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The relative importance of natural and human-induced environmental conditions for species richness distribution patterns in South Africa

by

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The relative importance of natural and human-induced environmental conditions for species richness distribution patterns in South Africa

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Abstract

I studied the spatial distribution of South African avian species richness from the viewpoint that humans are a substantial modifying force on earth, and have also modified the historical spatial distribution of species richness. The main aim of the thesis is to investigate the way in which humans have modified avian species richness patterns in South Africa at the quarter-degree square (QDS) resolution, which is a phenomenon that has been either overlooked, or not completely clarified, in many previous studies of the same region and data at the same resolution. In particular, I investigated hypotheses that were proposed to explain the maintenance of a positive relationship between native species richness and human population density in the face of negative human impacts. Further, I investigated which of the possible anthropogenic and natural environmental factors determine spatial distribution in exotic bird species. Highlighted from these studies are that substantial positive and negative human influences on bird species richness distribution patterns are observable at the QDS resolution, that there are differences between common native birds and rare native birds with regard to their relationships with anthropogenic environmental conditions and exotic bird species, and that the particular combination of environmental covariates that is important for the spatial distributions of exotic species is taxon- and scale-dependent. Even though these results have contributed much towards our understanding on how human modifications have affected species richness patterns, this thesis leaves some unanswered questions. Finer resolution studies and temporal studies are needed to examine many of these questions. Further, an interdisciplinary approach incorporating politics and economics into ecological studies is needed to enhance our understanding of the factors that modify the distribution of humans and their associated threats and benefits to species richness.

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Disclaimer

This thesis mainly consists of two papers that have been prepared for submission to, or publication in, scientific journals. As a result overlap may occur to secure publication entities.

Declaration

I, the undersigned, hereby declare that this thesis is my own work. I have not previously submitted it to any other institution.

Signed: ______________________ Date: ______________________

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CHAPTER 1

General Introduction

The generally negative impact of human activities on biodiversity is a well-known phenomenon. Humans are a substantial modifying force on earth, responsible for habitat transformation, degradation, and destruction, overexploitation of natural resources including species, the introduction of harmful invasive alien species, and ultimately, global climate change and an abnormally rapid rate of global species extinction (see Vitousek *et al.*, 1997, for a review). Many studies have found a positive correlation between human population density in an area, and the proportion of species that are threatened with extinction (Thompson & Jones, 1999; McKinney, 2001; McKee *et al.*, 2003; Luck *et al.*, 2004). Further, human density and activity is widely associated with a reduction in the numbers of individuals of species, whether it is caused directly (e.g., hunting or persecution) or indirectly through habitat transformation or biological invasion (Fisher & Shaffer, 1996; Hobbs & Mooney, 1998; Harcourt *et al.*, 2001; Gaston *et al.*, 2003).

Irrespective of these negative anthropogenic–biodiversity interactions, an unexpected but recurrent theme emerging from recent studies is that, at least at the regional scale, a positive spatial correlation exists between numbers of species of various taxa and human population density (Balmford *et al.*, 2001; McKinney, 2001; Araújo, 2003; Chown *et al.*, 2003; Luck *et al.*, 2004; Stohlgren *et al.*, 2006). It is commonly believed that this correlation arose due to the similar response of humans and other species to spatial variation in natural (i.e., as opposed to human-induced or anthropogenic) environmental conditions such as primary productivity, energy availability, and habitat heterogeneity (Currie, 1991; Mace & Pagel, 1995; Balmford *et al.*, 2001; Moore *et al.*, 2002; Chown *et al.*, 2003; Evans & Gaston, 2005; Stohlgren *et al.*, 2006). In other words, humans and other species are generally attracted to and have colonized areas with the most favourable environmental conditions, a scenario referred to as ‘the good life’ by Stohlgren and coworkers, who investigated the distribution of species richness and density of several taxa in relation to each other and abiotic conditions (Stohlgren *et al.*, 2006).

Following from studies on the spatial covariation of human density and species richness, and the related threats posed by the former, conflicts between human development needs and areas important for the conservation of biodiversity have long been, and still is, an important topic faced by decision makers (e.g., Terborgh, 1971; Bell, 1987; Balmford *et al.*, 2001; Chown *et al.*, 2003; Luck *et al.*, 2004; Davies *et al.*, 2006; Luck, 2007). Indeed, while human activities are linked to ecosystem and biodiversity degradation, human well-being is dependent on the services provided by healthy ecosystems of which biological diversity is an essential part as emphasized by the Millennium Ecosystem Assessment (Scholes *et al*., 2005). For example, invasive plant species in South Africa is a potential threat to not only natural biodiversity and ecosystems, but also ecosystem services supporting fresh water sources and livestock production, that are directly related to human well-being (van Wilgen *et al*., 2007).

Irrespective of progress made in the field of conservation planning, many questions related to ecological patterns and processes that could assist with systematic conservation planning strategies remain unanswered. For example, although several hypotheses have been suggested (see, e.g., Chown *et al*., 2003; Gaston, 2005), questions remain as to how a positive relationship between species richness and human population density is maintained in the face of current levels of human threat, and how this pattern could be incorporated into conservation networks that are sensitive to human development needs.

Spatial distribution of exotic species richness

One such hypothesis states that human activity increase species richness in densely populated areas by introducing exotic species and facilitating their establishment and spread (Hodkinson & Thompson, 1997; McKinney, 2001; McKinney, 2002; Pyšek *et al*., 2002; Richardson *et al*., 2005; Williams *et al*., 2005; Stohlgren *et al*., 2006). The argument goes that, even though invasions may cause local extinctions (McKinney, 2002; Clavero & García-Berthou, 2005), the number of additions of exotic species to a local species assemblage may still be greater than extinctions from that assemblage (Hobbs & Mooney, 1998; Sax *et al*., 2002; Sax & Gaines, 2003; Stohlgren *et al*., 2006). In addition, seeing that humans have preferentially colonized areas rich in native species, a positive correlation between exotic and native species richness is often found (McKinney, 2001; Pyšek *et al*., 2002; Richardson *et al*., 2005; Williams *et al*., 2005).

It can be seen, therefore, that exotic species pose a substantial threat to native species richness. Many studies investigate the anthropogenic and natural environmental factors responsible for facilitating the colonization and spread of exotic species, to predict the level and spatial variation in threat that they pose to native species (Hodkinson & Thompson, 1997; Stohlgren *et al*., 1999; McKinney, 2001; McKinney, 2002; Pyšek *et al*., 2002; Evans *et al*., 2005; Richardson *et al*., 2005; Williams *et al*., 2005). Most of the studies on exotic species richness mentioned up to this point focus on exotic plant species, probably because of data availability and the relatively greater threat from exotic plants compared with exotic animals (see, e.g., Le Maitre *et al*., 2000; Richardson *et al*., 2005). Results from studies on plants are often extrapolated to exotic animal species that are less well studied (e.g., Evans *et al*., 2005).

Richardson *et al*. (2005) have investigated the environmental correlates of exotic plant species richness in South Africa. The Southern African Bird Atlas Project (SABAP, Harrison *et al.,* 1997), which includes the distribution of 11 alien bird species across South Africa, provides an opportunity for such a study on exotic bird species richness. However, the suggestion that exotic bird species might be responsible for the maintenance of the positive bird species richness–human density relationship is unlikely for the current situation in South Africa because of the small number of exotic bird species recorded in South Africa.

Spatial distribution of native species richness

It has been found that a positive relationship is also maintained between human population density and native bird species in South Africa (Chown *et al*., 2003), and between human density and a variety of native species in other parts of the world (Balmford *et al*., 2001; Araújo, 2003; Luck *et al*., 2004). Some of the hypotheses proposed to explain this relationship highlight the role of conservation measures and remaining natural habitat patches (Gaston, 2005; Pautasso, 2007), and beneficial human activities that cause, for example, increased habitat heterogeneity (Andren, 1994) and increased primary productivity (Shochat *et al.,* 2006), in maintaining or promoting observed levels of species richness. Others argue that the influence of human activities may be more subtle and not necessarily manifested as a change in the form of the relationship between species richness and human density (e.g., Gaston, 2005). The positive correlation could even be the result of a sampling artefact caused by a greater sampling effort in areas with greater numbers of people (Stadler *et al*., 2000).

Even considering the importance of humans as a modifying force, evidence of a human influence on the spatial distribution patterns of species richness is often overlooked, even in studies that specifically searched for this influence. For example, according to van Rensburg *et al*. (2002, 2004) and Chown *et al*. (2003), coarse resolution and broad-scale natural environmental factors such as energy availability seems to have an overwhelming influence on South African native bird species richness, so that spatial distribution patterns remain similar to that before human domination of earth. Even so, the absence of any human influence should be doubted. After taking natural environmental gradients into account, Fairbanks *et al*. (2002) found indications of a positive human influence on spatial distribution in South African bird species richness though habitat creation. Also, Real *et al*. (2003) showed that human activity significantly disrupted the historical spatial distribution of certain mammal taxa in Argentina, and Evans & Gaston (2005) found that humans modified the bird species richness–energy relationship in Britain.

Objectives

In this work, I explicitly incorporate the idea that humans are a substantial force influencing species richness distribution patterns. I investigate South African native bird species richness distribution patterns, based on several hypotheses that were proposed in previous studies to explain how the positive relationship between native species richness and human population density is maintained. I thereby investigate the relative importance of several anthropogenic benefits and threats to bird species richness, and how these factors might have modified spatial distribution in bird species richness. Further, I investigate the role of anthropogenic and natural environmental factors in determining alien bird species richness, to determine whether the spatial distribution of exotic plant species, exotic bird species and native bird species are governed by similar factors.

Spatial distribution in native South African bird species richness has been the topic of research in several other studies, and their results provide the basis on which to further build our understanding of conservation planning systems and the factors that govern species richness patterns (e.g., Fairbanks *et al*., 2002; Rodrigues & Gaston, 2002; van Rensburg *et al*., 2002; Chown *et al*., 2003; van Rensburg *et al*. 2004). These studies used a reliable bird species distribution atlas – the Southern African Bird Atlas Project (Harrison *et al*., 1997) – and were mainly conducted at the quarter-degree square resolution. It is for these reasons that I also focus on bird species distribution in South Africa at the quarter-degree square resolution.

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CHAPTER 2

The maintenance of a positive spatial correlation between South African bird species richness and human population density

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ABSTRACT

Aim To investigate explanations for the maintenance of a positive spatial species richness–human population density correlation at broad scales, despite the negative impact of humans on species richness. These are (hypotheses 1 – 4): (1) human activities that create a habitat mosaic and (2) a more favourable climate, and (3) adequate conservation measures (e.g. sufficient natural habitat), maintain the positive species richness–human density correlation; or (4) the full range of human densities decrease the slope of the correlation without changing its form.

Location South Africa

Methods Avian species richness data from atlas distribution maps and human population density data derived from 2001 census results were converted to a quarter-degree resolution. We investigated the number of land transformation types (anthropogenic habitat heterogeneity), irrigated area (increasing productivity), and other covarying factors (e.g. primary productivity) as predictors of species richness. We compared species richness–human density relationships among regions with different amounts of natural habitat, and investigated whether the full range of human densities decrease species richness in relation to primary productivity.

Results Hypotheses 1, 2 and 3 were supported. Human densities and activities that increase habitat heterogeneity and productivity are important beneficial factors to common species, but not to rare species. The species richness–human density relationship persists only at low land transformation levels, and no significant relationship exists at higher levels. For common species, the relationship becomes non-significant at lower land transformation levels than for rare species.

Main conclusions The persistence of the species richness–human density relationship depends mostly on the amount of remaining natural habitat. In addition, certain human activities benefit especially common species. Common species seem to be more flexible than rare species in response to human activity and habitat loss.

Keywords Bird species richness, habitat heterogeneity, human population density, irrigated area, land transformation, primary productivity.

Running title Birds and humans in South Africa

INTRODUCTION

A recurrent theme emerging from recent studies is that, at least at the regional scale, a positive correlation exists between numbers of native species and human population density. Such a relationship has been found for a number of taxa including mammals, birds, reptiles and amphibians (Balmford *et al.*, 2001; Araújo, 2003; Chown *et al.*, 2003; Luck *et al.,* 2004; Evans & Gaston, 2005). The phenomenon has been studied at a number of spatial resolutions, varying from finer 10km grid scales (e.g., Evans & Gaston, 2005), to the coarse resolution of whole countries (e.g., Gaston & Evans, 2004).

It is commonly believed that similar responses to environmental conditions have determined the historical colonization of an area by humans and other species, resulting in the observed pattern (Moore *et al.*, 2002). Productivity and energy availability and habitat heterogeneity are examples of environmental factors that influence the distribution of humans and other species (Currie, 1991; Mace & Pagel, 1995; Balmford *et al.*, 2001; Chown *et al.*, 2003; Evans & Gaston, 2005). In most cases, the influences of more than one environmental factor can be seen, often with different factors being more important at different scales (e.g. van Rensburg *et al.*, 2002). According to Gaston (2005), energy and resource (i.e. primary productivity) limitation is the most widely accepted explanation for patterns of variation in species richness. Although some studies found that humans and species richness peak at intermediate productivity levels (e.g. Balmford *et al.*, 2001), it is known that in South Africa, human density and native avian species richness both have a positive correlation with primary productivity (Chown *et al.*, 2003).

