***	−0.6739	0.067	< 0.001	1.00
Soil pH***	0.6205	0.082	< 0.001	1.00
Litter cover*	0.0045	0.002	0.02	0.19
Litter depth	0.0320	0.024	0.21	0.13
Range temp.	−0.0210	0.016	0.22	0.13
Reptile species richness				
Intercept	0.5251	0.983	0.61	
Litter cover	−0.0030	0.004	0.46	0.17
Litter depth	0.0250	0.065	0.71	0.15
Range temp.	0.0145	0.027	0.61	0.11
Herb cover	−0.0015	0.005	0.76	0.10
Soil pH	0.0474	0.167	0.79	0.10
Mean temp.	−0.0083	0.113	0.94	0.10
Reptile abundance				
Intercept	0.7376	1.001	0.48	
Range temp.	0.0214	0.024	0.40	0.16
Soil pH	0.1129	0.157	0.49	0.15
Litter cover	−0.0022	0.003	0.50	0.11
Herb cover	−0.0029	0.004	0.51	0.11

Mean temp.	−0.0294	0.100	0.78	0.10
Litter depth	−0.0068	0.052	0.90	0.09
Functional group F1				
Intercept	6.0830	7.330	0.41	
Herb cover**	−0.0336	0.012	0.01	0.98
Mean temp.*	−0.4645	0.224	0.05	0.55
Soil pH	0.4299	0.243	0.09	0.39
Litter cover	−0.0102	0.006	0.10	0.32
Range temp.	0.0297	0.060	0.63	0.16
Litter depth	0.0044	0.103	0.97	0.13
Functional group F2				
Intercept*	9.7936	3.835	0.01	
Mean temp.***	−0.7106	0.136	< 0.001	1.00
Soil pH***	1.1252	0.194	< 0.001	1.00
Litter cover***	0.0216	0.006	< 0.001	0.76
Herb cover***	−0.0147	0.004	< 0.001	0.46
Range temp.	−0.0633	0.055	0.26	0.21
Litter depth	−0.0673	0.050	0.20	0.13
Functional group F3				
Intercept***	13.9233	2.229	< 0.001	
Herb cover***	−0.0233	0.004	< 0.001	1.00
Mean temp.***	−0.5720	0.088	< 0.001	1.00
Soil pH***	0.3597	0.096	< 0.001	1.00
Litter cover	0.0008	0.002	0.75	0.13
Litter depth	−0.0089	0.036	0.81	0.13
Range temp.	0.0036	0.022	0.87	0.13
Functional group F4				
Intercept	−6.4449	8.053	0.44	
Litter depth*	0.3902	0.189	0.05	0.83
Litter cover	0.0592	0.093	0.54	0.34
Soil pH	0.8544	0.837	0.33	0.31
Range temp.	−0.0959	0.131	0.48	0.20
Herb cover	0.0062	0.013	0.66	0.13
Mean temp.	−0.0864	0.437	0.85	0.09
Functional group R1				
Intercept	−18.8485	30.801	0.55	
Litter cover	0.1255	0.179	0.50	0.53

Herb cover	−0.0328	0.028	0.27	0.39
Mean temp.	1.1571	1.054	0.29	0.38
Range temp.	−0.2075	0.192	0.30	0.34
Litter depth	0.2913	0.241	0.25	0.34
Soil pH	0.4639	0.759	0.56	0.19
Functional group R2				
Intercept	4.9901	7.682	0.52	
Litter cover	0.0240	0.013	0.08	0.78
Mean temp.*	−0.4551	0.224	0.05	0.63
Herb cover	−0.0079	0.008	0.37	0.17
Soil pH	0.1740	0.246	0.50	0.14
Litter depth	−0.0218	0.095	0.83	0.12
Range temp.	−0.0112	0.048	0.82	0.12
Functional group R3				
Intercept	0.6984	1.755	0.70	
Litter cover**	−0.0161	0.005	< 0.01	0.81
Range temp.	0.0545	0.056	0.34	0.17
Litter depth	−0.0954	0.139	0.50	0.15
Mean temp.	−0.0925	0.154	0.57	0.10
Herb cover	0.0026	0.006	0.70	0.09
Soil pH	0.0372	0.258	0.89	0.09
Functional group R4				
Intercept	−4.6615	5.326	0.39	
Range temp.	0.0980	0.063	0.14	0.42
Mean temp.	0.3395	0.226	0.15	0.39
Litter depth	0.0835	0.159	0.61	0.16
Litter cover	−0.0024	0.009	0.79	0.13
Soil pH	−0.1205	0.329	0.73	0.12
Herb cover	0.0004	0.012	0.98	0.12

[a] Significance of each variable in models is indicated by * $p \le 0.05$, ** $p \le 0.01$, *** $p \le 0.001$.

[b] Relative importance reflects the sum of Akaike weights of models in each set containing each variable.

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Chapter 4. Decline of Birds in a Human-Modified Coastal Dune Forest Landscape in South Africa

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Abstract

Previous studies demonstrate that old-growth forest remnants and vegetation regenerating after anthropogenic disturbance provide habitat for birds in a human-modified coastal dune forest landscape in northern KwaZulu-Natal, South Africa. However, occurrence does not ensure persistence. Based on a 13-year monitoring database I calculated population trends for 37 bird species and general trends in overall bird density in different vegetation types. I evaluated species characteristics as covariates of population trend and assessed changes in rainfall and proportional area and survey coverage per vegetation type. Seventy-six percent of species assessed have declined, 57% significantly so at an average rate of 13.9% per year. Overall, bird density has fallen at 12.2% per year across old-growth forest and woody regenerating vegetation types. Changes in proportional area and coverage per vegetation type may partly explain trends for a few species but are unlikely to account for most. Below average rainfall may have contributed to bird declines. However, other possibilities

warrant further investigation. Species with larger range extents tended to decline more sharply than did others, and these species may be responding to environmental changes on a broader geographical scale. My results cast doubt on the future persistence of birds in this human-modified landscape. More research is needed to elucidate the mechanisms driving population decline in the study area and to investigate whether the declines identified here are more widespread across the region and perhaps the continent.

Introduction

Coastal dune forest is one of South Africa's rarest vegetation types; restricted to the eastern coast, it covers less than 1000 km^2. It is also biogeographically important, and occurs within the Maputaland Center of endemism (van Wyk 1996) and the Maputaland–Pondoland–Albany biodiversity hotspot (Küper et al. 2004, Steenkamp et al. 2004). While South African coastal dune forest is relatively well protected with 9.51% conserved, 43% has been transformed (Low and Rebelo 1998). The coastal location on the Indian Ocean accounts for the biggest threats to coastal dune forests—holiday resort expansion, dune mining, and firewood collection and clearing for agriculture by local communities (Low and Rebelo 1998). Additionally, the narrowness and linear nature of the coastal dune forest belt might make it particularly susceptible to edge effects, fragmentation, and isolation (see Eeley et al. 1999).

Forest conservation depends on maintaining both the land covered by forests and the ecological processes necessary for plant regeneration and gene flow (Low and Rebelo 1998). Thus, isolated stands of protected coastal dune forests may be insufficient for their long-term conservation (Low and Rebelo 1998) because dispersal ability of many tree species is constrained by distance between forest patches (Grainger et al. 2011). Due to their vagility and role in seed dispersal (Coates-Palgrave 2003), birds may enhance connectivity of coastal dune forest fragments (see Grainger et al. 2011). Thus, promoting persistence of coastal dune forest birds beyond protected areas may be important for both bird and forest conservation and is in line with recent shifts in conservation ideology from a strictly protected area based approach to a wider consideration of biodiversity in human-modified landscapes (Daily 2001, Daily et al. 2001). Land-use options that incorporate coastal dune forest elements such as remnant forest patches in agricultural landscapes or active regeneration after anthropogenic disturbances may allow bird populations to persist beyond protected areas. This may be the case in South Africa's northern coastal dune forests.

North of Richards Bay, on the coast of KwaZulu-Natal province, opencast surface mining of sand dunes has occurred since 1977 and has been followed by an active rehabilitation program to return indigenous coastal dune vegetation to one third of the mined area (see van Aarde et al. 1996a for program description). Earlier work showed that, with age, bird communities in the successional sere of known-aged regenerating sites become more similar to that of old-growth coastal dune forest (van Aarde et al. 1996a, Kritzinger and van Aarde 1998, Wassenaar et al. 2005, Grainger and van Aarde 2012). These observations suggest that post-mining regenerating forests and old-growth forest remnants provide refuge for coastal dune forest birds beyond protected areas—*e.g.* the Richards Bay Game Reserve ~20 km to the southwest and the iSimangaliso Wetland Park and World Heritage Site ~5 km to the northeast. However, these studies were based on snapshots of bird occurrence, and occurrence of species does not ensure their persistence (see Daily et al. 2001, Hughes et al. 2002). Assessing changes in population size over time is a step towards understanding the processes (*e.g.* survival, fecundity, and dispersal (see Hughes et al. 2002, Komar 2006)) that affect patterns of species occurrence and persistence in human-modified landscapes.

Based on 13 years of quantitative monitoring of forest birds, I calculated population trends for birds found commonly in old-growth coastal dune forest and woody regenerating vegetation types. I also calculated general trends of overall bird densities over time in old-growth forest and woody regenerating vegetation types. I investigated how species' characteristics known to be associated with extinction proneness of forest birds—*i.e.* clutch size, habitat affinity, diet, tolerance of human-modified landscapes, and range extent (see Sodhi et al. 2004 and references therein)—related to population trend and assessed changes in rainfall, and proportional area and survey coverage per vegetation type as possible determinants of population and general trends.

Methods

Bird data

I used data collected as part of a long-term monitoring program designed to assess the success of coastal dune forest rehabilitation after dune mining (see van Aarde et al. 1996a, Wassenaar et al. 2005 for a description of the program and map of the study area). Between 1997 and 2009, birds were surveyed via transect counts in 9 survey years at two relatively pristine old-growth coastal dune forest sites and nine regenerating forest sites of known age (Table S.4.1) within a mining lease area maintained by Richards Bay Minerals (RBM).

Forest regeneration in the area follows a trajectory of vegetation types from grassland (~1–5 years old), to thicket (~6–12 years old), to an early woodland stage dominated by *Acacia karroo* (~12–20 years old), to a late woodland stage in which *Acacia karroo* individuals have senesced and been replaced by coastal dune forest trees (~20–35 years old) (see van Aarde et al. 1996a, Grainger et al. 2011). Experienced observers walked 250–500 m transects randomly located at least 200 m apart within vegetation types (Table S.4.1) and recorded birds seen and distance from the transect. In most years, exact distances were recorded up to 60 m but in 1997 and 2006, distance intervals were used with cut points 2, 5, 10, 20, and 40 m and 5, 10, 15, 20, 25, and 30 m respectively. Birds flying over the canopy and all raptors, aerial feeders, and nocturnal birds were excluded. All surveys were conducted in the early morning under favorable weather conditions and took place between November and February.

Throughout the study period, 102 species were represented in 7890 sightings. I narrowed the species list to focal species typical of old-growth forest and the woody regenerating vegetation types—thicket, early woodland, and late woodland. To do this, I assessed the affinity of each species towards different vegetation types. For each species, I calculated the overall number of sightings/km of transect in each vegetation type—grassland, thicket, early woodland, late woodland, and old-growth forest. Twenty-seven species had ≥ 60% of their sightings/km in grassland, and I excluded all but two of these species from further analyses. I retained Red-eyed Dove and Yellow-eyed Canary because, although the majority of sightings were in grassland, they were also quite common in old-growth forest with > 20% sightings/km. I also excluded Lesser-masked Weaver *Ploceus intermedius* (predominantly found in thicket) from further analysis because observers in different years variably distinguished between Lesser-masked and other similar looking weavers predominantly found in grassland (*i.e.* Village Weaver *Ploceus cucullatus* and Yellow Weaver *Ploceus subaureus*). Thus, 6868 sightings of 76 species were retained for further analysis. I separated these species into two groups—39 relatively rare species (recorded ≤ 20 times throughout the study period) and 37 relatively common species (recorded > 20 times). Common and scientific names are provided in Table 4.1 for relatively common species and Table S.4.2 for relatively rare species.

To my knowledge, this is one of few long-term quantitative bird monitoring datasets for Africa. However, some aspects of the survey methodology might introduce bias. Differences in observers and vegetation types may lead to variation in the probability of detecting birds, which could bias inferences on the change in bird densities over time (Marques et al. 2007). I used distance sampling techniques to account for variability in detection probability to generate more reliable density estimates than unadjusted counts provide. Distance sampling relies on creating a detection function of the frequency of observations on distance from the transect line to estimate the average detection probability $\hat{P}_a$ of observing a bird given it is within the truncation point w of the line transect (Buckland et al. 2001).

To calculate reliable detection functions, 60–80 observations are necessary (Buckland et al. 2001), but in my study, most species were recorded far less often than 60 times per year. Similarly detectable species can be grouped together to achieve sufficient sample size to calculate a common detection function (Buckland et al. 2001). Thus, I grouped the 37 relatively common species (those recorded > 20 times) into three species pools: furtive species generally seen very close to the transect line, species that are intermediately visible, and conspicuous species frequently seen far from the transect line (Table 4.1). For each of these species pools, I used the Multiple-Covariate Distance Sampling (MCDS) engine in the program DISTANCE, version 6.0 (Thomas et al. 2009) to fit four detection function models for each year: a half-normal key model, a hazard-rate key model, and each with vegetation type as a factor covariate. Additionally, for 2007–2009 when two observers conducted surveys, I also fitted a half-normal and hazard-rate model with observer as a factor covariate and with both observer and vegetation type as factor covariates. Estimating a single detection function per year by pooling over vegetation types and observer differences should give adequate global estimates due to the pooling robustness property of distance sampling, but including these variables in MCDS can lead to increased estimate precision (Marques et al. 2007). I did not use adjustment terms in the models to avoid implausible, non-monotonic function results (Marques et al. 2007). To achieve adequate model fit and estimator robustness, I set distance intervals and truncation points to accommodate characteristics of species pools (*e.g.* shorter truncation point for furtive species), occasional issues with distance heaping and evasive movement of birds away from the transect line, and distance data collection intervals for 1997 and 2006. Models were post-stratified by species, but estimates were made at the global level, meaning that species in the same pool had a common detection function per year. I selected the best model per year based on AIC and extracted an estimate for $\hat{P}_a$ and its SE.

I assessed support for my assumption that species within each pool shared similar detectability by fitting detection functions to the total dataset (years pooled). I used the MCDS engine to fit for each species pool half-normal and hazard-rate key models, each with vegetation type as a factor covariate, each with observer as a factor covariate and each with species as a factor covariate. I then compared the models with AIC to assess whether pooling species was a reasonable assumption.

I was also interested in annual estimates specific to vegetation types. I modeled the per year, per vegetation type detection functions for birds in general (all 76 species pooled). I used the MCDS engine to fit for each year a half-normal key model and a hazard-rate key model and, for 2007–2009, each with observer as a factor covariate. Again, I did not use further adjustment terms and selected the best model per year based on AIC. Models were post-stratified by vegetation type with estimates made at the vegetation type stratum level. This generated an estimate for $\hat{P}_a$ and its SE of birds in general per vegetation type per year.

Trends and determinants

I assessed population trends over time for the 37 species recorded > 20 times. I used quasi-Poisson generalized linear modeling (GLM) with log-link function and standard errors corrected for over-dispersion (Zuur et al. 2009) and detection probability incorporated as an offset term (Buckland et al. 2004). I fitted the model $n_{t,s} = \exp(\log_e(2L_t w_t \hat{P}_{a,p,t}) + \beta_0 + \beta_1 t) + \varepsilon_t$ where $n_{t,s}$ is the number of birds of species s counted in year t, L_t is the line length surveyed at time t, w_t is the truncation distance, $\hat{P}_{a,p,t}$ is the estimated mean probability of detection for species in pool p in the covered region a in year t, and $\log_e(2L_t w_t \hat{P}_{a,p,t})$ is the offset term (modified from Buckland et al. 2004). In GLM, offsets are assumed known, but $\hat{P}_{a,p,t}$ is an estimate (Buckland et al. 2004). To account for uncertainty in the estimate of $\hat{P}_{a,p,t}$, I randomly resampled each estimate 999 times from a lognormal distribution and refit the GLM to each resample. I then estimated population trend and SE as the mean slope parameter and SE estimates from 999 fitted GLM's for each species. Population trends were deemed significant when population trend ± 1.96 SE did not include 0. Percent change per year was calculated as (exp(population trend) – 1)*100.