The generally negative impact of human activities on native biodiversity is another well-known phenomenon. Humans are responsible for habitat transformation, degradation, and destruction, overexploitation of natural resources including species, the introduction of harmful invasive alien species and, ultimately, global climate change and an abnormally rapid rate of global species extinction (see Vitousek *et al.*, 1997, for a review). Real *et al.* (2003) showed that human activity can significantly disrupt the historical spatial distribution of certain taxa. Further, many studies have found a positive correlation between human population density in an area, and the proportion of species that are threatened with extinction (Thompson & Jones, 1999; McKinney, 2001; McKee *et al.*, 2003; Luck *et al.*, 2004). In addition, human density and activity is widely associated with a reduction in the numbers of individuals of species, whether it is caused directly (e.g. hunting or persecution) or indirectly through habitat transformation or biological invasion (Fisher & Shaffer, 1996; Hobbs & Mooney, 1998; Harcourt *et al.*, 2001; Gaston *et al.*, 2003).

Considering that human activity reduces biodiversity in such manner that the effect increases with an increase in human numbers, why then does a positive correlation between human density and native species richness still persist in such a widespread manner? Many possible reasons have been suggested for why the negative human impact does not usually result in the elimination of a positive correlation. First, human activity might increase habitat heterogeneity, enabling the coexistence of more species and inflating species richness (Andren, 1994; Araújo, 2003). For example, Fairbanks (2004) indicated that this is likely for South African bird species, after showing that an increase in bird species richness coincided with an increase in various types of land transformation. Humans may increase habitat heterogeneity through habitat transformation if it results in the creation of a mosaic of natural and artificial (i.e. anthropogenic) habitat types where different species may coexist. Species richness might be increased if the beneficial effect of increased habitat heterogeneity is stronger than the negative effect of the loss of natural habitat through transformation.

Second, human activity might result in a local change in the climate of densely populated areas to a climate that is more favourable to species. Examples include a heat island effect or irrigation in urban areas, which may act to increase the productivity and lengthen the growing season (weakening natural seasonal effects) of that system (Shochat *et al*., 2006). For animals, this would translate to a lengthening of the breeding season, a more constant and predictable food supply and a higher survival rate of young. Similar to the first explanation, if the beneficial effect on species richness is stronger than any negative effect of human activity then species richness might be increased or at least be allowed to persist.

Third, levels of species richness could be determined by the strength of conservation measures in a given area rather than by human density *per se* (Gaston, 2005). It is predicted that the form of the observed relationship would vary among regions depending on the strength of conservation activities in those regions. In other words, a strong positive correlation might persist where conservation measures are adequate, regardless of human density, whereas the relationship might negative or unimodal where conservation measures are poor.

Fourth, humans could have a negative impact on species richness over the full range of the correlation, i.e. although higher human densities have a greater impact on biodiversity, even low human densities act to decrease species richness (Gaston, 2005). In other words, at any given value of human density, detrimental human activities prevent species richness from obtaining its maximum possible value that it would have obtained if human densities had no influence on species richness. Consequently, even though a positive correlation between species richness and human density may still be found, the slope of such a relationship would be lower than it would have been in the absence of a human influence.

Fifth, the relationship may be positive at the coarse spatial resolutions in which most of the studies were conducted, although it would be negative or unimodal at finer resolutions (Gaston, 2005). This is because, if viewed at coarse spatial resolutions, areas of high human density may still include substantial patches of natural habitat for biodiversity to be maintained (see Pautasso, 2007, for further information and support on this hypothesis).

Here we assess the nature of the relationship between species richness and human population based on the hypotheses stated. As a case study, we used data on the distributions of native bird species in South Africa provided by the Southern African Bird Atlas Project (SABAP, Harrison *et al.*, 1997) at a quarter-degree square (QDS) resolution.

METHODS

Hypothesis 1

Human activity increase habitat heterogeneity, enabling the coexistence of more species and inflating species richness in densely populated areas.

To test this hypothesis, hereafter referred to as the 'habitat heterogeneity' hypothesis, and all subsequent hypotheses, we used the same avian species richness (SABAP, Harrison *et al.*, 199; Appendix, Map 1) and 2001 human population density (Anonymous, 2001; Appendix, Map 2) data at the QDS resolution (the area of QDS grid cells in South Africa vary from 635 km^2 in the south to 712 km^2 in the north) as used by Chown *et al.* (2003) and Evans *et al.* (2006). In some cases the positive species richness–human density relationship has been found to be an artefact of sampling bias. That is, areas with a higher human density may have been sampled more thoroughly than areas where human density is low, and therefore species richness numbers were inflated artificially in the former areas (see, e.g., Stadler *et al.*, 2000). This is unlikely to be a problem for the SABAP data set however, as it has been demonstrated to be a reliable representation of bird distribution in many previous studies (see Evans *et al.*, 2006, who tested the influence of low reporting on data quality).

It is important to separate the potential positive influence of artificial habitat heterogeneity from that of productivity and natural habitat heterogeneity, which has been shown to be positively correlated to each other and to bird species richness (van Rensburg *et al.*, 2002). Also, it is important to determine whether artificial habitat heterogeneity is indeed determined by human density at a QDS resolution. Therefore, all combinations of the variables human density, natural habitat heterogeneity and productivity were investigated as predictors of artificial habitat heterogeneity. Next, we investigated all combinations of all four variables (i.e. including artificial habitat heterogeneity) as predictors of bird species richness.

We used the number of land transformation types within each QDS to represent artificial habitat heterogeneity (Appendix, Map 3), based on six types of transformed land-cover classes (cultivated land, degraded land, plantations, water bodies, urban build-up, and mines and quarries) captured by Landsat TM satellite imagery mainly between 1994 and 1995, and provided by Thompson (1996). We used the number of vegetation types within each QDS, based on Low & Rebelo's (1996) classification of 68 different vegetation types for the study area, to represent natural habitat heterogeneity (Appendix, Map 4).

Hypothesis 2

Human activities might result in a local change in the climate of densely populated areas to a climate that is more favourable. Hereafter, this hypothesis is referred to as the 'productivity increase' hypothesis.

Most previous studies focused on local, fine-resolution climate change caused by urbanization through heating and irrigation (Shochat, 2004; Shochat *et al.*, 2006). However, at the QDS resolution in South Africa, cultivated area is a more pervasive land transformation type, at 18% of the area studied, than urbanization at less than 1 % (according to the land transformation data set; Thompson, 1996). Also, the heat island effect is more likely in cold-climate regions, whereas productivity is limited instead by water availability in a warmer and drier country such as South Africa (van Rensburg *et al.*, 2002). Therefore, to test the productivity increase hypothesis we used the spatial distribution of irrigation for the purpose of boosting the productivity of cultivated areas, expressed as percentage irrigated area per QDS (Appendix, Map 5).

Even though the increased productivity caused by irrigation is likely to be beneficial to biodiversity (e.g. irrigation increased resources and biodiversity in oases in Tunisia; Selmi & Boulinier, 2003), it is also associated with a host of damaging environmental effects such as agricultural intensification and further transformation of previously non-arable land to cultivated land, polluted run-off, erosion, water extraction and changing flow regimes in wetlands (Brotons *et al.*, 2004; Hart, 2004). Irrigation is thus regarded as an anthropogenic environmental factor that may either benefit species richness or threaten it.

First, we needed to determine whether irrigation cause a significant increase in productivity at the QDS resolution. We did this by correlating precipitation (as the limiting factor of productivity) and percentage irrigated area, and a combination of these two predictors, with productivity. Next, as for the habitat heterogeneity hypothesis, it is important to separate the influence of irrigation from a number of other variables. Thus we determined whether irrigation is spatially associated with human density and productivity. Further, we determined whether irrigation is associated with extent of cultivated area (taken from the land transformation dataset; Appendix, Map 6), as an increase in cultivated area would imply a decrease in pristine natural habitat. Therefore, we investigated all combinations of the variables human density, productivity and cultivated area as predictors of irrigated area. Last, we investigated all combinations of these variables, except precipitation, as predictors of species richness.

We used data on January normalised difference vegetation index (NDVI) values averaged between 1982 and 1991 as a measure of primary productivity in this and all other hypotheses (Appendix, Map 7). NDVI is obtained by satellite imaging, and it correlates strongly with net primary production and plant biomass (Kerr & Ostrovsky, 2003). The NDVI values used in the current study, were obtained from the African Real Time Environmental Monitoring using Meteorological Satellites (Artemis) program of the Food and Agriculture Organization (FAO; http://www.fao.org/geonetwork/srv/en/main.home). We specifically used NDVI for January, because compared with other NDVI metrics, it exhibits the most marked spatial variation and explains more of the spatial variation in human density and avian species richness (Evans *et al*., 2006).

Precipitation (mm year^{-1}) was calculated from monthly data based on interpolated climate surfaces for the past 30 – 50 years, and supplied by the South African Computing Centre for Water Research (Schulze, 1997; Appendix, Map 8). A spatial distribution map of irrigated areas for South Africa was published by the Agricultural Research Council – Institute for Soil, Climate, and Water (2000) and was downloaded from the Agricultural Geo-Referenced Information System (AGIS) website (http://www.agis.agric.za/agis_metadata/).

Hypothesis 3

The form and the strength of the observed species richness – human density relationship could vary according to the strength of the conservation measures in an area. Hereafter, this hypothesis is referred to as the ‘species conservation’ hypothesis.

Conservation measures may include the establishment and maintenance of protected areas and conservation activities that may be applied outside protected areas, such as environmental protection laws and environmentally friendly urban development and farming (Linnell *et al*., 2001; Green *et al*., 2005; Lenth *et al*., 2006). Although percentage protected area is an easily quantifiable spatial measure of conservation strength, we decided not to use it, because although South Africa is still relatively untransformed, little of it is formally protected in national parks or game reserves for example. Even though according to the land transformation data set about 78% of the area investigated is pristine natural habitat, according to the World Data Base on Protected Areas (WDPA, 2004) only about 6% is formally protected (see also Reyers *et al*., 2001). Further, when working with a taxon group such as birds for which range sizes are often not being restricted by game fences, one should rather be interested in the number of available natural ecosystems within protected areas and the matrix within which they reside. Therefore, to quantify the number of natural ecosystems available within a given area (representing conservation strength), we summed the percentage area covered by the six types of transformed land-cover classes used for the habitat heterogeneity hypothesis to obtain the total percentage of land transformation (Appendix, Map 9). Remaining natural habitat currently situated outside protected areas might not be protected from future transformation; however, as there is no temporal component in the current study, natural habitat would adequately represent areas that were protected from transformation at the time of measurement.

To compare the form and the strength of the observed species richness–human density relationship among regions with different land transformation levels (i.e. different conservation strengths) the available QDSs were divided into 10 interval classes according to the total percentage of transformation in each QDS (0-10% transformed, 10% - 20%, etc.). However, because available data (i.e. actual number of QDSs) generally decline as percentage transformation increases, it was necessary to pool the data from the two highest transformation classes to make one class (80% - 100% transformation) in order to conduct the analyses with a reasonable number of data points. The form and the strength of the relationship between bird species richness and human population density were compared among the different land transformation classes.

Hypothesis 4

Although a positive correlation persists between species richness and human density, because of a negative human impact caused by the whole range of human densities, the slope of such a relationship might be lower than it would have been if human densities had no influence on species richness. Hereafter, this hypothesis is referred to as the ‘reduced slope, hypothesis.

To investigate the way various human densities decrease species richness it would be ideal to compare the form, slope and strength of the species richness–human density relationship between areas where human densities have a negative impact on native species richness and areas where similar human densities have no influence on species richness. However, we decided not to use this method, as the identification of an area where the resident humans do not influence species richness would be difficult because of the pervasiveness of human influence.

However, another option for testing this hypothesis in a more indirect way is provided by the finding that South African avian species richness and human density covary with primary productivity (Chown *et al.*, 2003), suggesting that the positive bird species richness–human density correlation is merely an artefact caused by this covariation. Evans & Gaston (2005) have found for British birds that human density is capable of influencing the observed species–energy relationships. Therefore, instead of making use of the species richness–human density relationship to measure human impacts on species richness patterns, we analysed the degree to which human density modifies the species richness–productivity relationship at the QDS resolution. Following Evans & Gaston (2005), we compared the effect that productivity has on the distribution of avian species richness between statistical models that either take into account or ignore human density. In their study, Evans & Gaston (2005) found that the slope of the species richness–energy relationship is significantly reduced in the models that include human density. Thus we expected to obtain a decreased slope for the species richness–productivity relationship in the presence of humans. This would indicate that any given value of human density prevents species richness from obtaining its maximum possible value in relation to primary productivity.

Hypothesis 5

Species richness is maintained in natural habitat patches undetected at a coarse resolution. A negative or unimodal species richness–human density relationship will be detected at finer resolutions.

This hypothesis was not investigated, because the only finer-resolution bird species richness data set available for South Africa (the Pretoria Conservation Challenge, PCC 2006, recorded at 3' grid cell resolution in parts of Gauteng and the surrounding provinces) was demonstrated to be of poor quality in preliminary analyses; it was impossible to adequately represent the true spatial distribution of bird species.

Analyses

We examined three species richness categories representing different range size categories seeing that common and rare species are known to react differently to anthropogenic disturbance (see e.g. Balmford *et al.*, 2001). In particular, common species, many of which are generalists with large range sizes, are often able to take advantage of habitats that have been altered by human activities, whereas rare or specialist species, often characterized with small range sizes, usually become rarer (McKinney & Lockwood, 1999; Fairbanks *et al.*, 2002; Davies *et al.*, 2004). Also, although the distribution patterns of common and rare species differ, common species contribute more towards overall species richness distribution patterns than rare species. In particular, most of the spatial variation is caused by a minority of the most common species (Lennon *et al.*, 2004; Vázquez & Gaston, 2004). The three avian species richness categories calculated for each QDS were: (1) all 651 species (Appendix 1, Map 1), (2) the 25% most widespread species (each occupying a minimum of 610 QDSs) representing the category 'common species' (Appendix, Map 10), and (3) the 25% most range-restricted species (each occupying a maximum of 98 QDSs) representing the category 'rare species' (Appendix, Map 11). Although these cut-off percentages are arbitrary, they are widely used to define range size categories (see Gaston, 1994).

All spatial information data sets have been converted to a QDS resolution using ArcView GIS 3.3 (ESRI Inc. 1998). We removed QDSs overlapping the border of the country (i.e. those overlapping with the coast or neighbouring countries) from the data sets, because information in these QDSs is incomplete and could therefore be misleading (n = 1669 QDSs were used in analyses).

We reduced heteroscedasticity in all variables by logarithmically transforming the data to the base 10 before applying the relevant statistical procedures. If zero values were present within a data set, we added the incremental value, 1, to all values in that data set before applying log transformation.

To detect collinearity, we examined the tolerance value for each predictor variable. Tolerance, as defined by Neter *et al*. (1996), is 1 minus the squared multiple correlation of a predictor variable with all other independent variables in the regression equation (Statsoft Inc., 1999); the lower the tolerance of a given variable, the stronger the correlation between the variable in question and one or more of the other predictors (Quinn & Keough, 2002). Following Quinn & Keough (2002), those variables with tolerance values < 0.1 should be eliminated from subsequent analyses. However, as none of the explanatory variables were found to be redundant, all were included in the subsequent analyses (Table 1). All analyses were conducted using the SAS version 9.1 procedure ‘PROC MIXED’ (SAS Institute Inc., 2002).

Data from contiguous grid cells are often spatially autocorrelated, which violates the assumptions of independent errors on which many classical statistical tests are based (Legendre *et al*., 2002). Therefore, we implemented spatial correlation models in which spatial variation in the response variable is tested for spatial autocorrelation (null spatial models are compared with models assuming independent errors with a likelihood ratio test giving a χ^2 value and level of significance), and a spatial covariance matrix is fitted to the data to adjust the test statistics (Littell *et al*., 1996). We used an exponential spatial covariance structure in all spatial analyses, as it always provided a better fit to the null model compared with the five others: spherical, Gaussian, linear, linear log and power. Except for the land transformation classes 60% to 70% and 70% to 80% in the rare species category of the species conservation hypothesis, variation in the response variable was significantly ($P<0.05$) spatially autocorrelated in each analysis.

To test the ‘goodness of fit’ of different models, ‘PROC MIXED’ supplies Akaike’s information criterion (AIC) values, of which smaller (or more negative) values indicate a better model. AIC values do not mean anything by themselves and are used to compare models with different predictor variables (SAS Institute Inc., 2004). Thus, AIC values can not be compared between models with different response variables (e.g. for which ‘all’, ‘common’ or ‘rare’ species richness are response variables) or between different data sets (e.g. the different transformation classes of the species conservation hypothesis that are different subsets of a data set). If such comparisons were required, we used the significance level (P) as an indication of the strength of a relationship. AIC values were used to choose the best models for the habitat heterogeneity and productivity increase hypotheses. However, AIC values were usually not reported, except where the best models predicting bird species richness could be compared between the habitat heterogeneity and productivity increase hypotheses.

Table 1 Tolerance values are used to detect collinearity between the predictor variables investigated in this chapter (Neter *et al*., 1996; Quinn & Keough, 2002). A tolerance value lower than 0.1 would have indicated that a predictor variable is redundant; however, all predictor variables used in this chapter could be included in the analyses (Quinn & Keough 2002).

Predictor	Tolerance value
Human density	0.27
Primary productivity	0.17
Anthropogenic habitat heterogeneity	0.38
Vegetation heterogeneity	0.83
Precipitation	0.16
Cultivated area	0.46
Irrigated area	0.79

To detect simple nonlinear relationships, we included the square term of each predictor variable in the models together with the variable concerned (Evans & Gaston, 2005). A significant improvement in the 'goodness of fit' (i.e. a decrease in the AIC value) after adding the square term would indicate a nonlinear relationship. However, unless otherwise stated and reported in the Results section, all relationships reported should be assumed to be positive and linear (i.e. the square term did not contribute significantly towards improving the model).

Finally, for all analyses, a probability level of 0.05 was accepted as indicating statistical significance. We used the confidence limits of the estimated slopes to indicate a significant difference between the slopes of different correlations (the reduced slope hypothesis). In this method, the difference can be considered significant if the confidence intervals do not overlap. However, as a 95% confidence interval would result in a significance threshold lower than 0.05, we used the 84% level of confidence, which provides the 0.05 significance threshold (Payton *et al.*, 2003; Evans *et al.*, 2006).

RESULTS

Hypothesis 1: habitat heterogeneity

Spatial distribution in artificial habitat heterogeneity was best predicted by a combination of human density and productivity, with human density contributing most to the model, as indicated by the *F* value (Table 2). This suggests that a greater variety of transformation types, thus a more diverse artificial habitat mosaic, tends to occur in areas with higher human densities and, secondly, higher productivity.

The best model predicting the spatial distribution of all species included human density, productivity and its square term, and artificial heterogeneity (Table 3). The best model for common species included human density and its square term, productivity and artificial heterogeneity (Table 3). Thus, artificial heterogeneity makes an important contribution towards explaining the distribution of all and common species; however, when considering the *F* values, it plays a secondary role to human density. It is also less important than productivity for all species, but seems to be similar in importance to productivity for common species (Table 3). Natural habitat heterogeneity did not seem to have a significant influence on all and common species richness patterns. This is consistent with van Rensburg *et al.* (2002), who showed that although natural habitat heterogeneity (i.e. the same vegetation heterogeneity data set as used in the current study) has an important effect on bird species distribution at the coarser 1° resolution, it is less important at the QDS resolution. In contrast, for rare species the best model included productivity and its square term, with a smaller contribution also made by natural heterogeneity (Table 3). If we take these two predictors into account, human density and artificial habitat heterogeneity have no significant influence on

Table 2 F ratios and associated significance levels for the best models explaining the spatial distribution of artificial habitat heterogeneity, primary productivity (NDVI) and irrigated area. For all F tests, the numerator degrees of freedom equals 1 and the denominator degrees of freedom is more than 1664. All predictor and response variables are logarithmically transformed to the base 10.

Response variable	Human population	NDVI	NDVI^2	Precipitation	Irrigated area	Cultivated area	Cultivated area^2
Artificial habitat heterogeneity	F=399.89****	F=47.69****	n.i.	n.a.	n.a.	n.a.	n.a.
NDVI	n.a.	n.a.	n.a.	F=645.90****	F=30.01****	n.a.	n.a.
Irrigated area	n.i.	F=6.67**	F=3.86**	n.a.	n.a.	F=197.04****	F=43.73††††

Significance levels: positive effects, **$P < 0.01$; ****$P < 0.0001$; negative effects, †††† $P < 0.0001$.

Abbreviations: n.i., not included in the model; n.a., not applicable; NDVI, normalized difference vegetation index.

Table 3 *F* ratios and associated significance levels of the best models predicting spatial distribution in avian species richness (all, the 25% most common and the 25% rarest) for the habitat heterogeneity hypothesis (hypothesis 1) and the productivity increase hypothesis (hypothesis 2). For all *F* tests, the numerator degrees of freedom equals 1 and the denominator degrees of freedom is more than 1007. All predictor and response variables are logarithmically transformed to the base 10.

Hypothesis	Human population	Human population ^{2}	NDVI	NDVI^2	Vegetation heterogeneity	Artificial heterogeneity	Irrigated area	AIC
All species								
1	*F*=78.56****	n.i.	*F*=23.69****	*F*=6.48*	n.i.	*F*=11.17***	n.a.	-2709
2	*F*=97.30****	n.i.	F=21.44****	*F*=5.39*	n.a.	n.a.	F=38.89****	-2733.2
Common species								
1	*F*=48.57****	*F*=21.82††††	*F*=14.60***	n.i.	n.i.	*F*=14.25***	n.a.	-3319.2
2	*F*=45.00****	*F*=18.57††††	*F*=13.10***	n.i.	n.a.	n.a.	*F*=39.36****	-3342.9
Rare species								
1	n.i.	n.i.	*F*=59.97****	*F*=31.96****	*F*=12.06***	n.i.	n.a.	387.1
2	n.i.	n.i.	*F*=62.46****	*F*=32.73****	n.a.	n.a.	*F*=6.42*	393.9

Significance levels: positive effects, *$P < 0.05$; ***$P < 0.001$; ****$P < 0.0001$; negative effects, †††† $P < 0.0001$.

Abbreviations: n.i., not included; n.a., not applicable; NDVI, normalized difference vegetation index; AIC, Akaike's information criterion (smaller or more negative values indicate a better model).

rare species richness patterns and are therefore excluded from the model.

Human density had a nonlinear relationship with common species: the form of the relationship was positive only in areas with relatively low human density values above which an asymptote was reached (between *c*. 320 and 3175 humans per QDS) with some weak signs of a negative relationship in the areas with high human density (Fig. 1). Further, productivity had a nonlinear relationship with all and rare species, and Fig. 2 indicates that high-productivity areas may contain any value of rare species richness, from the lowest to the highest.

Hypothesis 2: productivity increase

The best model predicting the spatial distribution of primary productivity included both precipitation and irrigated area, though precipitation contributes most to the model (Table 2). Thus, irrigation seems to significantly raise productivity above that expected from precipitation alone, although this increase is unremarkable at the QDS resolution, possibly because only small areas of many QDSs are irrigated (Table 2; Appendix, Map 5).

The best model predicting percentage irrigated area per QDS included cultivated area (contributing most) and productivity with their square terms (Table 2). It can therefore be seen that irrigation is mainly associated with cultivated area, but also tends to be more prevalent in areas with higher productivity, though both predictors had a nonlinear relationship with irrigated area. Although human density did not seem to have a significant direct influence on spatial distribution in irrigation, it can still be assumed that a positive correlation exists between these two variables because of their covariation with productivity.

The best model predicting the spatial distribution of all species included human density, irrigation and productivity with its square term (Table 3). The best model for common species included human density and its square term, irrigation, and productivity (Table 3). Thus irrigation makes an important contribution towards explaining the distribution of all and common species. Although it is less important than human density (i.e. it contributes less to the model), it is more important than productivity for all and common species (Table 3). In addition, if the AIC values in Table 3 are compared between the best models of the habitat heterogeneity and productivity increase hypotheses, irrigation seems to be even more important than artificial habitat heterogeneity in determining species richness patterns. In contrast, even though the best model for rare species included irrigated area and productivity with its square term (Table 3), irrigated area makes a much smaller contribution to rare species distribution patterns than productivity. Again, human density was excluded from the model. Finally, cultivated area had no significant influence on any measure of bird species richness if the other predictors are taken into account.

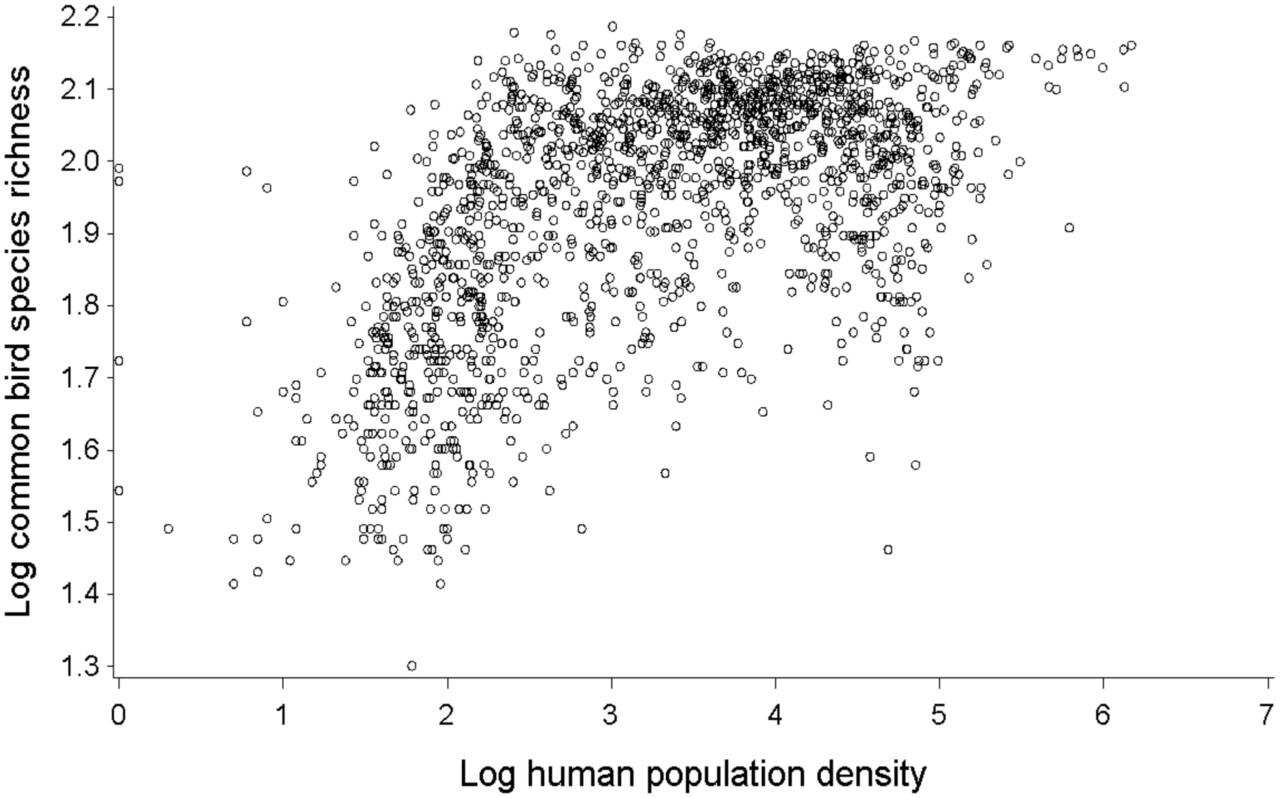

Figure 1 A nonlinear relationship exists between the spatial distribution of number of common bird species and number of humans per quarter-degree square. The form of the relationship was positive only in areas with relatively low numbers of humans after which an asymptote was reached.