I followed the same procedure to estimate general trends in bird density in each vegetation type by substituting into the GLM equation $n_{t,v}$, number of bird sightings per vegetation type v in year t, and $\hat{P}_{a,p,t}$ the estimated mean probability of detection of birds in vegetation type v in the covered region a in year t. Subsequently, I checked for significant differences of slopes and intercepts between vegetation types with a GLM of $n_{t,v}$ on t with an offset as described previously, a categorical variable of vegetation type v, and an interaction term between t and v. Significance of the interaction term indicates significantly different slopes.

I only calculated population trends for species recorded > 20 times. To infer what might be happening to the 39 relatively rare species, I assessed how commonness influenced population trend estimates. To do this, I regressed population trend estimate and SE on $\log_e$ of the cumulative number of sightings per species throughout the study period.

Variables that are intrinsic to species might explain variation in population trends. These include habitat affinity (Julliard et al. 2003), mean clutch size and bird weight (proxies for life history characteristics (Saether and Bakke 2000)), diet (Sekercioglu 2002, Sigel et al. 2006), tolerance of human-modified landscapes (Petit et al. 1999), and range extent (Mehlman 1997). I assigned habitat affinity as a categorical variable—predominant habitat—based on the vegetation type in which a species had the highest proportion of sightings/km. I also quantified affinity for old-growth forest as the proportion of sightings/km in old-growth forest. I sourced clutch size, weight, diet, and tolerance data for relevant species (Hockey et al. 2005). Based on the predominant food items listed, I distinguished three diet preference classes: insects and other invertebrates; plant material; and omnivorous/carnivorous. I considered species listed to occur in gardens, parks, plantations, and cultivated areas tolerant of human-modified landscapes while others were deemed intolerant. Finally, I noted the extent of each species' resident range (IUCN 2008). I assessed the relationship between population trend and range extent, affinity for old-growth forest, clutch size, and weight with linear regression. I used t-tests to compare population trends between species with predominant habitat in old-growth forest and those with predominant habitat in one of the regenerating vegetation types and between species that are tolerant and intolerant of human-modified landscapes. I used ANOVA to compare population trends between the three diet preference classes. Some caution is required in comparing population trends among species because pooling species to calculate detection functions means that annual density estimates from the same pool are not independent (Buckland et al. 2001). Therefore, species pooling could influence trend estimates. Thus, I used ANOVA to compare population trend estimates between the three species pools.

I also assessed factors that might influence both population trends and general trends —changes in rainfall (Faaborg 1982), area of each vegetation type (Askins and Philbrick 1987, Haskell et al. 2006), and transect coverage per vegetation type. I quantified mean annual rainfall as the residual cumulative annual rainfall (January–December) compared to the long-term mean annual rainfall (1977–2009). Rainfall data (provided by RBM) was unavailable for 2008. Proportional area of each vegetation type was calculated based on the area and age of each site in each year, and I assessed change over time with linear regression. Coverage per year was calculated as the proportion of km's of transect in each vegetation type per year. I assessed whether changes in coverage have generally matched changes in area by regressing proportional coverage divided by proportional area on year for each vegetation type.

Results

Habitat affinity

Of the 37 commonly observed species, 3 were only recorded in old-growth forest and 4 more had ≥ 80% of their sightings/km in old-growth forest. The majority of species (24) were often recorded in old-growth forest (≥ 20%, < 80% sightings/km) but also frequently seen in regenerating vegetation types. Six species were rarely seen in old-growth forest (< 20% sightings/km) including one species never recorded there (Table 4.1). Habitat affinities should be taken as an index comparable among species rather than as an absolute measure of species' habitat preferences because sightings/km were not corrected for variability in detection probability among vegetation types. I did not assess the habitat affinities of the 39 rarely observed species (those recorded ≤ 20 times) because so few sightings are unlikely to be representative of the species' occurrence in different vegetation types.

Distance sampling

I fitted detection functions for each of the three species pools in each year (Table 4.1, Table S.4.3). Detection probability varied among species pools with furtive species being the least detectable and conspicuous species the most, although estimates are not directly comparable due to variability in truncation distance (Table S.4.3). My assumption of relatively similar bird detectability within pools was supported, and models with species as a covariate were the least likely compared to models with a vegetation type covariate, an observer covariate and no covariate for all three species pools (Table S.4.4). I also fitted detection functions for birds in general (76 species pooled) for each vegetation type in each year (Table S.4.5). As expected, detection probability was generally high in early and late woodland, low in thicket, and intermediate in old-growth forest. There were too few observations in grassland to fit per year detection functions.

Population trends and determinants

I estimated population trends for the 37 relatively common species (recorded > 20 times) (Table 4.1, Fig. 4.1). Twenty-eight of these species (76%) decreased, 21 significantly so at an average rate of 13.9% per year. Nine species (24%) increased but only one significantly so. Population trend estimates were not significantly related to the $\log_e$ of the cumulative sightings/species (slope = −0.003, $p = 0.88$). However, as expected, SE of population trend estimates decreased with an increasing $\log_e$ of cumulative sightings/species (slope = −0.02, $r^2 = 0.41$, $p < 0.01$).

Population trend estimates for 30 species were acceptably reliable (SE < 0.08) for further analyses regarding the potential determinants of population trends. I investigated the relationship between population trends and characteristics of these species—range extent, affinity for old-growth forest, predominant habitat, clutch size, weight, predominant diet, and tolerance for human-modified landscapes. Range extent was significantly related to population trend (slope = -7.63×10^{-9}, $r^2 = 0.18$, $p < 0.05$) and was significantly correlated with affinity for old-growth forest (Pearson $r = -0.46$, $p < 0.05$). However, affinity for old-growth forest was not significantly related to population trend (slope = -0.075, $p = 0.23$). Generally, species with larger ranges had lower population trends (*i.e.* more negative) and a lower affinity for old-growth forest. Species with predominant habitat among regenerating vegetation types had larger range extents than species with predominant habitat in old-growth forest (mean range extent per vegetation type: old-growth = 3.10×10^6 km^2, n = 20; regenerating = 9.03×10^6 km^2, n = 10; $r^2 = 0.33$; $p < 0.01$). Furthermore, species with predominant habitat among regenerating vegetation types had significantly lower population trends (*i.e.* more negative) than those with old-growth forest as predominant habitat (mean population trend per vegetation type: old-growth = -0.08, n = 20; regenerating = -0.16, n = 10; $r^2 = 0.16$; $p < 0.05$). Weight (slope = -2.5×10^{-6}, $p = 0.99$), clutch size (slope = 0.016, $p < 0.57$), predominant diet (mean population trend per diet class: insects = -0.12, n = 16; plants = -0.10, n = 10; omnivorous/carnivorous = -0.073, n = 4; $p = 0.68$), and tolerance for human-modified landscapes (mean population trend per class: tolerant = -0.13, n = 13; intolerant = -0.09, n = 17; $p = 0.30$) were not significantly related to population trend. Furthermore, species pool was not significantly related to population trend (mean population trend per pool: pool A = -0.104, n = 5; pool B = -0.127, n = 11; pool C = -0.090, n = 14; $p = 0.61$).

I also assessed general trends of overall bird density (76 species pooled) in the different vegetation types—thicket, early woodland, late woodland, and old-growth forest. Grassland had too few sightings/year to estimate detection functions. Birds declined significantly in early woodland, late woodland, and old-growth forest with mean general trend and SE from 999 detection probability resamples and GLM refittings of −0.13 ± 0.03, −0.09 ± 0.04, and −0.14 ± 0.03 respectively. Birds also declined in thicket but not significantly so with mean general trend and SE = −0.15 ± 0.10. However, general trends in different vegetation types did not differ significantly although the intercepts did. Thus, the overall general trend across old−growth, late woodland, early woodland, and thicket was −0.13 ± 0.01 (Fig. 4.2).

I assessed changes in rainfall, area of vegetation types, and transect coverage per vegetation type over time as potential factors that could influence both population trends and general trends of overall bird density. Mean annual rainfall did not change significantly over time (slope = −62.10, $p = 0.05$). However, for 9 of 12 years for which I have rainfall data (1997–2009 excluding 2008 when data were unavailable), mean annual rainfall was lower than the long-term mean (Fig. S.4.6). Furthermore, mean annual rainfall has been below the long-term mean every year since 2002. Proportional area of regenerating vegetation types changed over time as regenerating sites aged. Proportional area increased significantly over time for late woodland (slope = 0.019, $r^2 = 0.91$, $p < 0.01$) and thicket (slope = 0.005, $r^2 = 0.55$, $p < 0.05$) and decreased for early woodland (slope = −0.005, $r^2 = 0.52$, $p < 0.05$), while proportional area of grassland did not change significantly (slope = 0.001, $p = 0.76$). However, transect coverage per vegetation type, generally matched these changes with proportional coverage/proportional area per vegetation type not changing significantly over time for any vegetation type (old-growth forest: slope = −0.002, $p = 0.86$; late woodland: −0.024, $p = 0.74$; early woodland: slope = −0.033, $p = 0.31$; thicket: slope = −0.043, $p = 0.08$) except grassland (slope = −0.146, $r^2 = 0.58$, $p < 0.05$).

Discussion

The birds inhabiting the old-growth coastal dune forests and coastal woody regenerating vegetation types (thicket, early woodland, and late woodland) have generally declined since 1997. Of the 37 relatively common species, 21 have declined significantly at rates between 7.9 and 27.8% per year while only one species has increased significantly. Furthermore, Rudd's Apalis, the only one of the four restricted-range bird species of the Maputaland Centre of endemism (Steenkamp et al. 2004) to occur at the study site, has declined significantly at a rate of 10.9% per year. None of the species for which I assessed population trends are globally threatened (IUCN 2008), but they were, by necessity of the trend analysis procedure, relatively common in the study area. Species with reliable population trend estimates (SE < 0.08) tended to be the most often recorded among the relatively common species because SE of population trend estimates decreased with increasing cumulative records per species. However, population trend estimate itself was not dependent on cumulative records per species, so there is no indication that populations of the 39 relatively rare species have fared better than the relatively common species.

Earlier studies show that forest regeneration in the area results in increased bird species diversity with regeneration age, while overall density remains relatively stable (Kritzinger and van Aarde 1998) as the bird community undergoes a compositional shift from grassland and pioneer species to secondary forest species (van Aarde et al. 1996a, Grainger and van Aarde 2012). Thus, from a site-specific perspective, a few species characteristic of early successional stages should decrease over time while many forest species increase as the regenerating vegetation becomes more similar to old-growth coastal dune forest. However, I took a study area wide view of population trends (necessitated by sample size requirements of distance sampling) rather than a site-specific approach. Therefore, successional changes in regenerating sites should not affect population trends unless area or transect coverage per vegetation type changes over time. While changes in area of vegetation types could result in real changes in population densities (Askins and Philbrick 1987, Haskell et al. 2006), changes in coverage per vegetation type could generate false trends. Changes in coverage mirrored changes in area for all vegetation types except grassland, which became less well represented in sampling over time. Thus, population trend estimates for the birds found commonly in grasslands could have been negatively biased—primarily Red-eyed Dove, Yellow-fronted Canary, and Tawny-flanked Prinia with 68, 60, and 44% of their sightings/km in grassland respectively. Late woodland increased substantially in proportional area (0.02 per year), and the only bird to increase significantly, Golden-tailed Woodpecker, was also the only bird with predominant habitat in late woodland. While thicket increased significantly and early woodland decreased significantly in proportional area, the change was not substantial (−0.005 and +0.005 per year respectively).

Of the species' characteristics I assessed as potential determinants of population trends, only predominant habitat and range extent were related to population trend. Range extent was inversely proportional to population trend and to species' affinity for old-growth forest.

Additionally, species found predominantly in regenerating vegetation types had lower population trend estimates (*i.e.* more negative) and larger ranges than species found predominantly in old-growth forest. Species with large range extents tend to be generalists and are expected to have broad environmental tolerances (Jetz et al. 2007), so specialists are generally more extinction prone (Sekercioglu et al. 2004). Thus, it is surprising that species with large range extents tended to decline more sharply in my study than species with smaller geographic distributions. One possible explanation is that habitat degradation or destruction outside the study sites but in the local area has affected grassland, thicket, and woodland more so than old-growth remnant patches, resulting in more severe population declines for species found predominantly in regenerating vegetation types. In this scenario, the significance of range extent would be largely coincidental. However, range extent could conceivably be more directly impinging on local population trends. The magnitude of change in bird density in response to broad-scale environmental change is generally greatest at the edge of a species' range, and environmental change that negatively affects species tends to result in a contraction of the range towards the core (Mehlman 1997). Because the study site is on the Indian Ocean coast and relatively near the southern most point of the African continent, the forests are at the edge of the range of many species. Thus, the range extent variable generally reflects the distance between the study site and the central point of the range. It might be that change in abundance is not only greatest at the edge but also dependent on how far away the edge is from the core. However, whether the central point of the ranges of species in my analysis corresponds to core range requires further investigation, although there is some evidence that it should be so (Lawton 1993).

That species with predominant habitat in regenerating vegetation types tended to decline more than others did should not overshadow the conclusion that most birds, regardless of habitat affinity, have declined. Overall density of the 76 bird species assessed declined significantly at an alarming rate of 12.2% per year across old-growth coastal dune forests and woody regenerating vegetation types. Recent below average mean annual rainfall might be expected to affect most bird species via effects on survival and breeding success (see Faaborg 1982) and thus, might have contributed to the widespread decline across species and vegetation types. If so, predictions of climate change induced rainfall reductions (see de Wit and Stankiewicz 2006) are concerning. It is also possible that the bird declines are merely temporary responses to drought. However, there are other possibilities that warrant further research including extinction debt (Kuussaari et al. 2009), ecological traps or sinks (Battin 2004), and broad-scale habitat change. Habitat destruction and environmental change at a macroecological scale could be affecting population trends at the local scale as reported elsewhere (Mehlman 1997). This hypothesis is in line with the importance of range extent in my analysis and implies that bird population declines are much more widespread across the region and perhaps the continent.

Severe and widespread declines of bird populations have been recorded throughout the world (e.g. Dunn 2002, BirdLife International 2004, Gregory et al. 2005, Olsen 2008, North American Bird Conservation Initiative 2009), and identification of these declines was largely the result of massive survey efforts in decades-long, nationwide programs such as the Breeding Bird Survey and Common Bird Census in the United Kingdom and the North American Breeding Bird Survey in the United States and Canada (Peakall 2000, North American Bird Conservation Initiative 2009). That similar declines have not been identified in Africa might be due to a lack of monitoring data, though some studies report declines of single species or small groups of species (Nel et al. 2002, Underhill and Crawford 2005, Thiollay 2006), and the decline of migratory bird populations in Europe indicate potential problems in wintering grounds in Africa (Sanderson et al. 2006).

Other studies show that many forest bird species occur in human-modified landscapes that appear, from a human perspective, quite different from undisturbed forest (e.g. Daily et al. 2001, Hughes et al. 2002, Ranganathan et al. 2008). Likewise, few species for which I assessed habitat affinities were strictly found in old-growth coastal dune forest while most were also found in woody regenerating vegetation. Thus, regenerating vegetation and remnant old-growth forests at the study site might provide valuable habitat for birds in a human-modified coastal dune forest landscape. However, the decline of birds across the study site draws their persistence into question. While assessing population trends over time is a step towards understanding the processes that determine occurrence and persistence of birds in human-modified landscapes, much more research is needed to elucidate the underlying mechanisms that generate trends—breeding success, survival, and dispersal.

In conclusion, remnant patches of old-growth forest and sites regenerating after mining in a human-modified coastal dune forest landscape might provide valuable habitat for birds. Persistence of these bird communities might contribute to conservation not only of birds but also forests by enhancing functional connectivity between coastal forests in protected areas and other remnant patches through seed dispersal and pollination. However, further assessment of long-term monitoring data revealed population declines of most bird species assessed and a consistent reduction in bird density across vegetation types. Birds are sensitive to a host of ecological threats (see Gregory et al. 2005) including habitat degradation (Robbins et al. 1989) and fragmentation (Robinson et al. 1995), invasive species (van Aarde 1980, Gurevitch and Padilla 2004), climate change (Veit et al. 1996, Sekercioglu 2002, Green et al. 2008), emergent disease (Wikelski et al. 2004, LaDeau et al.

2007), and pollution (Fry 1995, Camphuysen and Heubeck 2001), so bird declines identified here are a warning of environmental problems. Probable loss of valuable ecosystem services such as pollination, seed dispersal, and nutrient recycling with bird declines are also worrying (Sekercioglu et al. 2004) and might even threaten the coastal dune forest rehabilitation program which relies on processes of natural succession (van Aarde et al. 1996b, van Aarde et al. 1996a). More research is urgently needed to elucidate the mechanisms driving the decline and to assess whether declines are a local phenomenon or are also occurring at a broader geographical scale.

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Author contributions: Conceived and designed the experiments: MJT RJvA. Performed the experiments: MJT RJvA. Wrote the paper: MJT RJvA.