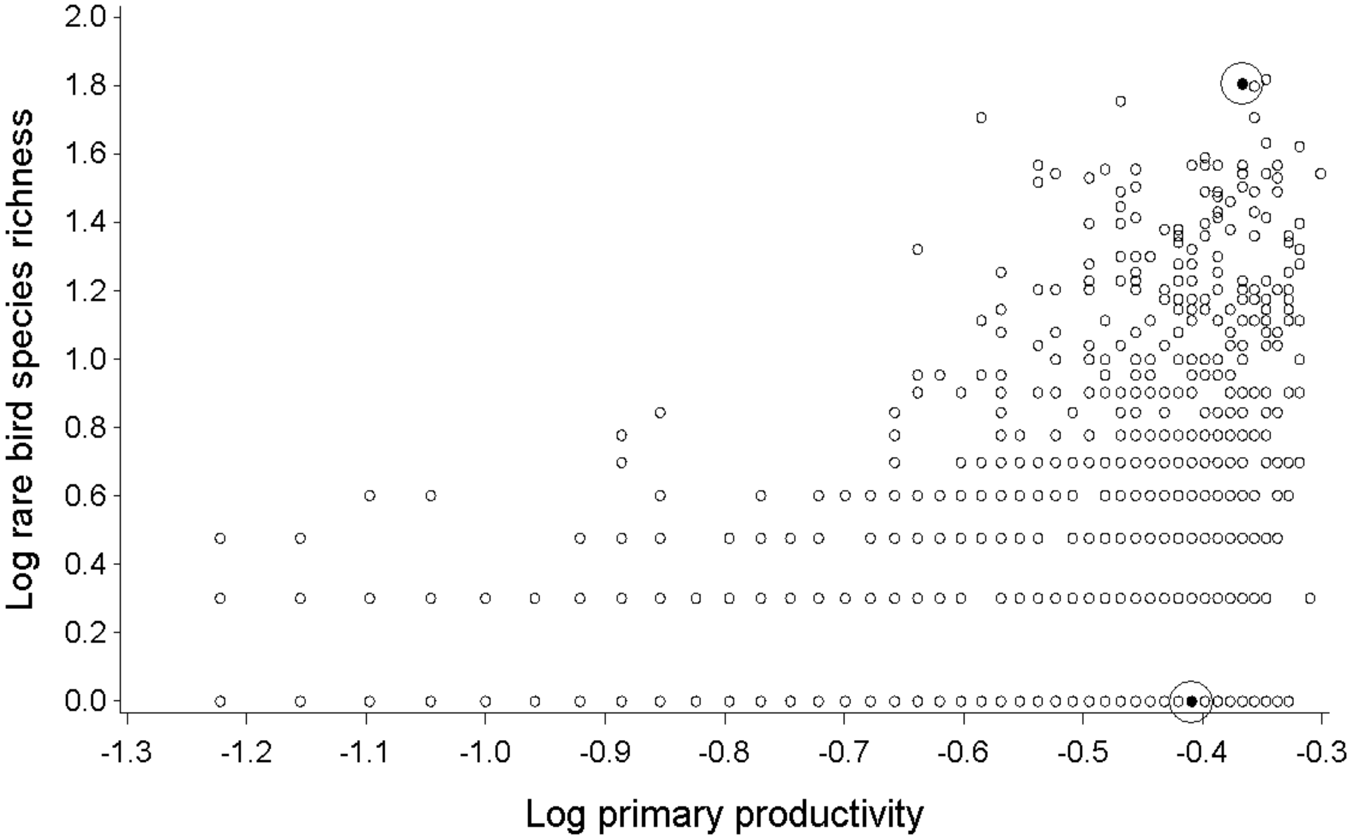

Figure 2 A nonlinear relationship exists between the spatial distribution of number of rare bird species and level of primary productivity [i.e. normalized difference vegetation index (NDVI) value, see Methods section] per quarter-degree square (QDS). Whereas low-productivity areas usually contain few rare species, high-productivity areas may contain any number of rare species, from the lowest to the highest. The points indicated by circles are QDSs located adjacent to one another and have similar levels of primary productivity, yet one contains 64 rare bird species whereas the other contains only one rare bird species. These two points are discussed more thoroughly in the Discussion section.

Hypothesis 3: species conservation

The significance levels of the positive species richness–human density relationship showed an overall decrease (i.e. increasing *P* values) with increasing transformation (Table 4). Important exceptions to this pattern of decrease were (i) the land transformation class 30%–40%, for which the *P* values were higher than the adjacent 40%–50% transformation class, and (ii) the transformation class 80%–100%, for which *P* values were lower than the adjacent 70%–80% class (Table 4). These exceptions were true for all three species richness categories. Further, the pattern of decrease in the level of significance was most consistent for all species and common species, whereas the pattern of decrease was less clear for rare species. Significance levels of the species richness–human density relationship for rare species were generally higher across the full gradient of land transformation classes, compared to the significance levels for the all species and common species categories.

More important support for this hypothesis is that, although mainly positive and significant species richness–human density relationships persisted at lower land transformation levels, the relationship becomes invariably non-significant at and above a certain threshold of transformation. In other words, as predicted, a change in the form of the relationship occured, in this case from significantly positive to non-significant. In QDSs below the transformation level threshold, the distribution of humans and bird species follow spatial patterns that are significantly similar (probably due to the similar response of both to environmental factors; see Balmford *et al.*, 2001, for sub-Saharan Africa and Chown *et al.*, 2003, for South Africa), whereas in QDSs at and above the threshold, a large enough proportion of species is in some way affected by land transformation to result in a breakdown of the positive species richness–human density correlation. Thus, this result suggests that higher levels of land transformation have the power to obscure the influence of environmental factors that cause the well-known covariation of human density and species richness. We tested whether decreasing sample sizes (i.e. decreasing number of QDSs with increasing transformation, Table 4) influenced *P* values, and found that this influence was negligible.

The concept of land transformation thresholds is not unique to the current study. Franklin & Forman's (1987) and Andren's (1994) simulations of increasing habitat loss both show a threshold at which the continuous original habitat becomes fragmented followed by a rapid decrease in habitat patch size, and a second threshold after which the distances between habitat patches begin to increase. Species are mainly affected by habitat loss until the thresholds are reached, after which the negative effects of size and isolation of remaining habitat patches (i.e. probability of persistence and colonization ability, respectively) are added to habitat loss (Andren, 1994).

The transformation level threshold found in the current study was unique for each species richness group: highest for rare species (70%–80% transformed area), lowest for

Table 4 The significance levels (*P* values) of correlations between avian species richness (all species and the 25% most common and 25% rarest species) and human population density at different levels of land transformation.

Land transformation class (%)	All species	Common species	Rare species
0 -10	<0.01 (926)	<0.01 (926)	<0.01 (458)
10 - 20	<0.01 (176)	<0.01 (176)	<0.01 (116)
20 - 30	<0.01 (146)	0.01 (146)	0.03 (118)
30 - 40	0.13 (102)	0.73 (102)	0.34 (85)
40 - 50	0.04 (111)	0.37 (111)	0.02 (83)
50 - 60	0.13 (68)	0.61 (68)	0.02 (56)
60 - 70	0.21 (58)	0.78 (58)	<0.01 (39)
70 - 80	0.34 (50)	0.58 (50)	0.29 (34)
80 - 100	0.07 (32)	0.20 (32)	0.06 (23)

Sample sizes (i.e. number of quarter-degree squares) are given in parentheses after each *P* value.

common species (30%–40%) and intermediate for all species (50%–60%) (Table 4). It seems that common species are influenced by lower levels of transformation, whereas rare species seem to be more resistant to the effects of transformation. This observation conflicts with the widely accepted assumption that rare species are mainly specialist species dependent on a specific set of environmental conditions, and are therefore usually not as well adapted to human activity as common species (McKinney & Lockwood, 1999; Davies *et al.*, 2004; but see La Sorte, 2006).

Hypothesis 4: reduced slope

Compared with the models that exclude human density, the estimated slopes of the positive relationships that bird species richness have with productivity were reduced for all and common species and slightly increased for rare species in the models that include human density (Table 5). However, these changes were insignificant, i.e. the 84% confidence intervals overlapped for all richness measures (Table 5). Therefore, the reduced slope hypothesis is not supported.

DISCUSSION

The observations of the habitat heterogeneity and productivity increase hypotheses indicate that common species benefit directly from human density and environmental effects that are caused by human activities, such as artificially increased habitat heterogeneity and productivity. The fact that human density contributes more to predicting common species distribution than the other two variables suggests the influence of other beneficial human activities that are not considered in the current study. All these benefits are large enough to overwhelm both the negative effects of human impact and the natural variation of common species with productivity, so that a relatively strong positive, though nonlinear, common species richness–human density relationship is promoted at the national scale. In contrast, the results indicate that although rare species are strongly dependent on natural productivity, and to a much smaller extent on artificially inflated productivity (i.e. irrigation) and natural habitat heterogeneity, human density and human-caused habitat heterogeneity play no beneficial role. These results are therefore consistent with the assumption stated in the Results section (where the results of the species conservation hypothesis are reported), that rare species are less able to adapt well to human activity. In addition, the idea stated in the Methods section, that general species richness patterns are mostly determined by common species, is reflected in the current study by the similarities between the two species richness measures – all species and common species – with regard to their responses to natural and human-caused environmental factors.

Spatial patterns in habitat transformation are often positively correlated with human

Table 5 A comparison of the slope estimates and their associated 84% confidence intervals of the species richness–productivity relationships in models with or without human population density. Any overlap in the relevant confidence intervals indicates that the differences between the slopes of models that include or exclude human density are not significant.

Group	Human density	Slope estimate	Confidence intervals
All	Excluded	0.53	0.46–0.60
	Included	0.43	0.36–0.49
Common	Excluded	0.26	0.20–0.32
	Included	0.17	0.12–0.23
Rare	Excluded	4.13	3.47–5.00
	Included	4.16	3.39–4.92

population densities (Chown *et al*., 2003; Vázquez & Gaston, 2006). That common species benefit from human density and, by implication, land transformation, is consistent with previous studies demonstrating that it is mainly common species that expand their ranges by colonizing areas affected by land transformation (Fairbanks *et al*., 2002; Fairbanks, 2004; La Sorte & Boecklen, 2005; La Sorte, 2006). However, it seems that not all common species benefit from all land transformation types. Where negative human activities are too severe (e.g. areas with high transformation levels, species conservation hypothesis), beneficial human activities cannot counter the negative effects, perhaps because not enough natural habitat patches are present with the artificially created habitats, increased productivity and other beneficial factors (see Andren, 1994). This is indicated by the breakdown of the species richness–human density relationship at higher transformation levels (species conservation hypothesis), the asymptote reached by common species at high human densities (Fig. 1), and the fact that it is the irrigation of cultivated area that promotes species richness rather than cultivated area (i.e. agricultural intensification, see Methods section) *per se* (productivity increase hypothesis). The non-significant species richness–human density relationship found in those areas with land transformation values above the various thresholds (species conservation hypothesis), is most likely caused by a combination of positive, negative and neutral effects between the bird assemblages found in these areas (with different habitat requirements) and the various types and amounts of land transformation. This is consistent with Fairbanks *et al*. (2002) who showed that transformation generally acts to increase the abundance of a small number of generalist species (i.e. only a fraction of those that would be classified as ‘common’), thereby decreasing evenness and increasing the prevalence of assemblages dominated by a single species. Likewise, there are numerous studies suggesting similar patterns, as was shown in our study, of the way in which common and rare species may experience range expansion or contraction related to various land-use activities (see, e.g., Andren, 1994; Armstrong & van Hensbergen, 1994; Allan *et al*., 1997; Gaston *et al*., 2003; Fairbanks, 2004).

The finding in the current study that common and rare species differ in their response to transformation in the current study (e.g. their different transformation thresholds) probably indicates that common species are more flexible than rare species in the presence of transformation rather than more vulnerable, as it may seem at first. Figure 2 shows that low species richness values for rare species also exist in certain high-productivity areas, indicating that not all of these areas are suitable for or contain rare species. Rare species are highly dependent on specific original habitat types (see, e.g., Armstrong & van Hensbergen, 1994; Allan *et al*., 1997). High-productivity zones, where many rare species are expected to occur according to certain observations from the current study, are often severely transformed and densely populated by humans, possibly making them unsuitable to support rare species. Two neighboring QDSs in KwaZulu–Natal with similar levels of primary productivity (indicated in Fig. 2) illustrate situations at both ends of the spectrum. In the relatively untransformed QDS (with its midpoint at 32º 7´ 30´´ S and 27º 37´ 30´´ E, and *c*.12% transformed area), 64 rare bird species coexist with 23,135 humans, whereas the highly transformed QDS (with its midpoint at 31º 52´ 30´´ S and 27º 52´ 30´´ E, and *c*. 74% transformed area) that includes 55,575 humans, has only one rare species. Many rare species might be unable to avoid competition with habitat transformation by dispersal, which involves crossing inhospitable surroundings to find a patch suitable for their specific requirements, while competing with the common species already present in the patch and surrounding habitat (MacArthur & Wilson, 1967). In contrast, common species are less dependent upon productive areas and are able to successfully colonize a wider variety of habitats. Therefore, although certain common species thrive in modified habitats, those that are negatively affected are able to disperse more easily than rare species (Gaston, 1994; MacArthur & Wilson, 1967). Important future work on South African bird species should include an investigation of the degree of aggregation and concentration of: (1) natural habitat fragments, (2) transformed habitat fragments, and (3) different human densities within QDSs, and their effect on species richness persistence. The results of similar previous studies for other parts of the world are often conflicting; however, a common feature is that different species vary with regard to their response to these aspects of land transformation (Franklin & Forman, 1987; Green *et al*., 2005; Lenth *et al*., 2006).