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Figures

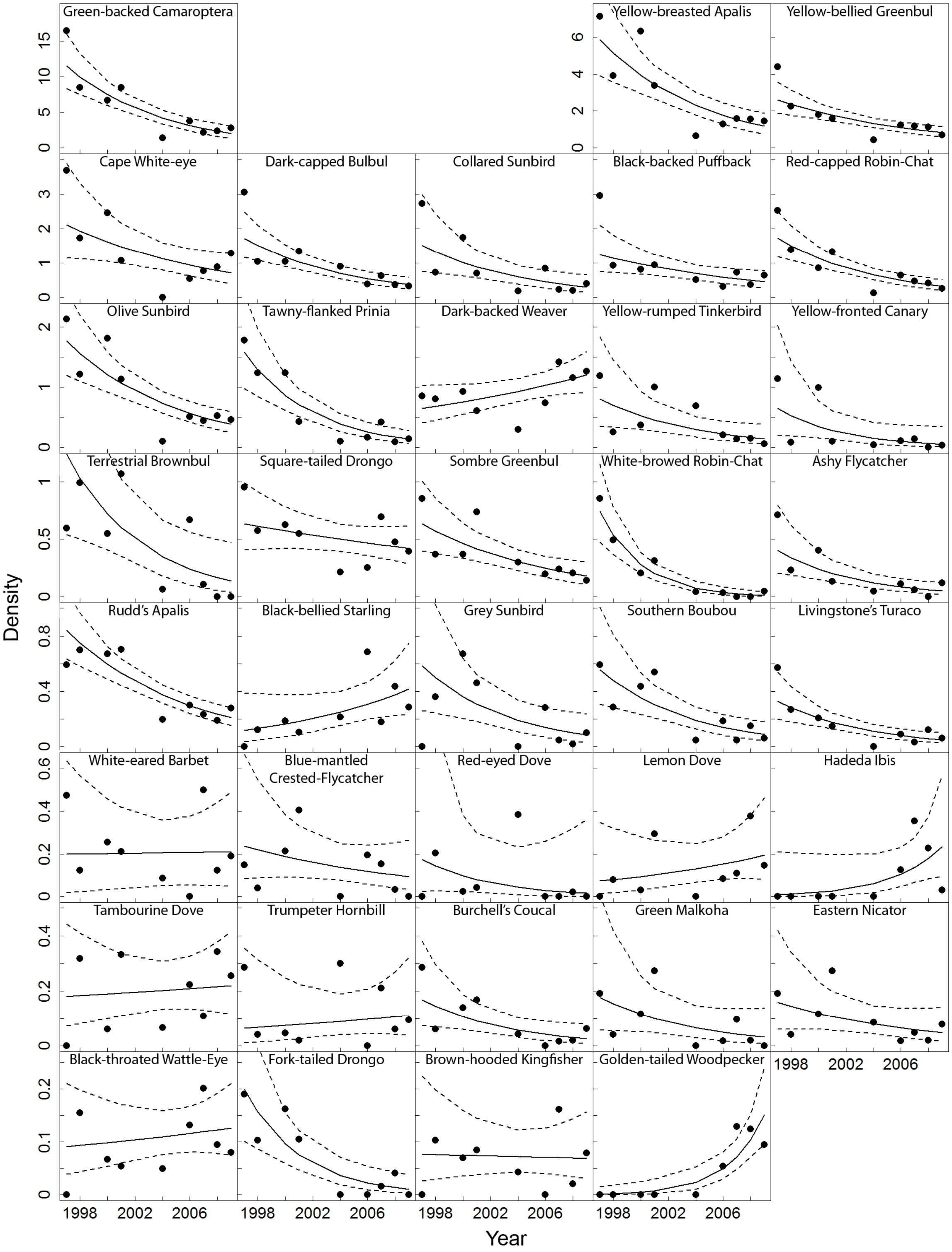
Green-backed Camaroptera
Yellow-breasted Apalis
Yellow-bellied Greenbul
Cape White-eye
Dark-capped Bulbul
Collared Sunbird
Black-backed Puffback
Red-capped Robin-Chat
Olive Sunbird
Tawny-flanked Prinia
Dark-backed Weaver
Yellow-rumped Tinkerbird
Yellow-fronted Canary
Terrestrial Brownbul
Square-tailed Drongo
Sombre Greenbul
White-browed Robin-Chat
Ashy Flycatcher
Rudd's Apalis
Black-bellied Starling
Grey Sunbird
Southern Boubou
Livingstone's Turaco
White-eared Barbet
Blue-mantled Crested-Flycatcher
Red-eyed Dove
Lemon Dove
Hadeda Ibis
Tambourine Dove
Trumpeter Hornbill
Burchell's Coucal
Green Malkoha
Eastern Nicator
Black-throated Wattle-Eye
Fork-tailed Drongo
Brown-hooded Kingfisher
Golden-tailed Woodpecker
Density
Year
1998
2002
2006
0
5
10
15
2
4
6
1
3
0.5
0.4
0.8
0.2
0.6
0.1

Fig. 4.1. Population trends. Change in density/ha over time for relatively common species with fitted GLM trend line and 95% CI (stippled lines) from the original offset estimate. Density was estimated by $n_{t,s} / 2L_t w_t \hat{P}_{a,p,t}$ where $n_{t,s}$ is the number of sighting per species per year, $2L_t w_t$ is the area of transect coverage in hectares and $\hat{P}_{a,p,t}$ is the detection probability over the area covered per pool per year. See Table 4.1 for trend estimates and SE's calculated based on 999 resamples of $\hat{P}_{a,p,t}$.

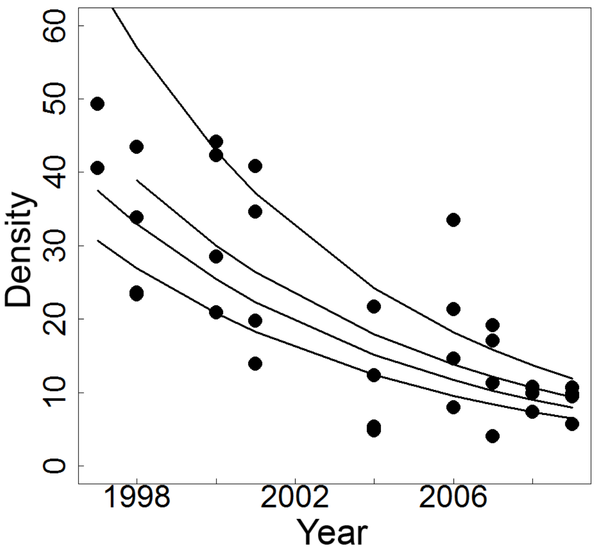

Fig. 4.2. Vegetation type specific trends. Change in density/ha of birds in general over time in different vegetation types with fitted GLM trend lines of slope −0.13 ± 0.01. Density was estimated by $n_{t,v} / 2L_t w_t \hat{P}_{a,p,t}$ where $n_{t,v}$ is the number of bird sightings per vegetation type per year, $2L_t w_t$ is the area of transect coverage in hectares and $\hat{P}_{a,p,t}$ is the detection probability over the area covered per vegetation type per year. Intercepts are significantly different and trend lines are for, from highest to lowest density, old-growth forest, late woodland, thicket, and early woodland.

Tables

Table 4.1. Population trends and covariates for relatively common species. Species names follow Hockey et al. (2005). Pool codes are A = furtive species, B = intermediate, C = conspicuous. * indicates statistically significant trends. Predominant habitat is the vegetation type in which a species has the greatest proportion of sightings/km, and the proportion is given in parentheses. Vegetation type abbreviations as follows: OG = old-growth coastal dune forest, LW = late woodland, EW = early woodland, T = thicket, G = grassland. OG affinity is the proportion of sighting/km in old-growth forest.

Common name	**Scientific name**	**Pool**	**Trend**	**SE**	**Range (km2)**	**Predominant habitat**	**OG affinity**
Black-bellied Starling	*Lamprotornis corruscus*	C	0.104	0.063	350000	OG (0.54)	0.54
Ashy Flycatcher	*Muscicapa caerulescens*	B	−0.171*	0.055	7700000	EW (0.47)	0.21
Black-backed Puffback	*Dryoscopus cubla*	C	−0.083*	0.037	5400000	OG (0.34)	0.34
Black-throated Wattle-Eye	*Platysteira peltata*	B	0.027	0.048	3100000	OG (0.81)	0.81
Blue-mantled Crested-Flycatcher	*Trochocercus cyanomelas*	A	−0.077	0.073	1200000	OG (1)	1.00
Brown-hooded Kingfisher	*Halcyon albiventris*	C	−0.008	0.067	3800000	EW (0.39)	0.08
Burchell's Coucal	*Centropus burchellii*	C	−0.153*	0.067	5000000	OG (0.42)	0.42
Cape White-eye	*Zosterops virens*	B	−0.090*	0.042	1300000	OG (0.38)	0.23
Collared Sunbird	*Hedydipna collaris*	B	−0.132*	0.051	5500000	OG (0.52)	0.52
Dark-backed Weaver	*Ploceus bicolor*	C	0.051	0.027	1100000	OG (0.33)	0.33
Dark-capped Bulbul	*Pycnonotus tricolor*	C	−0.126*	0.029	19000000	G (0.25)	0.23
Eastern Nicator	*Nicator gularis*	C	−0.098	0.071	4000000	OG (0.38)	0.38
Fork-tailed Drongo	*Dicrurus adsimilis*	C	−0.243*	0.071	14000000	EW (0.67)	0.09
Golden-tailed Woodpecker	*Coampethera abingoni*	C	0.377*	0.104	3880000	LW (0.56)	0.27
Green Malkoha	*Ceuthmochares aereus*	C	−0.141	0.091	5400000	OG (0.82)	0.82

Green-backed Camaroptera	*Camaroptera brachyura*	A	−0.144*	0.029	16000000	EW (0.3)	0.18
Grey Sunbird	*Cyanomitra veroxii*	B	−0.160*	0.064	170000	OG (0.47)	0.47
Hadeda Ibis	*Bostrychia hagedash*	C	0.270	0.153	16000000	G (0.32)	0.25
Lemon Dove	*Aplopelia larvata*	A	0.082	0.089	2000000	OG (1)	1.00
Livingstone's Turaco	*Tauraco livingstonii*	C	−0.154*	0.042	5000000	OG (1)	1.00
Olive Sunbird	*Cyanomitra olivacea*	B	−0.127*	0.029	570000	OG (0.45)	0.45
Red-capped Robin Chat	*Cossypha natalensis*	A	−0.137*	0.031	3600000	OG (0.58)	0.58
Red-eyed Dove	*Streptopelia semitorquata*	C	−0.197	0.182	10000000	G (0.68)	0.26
Rudd's Apalis	*Apalis ruddi*	B	−0.116*	0.021	76000	T (0.46)	0.20
Sombre Greenbul	*Andropadus importunes*	C	−0.105*	0.035	1200000	OG (0.52)	0.52
Southern Boubou	*Laniarius ferrugineus*	B	−0.153*	0.046	580000	OG (0.7)	0.70
Square-tailed Drongo	*Dicrurus ludwigii*	C	−0.034	0.029	4300000	OG (0.37)	0.37
Tambourine Dove	*Turtur tympanistria*	A	0.018	0.057	7400000	OG (0.41)	0.41
Tawny-flanked Prinia	*Prinia subflava*	B	−0.202*	0.042	14000000	G (0.44)	0.12
Terrestrial Brownbul	*Phyllastrephus terrestris*	A	−0.181*	0.073	2400000	OG (0.9)	0.90
Trumpeter Hornbill	*Bycanistes bucinator*	C	0.045	0.098	2900000	OG (0.96)	0.96
White-browed Robin-Chat	*Cossypha heuglini*	C	−0.326*	0.058	8800000	T (0.49)	0.00
White-eared Barbet	*Stactolaema leucotis*	C	0.005	0.071	710000	OG (0.59)	0.59
Yellow-bellied Greenbul	*Chlorocichla flaviventris*	C	−0.095*	0.024	3800000	OG (0.49)	0.49
Yellow-breasted Apalis	*Apalis Favida*	B	−0.133*	0.031	5600000	EW (0.38)	0.13
Yellow-fronted Canary	*Crithagra mozambicus*	C	−0.207	0.108	9500000	G (0.6)	0.22
Yellow-rumped Tinkerbird	Pogoniulus bilineatus	B	−0.142*	0.063	6600000	OG (0.75)	0.75

Supplementary Material

Table S.4.1. Transects per site per year in regenerating and old-growth sites. RegX sites are regenerating after mining; numbers in parentheses represent the regeneration age since mining as of 2009. OG sites are old-growth forests. [a] indicates transect length of 250 m, [b] indicates transects length of 500 m, and [c] indicates transect length of 300 m.

Year	Observer	Transects per site										
		Reg1 (32)	Reg2 (29)	Reg3 (25)	Reg4 (21)	Reg5 (17)	Reg6 (13)	Reg7 (9)	Reg8 (6)	Reg9 (3)	OG1	OG2
1997	A	2[a]	2[a]	2[a]	2[a]	1[a]	4[a]	-	-	-	1[a]	2[a]
1998	A	4[a]	4[a]	4[a]	4[a]	4[a]	3[b]	-	-	-	4[a]	8[a]
2000	A	4[a]	4[a]	4[a]	4[a]	4[a]	3[b]	-	-	-	4[a]	4[a]
2001	A	4[a]	4[a]	4[a]	4[a]	4[a]	2[b]	-	-	-	4[a]	10[a]
2004	B	2	3	2	2	3	2	3	3	-	-	5
2006	C	4	5	4	4	5	4	5	-	-	5	10
2007	D & E	6	7	7	11	4	4	7	6	3	11	9
2008	D & E	4	5	4	4	6	7	6	4	-	8	6
2009	D & E	6	6	6	4	5	^{6}	5	4	9	4	8

Table S.4.2. Relatively rare species. Species names follow Hockey et al. (2005).

Common name	**Scientific name**
Bearded Scrub-Robin	*Cercotrichas quadrivirgata*
African Dusky Flycatcher	*Muscicapa adusta*
African Emerald Cuckoo	*Chrysococcyx Cupreus*
African Green-Pigeon	*Treron calvus*
African Paradise-Flycatcher	*Terpsiphone viridis*
African Pygmy-Kingfisher	*Ispidina picta*
Bar-throated Apalis	*Apalis thoracica*
Brimstone Canary	*Crithagra sulphurata*
Broad-billed Roller	*Eurystomus glaucurus*
Buff-spotted Flufftail	*Sarothrura elegans*
Cape Batis	*Batis capensis*
Cape Turtle-Dove	*Streptopelia capicola*
Cardinal Woodpecker	*Dendropicos fuscescens*
Chorister Robin-Chat	*Cossypha dichroa*
Common Cuckoo	*Cuculus canorus*
Crested Guineafowl	*Guttera edouardi*
Crowned Hornbill	*Tockus alboterminatus*
Eastern Bronze-naped Pigeon	*Columba delegorguei*
Eurasian Golden Oriole	*Oriolus oriolus*
Garden Warbler	*Sylvia borin*
Giant Kingfisher	*Megaceryle maxima*
Gorgeous Bush-Shrike	*Telophorus viridis*
Green Twinspot	*Mandingoa nitidula*
Grey Waxbill	*Estrilda perreini*

Icterine Warbler	*Hippolais icterina*
Klaas's Cuckoo	*Chrysococcyx klaas*
Lesser Honeyguide	*Indicator minor*
Long-billed Crombec	*Sylvietta rufescens*
Narina Trogon	*Apaloderma narina*
Neddicky	*Cisticola fulvicapilla*
Purple-banded Sunbird	*Cinnyris bifasciatus*
Purple-crested Turaco	*Gallirex porphyreolophus*
Red-chested Cuckoo	*Cuculus solitarius*
Red-fronted Tinkerbird	*Pogoniulus pusillus*
Southern Black Flycatcher	*Melaenornis pammelaina*
Spectacled Weaver	*Ploceus ocularis*
Spotted Flycatcher	*Muscicapa striata*
Swee Waxbill	*Coccopygia melanotis*
Woodwards' Batis	*Batis fratrum*

Table S.4.3. AIC selected detection function models for species pools. See (Table 4.1) for species pool composition. Pool A comprises furtive species, Pool B intermediate, and Pool C conspicuous. Model details are described by $\hat{P}_{a,t}$, the estimated mean probability of detection for species in the covered region *a* in year *t*; its SE; L_t, the line length surveyed at time *t*; w_t, the truncation distance; and the model key function and covariates. Model abbreviations as follows: “HR” for hazard-rate key, “HN” for half-normal key, “+ V” for vegetation type as factor covariate, and “+ O” for observer as factor covariate.

Grouping	**Model details**	**1997**	**1998**	**2000**	**2001**	**2004**	**2006**	**2007**	**2008**	**2009**
Pool A	$\hat{P}_{a,t}$	0.208	0.332	0.482	0.357	0.254	0.435	0.255	0.225	0.198
	SE	0.018	0.017	0.027	0.017	0.039	0.018	0.019	0.023	0.080
	Best Model	HN + V	HN + V	HR	HN + V	HN	HR	HR + O	HR	HR
	L_t (m)	4000	9500	8500	9500	7500	13800	22500	16200	17400
	w (m)	40	40	40	40	40	30	40	40	40
Pool B	$\hat{P}_{a,t}$	0.260	0.509	0.438	0.488	0.339	0.643	0.359	0.408	0.359
	SE	0.016	0.018	0.016	0.019	0.040	0.040	0.014	0.023	0.025
	Best Model	HN	HR + V	HN + V	HR + V	HN	HR	HR	HN + O	HR
	L_t (m)	4000	9500	8500	9500	7500	13800	22500	16200	17400
	w (m)	40	40	40	40	40	30	40	40	40
Pool C	$\hat{P}_{a,t}$	0.324	0.512	0.508	0.501	0.311	0.670	0.275	0.299	0.364
	SE	0.028	0.021	0.021	0.020	0.030	0.044	0.012	0.029	0.025
	Best Model	HR	HR + V	HR + V	HN + V	HN + V	HR	HN + O + V	HR + O + V	HN + O + V
	L_t (m)	4000	9500	8500	9500	7500	13800	22500	16200	17400
	w (m)	40	50	50	50	50	30	50	50	50

Table S.4.4. AIC model selection for validating species pooling assumption. ΔAIC = 0 indicates the most supported model of the detection function for each species pool over the study period (years pooled with 1997 and 2006 excluded due to constraint in setting reasonable cutpoints). See (Table 4.1) for species pool composition. Pool A comprises furtive species, Pool B intermediate, and Pool C conspicuous. Model abbreviations as follows: "HR" for hazard-rate key, "HN" for half-normal key, "+ V" for vegetation type as factor covariate, "+ O" for observer as factor covariate, and "+ S" for species as factor covariate. Models including species as a factor covariate had the highest ΔAIC in support of my species pooling assumptions. The half-normal key model with observer as a factor covariate failed to converge for Pool A.

	ΔAIC		
Model	Pool A	Pool B	Pool C
HN	143.59	48.7	117.96
HN + V	102.38	5.47	48.17
HN + O	-	0	0
HN + S	138	55.38	90.84
HR	129.73	62.05	116.75
HR + V	133.45	2.61	145.27
HR + O	0	6.21	143.55
HR + S	141.16	72.21	171.47

Table S.4.5. AIC selected detection function models stratified by vegetation type (76 species pooled). Model details are described by $\hat{P}_{a,t}$, the estimated mean probability of detection for species in the covered region a in year t; its SE; L_t, the line length surveyed at time t; w_t, the truncation distance; and the model key function and covariates. Model abbreviations as follows: "HR" for hazard-rate key, "HN" for half-normal key, and "+ O" for observer as factor covariate.

Grouping	**Model Details**	**1997**	**1998**	**2000**	**2001**	**2004**	**2006**	**2007**	**2008**	**2009**
	Best Model	HR	HR	HR	HR	HR	HR	HN	HR	HN + O
	w (m)	40	40	40	40	40	30	40	40	40
Old-growth	$\hat{P}_{a,t}$	0.270	0.467	0.571	0.465	0.380	0.579	0.335	0.430	0.382
	SE	0.016	0.022	0.025	0.019	0.039	0.030	0.015	0.030	0.030
	L_t (m)	750	3000	2000	3500	1500	4500	6000	4200	3600
Late woodland	$\hat{P}_{a,t}$		0.728	0.417	0.751	0.162	0.573	0.394	0.643	0.588
	SE		0.047	0.028	0.040	0.298	0.035	0.017	0.057	0.028
	L_t (m)		1000	1000	2000	1500	3900	6000	3900	6600
Early woodland	$\hat{P}_{a,t}$	0.346	0.674	0.787	0.676	0.450	0.712	0.348	0.388	0.614
	SE	0.021	0.029	0.037	0.045	0.080	0.079	0.022	0.064	0.086
	L_t (m)	1500	2000	2000	2000	1200	2700	4500	3000	1500
Thicket	$\hat{P}_{a,t}$	0.213	0.355	0.581	0.408	0.463	0.142	0.429	0.361	0.360
	SE	0.034	0.024	0.029	0.030	0.082	0.438	0.050	0.050	0.031
	L_t (m)	500	2000	2000	1000	1500	2700	3300	3900	4500

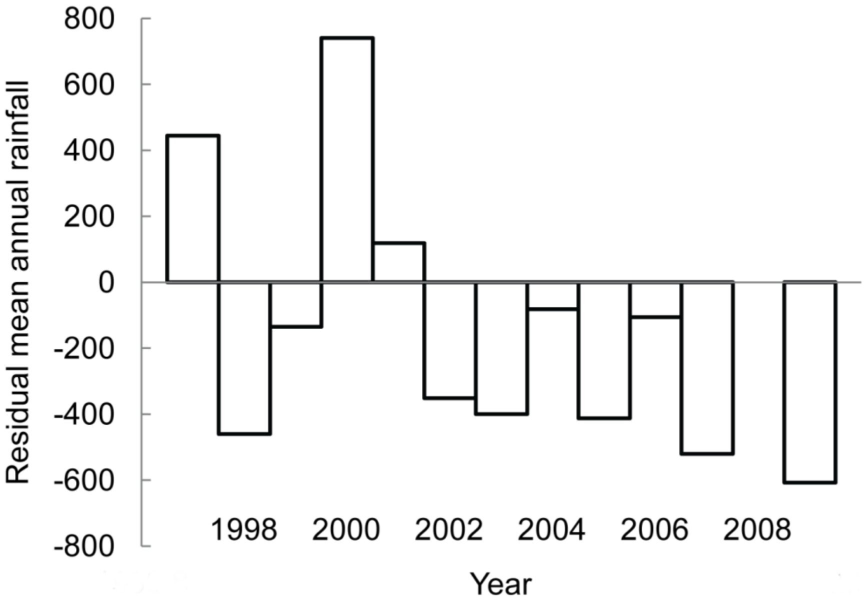

Figure S.4.6. Change in rainfall over time. Bars represent residual mean annual rainfall from the long-term (1977–2009) mean in mm.

Chapter 5. Geographical and Taxonomic Biases in Research on Biodiversity in Human-Modified Landscapes

Publication Details

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Abstract

Biodiversity persistence in human-modified landscapes is crucial for conservation and maintaining ecosystem services. Studies of biodiversity in landscapes where humans live, work, and extract resources could support defensible policy-making to manage land use. Yet, research should cover relevant regions, and biases in study topics should not lead to gaps in the evidence base. I systematically reviewed the literature of biogeography in human-modified landscapes published in eight eminent biogeography, conservation, and ecology journals to assess geographical bias among biomes and geopolitical regions and taxonomic bias among species groups. I compared research output per biome to area, biome type, species richness, proportion of transformed land, and the ratio of transformed to protected land. I also compared research output per geopolitical region to area, proportion of transformed land, the ratio of transformed to protected land, and human population density. Research output was distributed unequally among biomes, geopolitical regions, and species groups. Biome type was a clear factor in research bias, and forest biomes were the subject of 87% of papers, while species richness was not generally associated with bias. Conservation in human-modified landscapes is most important in regions with low protected area coverage, high land conversion, and high pressure from human populations, yet the distribution of published papers did not generally reflect these threats. Seventy-five percent of studies focused on the Americas and Europe, while Africa and Asia were critically understudied. Taxonomically, plants and invertebrates were the most studied groups; however, research output was not correlated with species richness per group. Protected areas alone will not conserve biodiversity in the long term. Thus, a strong biogeographical evidence base is required to support policies for biodiversity maintenance on human-modified land. Under-studied regions and species groups deserve further research to elucidate what, where, and how biodiversity persists in human-modified landscapes to inform conservation policy and enhance efficacy.

Introduction

Conservation actions should be based on scientific evidence to achieve the best possible outcomes and avoid squandering resources (Sutherland 2004). However, science-based decision-making relies on a solid foundation of relevant evidence, often an assemblage of peer-reviewed studies (Sutherland 2004, Pullin and Knight 2009). Scientists, funding agencies, and publishers hold sway over the composition of the evidence base through their influence on which studies are conducted and published (Lawler et al. 2006). If research interests are misaligned with research needs, gaps in the evidence base could compromise conservation efforts. Thus, it is important to monitor the distribution of published research in comparison to emerging research requirements (Lawler et al. 2006).

I performed such an assessment for an increasingly important field of inquiry—biogeography of human-modified landscapes—concerned with biodiversity patterns and the processes that maintain them in areas where humans live, work, and extract resources. Though the conservation literature has traditionally focused on large, relatively pristine study sites (Fazey et al. 2005a, Felton et al. 2009), research on the biogeography of human-modified landscapes is accumulating (see Daily 1999, Daily et al. 2001, Rosenzweig 2003). In line with research needs(Chazdon et al. 2009), these studies seek to define where, what, and how biodiversity persists in human-modified landscapes; how different aspects of diversity co-vary; and how human actions drive these patterns.

Protected areas (PAs) are an essential part of the overall conservation strategy, but alone, in the long-term, they are unlikely to conserve biodiversity for several reasons including constraints of location, size, and configuration (Bengtsson et al. 2003, Brooks et al. 2004, Joppa and Pfaff 2009); ongoing management challenges and outside pressures (Kareiva et al. 2007); and climate change (Loarie et al. 2009). Most compellingly, if species cannot persist beyond PA boundaries, loss of speciation rates and pools of potential immigrants to PAs means that conserving, for example, 10% of the Earth's surface (see Brooks et al. 2004) is likely to result in 90% loss of species (Rosenzweig 2003). Already, humanity has commandeered roughly 40% of Earth's land surface for crops and pastures alone (Millennium Ecosystem Assessment 2005), and demand will escalate for food, fiber, fuel, shelter, space, and freshwater (Tilman 2001). Calls for conservation beyond the boundaries of PAs are not novel (e.g. Leopold 1949), but as humans continue to transform natural ecosystems, conservation efforts in rural villages, logging concessions, pastures, fields, and the like will become increasingly important, not only for conservation's sake but also to sustain valuable ecosystem services (e.g. pollination, decomposition, nutrient cycling) (Tscharntke et al. 2005).

Studies on the biogeography of human-modified landscapes provide an evidence base to support land-use planning decisions meant to render human dominated land as amenable as possible to biodiversity. For example, studies demonstrate that agroforestry systems maintain on average > 60% of the species richness of primary tropical forests (Bhagwat et al. 2008), oil palm plantations support less forest biodiversity than do other tree crops (Fitzherbert et al. 2008), and scattered remnant trees in fields or pastures help maintain forest diversity (Dunn 2000, Fischer et al. 2010). Yet, to achieve success in supporting policy, the evidence base must cover relevant geographical regions and taxonomic groups and be sufficiently comprehensive; conservation decisions ought to be based on adequate understanding of local biodiversity features and the processes that maintain their viability rather than global generalizations (Svancara et al. 2005). While no topic is likely “over-studied”, when scientific output is severely biased, “under-studied” topics could hamper conservation efforts. For instance, research on human-modified forest ecosystems guides strategies to manage plantations to encourage persistence of forest biodiversity. However, managers have applied the same strategies to plantations embedded in grasslands with dubious efficacy (Pryke and Samways 2003, Lipsey and Hockey 2010).

Unfortunately, biases in the topics that scientists study are common, and the drivers of bias are varied. For example, the distribution of research output among species is uneven (Bonnet et al. 2002, Clark and May 2002, Fazey et al. 2005a, Lawler et al. 2006, Pyšek et al. 2008, Felton et al. 2009, Trimble and van Aarde 2010, Griffiths and Dos Santos 2012). Threatened status, economic importance, or ecological impact drive biases somewhat, but so too, and apparently more so, do personal affinities of scientists, funders, and reviewers toward certain species characteristics that may be unrelated to research needs (Bonnet et al. 2002, Lawler et al. 2006, Trimble and van Aarde 2010). There are also clear geographical biases in ecological research. For instance, the study of invasive species is concentrated in the Americas and Europe with little research conducted in Africa and Asia (Pyšek et al. 2008), a pattern that holds for landscape research, climate change ecology, and conservation biology as a whole (Lawler et al. 2006, Felton et al. 2009, Conrad et al. 2011). If studies of biogeography of human-modified landscapes are biased towards certain topics, scientists and funding agencies may wish to refocus their efforts to ensure sufficient science is available to support conservation in human-modified landscapes where it is most needed. Specifically, research on biogeography in human-modified landscapes should be prioritized in areas (or for species groups) where the topic is little studied despite high threat.

I systematically reviewed the literature on the biogeography of human-modified landscapes to assess the distribution of research output ecologically, among terrestrial biomes; geopolitically, among UN GeoScheme sub-regions; and taxonomically, among species groups. The ecological subdivision is important because I expect biodiversity to respond more similarly to land-use management within than among ecosystem types, while the geopolitical comparison may be more relevant to policy-makers and funding agencies. I investigated the relationship between the distribution of research and the area and species richness per region and biome type. I also compared the distribution of research to the estimated importance of countryside biogeography in each region based on population density, proportion of land converted, and the ratio of land area converted to area protected.

These metrics provide a rough quantification of the risk of biome-wide biodiversity loss and, thus, the importance of conservation outside PAs. I also assessed the distribution of research among seven species groups: birds, fish, fungi, herpetofauna, mammals, plants, and invertebrates.

Methods

Literature search

I searched the ISI Web of Knowledge (covering 1950–2010) in May 2012 with keywords "biodiversity" or "conservation" and each of the following terms: "agricultur*", "agroforest*", "crop$land", "farm*", "forestry", "human$modified", "multiple$use management", "range$land", "rural", "sub$urban", and "urban" ("*" is a wildcard indicating any group of characters, and "$" represents zero or one character). I limited my assessment to eight conservation, biogeography, and ecology journals: *Biodiversity and Conservation, Biological Conservation, Conservation Biology, Diversity and Distributions*, *Journal of Applied Ecology*, *Journal of Biogeography*, *Ecological Applications,* and *Ecology*. From the initial search, I retained primary research papers that assessed occurrence or persistence of multi-species assemblages on human-modified land under current use. Thus, I excluded studies of abandoned landscapes, restoration projects that excluded human use, and fragmentation studies that did not explicitly consider biodiversity in the human-modified areas surrounding the fragments.

The choice of keywords and journals searched was a compromise between practicality and comprehensiveness. My keywords were, by necessity, not overly specific to avoid biasing search results. Thus, my keywords returned many papers not relevant to the topic, and practicality dictated that I limit the number of journals searched to prevent an unwieldy number of search results. I selected eight journals that I expected to be among the least biased towards particular biome types, regions, or taxonomic groups.

To assess how research output on the topic of biogeography of human-modified landscapes has changed over time in these journals, I calculated the number of papers per year identified in my literature search, and I noted the total number of papers published per year available on the ISI Web of Knowledge for each journal. I used linear regression to assess changes over time in the proportion of the total research output that was composed of studies on the biogeography of human-modified landscapes.

Geographical distribution of research output

I assessed the geographical distribution of research output both politically and ecologically. For each paper identified by my search, I noted the geopolitical region or regions where the study was carried out based on an intermediate scale of subdivision, the UN GeoScheme categorization (UNSD 2011; Micronesia, Melanesia, and Polynesia combined to yield 19 geopolitical regions). To assess the ecological distribution, I noted the terrestrial biome or biomes in which research was conducted (Olson et al. 2001, WWF 2001). In the few cases where studies assessed biodiversity in aquatic ecosystems, I allotted terrestrial biomes based on the location of the water bodies.

Many papers identified in the literature search, especially of European origin, considered “farmland biodiversity” in semi-natural landscapes with no reference to any natural ecosystem. These studies may not represent useful information on conserving the biodiversity of the original biome; for example, studies of biodiversity in extensive semi-natural grasslands under varying management regimes may or may not inform the conservation of the biodiversity of boreal forests in which the grasslands are embedded. Thus, to assess the effect of the inclusion of such studies on further analyses, in addition to recording the biome in which they took place, I also categorized them as “no comparison” (in contrast to “natural comparison”). “Natural comparison” studies compared biodiversity patterns or processes to those of a natural baseline, either analytically or conceptually, and “no comparison” studies did not.