In conclusion, the three hypotheses that were supported by the data (the habitat heterogeneity, productivity increase and species conservation hypotheses) supplement one another in explaining a complex system. The amount of remaining natural habitat seems to be the most important factor determining whether the positive bird species richness–human population density relationship is maintained, regardless of rarity. However, the relative importance of potentially beneficial human activities, such as artificial habitat heterogeneity and irrigated area, in explaining bird species richness patterns depends on the rarity or degree of specialization of the species investigated. Often beneficial human activities contribute significantly to maintaining at least common bird species, which might be a reason why the reduced slope hypothesis is not supported. Lower human densities could possibly provide more positive than negative factors; thus one of the assumptions on which this hypothesis is based is invalid. However, even beneficial human factors are insufficient to maintain species richness in situations of severe habitat loss, emphasizing the value of protecting at least part of an area from habitat transformation. In addition, it is clear that the pervasive influence of common species on general species distribution patterns would obscure the more severe impact humans may have on rare species in studies that do not distinguish between these two species richness categories. Certain populations of rare species are likely to be vulnerable to any future increase in habitat transformation, although it may not be clearly visible from current national-scale rare species distribution patterns. Rare species might face a future contraction in range size or even extinction if measures are not taken to prevent habitat transformation in areas important to rare birds. However, considering the increase in human population size and resource demands, options to expand on existing reserve systems in order to include such areas appear to be limited, and it is increasingly difficult for conservation to compete with the expansion of other land uses (Chown *et al*., 2003). Decision makers are therefore faced, now more than ever before, with the challenge to further off-reserve conservation strategies (e.g., by integrating human development with biodiversity conservation) in order to achieve long term conservation goals (Kepe *et al*., 2004).

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CHAPTER 3

Exotic and native birds in South Africa: patterns, processes and conservation

ABSTRACT

Aim The spatial distribution of exotic species richness often correlates positively with native species richness, and reflects the role of human density and activity, and primary productivity and habitat heterogeneity, in facilitating the establishment and spread of exotic species. Here, I investigate the relationship between the spatial distribution of exotic bird species, native bird species richness, and anthropogenic and natural environmental conditions.

Location South Africa

Methods Using correlative analyses that take spatial autocorrelation into account, all combinations of the variables human density, primary productivity, anthropogenic and natural habitat heterogeneity, and urban, cultivated, irrigated and total transformed area, were investigated as predictors of the spatial distribution of exotic bird species richness. Further, I examined the relationship between each separate exotic species and the abovementioned predictor variables using logistic regression procedures based on binary presence-absence data. Finally, I examined the relationship between exotic species (i.e. individual species and species richness) and native species richness.

Results A combination of human density and natural habitat heterogeneity best explained the spatial distribution of exotic species richness. This contrasts with the results for individual exotic species and with previous studies on other non-native taxa showing the importance of primary productivity and anthropogenic habitat modification as explanatory variables. In general, native species richness is an important correlate of spatial variation in exotic species richness and individual exotic species, with exotic species being more similar to common species than to rare species.

Main conclusion Factors that govern spatial distribution in exotic species differ between taxa and species, and individual exotic bird species differ with exotic bird species richness. Despite these differences, spatial variation in exotic bird species seems to be most similar to variation in human density and common native species richness.

Keywords exotic birds, habitat heterogeneity, human activities, human population density, native birds, primary productivity, species richness.

Running title Exotic and native birds in South Africa

INTRODUCTION

Many studies indicate a positive spatial correlation between native and exotic species richness at coarse resolutions and the regional scale (Lonsdale 1999; Stohlgren *et al*., 1999; McKinney, 2001; Pyšek *et al*., 2002; Stohlgren *et al*., 2003; Evans *et al*., 2005; Richardson *et al*., 2005; Williams *et al*., 2005; Stohlgren *et al*., 2006). The opposite effect is often expected due to local competitive exclusion of exotic species (also known as alien species or introduced species) by natives; however, competitive exclusion by natives appears to be a relatively weak force that is mainly manifested at fine resolutions, if at all (Case, 1996; Stohlgren *et al*., 1999; Kennedy *et al*., 2002; Levine *et al*., 2004). A coarse resolution positive relationship is not necessarily causal (Lonsdale, 1999; Stohlgren *et al*., 1999). Indeed, Duncan *et al*. (2003) suggest that factors such as natural and anthropogenic environmental conditions and introduction effort are much more important than species traits and interactions in determining the colonization and distribution of exotic bird species. It is more likely that exotic and native species richness covary at regional spatial scales due to positive responses to similar environmental conditions, leading to higher native and exotic species richness in areas with a great diversity of habitat types and favourable environmental conditions such as high primary productivity or energy availability (Lonsdale, 1999; Stohlgren *et al*., 1999; Evans *et al*., 2005; Richardson *et al*., 2005; Williams *et al*., 2005; Stohlgren *et al*., 2006).

Exotic species richness is often higher in areas with high human density, because humans and human activities are often the source of exotic species (Hodkinson and Thompson, 1997; Dean, 2000; McKinney, 2001; McKinney, 2002; Pyšek *et al*., 2002; Le Maitre *et al*., 2004; Richardson *et al*., 2005; Williams *et al*., 2005; Stohlgren *et al*., 2006). Further, disturbance of natural habitat by humans also facilitate the colonization and spread of exotic species (Case, 1996; Dean, 2000; Fine, 2002; Le Maitre *et al*., 2004). Spatial variation in human density is, in turn, often determined by the same environmental conditions that determine native and exotic species richness, further promoting a widespread positive correlation between these variables (McKinney, 2001; Moore *et al*., 2002; Chown *et al*., 2003; Evans & Gaston, 2005). Thus, areas with high native species richness are most at risk from the harmful effects of invasive exotic species and human activities such as habitat transformation, degradation, and destruction, and overexploitation of natural resources including species (see Vitousek *et al*., 1997, for a review).

Most of the studies mentioned so far focussed on or included exotic plant species richness, for which adequate distribution atlases are often available (e.g., the Southern African Plant Invaders Atlas used by Richardson *et al*., 2005). These studies are essential because of the high prevalence of exotic plant species (Rapoport, 2000; Richardson *et al*., 2005) and the severity of detrimental ecological and economical impacts caused by exotic plant invasions (Gordon, 1998; van Wilgen *et al*., 2001; Le Maitre, 2004). Spatial distribution of exotic plant species richness in South Africa is determined by the natural environmental factors primary productivity and habitat heterogeneity, and the human factors population density, road density, and percentage urban and transformed area (Richardson *et al*., 2005).

Fewer studies have been done on the spatial distribution of exotic animal species richness, examples being studies done on fish (McKinney, 2001; McKinney, 2002; Irz *et al*., 2004; Stohlgren *et al*., 2006), and birds (Case, 1996; Evans *et al*., 2005; Stohlgren *et al*., 2006). The basic variables and mechanisms found to govern the spatial distribution of exotic plant species richness are often extended in the literature to animal species (e.g. Evans *et al*., 2005; Stohlgren *et al*., 1999), one difference being that animals are known to have greater dispersal abilities than plants (Rapoport, 2000). The spatial distribution pattern of exotic animal species richness is therefore assumed to be similar to native animal species richness distribution patterns, and to reflect the response of exotic species to environmental conditions (e.g. primary productivity and habitat heterogeneity), their source of introduction (e.g. humans and human activities), and anthropogenic disturbance to ecosystems (e.g. habitat transformation).

Data on South African birds provide an ideal opportunity to investigate these assumptions and as far as I am aware, no studies have been done on the spatial patterns and the underlying mechanisms of exotic animal species richness at the national scale for South Africa. The Southern African Bird Atlas Project (SABAP, Harrison *et al*., 1997) provides reliable bird distribution data at the quarter-degree square (QDS) resolution (the area of QDS grid cells in South Africa vary from 635 km^2 in the south to 712 km^2 in the north), and includes 11 bird species that are non-native (Hockey *et al*., 2005).

METHODS

It is known that in South Africa, human density and native avian species richness are positively correlated to primary productivity and natural habitat heterogeneity (van Rensburg *et al*., 2002; Chown *et al*., 2003). Habitat transformation, which is positively correlated to human density and productivity (Chown *et al*., 2003), could be regarded as a form of habitat disturbance, which, as mentioned in the Introduction section, is a factor that may benefit exotic species. Further, certain human activities, such as increased habitat heterogeneity in terms of number of different land transformation types, and increased primary productivity associated with irrigation, have been found to benefit South African native bird species, and accordingly, perhaps also exotic bird species (Chapter 2). In addition, not all exotic bird species invade natural habitat, but are rather associated with urban and cultivated areas (Case, 1996; Dean, 2000; Hockey *et al*., 2005). Thus, to determine the relative importance of different anthropogenic and natural environmental factors to spatial distribution in exotic species, I investigated human density, primary productivity, natural and anthropogenic habitat heterogeneity, and urban, cultivated, irrigated, and total transformed area as predictors of the spatial distribution of total number of exotic bird species per QDS (i.e. exotic species richness). In addition to this, following Evans *et al*. (2005), I modelled each exotic species as individual response variables in relation to the predictor variables mentioned above. Doing this would allow the exploration of their separate contributions to the overall spatial distribution of exotic species richness (i.e. exotic species combined). For these two sets of multivariate regression analyses I report only the models that best predicted variation in the response variables. 'Best' models included only predictors that contribute significantly to the model.

Primary productivity was represented by January normalised difference vegetation index (NDVI) values averaged between 1982 and 1991 (Appendix, Map 7). NDVI is obtained by satellite imaging, and it correlates strongly with net primary production and plant biomass (Kerr and Ostrovsky, 2003). The NDVI values used in the current study were obtained from the African Real Time Environmental Monitoring using Meteorological Satellites (Artemis) program of the Food and Agriculture Organization (http://www.fao.org/geonetwork/srv/en/main.home). I specifically used NDVI for January, because compared with other NDVI metrics, it exhibits the most marked spatial variation and explains more of the spatial variation in human density and avian species richness (Evans *et al*., 2006). Natural habitat heterogeneity was represented by the number of vegetation types in each QDS according to Low and Rebelo (1996) (Appendix, Map 4).

Human population density values were derived from the 2001 national population census (Anonymous, 2001; Appendix, Map 2). Total percentage land transformation per QDS (Appendix, Map 9) and percentage cultivated (Appendix, Map 6) and urban area (Appendix, Map 12) per QDS were based on the transformed land-cover data captured by Landsat TM satellite imagery (six main land cover types were recorded mainly between 1994 and 1995: cultivated land, degraded land, plantations, water bodies, urban build-up, and mines and quarries), provided by Thompson (1996). I calculated anthropogenic heterogeneity as the number of transformed land cover types in each QDS (Appendix, Map 3). A spatial distribution map of irrigated areas (Appendix, Map 5) was published by the Agricultural Research Council – Institute for Soil, Climate, and Water (2000), and was downloaded from the Agricultural Geo-Referenced Information System (AGIS) website (http://www.agis.agric.za/agis_metadata/).

To study the spatial relationship between exotic and native bird species richness, I investigated native species richness as a predictor of the spatial distribution of exotic species richness (response). Further, I investigated native species richness as a predictor of the spatial distribution of each exotic species separately (Evans *et al*., 2005). I investigated three native species richness categories, representing different range size categories calculated for each

QDS: (i) all 651 species (Appendix 1, Map 1), (ii) the 25% most widespread species (each occupying a minimum of 610 QDSs) representing the category 'common species' (Appendix, Map 10), and (iii) the 25% most range restricted species (each occupying a maximum of 98 QDSs) representing the category 'rare species' (Appendix, Map 11). This was done because the distribution patterns of common and rare species differ, and common species contribute more towards overall species richness distribution patterns than rare species (i.e., most of the spatial variation is caused by a minority of the most common species) with the result that rare species distribution patterns would be obscured in an analysis that do not separate the two (Lennon *et al*., 2004; Vázquez and Gaston, 2004). Although the 25% cutoff values are arbitrary, they are commonly used to define range size categories (see Gaston, 1994). For these two sets of analyses, I report all models regardless of whether the predictor was significant.

All spatial information datasets have been converted to a QDS resolution using ArcView GIS of ESRI Inc. (1998). I removed QDSs overlapping the border of the country (i.e. those overlapping with the coast or neighbouring countries) from the datasets (Fig. 1), as information in these cells are incomplete and could be misleading (n = 1669 QDSs used). For this reason exotic species restricted to the coast (Chaffinch, *Fringilla coelebs*; Chukar partridge, *Alectoris chucar*; House Crow, *Corvus splendens*) were omitted from the study and only eight exotic species were included (Table 1, Fig. 2).