I expected the area of regions to determine the distribution of research among biomes and geopolitical units if research efforts were randomly distributed geographically. The area covered by the largest biome, deserts and xeric shrublands, eclipses the smallest in my study, tropical and subtropical coniferous forests, by 39 times. Similarly, the largest geopolitical region, Northern America, is 87 times the area of the Caribbean. Thus, I regressed the number of papers per region on area of biomes (Olson et al. 2001, WWF 2001) and geopolitical regions (UNEP 2011a). I then calculated area-corrected estimates of research output as the number of studies per million km^2 for biomes and geopolitical regions to investigate whether other factors were related to bias in research output.

For biomes, these factors included biome type (i.e. forest or other), species richness per biome, and the estimated importance of research in a biome. I compared the area-corrected estimates of research output between the seven forest biomes (i.e. three tropical, two temperate, boreal, and Mediterranean forests) and the six other biomes (i.e. montane, flooded, tropical, and temperate grasslands; tundra; and deserts). To evaluate whether research output was skewed towards biomes with higher species richness, I used Spearman rank correlation to compare the total studies per biome to the estimated total number of mammal, bird, reptile, and amphibian species per biome (Hassan et al. 2005). I also compared area-corrected studies per biome to an estimate of the biome-specific z-value from the power model of the species–area relationship for vascular plants calculated by Kier et al. (2005) (I averaged the four sub-regional z-values for the tropical and subtropical dry broadleaf forests). I reasoned that biogeography of human-modified landscapes should be most important in biomes that have been heavily transformed and especially in those that also have low PA coverage. Therefore, I used Spearman rank correlation to compare area-corrected research output to the proportion of transformed land per biome and to the ratio of converted to protected land (i.e. the Conservation Risk Index (CRI) calculated by Hoekstra et al. (2005)). I then used Mann–Whitney U tests to compare the two species richness metrics, CRI, and proportion of transformed land between forest and other biomes.

For geopolitical regions, I used Spearman rank correlation to assess whether area-corrected research output was correlated with the proportion of agricultural land conversion (World Bank 2009), the geopolitical CRI (the ratio of land conversion to PA coverage (UNSD 2010)), and population density (UNEP 2011b). I reasoned that conservation beyond PAs would be both particularly important and challenging in geopolitical regions with high population density.

Distribution of research output among species groups

I categorized the species group or groups assessed in each paper as birds, fish, fungi, herpetofauna, mammals, plants, or invertebrates. I then calculated the percent of total, “natural comparison”, and “no comparison” studies that assessed each group. I used Spearman rank correlation to assess whether the proportion of all studies that assessed each species group was correlated with the proportion of described species comprised by each group (Vie et al. 2009).

Results

I assessed the distribution of research output over time, by geo-ecological region (i.e. biome), by geopolitical region, and by taxonomic group with respect to a number of potential explanatory variables summarized in Table 5.1 and discussed below.

Of the 2521 references returned by my literature search, 681 assessed the occurrence and/or persistence of biodiversity in human-modified landscapes and met my inclusion criteria. These papers (published between 1984 and 2010) made up 4–7% of the total papers published over the same period in *Biological Conservation* (214 of 4890), *Biodiversity and Conservation* (168 of 2685), and *Journal of Applied Ecology* (110 of 2750). They comprised 1.5–2% of research output in *Ecological Applications* (64 of 2796), *Diversity and Distributions* (16 of 657), and *Conservation Biology* (77 of 4132), while they were less prevalent in *Ecology* (12 of 7385) and *Journal of Biogeography* (20 of 2837). Prevalence has increased over time, even after accounting for the increase in publishing output (Fig. 5.1). The yearly proportion of the total studies published by all eight journals comprised of studies identified in my literature review increased significantly with year ($F_{1,18} = 219.1$, $p < 0.001$, $r^2 = 0.90$, $y = 0.002x - 3.892$) although the pattern was clearly non-linear over the study period (Fig. 5.1).

I distinguished 218 papers as “no comparison” studies and 463 as “natural comparison”. I performed subsequent analyses both including and excluding “no comparison” studies. Seven percent of the total studies and 8% of “natural comparison” studies considered biodiversity of human-modified aquatic ecosystems, e.g. streams, wetlands, and ponds.

Geographical bias

The number of studies per biome (see Fig. 5.2) differed widely from one in tundra to 316 in temperate broadleaf and mixed forests, while tropical and subtropical moist broadleaf forests had the highest number of studies from the "natural comparison" category (169) (Fig. 5.3). The seven forest biomes were the subject of 87% of studies. Contrastingly, only 13% of papers assessed the other six biomes. While "no comparison" studies came almost exclusively from forest biomes (96%), excluding them did not remove the bias towards forests; 83% of "natural comparison" studies were conducted in forest biomes.

Research output was also uneven among geopolitical regions (Figs. 5.4 and 5.5), ranging from zero studies in Melanesia, Micronesia, and Polynesia to 163 in Northern Europe. Forty-two percent of the papers studied European regions (although 68% of these were "no comparison" studies), while a further 33% centered on regions in the Americas. Studies conducted in Australia and New Zealand, Africa, and Asia each made up < 10% of the total studies.

Research output was not randomly distributed among biomes or geopolitical regions. The number of studies per biome and geopolitical region were not related to area (biomes: $F_{1,11} = 1.87$, $p = 0.20$; geopolitical regions: $F_{1,18} = 0.07$, $p = 0.80$), even when "no comparison" studies were excluded (biomes: $F_{1,11} = 2.34$, $p = 0.15$; geopolitical regions: $F_{1,18} = 2.40$, $p = 0.14$).

The median number of studies per million km^2 of forest biomes (8.65) was much higher than for other biomes (1.49) (Mann–Whitney U = 1.00, $p < 0.01$) (Fig. 5.6). The difference remained substantial and significant even when "no comparison" studies were excluded (median studies in forest biomes = 8.46, other biomes = 1.49, Mann–Whitney U = 2.00, $p < 0.01$). If I categorized Mediterranean forests, woodlands, and scrub as "other" instead of "forest", research output remained biased towards forest in the total dataset (median studies in forest biomes = 8.55, other biomes = 1.54, Mann–Whitney U = 6.00, $p = 0.04$) and when "no comparison" studies were excluded (median studies in forest biomes = 7.16, other biomes = 1.54, Mann–Whitney U = 7.00, $p = 0.05$).

The number of studies per biome was not significantly correlated with estimated total mammal, bird, reptile, and amphibian richness including "no comparison" studies (Spearman r = 0.14, $p = 0.65$) or excluding them (Spearman r = 0.31, $p = 0.30$). However, the correlation between studies per million km^2 and biome-specific *z*-values for vascular plants was significant when "no comparison" studies were excluded (Spearman r = 0.56, $p = 0.05$), but not when they were included (Spearman r = 0.51, $p = 0.08$). However, *z*-values were higher in forest than other biomes (Mann–Whitney U = 5.50, $p = 0.03$), while total species of mammals, birds, reptiles, and amphibians did not differ significantly (Mann–Whitney U = 18.00, $p = 0.37$).

Area-corrected research output was not correlated with the per-biome CRI (Spearman r = 0.55, $p = 0.051$) unless "no comparison" studies were excluded (Spearman r = 0.63, $p = 0.02$) (Fig. 5.3). However, research output was correlated with proportion of land converted per biome both with and without "no comparison" studies (Spearman r = 0.65, $p = 0.02$; Spearman r = 0.73, $p < 0.01$). However, CRI did not differ significantly between forest biomes and others (Mann–Whitney U = 15.00, p = 0.43), nor did proportion of land converted (Mann–Whitney U = 12.00, p = 0.23). Additionally, area-corrected research output was not correlated with CRI per geopolitical region (all data: Spearman r = −0.18, p = 0.22; "no comparison" studies excluded: Spearman r = −0.15, p = 0.26), nor with proportion of land converted to agriculture (all data: Spearman r = 0.11, p = 0.32; "no comparison" studies excluded: Spearman r = 0.14, p = 0.27) (Figs. 5.4 and 5.5). However, area-corrected research output per geopolitical region was weakly correlated with population density (all data: Spearman r = 0.47, p = 0.04; "no comparison" studies excluded: Spearman r = 0.47, p = 0.03).

Taxonomic bias

Research output was not distributed evenly among seven major taxonomic groups (Fig. 5.7). Of the 681 papers indentified (13% of which studied multiple species groups), 36% assessed invertebrates. Birds and plants were each assessed in 31% of papers. Contrastingly, fewer studies assessed mammals (10%), herpetofauna (7%), fungi (3%), and fish (0.5%).

The 218 "no comparison" studies focused even more on invertebrates (47%) and plants (39%). Of "no comparison" studies, 25% assessed birds, while only 3%, 2%, 1%, and 0% covered mammals, herpetofauna, fungi, and fish respectively. Therefore, among the 463 "natural comparison" studies, research output was more evenly distributed among taxonomic groups (Fig. 5.7): birds (33%), invertebrates (31%), plants (27%), mammals (13%), herpetofauna (9%), fungi (4%), and fish (1%). However, the proportion of studies that assessed each group was not correlated with the proportion of described species per group (all data: Spearman r = 0.34, p = 0.44; "no comparison" studies: Spearman r = 0.40, p = 0.40; "natural comparison" studies: Spearman r = 0.11, p = 0.84).

Discussion

Biogeography of human-modified landscapes provides the evidence base required to support defensible policy-making to encourage biodiversity conservation beyond protected areas, an increasingly important objective. I have shown that it has been a growing sub-discipline in conservation biology over the past two decades, as reflected by publication trends in the eight journals included in my assessment. I have also demonstrated, however, that scientific research output is biased geo-ecologically, geopolitically, and taxonomically. Geo-ecologically, research output for forest biomes was disproportionately higher than for other biomes after correcting for area. In particular, temperate broadleaf and mixed forests and tropical and subtropical moist broadleaf forests garnered a large proportion of research output. Geopolitically, the bias was clearly towards Europe and the Americas, while substantially fewer studies came from Africa and Asia. Taxonomically, research attention among species groups was neither evenly distributed nor correlated with per-group richness, and invertebrates, plants, and birds were the most studied groups.

My literature search was extensive, covering 681 papers, though not comprehensive. I searched eight journals for a limited set of search terms because practicality dictated that I could not assess all papers ever published. I attempted to minimize bias as far as possible in my selection of relatively neutral keywords and journals. Additionally, the journals I selected are preeminent in conservation, ecology, and biogeography, and I expect them to be representative of the wider research base of high-quality studies available to and useful for policy-makers. Nonetheless, further consideration of less prestigious journals, the grey literature, and non-English language publications may influence the conclusions of this study.

“Natural comparison” versus “no comparison” studies

I identified two types of studies: “natural comparison” and “no comparison”. “Natural comparison” studies compared biodiversity between human land use and a baseline reference from relatively natural fragments of the biome in which the study was conducted. For example, many studies in tropical forests compared biodiversity among agroforestry plantations, crop fields, pastures, and nearby PAs or forest remnants (e.g. Zapfack et al. 2002, Wanger et al. 2010).

On the other hand, “no comparison” studies, which came predominantly from Europe, lacked direct reference to natural ecosystems. Many assessed the effects of agricultural management (e.g. organic versus conventional (e.g. Batary et al. 2010) or an intensification gradient (e.g. Kohler et al. 2007)) on “farmland biodiversity”, the suite of species occupying traditionally managed agro-ecosystems (see Bignal and McCracken 1996), without specific reference to the biomes in which the studies were conducted. Often, farmland itself is presented as a novel ecosystem worthy of conservation for its own sake (e.g. Stefanescu et al. 2005, Jay-Robert et al. 2008), best accomplished by promoting the traditional agricultural practices that created it over thousands of years (e.g. Bignal and McCracken 1996, Pykala 2000). For example, semi-natural grasslands created by traditional agricultural practices in Europe’s forest biomes are particularly important in conservation schemes (see Austrheim et al. 1999, Walker et al. 2004), and many papers compared biodiversity among varying management options for maintaining them (e.g. Poyry et al. 2005, Saarinen and Jantunen 2005).

Although such studies provide crucial support for conservation in Europe, their applicability elsewhere and relevance to the biome in which they were conducted cannot be assumed. Thus, I distinguished these studies in my analyses of research output bias and associated factors. Nonetheless, the recognized value of farmland biodiversity in landscapes long dominated by humans (see Bignal and McCracken 1996, Pykala 2000) testifies to the importance of the early consideration of biogeography of human-modified landscapes in land-use planning for regions that retain large tracts of relatively undisturbed land (*e.g.* wilderness areas (Mittermeier 2003)). A comparative approach is important to inform conservation strategies in human-modified landscapes because it allows for consideration of community composition and functional trait richness over space and time (e.g. Mayfield et al. 2006, Flynn et al. 2009), investigation of processes that link occurrence to persistence (e.g. Trimble and van Aarde 2011), and, to avoid biotic homogenization, distinction between land uses amenable to invasive or cosmopolitan species versus more localized species (see Filippi-Codaccioni et al. 2010).

Patterns of geographical bias in research output

I expected per-region area to determine the distribution of research output if research interest were distributed randomly geographically. However, this was not the case for biomes or geopolitical regions. For biomes, I investigated ecosystem type (forest or other), per-biome species richness, the proportion of transformed land, and CRI in relation to research distribution.

Area-corrected research output was clearly higher in forest than other biomes, a pattern also reported by Fazey et al. (2005a) in the conservation literature. Felton et al. (2009) subsequently found twice the degree of bias towards forests (38% of studies versus 20.5%) in the climate-change ecology literature. I found more than double that again (87% of studies) for the literature on biogeography of human-modified landscapes. The area-corrected number of studies per biome was positively correlated with the z-value from the power model of the species–area relationship for vascular plants (Kier et al. 2005) when “no comparison” studies were excluded. However, z-values were also significantly higher in forest biomes than other types. On the other hand, the per-biome number of mammal, bird, reptile, and amphibian species was not correlated with the number of studies per biome and did not differ significantly between forest and other types. Additionally, the overall bias towards forests could not be explained by an estimated increased importance of study there because forests did not tend to have a higher CRI or proportion of transformed land than did other biomes. Thus, while the high plant richness of forests may play some role in research bias, it seems a penchant for forests, rather than species richness or threat status per se, drives bias. Felton et al. (2009) suggested that the bias towards forests in the climate-change ecology literature was a result of the concomitant bias towards North American and European study sites. However, my results indicate that the forest bias is prominent in both temperate and tropical regions.

While research output per biome was correlated, based on rank, with CRI when “no comparison” studies were excluded and with proportion of transformed land, there did seem to be under-studied biomes. The temperate grasslands, savannas, and shrublands biome was the most glaring example, and tropical and subtropical dry broadleaf forests warranted more attention. The Mediterranean forests, woodlands, and scrub biome had a relatively high number of studies after correcting for area, but its CRI and the proportion of land converted were very high, warranting more research. Among the biomes on the lower end of the CRI scale, there was a relative excess of studies from the temperate conifer forests and the boreal forests, which both have low proportions of converted land. Contrastingly, tropical and subtropical grasslands, savannas, and shrublands; flooded grasslands and savannas; and deserts and xeric shrublands were under-studied relative to their CRI.

Geopolitical bias was towards Europe and the Americas with far less focus on Africa and Asia, a pattern previously demonstrated for other sub-disciplines of conservation and ecology (Pyšek et al. 2008, Felton et al. 2009, Conrad et al. 2011). Disconcertingly, area-corrected research output per geopolitical region was not correlated with CRI. Central Asia, Eastern Asia, Southern Asia, Northern Africa, and West Africa had a particularly low research output considering their high CRI. Additionally, while research output per region was weakly correlated with human population density, several regions with high population densities had low research output including Southern, Eastern, and South-eastern Asia and the Caribbean.

CRI, proportion of land converted, and population density are indices that I expect to highlight regions where conservation beyond PAs will be especially important due to extensive land conversion, little protection, and high threat. The general disparities in patterns of research output relative to these estimates of research importance could act as a guide to where additional research investment in the biogeography of human-modified landscapes may be most beneficial. There are, however, caveats to consider. Estimates of land conversion do not account for the likelihood of future conversion or intensification, and they likely underestimated land uses that did not totally transform the land, yet might result in substantial degradation, e.g. grazed rangelands, hunting grounds, and selectively logged forests (Hoekstra et al. 2005, World Bank 2009).

Additionally, the focus of this paper was terrestrial, but marine and aquatic ecosystems also warrant consideration. While 7% of studies from my search assessed biodiversity in human-modified ponds, streams, and wetlands, it was not feasible to include a more targeted search in this assessment. However, I predict that similar knowledge gaps exist regarding biogeography of human-modified aquatic biomes, an issue for future study.

Patterns of taxonomic bias

Unsurprisingly, research output was distributed unequally among seven taxonomic groups and was not correlated with per-group richness. However, the disparities did not mirror those found in other studies. I found that plants, invertebrates, and birds received the most attention, while mammals, herpetofauna, fish, and fungi were studied much less often. Contrastingly, Clark and May (2002) demonstrated that in the general conservation literature, vertebrate species command the attention of 69% of papers, while invertebrates (11%) and plants (20%) get less attention even though vertebrates comprise a small fraction of known species (3%) compared to invertebrates (79%) and plants (18%).

Also in contrast to my findings, other studies have demonstrated a strong bias towards mammals compared to other vertebrates (Bonnet et al. 2002, Clark and May 2002, Trimble and van Aarde 2010). In a survey of papers published in nine leading ecological journals, Bonnet et al. (2002) found that birds and mammals are over represented compared to their species diversity (with 44% and 27% of papers respectively yet only 20% and 9% of vertebrate species), while fish (14% of papers, 48% of species), reptiles (7% of papers, 14% of species), and amphibians (7% of papers, 9% of species) are underrepresented.

Therefore, within the field of biogeography of human-modified landscapes, research output among taxonomic groups may more closely mirror species richness among groups than does the general ecological or conservation literature. However, this reduced bias compared to other fields may be better explained by methodological constraints rather than a sense of fairness among researchers (Pawar 2003). Invertebrates, plants, and birds may be easier to survey than mammals, herpetofauna, and fish. The former groups may also be more likely than the latter to persist in and, thus, be available for study in human-modified landscapes.

Yet, species richness per taxonomic group may not be the best resource allocation metric for research. Although one aim of promoting biodiversity persistence in human-modified landscapes is to complement PAs in conserving species, the other is to maintain ecosystem services (Chazdon et al. 2009). That "no comparison" studies were more biased towards plants and invertebrates than "natural comparison" studies were is perhaps a reflection that these groups are most closely linked with ecosystem services, such as pollination and pest control, upon which agriculture relies (e.g. Albrecht et al. 2007, Bell et al. 2008).

Origins of bias and new directions for research

Although biome type, geopolitical region, and species group were related to bias, definitively determining the root cause of the biases in research output from the eight journals assessed here was beyond the scope of this paper. Research history and interests of individuals and organizations, priorities of funding agencies and governments, and the stance of journal editorial boards are all likely to play a role in influencing the type of research conducted and published (see Fazey et al. 2005b). So too are practical constraints such as the varying difficulty of conducting research in different geographical regions, varying support and capacity for science in different countries, and language barriers to publication (see Fazey et al. 2005b, Griffiths and Dos Santos 2012), in conjunction with regional disparities in economic incentives and resources (see Pyšek et al. 2008), to name just a few.

This systematic review has highlighted gaps in the evidence base of biogeography of human-modified landscapes that scientists, publishers, funding agencies, and governments may wish to consider when planning future research and making decisions that affect research output. While research output among taxonomic groups was not free from bias, I conclude that the geo-ecological and geopolitical biases are more immediate hurdles for science-based conservation action (see also Pyšek et al. 2008). Some biomes have attracted a good deal of research interest (particularly temperate broadleaf and mixed forests and the tropical and subtropical moist broadleaf forests), while other biomes were critically under-investigated. Similarly, research output was biased towards geopolitical regions in Europe and the Americas, yet Asian and African regions were generally severely underrepresented.

As conservation efforts beyond PAs become increasingly important globally, these deficiencies could have profound consequences. Conservation success on human-modified land depends on a sound and comprehensive evidence base and interdisciplinary collaboration to meet humanity's demands for resources while allowing the persistence of biodiversity. The evidence base to support sensible land-use policies needs to have been generated in an appropriate geo-ecological and geopolitical context and be extensive enough to allow systematic review or meta-analytical assessment to draw robust conclusions regarding management actions (Pullin and Knight 2009, Segan et al. 2011, Guldemond et al. 2012).

I hope this paper will be the first step towards rectifying the gaps in the evidence base that I have identified. Ideally, awareness of the current biases will lead researchers, funding agencies, editors, and publishers to choose, of their own volition, to prioritize biogeography of human-modified landscapes in under-studied regions and biomes, while continuing to develop and refine research and implementation strategies for the regions that have already attracted a good deal of research. Obviously, international funding agencies could do a great deal to support research in under-studied regions. Similarly, government policies and funding opportunities that encourage international scientific collaboration could help spread resources to under-studied regions, promote valuable knowledge exchange, and build local capacity (Fazey et al. 2005b). However, given that similar research biases have emerged repeatedly in the conservation and ecology literature (e.g. Fazey et al. 2005b, Lawler et al. 2006, Pyšek et al. 2008, Felton et al. 2009, Conrad et al. 2011), and little progress has been made (Griffiths and Dos Santos 2012), future work should specifically assess how to encourage research on topics in need of more attention.

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Figures

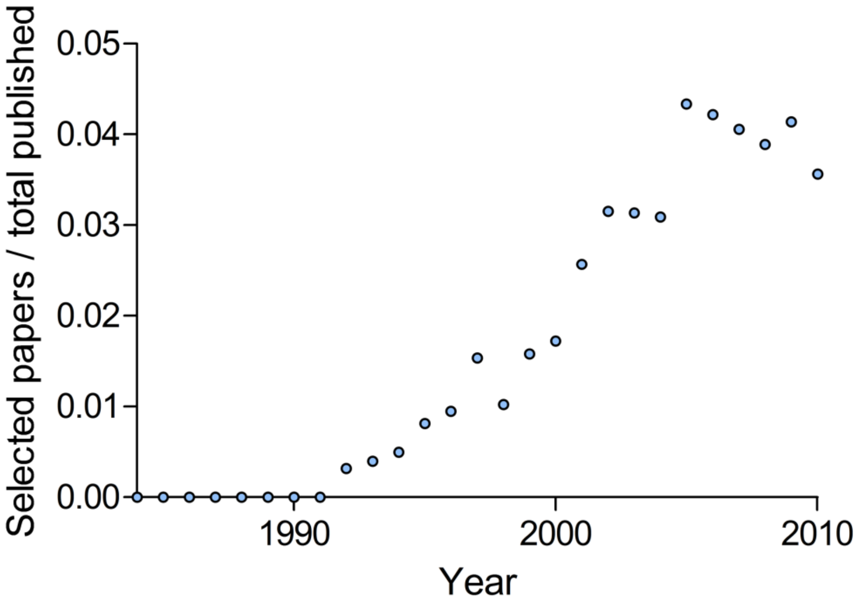

Fig. 5.1. Increase in studies of biogeography of human-modified landscapes over time. For the eight journals I considered, the proportion of the total studies published comprised by studies of the biogeography of human-modified landscapes identified in my review increased significantly over time.

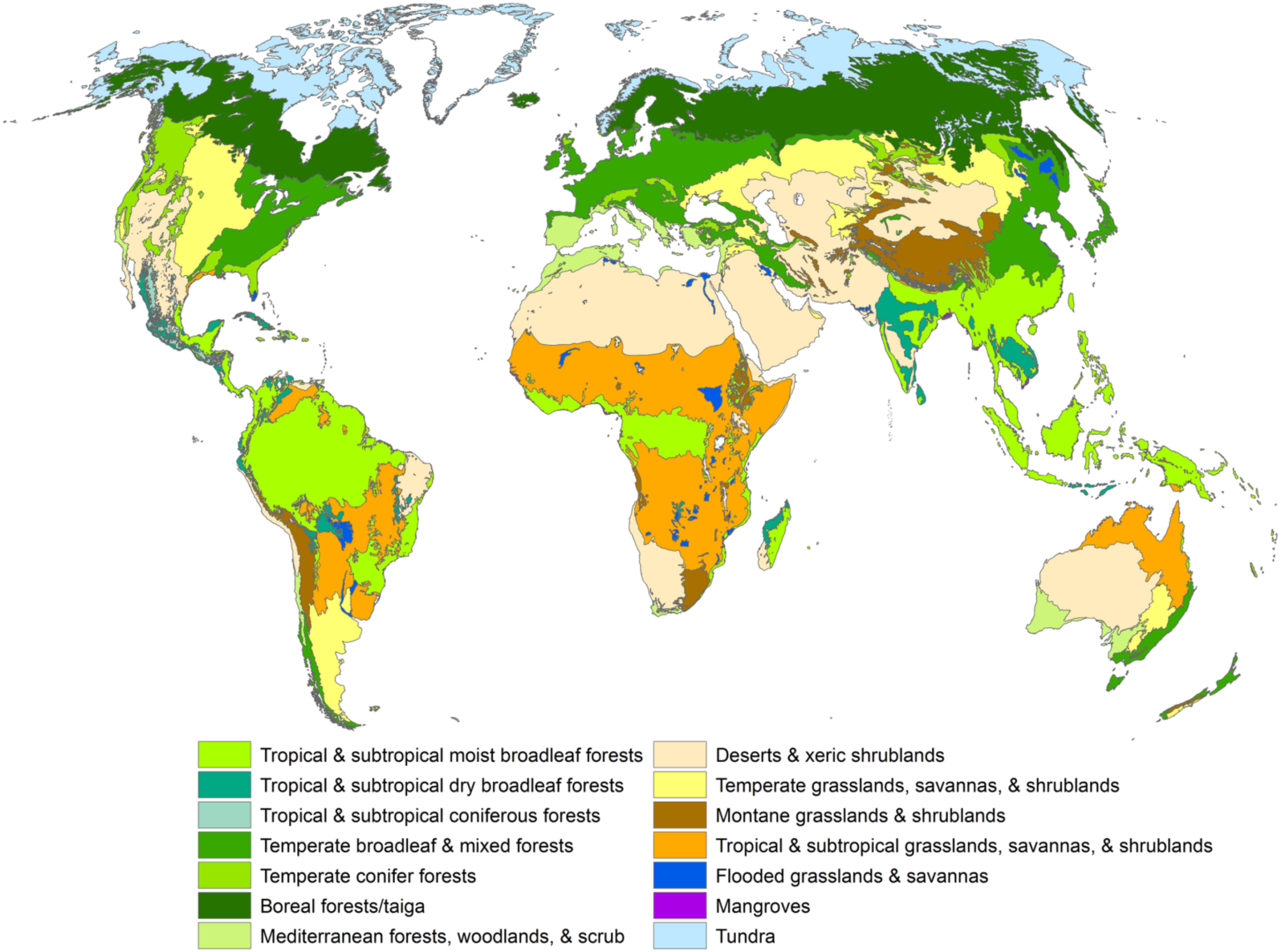

Fig. 5.2. World map of coverage of 14 terrestrial biomes. The 14 terrestrial biomes adapted from Olson et al. (2001).

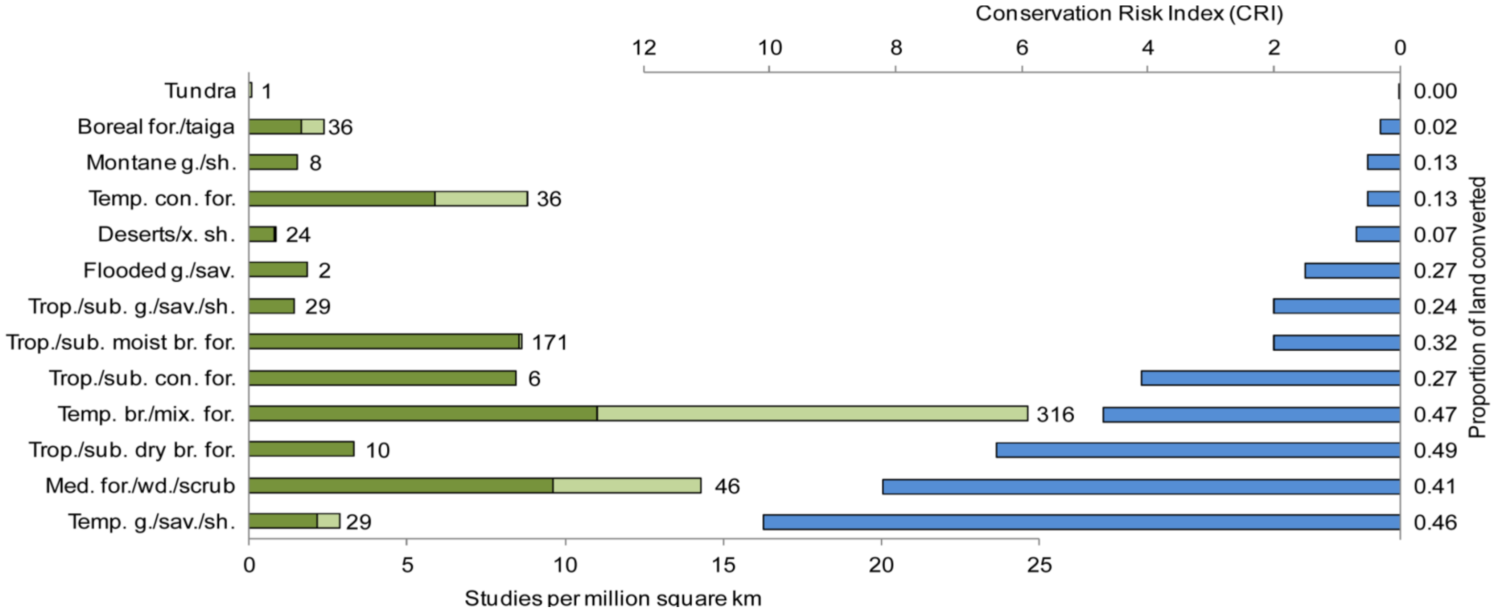

Fig. 5.3. Distribution of research output, CRI, and proportion of land transformed among biomes. Discrepancy between the number of biogeography of human-modified landscape studies per million km^2 (dark green = "natural comparison" studies; light green = "no comparison" studies; total number of studies listed to the right of bars) and Conservation Risk Index (CRI, blue bars) per terrestrial biome. Per-biome proportion of land that is transformed is listed on the right-hand axis. Biome abbreviations: Boreal for./taiga = Boreal forests/taiga; Montane g./sh. = Montane grasslands and shrublands; Temp. Con. For. = Temperate conifer forests; Deserts/x. sh. = Deserts and xeric Shrublands; Flooded g./sav. = Flooded grasslands and savannas; Trop./sub. g./sav./sh. = Tropical and subtropical Grasslands, savannas, and shrublands; Trop./sub. moist br. for. = Tropical and subtropical moist broadleaf forests; Trop./sub. con. for. = Tropical and subtropical coniferous forests; Temp. br./mix. for. = Temperate broadleaf and mixed forests; Trop./sub. dry br. for. = Tropical and subtropical dry broadleaf forests; Med. for./wd./scrub = Mediterranean forests, woodlands, and scrub; Temp. g./sav./sh. = Temperate grasslands, savannas, and shrublands.

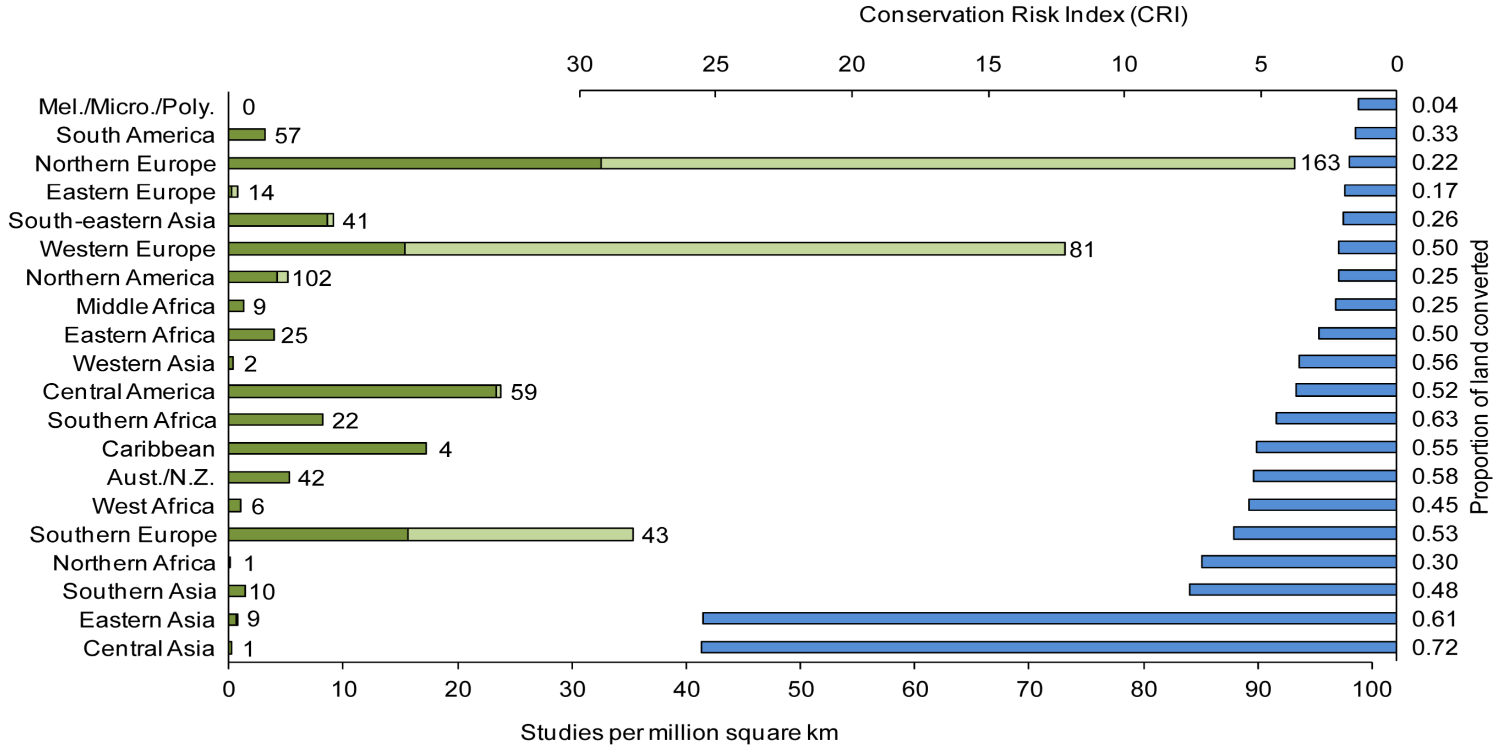

Fig. 5.4. Distribution of research output, CRI, and proportion of land transformed among geopolitical regions. Discrepancy between number of biogeography of human-modified landscape studies per million km^2 (dark green = “natural comparison” studies; light green = “no comparison” studies; total number of studies listed to the right of bars) and Conservation Risk Index (CRI, blue bars) per geopolitical region. Per-region proportion of land that is transformed is listed on the right-hand axis. Geopolitical region abbreviations: Mel./Micro./Poly. = Melanesia, Micronesia, and Polynesia; Aust./N.Z. = Australia and New Zealand.