I reduced heteroscedasticity in all variables by logarithmically transforming the data to the base 10, before applying the relevant statistical procedures. If zero values were present within a dataset, I added an incremental value, 1, to all values in that dataset before applying log transformation.

To detect collinearity, I examined the tolerance value for each predictor variable. Tolerance, as defined by Neter *et al*. (1996), is 1 minus the squared multiple correlation of a predictor variable with all other independent variables in the regression equation (Statsoft Inc., 1999); the lower the tolerance of a given variable, the stronger the correlation between the variable in question and one or more of the other predictors (Quinn and Keough, 2002). Following Quinn and Keough (2002), those variables with tolerance values smaller than 0.1, should be eliminated from subsequent analyses. However, as none of the explanatory variables were found to be redundant, all were included in the analyses (Table 2).

I used the SAS version 9.1 procedure 'PROC MIXED' (SAS Institute Inc. 2002) to investigate the spatial distribution of exotic species richness. Data from contiguous grid cells are often spatially autocorrelated, which violates the assumption of independent errors on which many classical statistical tests are based (Legendre *et al*., 2002). Therefore, using 'PROC MIXED', I implemented spatial correlation models in which spatial variation in the response variable is tested for spatial autocorrelation (null spatial models are compared with

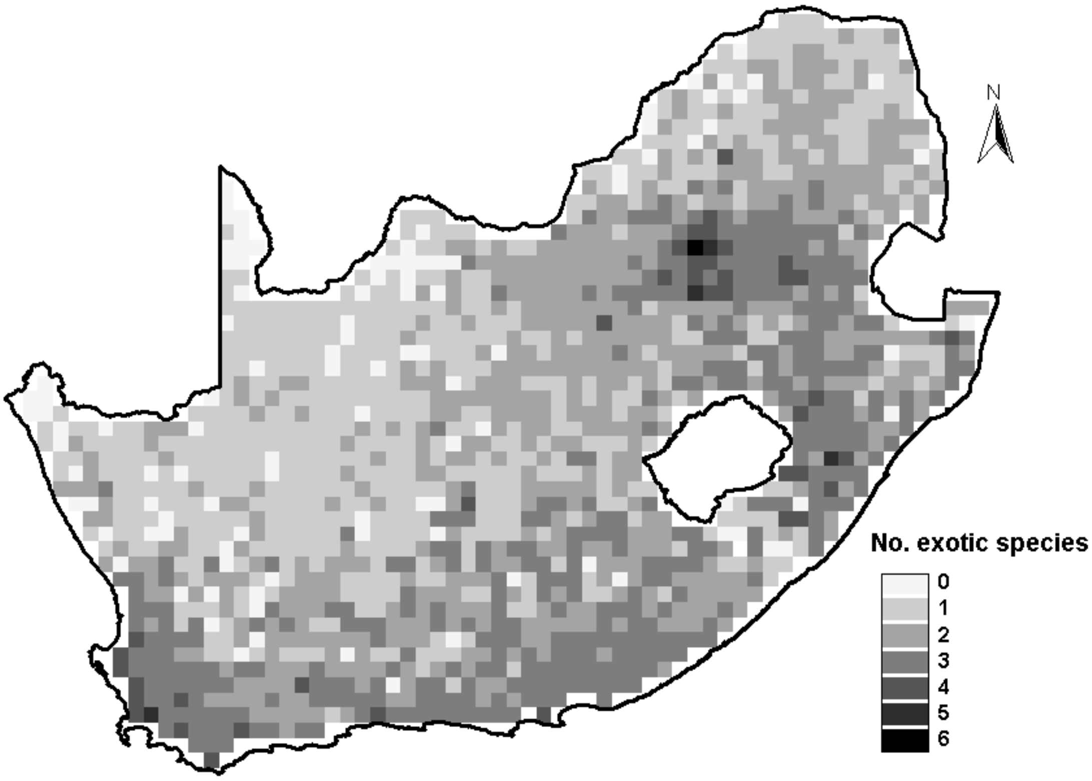

Figure 1 The number of exotic bird species per quarter-degree square in South Africa, as provided by the Southern African Bird Atlas Project (Harrison *et al.*, 1997).

Table 1 The eight exotic species investigated, as provided by the Southern African Bird Atlas Project (Harrison *et al*., 1997). Four of the species (a – d) are widespread in South Africa (see Fig. 2 a – d), whereas the other four (e – h) occupy much smaller areas of South Africa (i.e. only a few quarter-degree squares, see Fig. 2 e – h).

Species	Origins	Problem caused by species
Widespread		
a) Common Myna, *Acridotheres tristis*	India and central and southern Asia	Pest species, and suspected to compete with natives at a local scale.
b) Common Starling, *Sturnus vulgaris*	Eurasia	Agricultural pest species
c) House Sparrow, *Passer domesticus*	Eurasia and North Africa	No serious problems
d) Rock Dove, *Columba livia*	North Africa, Europe and South West Asia	No serious problems
Range restricted		
e) Budgerigar, *Melopsittacus undulates*	Semi-arid Australia	None
f) Mallard, *Anas undulata*	Holarctic	Threatens native ducks through hybridization.
g) Rose-ringed Parakeet, *Psittacula krameri*	North Africa in Sahel, and southern Asia	Potential agricultural pest species.
h) Mute Swan, *Cygnus olor*	Western Europe to China	None. Current populations are probably not self-sustaining

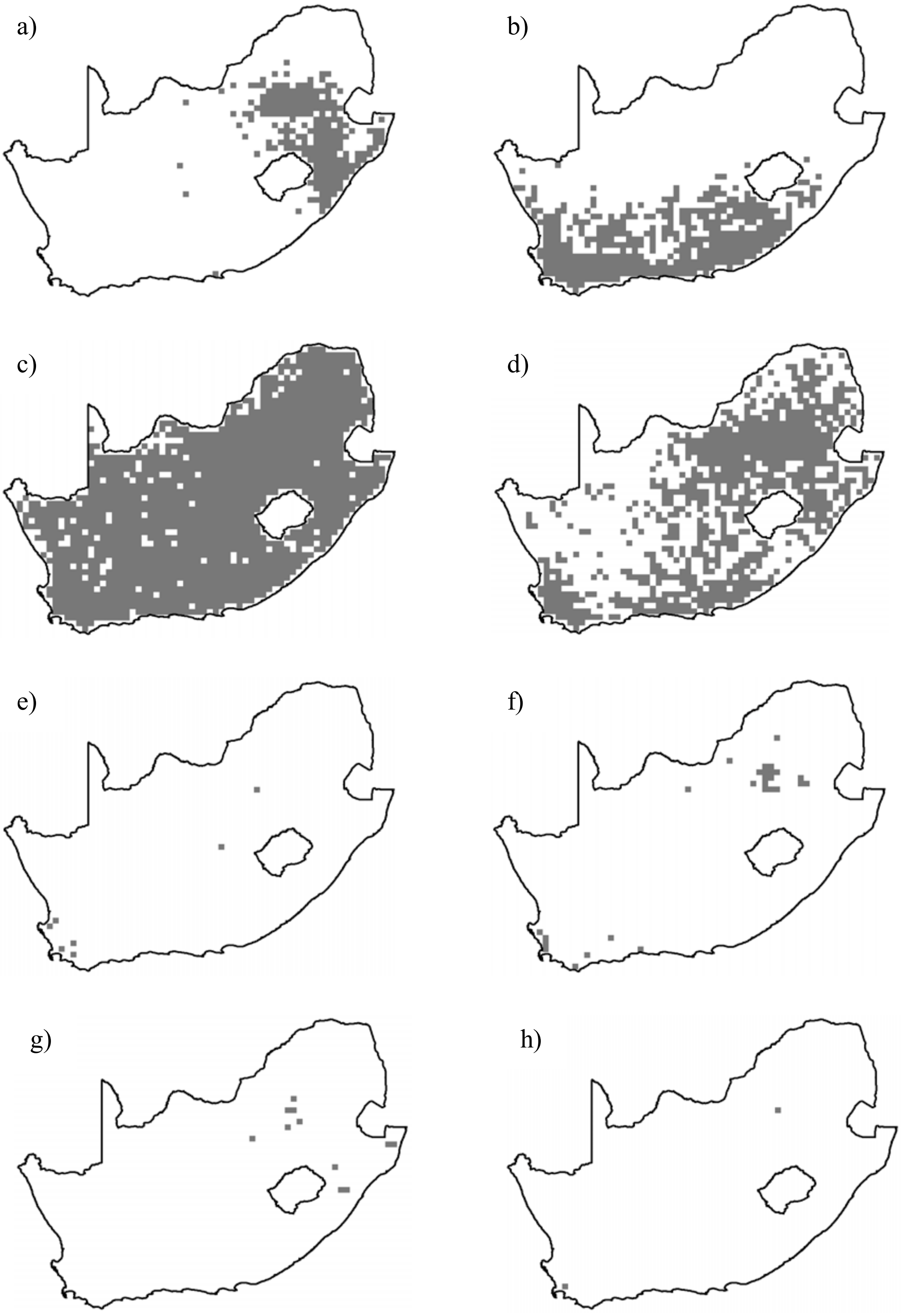

Figure 2 Quarter degree resolution distribution maps of 8 exotic bird species as provided by the Southern African Bird Atlas Project (Harrison et al., 1997): a) common myna, b) common starling, c) house sparrow, d) rock dove, e) budgerigar, f) mallard, g) rose-ringed parakeet, and h) mute swan.

Table 2 Tolerance values are used to detect collinearity between the predictor variables investigated in this chapter (Neter *et al.*, 1996; Quinn & Keough, 2002). A tolerance value lower than 0.1 would have indicated that a predictor variable is redundant; however, all predictor variables used in this chapter could be included in the analyses (Quinn & Keough, 2002).

Predictor	Tolerance value
Human density	0.23
Primary productivity	0.39
Vegetation heterogeneity	0.82
Cultivated area	0.22
Irrigated area	0.76
Urban area	0.60
Total transformed area	0.14
Anthropogenic heterogeneity	0.24

the independent errors models with a likelihood ratio test giving a χ^2 value and level of significance), and a spatial covariance matrix is fitted to the data to adjust the test statistics (Littell *et al*., 1996). I used an exponential spatial covariance structure in all analyses, as this always provided a better fit to the null model compared with the five others: spherical, Gaussian, linear, linear log and power. Variation in the response variable was significantly ($P<0.0001$) spatially autocorrelated in each analysis done with 'PROC MIXED' in this study. To investigate the spatial distribution of the individual exotic species I used the SAS version 9.1 procedure 'PROC LOGISTIC' (SAS Institute Inc. 2002), which is a logistic regression procedure that allows the use of presence-absence (i.e. binary) data to model the probability of occurrence of a species in relation to various predictor variables (Evans *et al*., 2005). Unfortunately, a test that controls for spatial autocorrelation is not available for binary regressions, and for analyses using 'PROC LOGISTIC' I could only report models based on the independent errors assumption.

To test the 'goodness of fit' of different models, the 'PROC MIXED' and 'PROC LOGISTIC' procedures supply Akaike's information criterion (AIC) values, of which smaller (or more negative) values indicate a better model. AIC values do not mean anything by themselves and are only used to compare models with different predictor variables and the same response variable (SAS Institute Inc., 2004). Thus, AIC values could not be used to compare relationship strength between different subsets of a dataset. For this reason, as rare species occupy fewer QDSs at the national scale (i.e. a subset of QDSs occupied by all and common species), the common and all species datasets were reduced so that the area covered matched that of the rare species in size and location (i.e. the same QDSs were analysed, n=1011), in order to use AIC to choose the native species richness category with a spatial distribution that is most similar to the response variables, individual exotic species and exotic species richness.

To detect simple nonlinear relationships, the square term of each variable was included into the models together with the variable concerned (Evans and Gaston, 2005). An increase in the 'goodness of fit' (i.e. a decrease in the AIC value), indicate a nonlinear relationship.

Finally, for all analyses, the 0.05 level of probability was accepted as indicating statistical significance.

RESULTS

Human density (F=181.83; P<0.0001) and natural habitat heterogeneity (F=13.39; P=0.0003) are the only human and natural environmental factors included in the best model explaining spatial distribution patterns in exotic species richness. Both have a positive correlation with exotic species richness. For both these predictors, n=1668, the numerator df = 1, and the denominator df = 1666.

Of all the predictor variables investigated, only total transformed area was not included in any model predicting the probability of occurrence of any given exotic bird species. The reason for this could be due to some level of collinearity with one or more of the other predictors, despite having a tolerance value larger than 0.1 (Table 2). Nevertheless, when examined individually, exotic bird species seem to differ substantially in terms of the combination of factors predicting their occurrence (Table 3). This result is supported by the fact that the distribution ranges of these exotic bird species in South Africa differ substantially and some, like common myna and common starling (Fig. 2 a and b respectively), hardly overlap with each other (Harrison *et al*., 1997).

The probability of occurrence of common myna (the response variable) was best predicted by a combination of human density, cultivated area, and primary productivity with which it was positively correlated, and urban build-up with which it was negatively correlated (Table 3). Judging from the Chi-square values, primary productivity was the predictor that contributed the most to the model. The square terms (which may or may not have been positively correlated to the response variable) of human density and urban build-up were included in the model, meaning that, compared to the remaining predictor variables, these predictors were nonlinearly correlated with the response variable.

The probability of occurrence of common starling was best predicted by human density, cultivated area, irrigated area, primary productivity and vegetation heterogeneity (Table 3). Primary productivity contributed most to the model, although it was negatively correlated to the probability of occurrence of common starling. Most of the other predictors had positive relationships with the response variable, except cultivated area. Human density, irrigated area and vegetation heterogeneity had nonlinear relationships with the response variable.

The probability of occurrence of the house sparrow was best predicted by human density and irrigated area to which it was positively correlated and cultivated area to which it was negatively correlated (Table 3). Cultivated area had a nonlinear relationship with the response variable. Human density seemed to have contributed most to the model.

The probability of occurrence of the rock dove was best predicted by all predictors except total transformed area and irrigated area (Table 3). Only cultivated area had a negative relationship with the response variable. Human density, cultivated area, and anthropogenic habitat heterogeneity had nonlinear relationships with the response variable. Human density contributed most to the model.

The probability of occurrence of the budgie was best predicted by human density, with which it was negatively correlated, and cultivated area, irrigation and urban build-up,

Table 3 The chi-square (χ^2) values and significance levels of all predictors included in the best model predicting the probability of occurrence of each exotic bird species. All predictors were log-transformed to the base ten.

Predictor	a) Common myna	b) Common starling	c) House sparrow	d) Rock dove	e) Budgerigar	f) Mallard	g) Rose-ringed parakeet
Human density	$\chi^2=4.73$*	$\chi^2=50.01$****	$\chi^2=20.70$ ****	$\chi^2=62.38$****	$\chi^2=12.71$†††	n.i.	$\chi^2=25.04$****
Human density^2	$\chi^2=3.89$†	$\chi^2=42.63$††††	n.i.	$\chi^2=45.61$††††	n.i.	n.i.	n.i.
Cultivation	$\chi^2=17.14$****	$\chi^2=7.09$††	$\chi^2=14.14$†††	$\chi^2=7.56$††	$\chi^2=10.85$**	$\chi^2=9.73$**	n.i.
Cultivation^2	n.i.	n.i.	$\chi^2=15.22$****	$\chi^2=14.53$***	n.i.	n.i.	n.i.
Irrigation	n.i.	$\chi^2=18.97$****	$\chi^2=11.23$***	$\chi^2=13.17$***	$\chi^2=15.38$****	n.i.	n.i.
Irrigation^2	n.i.	4.60†	n.i.	n.i.	n.i.	n.i.	n.i.
Urban build-up	$\chi^2=10.47$††	n.i.	n.i.	$\chi^2=34.47$****	$\chi^2=12.44$***	$\chi^2=56.99$****	n.i.
Urban build-up^2	$\chi^2=17.00$****	n.i.	n.i.	n.i.	n.i.	n.i.	n.i.
Primary productivity	$\chi^2=116.12$****	$\chi^2=95.46$††††	n.i.	$\chi^2=4.10$*	n.i.	n.i.	n.i.
Anthropogenic heterogeneity	n.i.	n.i.	n.i.	$\chi^2=7.94$**	n.i.	n.i.	n.i.
Anthropogenic heterogeneity^2	n.i.	n.i.	n.i.	$\chi^2=14.69$†††	n.i.	n.i.	n.i.
Vegetation heterogeneity	n.i.	$\chi^2=4.01$*	n.i.	$\chi^2=9.87$**	n.i.	n.i.	n.i.
Vegetation heterogeneity^2	n.i.	$\chi^2=12.80$***	n.i.	n.i.	n.i.	n.i.	n.i.

Significance levels: positive effects, *$P<0.05$; **$P<0.01$; ***$P<0.001$; ****$P<0.0001$; negative effects, †$P<0.05$; ††$P<0.01$; †††$P<0.001$; ††††$P<0.0001$. Abbreviation: n.i., not included.

with which it was positively correlated (Table 3). Irrigation contributed most to the model.

The probability of occurrence of the mallard was best predicted by cultivated area and urban build-up (Table 3). Both predictors had positive correlations with the response variable, and urban build-up contributed most to the model.

The probability of occurrence of the rose-ringed parakeet was best predicted by human density only, with which it had a positive relationship (Table 3).

Mute swan was omitted from this analysis because it is present in only two QDSs of the dataset (Fig.2 c), and thus does not provide enough data for the analysis to be conducted.

The spatial distribution of exotic species richness was significantly positively correlated to all three native species richness categories. Exotic species richness was linearly correlated to all native species richness (F=213.83; P<0.0001; AIC= -1467.6) and rare native species richness (F=61.55; P<0.0001; AIC= -1338.5); however, exotic species richness had a nonlinear correlation with common native species richness (log common species: F=10.87, P=0.001; log common species^2: F=19.47, P<0.0001; AIC= -1526.8). The AIC values indicated that common species richness and its square term were the predictors that best describe spatial patterns in exotic species richness, followed by all species richness, and then rare species richness. For all these analyses, n=1011, the numerator df = 1, and the denominator df > 1008.

Generally, the probability of occurrence of an exotic bird species in a QDS increased with an increase in the number of native bird species occurring in that QDS. However, negative relationships were found between the probability of occurrence of rock dove and common native species richness, and the probability of occurrence of house sparrow and all and common native species richness (Table 4). Further, the probability of occurrence of budgies increased significantly only with an increase in the number of common native species, whereas no significant relationships were found between budgies and all and rare native species richness (Table 4). Nonlinear relationships were present for the probability of occurrence of common myna (rare native species), common starling (all three native species richness categories), mallard (rare native species), rock dove (all categories), and house sparrow (all and common native species richness categories) (Table 4). As indicated by the AIC values, probability of occurrence of four species (budgie, mallard, rock dove and house sparrow) were best predicted by common native species richness, whereas probability of occurrence of three exotic species (common myna, common starling and rose-ringed parakeet) were best predicted by the native species richness category ‘all species’ (Table 4). Again, mute swan was omitted from this analysis.

Table 4 The probability of occurrence of each exotic bird species in relation to three categories of native bird species richness, all species, the 25% most widespread species (common species) and the 25% most range restricted species (rare species). Chi-square (χ^2) values and significance levels are provided for each predictor. All predictors were log-transformed to the base ten.

	Native species group	Native richness	Native richness^2	AIC
a) Common myna	All	χ^2=110.35****	n.i.	800.7
	Common	χ^2=76.02****	n.i.	852.5
	Rare	χ^2=38.28****	χ^2=15.06†††	889.4
b) Common starling	All	χ^2=74.77****	χ^2=76.27††††	1004.4
	Common	χ^2=8.81**	χ^2=7.71††	1075.8
	Rare	χ^2=19.62****	χ^2=26.06††††	1106.6
c) House Sparrow	All	χ^2=6.45†	χ^2=8.22**	399.5
	Common	χ^2=13.35†††	χ^2=16.00****	354.3
	Rare	χ^2=7.95**	n.i.	450.3
d) Rock Dove	All	χ^2=10.53**	χ^2=6.88††	1081.3
	Common	χ^2=21.35††††	χ^2=29.83****	893.9
	Rare	χ^2=44.49****	χ^2=21.88††††	1332.1
e) Budgerigar	All	χ^2=1.51 n.s.	n.i.	85.8
	Common	χ^2=4.49*	n.i.	78.5
	Rare	χ^2=1.30 n.s.	n.i.	86.4
f) Mallard	All	χ^2=13.91***	n.i.	240.6
	Common	χ^2=22.12****	n.i.	212.2
	Rare	χ^2=12.78***	χ^2=10.51††	234.5
g) Rose-ringed Parakeet	All	χ^2=18.19****	n.i.	89.6
	Common	χ^2=9.92**	n.i.	104.1
	Rare	χ^2=11.59***	n.i.	113.1

Significance levels: positive effects, *$P<0.05$; **$P<0.01$; ***$P<0.001$; ****$P<0.0001$; negative effects, †$P<0.05$; ††$P<0.01$; †††$P<0.001$; ††††$P<0.0001$.

Abbreviations: AIC, Akaike's information criterion (smaller values indicate a better model); n.i., not included; n.s., not significant.

DISCUSSION

One of the most noticeable results of this study is that there is limited agreement between the models concerning the spatial distribution of exotic bird species richness and the models concerning the spatial distributions of individual exotic bird species. Further, as mentioned in the Results section, models predicting the occurrence of individual exotic species differ substantially from one another. Generally, the models predicting the probability of occurrence of individual exotic species included more variables than the models that best predicted spatial variation in exotic species richness. It should be kept in mind that 'PROC LOGISTIC', used to model the distributions of each individual exotic species, is a less stringent analysis than the 'PROC MIXED' analysis that take spatial autocorrelation into account. For this reason, it is possible that the models concerning individual exotic species included some predictors that would have been excluded from a more stringent analysis. Therefore, one should be cautious when interpreting the results from the 'PROC LOGISTIC' analyses, and view the analyses concerning the probability of occurrence of individual exotic species only as a supplement to the analyses concerning the spatial distribution of exotic species richness.

The spatial distribution of exotic species richness in South Africa was mainly determined by human density, with which it had a positive correlation. A positive correlation between exotic species richness and human density is consistent with various other studies (McKinney, 2001; McKinney, 2002; Pyšek *et al.*, 2002; Richardson *et al.*, 2005; Stohlgren *et al.*, 1999). However, this result conflicts with Evans *et al.* (2005) who found that human density is not significantly correlated to exotic bird species richness in Britain if energy availability is taken into account. A positive exotic species richness–human density correlation is also generally consistent with the results for individual species, for which human density made a positive contribution to almost all models (human density was negatively correlated to budgie only) predicting the probability of finding an exotic species in a QDS. Further, local scale observations of all of the species included in the current study suggested that they tend to be closely associated with humans (Dean, 2000; Hockey *et al.*, 2005). Overall, human density seems to be an important variable determining the spatial distribution of exotic bird species.

Previous local scale studies (e.g. Case, 1996; Dean, 2000; Hockey *et al.*, 2005) also suggested that human settlements and human-modified landscapes are important habitats to exotic bird species. According to the results from the current study, and depending on the bird species in question, cultivated and irrigated area, urban build-up and anthropogenically created habitat heterogeneity all played a (usually positive) role in determining the probability of occurrence of an exotic bird species in South Africa at the QDS resolution. Thus, as suggested by previous studies (Case, 1996; Dean, 2000; Fine, 2002; Le Maitre *et al.*, 2004), certain exotic bird species may benefit from human activities and human-induced habitat modification. However, none of these human-caused factors made a significant contribution to explaining the spatial distribution of exotic species richness if human density was taken into account, which conflicts with the abovementioned studies.

It is likely that the positive exotic bird species richness–human density correlation is dependent on human activities other than those investigated in the current study. One possibility is a greater probability of introduction and establishment of new individuals in areas with high human densities. This is unlikely however, as, except for budgies, rock doves, and mute swans, no recent introductions have taken place (Hockey *et al.*, 2005). Further, common myna, common starling, house sparrow, rock dove and rose-ringed parakeet all have well-established populations that have expanded, and they are now found far from their initial sites of introduction (Hockey *et al.*, 2005). Another possibility is that humans provide one or more undiscovered (through the current study's methods) beneficial factors that promote exotic species richness. An example of such a beneficial factor is the feeding of animals, either directly (e.g. bird feeders) or indirectly through exotic vegetation or refuse (Emlen, 1974; Mills *et al.*, 1989; Morneau *et al.*, 1999, Jokimäki *et al.*, 2002). Dean (2000) and Hockey *et al.* (2005) report that the exotic species investigated in the current study often scavenge on human refuse, and feed from bird feeders and on the seeds and fruit of exotic vegetation and crops. Further, they use buildings, nest boxes, bridges and other man-made structures for nest sites, and incorporate man-made materials in their nests (Dean, 2000; Hockey *et al.*, 2005). These factors were determined from local scale observations, suggesting that the QDS resolution might have been too large to detect all of the factors that may promote a close association between exotic species richness and human density.

Natural habitat heterogeneity (i.e., vegetation type heterogeneity) also played a smaller significant role in explaining the spatial distribution of exotic species richness, consistent with Lonsdale (1999) and Richardson *et al.* (2005). In contrast, for the individual species analyses, natural heterogeneity seemed to play a small significant positive role only for common starling and rock dove.

Primary productivity was not a significant determinant of spatial distribution in exotic bird species richness in South Africa, which conflicts with studies on exotic plant species richness in South Africa (Richardson *et al.*, 2005) and California, USA (Williams *et al.*, 2005), and exotic bird species richness in Britain (Evans *et al.*, 2005), in which significant positive correlations between primary productivity or energy availability (as a limiting factor of primary productivity) and exotic species richness were reported. For the individual species analyses, primary productivity played an important positive role only for common myna, for which it is also the most important predictor. Dean (2000) suggested that common myna are restricted to the more productive and warmer regions in the East of South Africa, and did not invade the cooler southern regions of the country. Conversely, a strong negative relationship between common starling and primary productivity suggests that common starlings avoid areas with high primary productivity. A possible reason for this is that they were originally adapted to cooler climates and therefore they are restricted to the cooler parts of South Africa – they did not expand far into the productive warmer regions of KwaZulu-Natal in the East of South Africa, where common myna are present (Dean, 2000). Rock dove was the only other species for which primary productivity was included in the best model, and it only played a small role. The finding that primary productivity is generally unimportant to individual exotic bird species conflicts with Evans *et al.* (2005) in which energy availability was found to be important in predicting the probability of occurrence of all exotic bird species present in Britain. Evans *et al.* (2005) suggested that most of these species originated in countries that are warmer than Britain, hence the importance of energy availability. Dependence on humans and human activities for food and shelter, discussed previously, may also explain why the spatial distributions of exotic bird species in South Africa do not seem to depend on primary productivity, as Dean (2000) suggested for house sparrow and rock dove that seem to occur across the country in almost any kind of climate, provided that there are humans or man-made structures present.