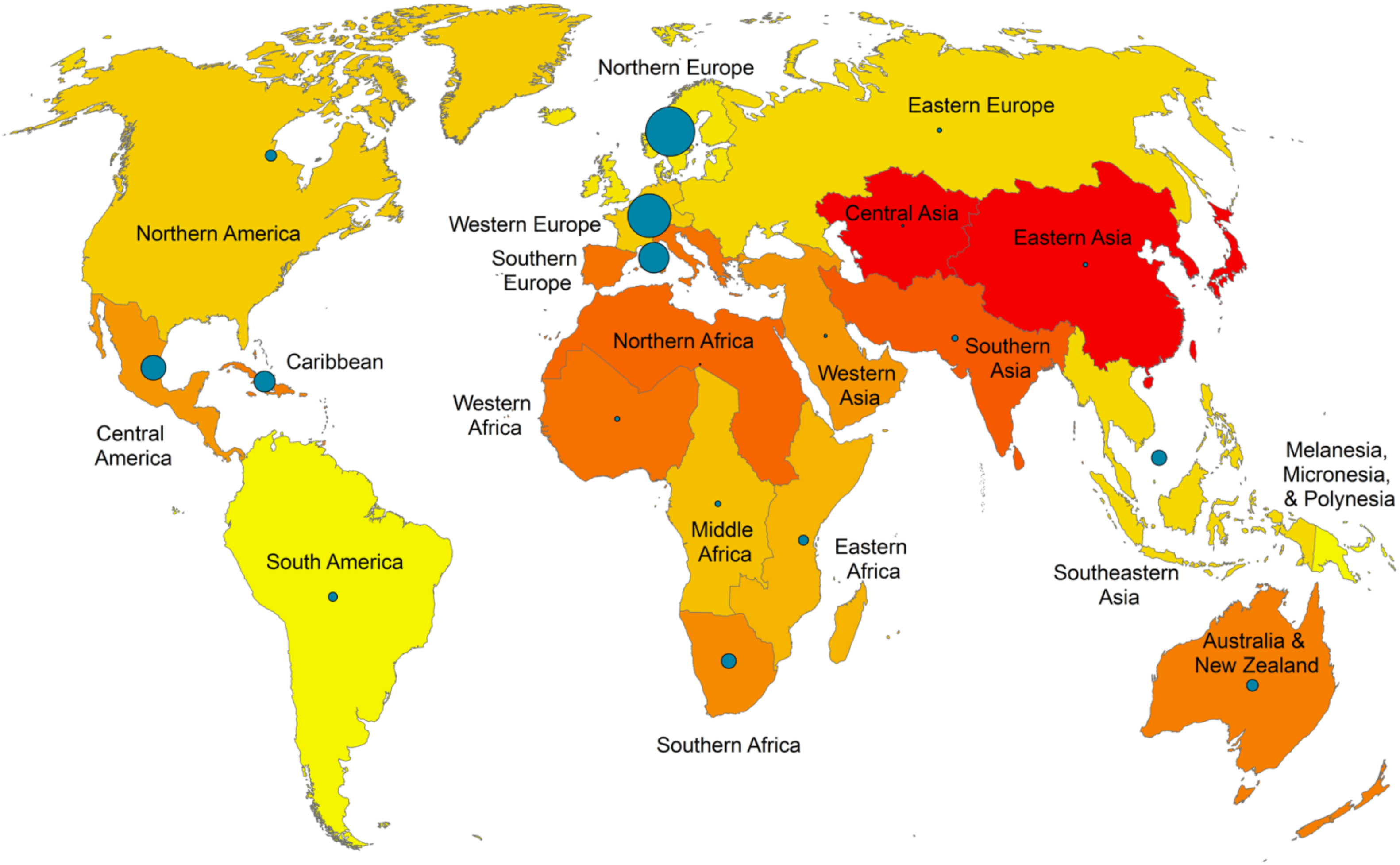

Fig. 5.5. World map of CRI and research output per geopolitical region. Geopolitical regions based on UN GeoScheme (UNSD 2011) colored according to their Conservation Risk Index (CRI) from low (yellow) to high (red); blue circles are proportional in size to the area-corrected research output per geopolitical region (refer to Fig. 5.4 for values).

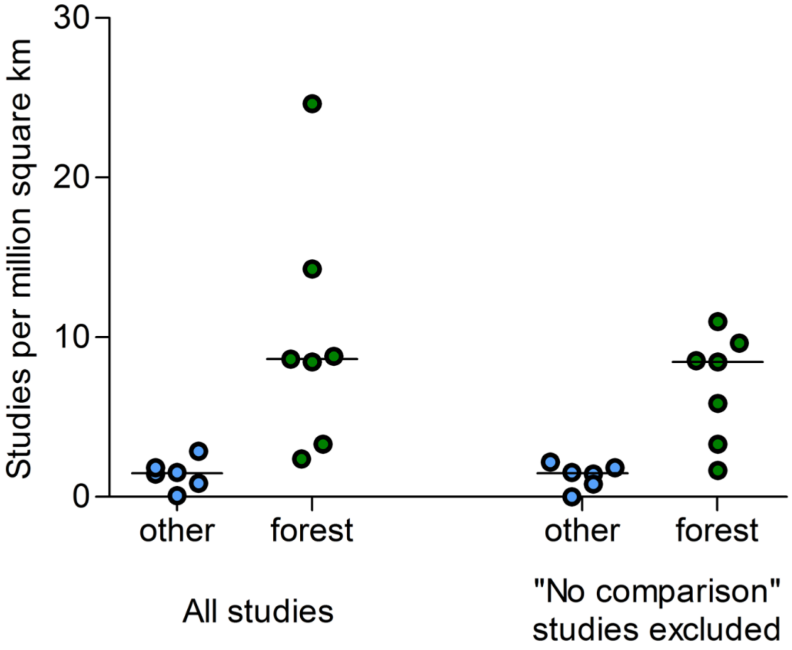

Fig. 5.6. Research output per biome type. Median number of studies per million km^2 in forest biomes was significantly higher than in other biomes both including and excluding “no comparison” studies.

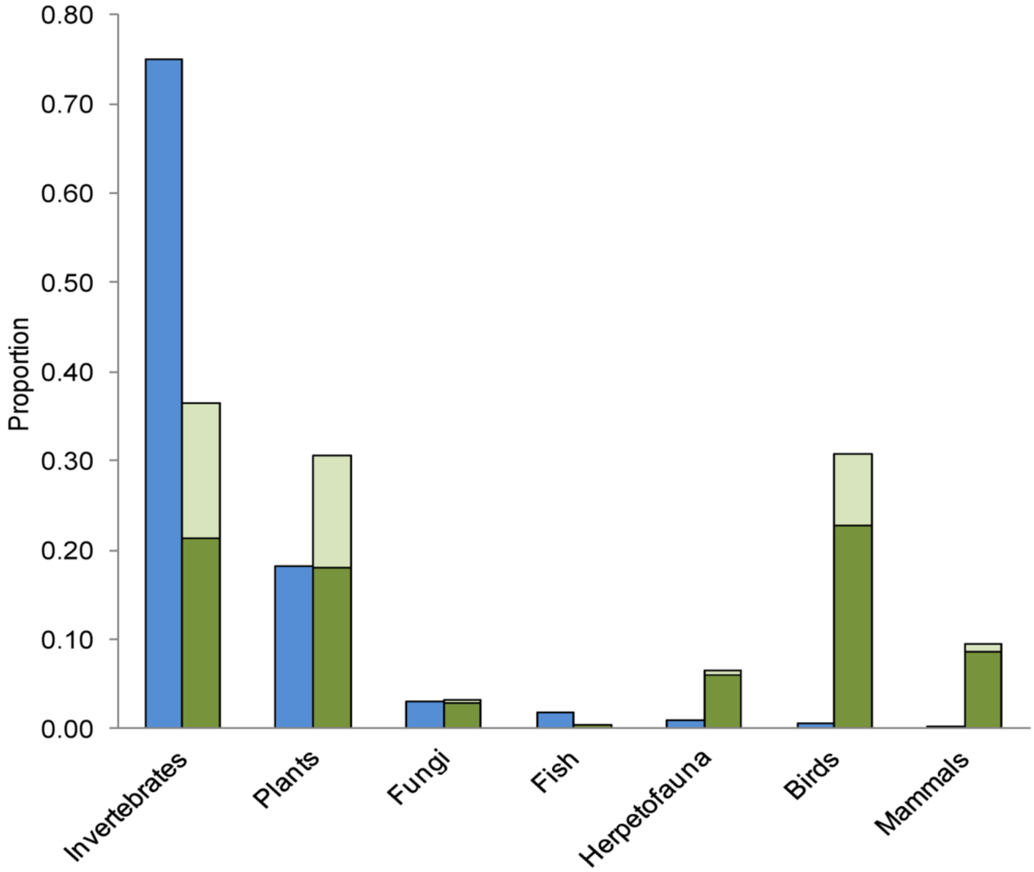

Fig. 5.7. Distribution of research output and estimated richness per taxonomic group. Discrepancy between the proportion of the 681 biogeography of human-modified landscape studies that assessed each taxonomic group (dark green = "natural comparison" studies; light green = "no comparison" studies) and the estimated proportion of richness per group (blue bars).

Tables

Table 5.1. Summary of variables considered and outcomes of statistical tests with respect to research output groupings of studies of biogeography in human-modified landscapes published in eight major journals.

Research output grouping	Variables considered	Compared to	Statistical test	Significance	
				All studies	Excluding "no comparison" studies
Year	year (time)	selected studies/total published	linear regression	***	NA
Biomes	area	studies per biome	linear regression	NS	NS
	biome type: forest or other	area-corrected studies per biome	Mann–Whitney	**	**
	mammal, bird, reptile, amphibian richness	studies per biome	Spearman	NS	NS
	z-value for vascular plants	area-corrected studies per biome	Spearman	NS	*
	proportion of land transformed	area-corrected studies per biome	Spearman	*	**
	CRI	area-corrected studies per biome	Spearman	NS	*
Geopolitical regions	area	studies per region	linear regression	NS	NS
	proportion of land transformed	area-corrected studies per region	Spearman	NS	NS
	CRI	area-corrected studies per region	Spearman	NS	NS
	human population density	area-corrected studies per region	Spearman	*	*
Taxonomic groups	described species per group	studies per group	Spearman	NS	NS

Notes: CRI stands for Conservation Risk Index, the proportion of transformed to protected land. NS is not significant, NA is not assessed, * indicated $p < 0.05$, ** $p < 0.01$, and ***$p < 0.001$.

Chapter 6. General Conclusions

In effect, the currency of biodiversity conservation is space. Increasing the total area dedicated to the protection of nature will, in theory (with provisos that additional areas are selected at random, are of a sufficient scale, and have not already lost their biodiversity), increase the proportion of the Earth's biodiversity that is conserved at the genetic, species, and ecosystem levels. Space encompasses environmental heterogeneity, provides the opportunity for speciation, and buffers biodiversity from stochastic phenomena that drive extinction; it is the underlying variable determining the steady-state diversity of Earth upon which species–area relationships rely and island biogeography theory depends (MacArthur and Wilson 1967, Rosenzweig 2001, Rosenzweig 2003). More space increases the likelihood of incorporating important variations in habitat quality that give rise to source–sink (Pulliam 1988, Liu et al. 2011), metapopulation (Hanski 1999, 2004), and patch dynamics (Pickett and White 1985), which contribute to long-term stability of populations and communities in temporally dynamic ecosystems (see Pickett and Thompson 1978, Falcy and Danielson 2011). Given the importance of space, efforts to stem biodiversity loss have focused on meeting benchmarks for protected area coverage, e.g. 10% of each terrestrial ecological region (Brooks et al. 2004, Chape et al. 2005).

Progress towards meeting the Convention on Biological Diversity's (CBD's) 2010 target to reduce the rate of global biodiversity loss was measured largely in terms of protected area coverage (Secretariat of the CBD 2010). With protected area coverage now approaching 13% of Earth's land surface (IUCN and UNEP-WCMC 2011), perhaps failure to hit the 2010 target, evidenced by the growing number of species facing extinction

(Butchart et al. 2010, Secretariat of the CBD 2010, IUCN 2012), can be attributed to a lack of focus on conservation beyond protected areas. The fate of wild species in the 87% of land area that is not formally protected will likely play a substantial role in determining the long-term maintenance of ecosystem services valuable to humanity and the persistence of biodiversity, even within protected areas (Daily 1999, Daily et al. 2001). Therefore, the CBD's proposed 2020 targets are a step in the right direction—considering biodiversity in "areas under agriculture, aquaculture, and forestry" and focusing on "the science base and technologies relating to biodiversity" (Perrings et al. 2010).

Conservationists now have the imperative to increase the focus of science and implementation towards biodiversity in landscapes where humans live, work, and extract resources (Foley 2005). That habitat degradation leads to extinctions and that protected areas prevent them epitomize a dogmatic dichotomy in conservation biology. However, real-world responses of species, and thus communities, to land-use change and protection are idiosyncratic with some species tolerating or even thriving in human-modified habitats (e.g. Sekercioglu 2012) and others succumbing to extinction despite protection (see Hansen and DeFries 2007). Therefore, use of the classic island biogeography theory to describe the effects of habitat fragmentation has had to evolve in recognition that the matrices surrounding fragments can play a substantial role in determining conservation outcomes (e.g. Pereira and Daily 2006). Ecological frameworks of source–sink, metapopulation, and patch dynamics that have traditionally been applied in relatively pristine natural habitats are equally, if not more, relevant to landscapes that have been substantially modified by human activities, but in which we still seek to maintain biodiversity. The management choices humans make in these landscapes will have profound consequences for biodiversity, and this thesis broadly focused on contributing to our understanding of the consequences of human land use for different components of biodiversity. The general focus in this thesis was at the species level of biodiversity; however, other levels should not be neglected in future developments of frameworks for considering biodiversity in human-modified landscapes.

In Chapter 2, I provided a qualitative review of the literature on biodiversity in sub-Saharan Africa's human-modified landscapes in relation to four broad ecosystem categorizations (rangelands, tropical forest, the Cape Floristic Region, and the urban and rural built environment) within which I expect similar patterns of biodiversity persistence in relation to specific human land uses and land management actions. The outcome of this chapter is that, while much more work is needed, I illustrated that available research on biodiversity in human-modified landscapes within all four ecosystem types provides general conclusions that could support policy-making. This is especially important in light of rapid development expected in many parts of Africa because a proactive approach to land-use planning for biodiversity persistence is likely to be more effective and efficient than a reactive approach requiring habitat restoration (Gardner et al. 2010). However, I also identified several constraints to conservation success in human-modified landscapes that require further scientific investment, including deficiencies in the available research, uncertainties regarding implementation strategies, and difficulties of coexisting with some species in some circumstances. However, information that is currently available can and should be used to support efforts at individual, community, provincial, national, and international levels to support biodiversity conservation in human-modified landscapes.

Chapters 3 and 4 delved into species-specific idiosyncrasies in responses to human land use in the forest belt skirting the southeastern coast of Africa, part of a biodiversity hotspot hosting many endemic species in a highly transformed landscape (see van Wyk 1996, Küper et al. 2004, Perera et al. 2011, van Aarde et al. 2013). As reported in Chapter 3, I sampled a rich and highly endemic herpetofaunal assemblage over a vegetation-type gradient representative of prevalent regional land uses (old-growth forest, degraded forest, acacia woodland (i.e. new-growth forest), eucalyptus plantation, and sugar cane cultivation). This topic, region, and taxon are drastically understudied even though both frogs and reptiles face global extinction crises. Besides comparing traditional community metrics along the gradient, I categorized species into trait-derived functional groups, and assessed abundance and richness of groups along the gradient to elucidate ecological underpinnings of species-specific responses. I further assessed the capacity of environmental variables to predict richness and abundance overall and for functional groups. The outcome was that overall, old-growth forest harbored the highest richness and abundance, and frogs and reptiles responded similarly to the gradient. Richness was low in cultivation and, somewhat surprisingly given other research (Gardner et al. 2007), in degraded forest but substantial in acacia woodland and exotic plantations. Composition differed between natural vegetation types (forest, degraded forest) and anthropogenic types (plantation, cultivation), while acacia woodland grouped with the latter for frogs and the former for reptiles. Functional group richness eroded along the gradient, a pattern driven by sensitivity of fossorial frogs and reptiles and vegetation-dwelling frogs to habitat change, which was a novel finding of the study. Environmental variables were good predictors of frog abundance, particularly abundance of functional groups, but less so for reptiles. The implications of this research for land-use planning in the region are that conserving forest and preventing degradation is essential, restoration and plantations have some conservation value, and cultivation is least amenable to forest herpetofauna. Furthermore, this study demonstrates the utility of function-related assessments, beyond traditional metrics alone, for understanding community responses to transformation. In particular, fossorial frogs and reptiles and vegetation-dwelling frogs should be closely monitored because they are especially disturbance-sensitive and many are species of conservation concern (IUCN 2012, Botts et al. 2013).

One shortcoming of the herpetofaunal sampling is that recording a species' presence in a given vegetation type does not imply that it is able to persist solely within that vegetation type. The value of land uses to particular species found within them could range from high, i.e. source habitat, which would be a boon to conservation; to intermediate, a sink habitat that relies on immigrants from the source; to negative, an ecological trap, which would result in population extinction (Battin 2004, Hansen 2011). Unfortunately, a snapshot assessment of species occurrence does not allow for differentiation along this gradient of habitat quality. Instead, a more in depth assessment of the determinants of population size, e.g. survival, fecundity, and immigration, and emigration, is required.

As discussed in Chapter 4, the avifaunal community in old-growth coastal dune forest remnants and in vegetation types regenerating after forest clearance for mining presents such an example where occurrence might not result in persistence. Based on occurrence data, previous research demonstrates that forest bird diversity increases with age along a successional sere of regenerating forest fragments and that the community becomes more similar to that of old-growth forest with time (van Aarde et al. 1996a, van Aarde et al. 1996b, Kritzinger and van Aarde 1998, Wassenaar et al. 2005). However, I assessed population trends for 37 bird species commonly found in old-growth forest and trends in overall bird density in different vegetation types. The outcome was that I found alarming population declines over a 13-year period; 76% of species I assessed declined, 57% significantly so at an average rate of 13.9% per year. Overall bird density also declined, both in old-growth forest and in woody regenerating vegetation types, at an average rate of 12.2% per year. These substantial declines call into question the likelihood of persistence of these species in the region, and loss of birds may threaten ecological processes, e.g. seed dispersal and pollination, important for functional connectivity between remnant forest fragments and for the natural successional pathways on which the forest restoration program depends (Grainger and van Aarde 2012).

As with the herpetofauna, I assessed species' traits as potential correlates of species' responses to their environment, in this case population trends, to try to elucidate ecological drivers of population decline. Interestingly, among the many traits I assessed, including proxies for life history characteristics, only range extent and habitat affinity were related to trend. Species with larger range extents (generally those with a greater affinity for regenerating vegetation types) tended to experience more severe population declines. Therefore, population declines in the study area could be reflecting changing environmental conditions on a regional scale, e.g. habitat loss or changing climatic conditions. Still the possibility that human-modified habitats may be acting as ecological traps should be investigated, especially given that population declines were similar both within old-growth remnants and in regenerating vegetation types (Battin 2004). It is also possible that population declines represent the realization of extinction debts following a reduction in the area of old-growth forest (Olivier et al. 2013); however, that species found predominantly in regenerating vegetation types tended to have lower trend estimates (more negative) than species found predominantly in old-growth forest suggests otherwise. Then again, more negative trends of species from regenerating vegetation types might reflect destruction of grassland, thicket, and woodland on a regional scale.

Unfortunately, the ultimate causes of the declines remain unknown, so more work is required to assess survival, fecundity, and dispersal rates for each species in each habitat type. This avifaunal case study serves as a reminder of the shortcomings of occurrence data and suggests the utility of monitoring programs for other species groups, e.g. herpetofauna, whose persistence locally may be threatened by regional forces. The case studies presented here contribute to the wider body of literature on biodiversity in human-modified landscapes that can provide evidence to support conservation-conscious decision-making by land-use planners and policy makers. Basing management decisions on scientific evidence of efficacy can prevent wasted resources and ensure the best possible outcomes (Sutherland 2004).

However, with limited resources for research, scientists should target the most relevant projects, and it is crucial to monitor the distribution of published research in comparison to emerging research needs to identify gaps (Lawler et al. 2006). Therefore, in Chapter 5, I presented an extensive systematic review of the global literature on biodiversity in human-modified landscapes. By comparing the research output per geopolitical region, biome, and taxonomic group to variables that could be considered indicative of research needs, e.g. species richness, area, human population density, and proportion of transformed and protected land, I discovered biases in the evidence base out of sync with conservation needs and identified topics deserving of future research. In particular, I found that 87% of research comes from forest biomes and 75% of studies were conducted in the Americas and Europe. Therefore, a greater research focus in non-forest biomes and in Africa and Asia is urgently required. This finding echoes calls for a greater focus on biodiversity in African human-modified landscapes, particularly within rangelands and the Cape Floristic Region, as discussed in Chapter 2.

In this thesis, I have provided case studies on biodiversity patterns and processes that can inform management within the biogeographically important coastal forest belt of southern Africa. More broadly, I have reviewed the current state of research on biodiversity in human-modified landscapes in Africa with recommendations for future work and discussion of the challenges of implementation. From a global perspective, I have systematically reviewed the literature to identify geographical and taxonomic biases in need of rectification, and ideally, this work will lead researchers, funding agencies, and publishers to prioritize under-studied topics. Conservation success in human-dominated land depends on a sound evidence base and collaboration between ecologists, agronomists, economists, social and political scientists, and policy-makers to meet humanity’s demands for resources while allowing as much biodiversity as possible to persist where we live, work, and extract resources. The future of most species depends on it (Rosenzweig 2003).

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Appendix A. Fences are More Than an Issue of Aesthetics

Publication Details

Trimble, M.J. & van Aarde, R.J. 2010. Fences are more than an issue of aesthetics. *BioScience*. 60: 486. doi: 10.1525/bio.2010.60.7.20

Letter

Licht and colleagues (*BioScience* 60: 147–153) identify South Africa's pioneering efforts to reintroduce top predators to small, fenced protected areas as a conservation model America might be wise to follow. However, South African success at large predator reintroduction is largely the result of ubiquitous fencing that generally prevents predator conflict with people and livestock (see Gusset et al. 2008).

The consequences of applying a similar paradigm in America are not only aesthetic, as implied by Licht, but could also compromise the long-term success of biodiversity conservation. A recent review of fencing for conservation concluded that fencing is an acknowledgment that we are failing to coexist with and successfully conserve biodiversity, and that the costs—economic and ecological—generally far exceed the benefits (Hayward and Kerley 2009). Ecological costs include fence-line mortalities, influences on natural behavior, impingement on natural mechanisms of population control, restriction of animal movements in response to environmental changes (e.g. fires, climate change, drought), limitation of migration and genetic flow, and impediment to recolonization and source–sink population dynamics.

Licht and colleagues stated that there are relatively few concerns in South Africa about the fence around Kruger National Park. This is incorrect—there are serious ecological concerns including extinction debt and species persistence of many iconic herbivores, even though the park covers nearly 20,000 square kilometers (Nicholls et al. 1996, Ogutu and Owen-Smith 2003). Fences around smaller protected areas can be even more problematic.

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Appendix B. A Note on Polyvinyl Chloride (PVC) Pipe Traps for Sampling Vegetation-Dwelling Frogs in South Africa

Publication Details

Trimble, M.J. & van Aarde, R.J. 2013. A note on polyvinyl chloride (PVC) pipe traps for sampling vegetation-dwelling frogs in South Africa. *African Journal of Ecology*, DOI: 10.1111/aje.12120.

Introduction

Vegetation-dwelling frogs are challenging to sample. They can climb out of traditional traps, and many are furtive (Myers et al. 2007, Pittman et al. 2008). PVC pipe traps, which mimic natural features frogs use for shelter, may provide a useful technique (e.g. Boughton et al. 2000). Pipe trapping has been used to sample treefrogs of the family Hylidae in the United States (e.g. Boughton et al. 2000, Liner et al. 2008, Farmer et al. 2009), but it is increasingly used elsewhere (e.g. Laurencio and Malone 2009, Ferreira et al. 2012), even for non-Hylids (Coqui Frog Working Group 2006).

African vegetation-dwelling frog genera, e.g. *Leptopelis, Afrixalus*, and *Hyperolius* (see Channing 2001, du Preez and Carruthers 2009), may be attracted to artificial refugia of PVC pipe traps. If so, pipe trapping would augment sampling techniques for African anurans, which are little studied (Trimble and van Aarde 2010, Trimble and van Aarde

2012) despite conservation needs (Measey 2011), and could facilitate sampling outside the breeding season, reduce observer and detection bias (see Bailey et al. 2004, Willson and Gibbons 2010), and allow fundamental and applied ecological studies, e.g. habitat selection (e.g. Johnson et al. 2007, Pittman et al. 2008), migration/dispersal (e.g. Johnson 2005), and management effects (e.g. Muenz et al. 2006, Rice et al. 2011). In this preliminary assessment, I provide the first evidence that it is possible to capture African frogs in PVC pipe traps in the field. However, capture success was low, so I encourage more research on alternate trap designs and in other habitats.

Methods

My study was conducted in the South African coastal forest within 2.3 km of the east coast, along a 25 km section between the Umlalazi River and Richards Bay Harbour. The area harbours a high species richness and concentration of threatened frogs (Maritz 2007, Measey 2011) (Table B.1).

I installed 30 pipe trap arrays in terrestrial habitats ≥ 300 m from water bodies and ≥ 500 m from each other, divided evenly among five vegetation types: coastal forest, degraded forest, acacia woodland, eucalyptus woodlot, and sugar cane cultivation. I placed a further six arrays in coastal forest ≤ 30 m from a water body and ≥ 50 m apart. Each array consisted of four, 60-cm-long, white PVC pipes. I inserted two pipes (one of 16 mm and 44 mm internal diameter) 10cm into the ground near the base of a tree. I attached another of each diameter pipe together and affixed them vertically from their top at a height of 2 m up the tree trunk. Caps on the bottom of these pipes allowed retention of standing water (added at installation), and a hole drilled 15 cm from the bottom prevented flooding (Boughton et al. 2000). I installed pipes on a variety of tree species (e.g. White Stinkwood *Celtis africana*, Horsewood *Clausena anisata*, Sweet Thorn *Acacia karroo,* and *Eucalyptus* sp.) with circumference at breast height of 10–200cm ($\bar{x}$ = 53.7 cm, sd = 41.2 cm). At five sugar cane cultivation arrays there were no trees, so all four pipes were inserted into the ground.

Pipe traps were installed progressively from February 17 to March 21, 2012 (summer/rainy season); I monitored arrays for 14–34 days ($\bar{x}$ = 21.7, sd = 7.3). As per agreements with landowners, arrays in cultivation and woodlots were removed after 14–15 days, while others remained for the study duration. I checked each array during daylight hours on an intermittent schedule as logistics allowed, i.e. 5–9 times per array at intervals of 1–9 days ($\bar{x}$ = 3.4, sd = 0.7). I identified and measured frogs found in traps and released them ≥ 50 m away. I also noted frogs observed incidentally (i.e. coincidentally or during casual searches) during the study period.

Results and Discussion

I checked 36 arrays 219 times over 34 days (43 times for the six arrays near water and 176 for the 30 terrestrial arrays). I caught five frogs in pipes (Table B.1), a trap success of 2.3% by array checking instances or 0.6% by pipe checking instances. One capture on the outside of a pipe was not included in calculations (Table B.1). Sparse captures prevented statistical analyses, but trap success appeared higher near water than away, 7% of array checking instances versus 1.1%. I incidentally observed eight species (Table B.1). Trapping success was lower than reported in the Americas, e.g. 79% (Bartareau 2004), 23% (Myers et al. 2007), 2.5–4.3% (Pittman et al. 2008), and 6% (Ferreira et al. 2012) (some of these studies included recaptures). Several factors might have contributed to my low trapping success.

(1) Pipes might not have provided attractive refugia. Frogs discriminate between refugia attributes (e.g. Boughton et al. 2000, Bartareau 2004, Johnson et al. 2007, Johnson et al. 2008, Hoffmann et al. 2009). Many design factors have been investigated in relation to capture success (e.g. diameter, length, and colour), and while 44 mm diameter pipes appeared more effective than 16 mm and ground and tree pipes both worked, other trap designs could be investigated (see Boughton et al. 2000, Bartareau 2004, Johnson et al. 2007, Myers et al. 2007, Johnson et al. 2008, Pittman et al. 2008, Ferreira et al. 2012).

(2) Natural refugia provided by plants may have outcompeted pipes (Hoffmann et al. 2009). *Dracaena aletriformis* and *Strelitzia nicolai* are prevalent in the undergrowth, and their leaf axils provide hiding places for frogs (du Preez and Carruthers 2009).

(3) The sampling period may have been too short for frogs to find the pipes (Myers et al. 2007), which could have compounded the effects of competition with natural refugia.

In conclusion, I caught three species in PVC pipe traps and found an additional species on the outside of a pipe, demonstrating that the technique can be used to trap African frogs of the family Hyperoliidae. However, trap success was low, and I captured species also encountered incidentally. I encourage further assessment of PVC pipe trapping for African vegetation-dwelling frogs to support amphibian ecological studies. Altering trap design, using traps in areas with less abundant natural refugia, and installing traps a few months prior to sampling should be investigated to improve success. Further experiments could elucidate which trap designs work for which species.

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Tables

Table B.1. Vegetation-dwelling frog species expected in the area, species incidentally recorded in the area during the survey (location of observation is denoted NW = near water, Tr = terrestrial, Tr/NW = terrestrial and near water), and inventory of captures in PVC pipe traps indicating array location (NW = near water, Tr = terrestrial), pipe diameter and location (G = ground, T = tree), Snout–urostyle length (SUL) of frog, and habitat type (AW = acacia woodland, DF = degraded forest, F = Forest).

Frog Atlas species [a]	**Incidentally recorded**	**Pipe trap captures**
Afrixalus delicates		
Afrixalus fornasinii	NW	NW (44 mm G pipe, SUL = 35 mm, F)
		NW (44 mm T pipe, SUL = 35 mm, F)
Afrixalus spinifrons	Tr	Tr (44 mm G pipe, SUL = 23 mm, DF)
Hyperolius argus	NW	
Hyperolius marmoratus	NW	NW (outside of T pipe, F)
Hyperolius poweri		
Hyperolius pickersgilli	NW	
Hyperolius pusillus	Tr/NW	
Hyperolius semidiscus		
Hyperolius tuberilinguis	Tr/NW	NW (44 mm T pipe, SUL = 27 mm, F)
		Tr (44 mm G pipe, SUL = 29 mm, AW)
Leptopelis mossambicus		
Leptopelis natalensis [b]	Tr/NW	

[a] The South African Frog Atlas Project recorded twelve species of *Leptopelis*, *Afrixalus*, and *Hyperolius* in the two quarter-degree squares spanned by the study area (ADU 2011). Nomenclature follows du Preez and Carruthers (2009) except *Hyperolius poweri* (see Channing et al. 2013).

[b] *L. natalensis* was not captured in pipes despite occurring in the area. Worth noting, however, is that on two occasions I released incidentally caught *L. natalensis* individuals at the base of tree in which I had hung a set of pipes, and both frogs climbed the tree, went into a pipe, and remained there for some time.