Although positively correlated to all three native species richness categories, spatial distribution in exotic species richness was more similar to that of common native species richness than rare native species richness, possibly indicating that exotic species behave more similarly to common species. This idea is supported by the fact that human density is an important correlate of spatial variation in both exotic (current study) and common native (Chapter 2) species richness. Further, the distributions of individual exotic species were generally most similar to the distribution of common native species richness, with some exceptions, and never most similar to the distribution of rare native species richness. These observations should be expected, as common and rare species are known to react differently to anthropogenic disturbance. In particular, common species, many of which are generalists, are often able to take advantage of habitats altered by human activities, whereas rare or specialist species usually become rarer (McKinney and Lockwood, 1999; Davies *et al.*, 2004; Fairbanks, 2004). Exotic bird species that are successful at establishing a population and spreading are often pre-adapted for invasion by being opportunistic generalists that are closely associated with humans and tolerant of a wide range of environmental conditions (Dean, 2000; Duncan *et al.*, 2003). Similarly, Dean (2000) suggested that common native species with the characteristics of a successful invader could also increase in number and expand their ranges. Thus invasive exotic species and common species with expanding ranges, as was shown for North America by La Sorte and Boecklen (2005) and La Sorte (2006), may share many traits and may both respond positively to human densities. The pied crow (*Corvus albus*) is an example of a generalist species native to South Africa that benefits to a large extent from human activities and has made use of the human modification of habitats to expand its range in South Africa (Harrison *et al*., 1997).

Even though invasions may cause local extinctions (McKinney, 2002; Clavero and García-Berthou, 2005), the number of additions of exotic species to a local species assemblage may still be greater than extinctions from that assemblage (Hobbs and Mooney, 1998). It can thus often be seen at both local scales and regional scales that species richness of an area increases through invasion whereas globally species richness decreases due to global extinctions (Stohlgren *et al*., 1999; McKinney, 2002; Sax *et al*., 2002; Sax and Gaines, 2003; Williams *et al*., 2005; Stohlgren *et al*., 2006). It is predicted that invasion may eventually cause homogenization of community assemblages across the globe, as the few species that are capable of thriving in habitats altered by human activity during the time of global change, replace the majority of species (McKinney and Lockwood, 1999). The invaders are usually widespread or opportunistic species (exotic or native), which are replacing range restricted, specialist species. In the current situation in South Africa, exotic bird species richness *per se* would not substantially increase local species richness because of the small number of exotic species recorded in South Africa. However, common native species with expanding ranges may have the potential to threaten South African bird assemblages with homogenization. Further, the population density of invasive exotic species and certain native generalists are often greater than the population density of rare species in transformed areas (e.g., Fairbanks *et al*., 2002), thus possibly threatening biodiversity through interspecific competition, and hybridization of exotic and native species (Emlen, 1974; Clout, 2002). It was however not possible to test this idea due to a lack of population density data and should be explored further.

Information on the habitat selection and opportunistic scavenging and nesting behaviour of individual exotic bird species mentioned previously throughout the Discussion section, have usually been obtained through direct local-scale observations of exotic species rather than a QDS resolution analysis (Dean, 2000; Hockey *et al*., 2005). Nevertheless, there is a lack of fine resolution and local-scale studies of exotic and native birds in South Africa. It can be seen that knowledge gained about the factors that correlate with exotic species at a QDS resolution differs slightly from that gained from local-scale observations reported in Hockey *et al*. (2005). For example, whereas the QDS-resolution analysis of common starling in the current study showed no effect of urban build-up and a negative effect of cultivated area, local-scale observations revealed that common starling are present in urban areas and agricultural fields (Hockey *et al*., 2005). Studies are needed to clarify this scale-dependent effect. Further, it is unclear how exotic bird species in South Africa interact with native species, although common mynas are suspected to displace natives at a local scale and mallards are known to hybridize with native *Anas* species (Dean, 2000; Hockey *et al*., 2005).

Local-scale studies are needed to examine the interactions between exotic and native species, and Dean (2000) argued that there is also a lack of studies on the impacts of exotic fauna on indigenous species and vegetation. In addition, there is a lack of local-scale and fine-resolution studies on exotic species richness, as opposed to species-specific studies.

Case (1996) conducted and reviewed local-scale studies, and reported that exotic and native birds occupy different habitats and use different resources at a local scale. Exotic bird species are usually not abundant in pristine natural habitats (Case, 1996; Dean, 2000; Hockey *et al*., 2005), and Dean (2000) suggests that exotic bird species in South Africa might be competitively dominant and more prevalent in human-modified habitats, whereas native species are competitively dominant and more prevalent in pristine natural habitat. Case's (1996) finding that exotic and native species occupy different habitats, implies that the spatial distributions of exotic bird species richness and native bird species richness in South Africa might be negatively correlated at finer resolutions, at which different habitat types could be distinguished more clearly. It is conceivable that, if interspecific competition would occur, it would be mainly between exotic birds and the few generalist native birds that are closely associated with humans and could therefore come into regular contact with exotic birds (Fairbanks *et al*., 2002).

In conclusion, not all assumptions regarding the factors that govern the spatial distribution in exotic species richness are relevant for all taxa and all situations. In accordance with many studies on plants and animals and in different locations around the world, exotic bird species richness in South Africa is significantly positively correlated to native species richness, natural habitat heterogeneity and human density. Further, common native species are more similar to exotic species than rare native species are, highlighting their potentially invasive and opportunistic natures. However, unexpectedly, neither primary productivity, nor any form of anthropogenic habitat modification considered in this study, contributes significantly to the observed spatial patterns of exotic bird species richness if human density and vegetation heterogeneity is taken into account. This unexpected observation also differs substantially from what was found for individual exotic bird species, and in addition, individual exotic bird species differ substantially from one another. Further, the results from this QDS-resolution analysis differ from previous local-scale observations. Therefore, this study leaves many unanswered questions, particularly those that can be elucidated with further local-scale and fine-resolution studies.

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CHAPTER 4

General Discussion

An essential component of effective biodiversity conservation is to understand patterns of species richness through space and time thus contributing towards the increasing need to understand the mechanisms underlying biodiversity, and human impacts on species and populations. Based on several hypotheses that have emerged from recent studies, this thesis has addressed the contribution of different natural and anthropogenic environmental factors to (i) the maintenance of a positive relationship between South African native bird species richness and human density, in the face of human-caused biodiversity threats, and (ii) the spatial distribution patterns of exotic bird species in South Africa.

Four main results can be highlighted. First, humans have substantial positive and negative impacts on native bird species richness distribution patterns that are observable at the quarter-degree square resolution. Chapter 2 of this thesis revealed the way in which humans influence native species richness more clearly than before. For example, whereas van Rensburg *et al.* (2004) found no significant effects of land transformation, Chapter 2 clearly indicate the role of land transformation in determining bird distribution patterns, perhaps due to differences in methodology. In particular, categorizing areas according to severity of pristine natural habitat loss, and perhaps using alpha instead of beta species diversity, has revealed the effect of land transformation on bird species more effectively in Chapter 2 than in van Rensburg *et al.* (2004).

Second, factors governing spatial distribution in exotic species richness are not entirely similar among different taxa or species, as is often assumed (Chapter 3). There are also indications that the particular combinations of environmental factors determining the spatial distributions of exotic species are scale-dependent (Chapter 3).

Third, native bird species richness is often reduced in areas that are highly transformed and contain little natural habitat (Chapter 2). Thus the main threat to native bird species richness in South Africa is land transformation, although low levels of transformation might increase the variety of habitats available for those species that are able to adapt to the novel conditions (Chapter 2). Being highly dependent on humans, exotic species seem to mostly avoid natural habitat, and seem to come into regular contact with native birds only in areas with a dense population of humans (Chapter 3). Either way, natural habitat remains important for maintaining current levels of native bird species richness.

Fourth, common bird species differ from rare bird species with regard to their response to natural and anthropogenic environmental factors (Chapter 2; but see also McKinney & Lockwood, 1999; Davies *et al.*, 2004; Fairbanks *et al.*, 2002), and common species contribute more to species richness distribution patterns than rare species (Chapter 2, see also Lennon *et al*., 2004; Vázquez & Gaston, 2004). This highlights the importance of separating rare and common species in species richness distribution studies, which is a method often used in recent studies (e.g., Balmford *et al*., 2001; Chown *et al*., 2003; Evans & Gaston, 2005). Otherwise, whereas common species distribution patterns would be understood well enough, the distribution patterns of rare species in need of conservation measures would be neglected. It should also be noted that common native species may be invasive when they shift their ranges, which is a trait more often associated with exotic species (Chapter 2 and 3; but see also La Sorte & Boecklen, 2005; La Sorte, 2006).

The studies included in this work do not address the main theme completely, but rather supply various further questions that are important for effective conservation of current levels of species richness and species richness distribution patterns. First, in Chapter 2, I speculate that common bird species are more easily able to modify their distribution in response to human activities than rare species, resulting in the observation that common species do not follow the positive species richness–human density relationship in highly transformed areas, whereas the relationship generally remains positive for rare species. This argument should be tested with a temporal study, comparing the way in which in the distribution ranges of common and rare species change in relation to changes in different types of land cover (see e.g., La Sorte & Boecklen, 2005; La Sorte, 2006). A more recent land cover dataset is already available for South Africa (the South African National Land Cover Database for 2000, provided by Landsat TM); however, a new bird distribution dataset is also needed. The second Southern African Bird Atlas Project (SABAP) was launched in July 2007, and after completion it could provide an opportunity to conduct such temporal studies. If it is true that bird species change their distribution range in response to changes in land cover, perhaps indicator bird species that could be used to assess habitat quality could be identified.

Second, studies and data at finer resolutions are urgently needed. A hypothesis relating to the species richness–human density relationship, requiring fine-resolution bird distribution patterns, is mentioned in Chapter 2. This hypothesis could not be tested for South Africa, because adequate finer resolution bird distribution data is not yet available. However, the second SABAP will provide bird distribution data at the 5 minute resolution instead of the quarter-degree resolution as for the first SABAP (Harrison *et al*., 1997). Further, fine-resolution data could also be used to study the degree of aggregation and concentration of natural habitat fragments, humans, and human activity within QDSs, and its effect on species richness (Franklin & Forman, 1987; Green *et al*., 2005; Lenth *et al*., 2006). Fine-resolution studies are also required to examine the previously mentioned scale-dependence of exotic bird species distribution patterns (Chapter 2). Further, fine-resolution can be used to examine habitat partitioning and interactions between exotic bird species and native bird species, to determine whether exotic bird species have a local negative impact on native species (Case, 1996; Dean, 2000).

Third, even though humans have generally preferred to colonize areas with favourable environmental conditions such as high primary productivity, the influence of lifestyle choices on per capita human impact and the influence of political and economic factors on human distribution patterns, should not be ignored. These factors are often substantial forces determining the impact of humans on the environment and changes in the historical distribution of species richness (Laurance *et al*., 2002; Real *et al*., 2003; Liu, 2004). In particular, inequality in the distribution of wealth and resources, resulting in vast differences between socioeconomic classes, is a prominent global problem occurring not only between developed and developing nations, but also between population groups within these nations (SARDC, 1994; Reed, 2002; Liu, 2004). This scenario is often linked to resource depletion, environmental degradation and loss of biodiversity, and is likely to become even more prevalent in the future (Miller *et al*., 1995; Perrings, 1995; Homer-Dixon, 1999; Scharlemann *et al*., 2004). Specifically, most benefits derived from ecosystem services is enjoyed by a disproportionately small section of the human population (high socioeconomic classes), whereas degradation of ecosystems and loss of biodiversity and other resources is more prevalent in areas with high poverty rates and a high dependence on local resources, so that poor communities bear most of the consequences of these detrimental impacts (Scholes *et al*., 2005). An example of the latter situation is the marginal and resource poor areas in South Africa known as the former homelands, where most of the rural poor are concentrated (SARDC, 1994; Homer-Dixon, 1999).

It can thus be argued that studying the human modification of species distribution patterns should also include studies on political factors and on the spatial distribution of different socioeconomic classes and consumption patterns (e.g., Fairbanks, 2004). This is especially true for South Africa, seeing that this country has one of the highest degrees of inequality in the world (May *et al*., 2000).

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APPENDIX

This appendix includes maps of the spatial distributions of all predictor variables used in this thesis at the quarter-degree square resolution. The maps were created using ArcView GIS 3.3 (ESRI Inc., 1998). All variables have been log transformed to the base ten, as this appeared to improve the visual representation of each predictor on the map.

Map 1	Number of native bird species per quarter-degree square (QDS) obtained by the Southern African Bird Atlas Project (Harrison *et al*., 1997).
Map 2	Number of humans per QDS as calculated from the 2001 national population census (Anonymous, 2001).
Map 3	Number of land-use types per QDS, based on six broad categories of transformed land-cover: cultivated land, degraded land, plantations, waterbodies, urban build-up, and mines and quarries (Thompson, 1996).
Map 4	Number of vegetation types per QDS as described by Low and Rebelo (1996).
Map 5	The percentage area per QDS that is irrigated (Agricultural Research Council – Institute for Soil, Climate, and Water, 2000; http://www.agis.agric.za/agis_metadata/).
Map 6	The percentage area per QDS that is cultivated (Thompson, 1996).
Map 7	Primary productivity per QDS as represented by the normalised difference vegetation index (NDVI) (Food and Agriculture Organization; http://www.fao.org/geonetwork/srv/en/main.home).
Map 8	Precipitation (mm^{-1}.year) per QDS (Schulze, 1997).
Map 9	The percentage area per QDS that has been transformed by the sum of the six broad categories of land-cover named for Map 3 (Thompson, 1996).
Map 10	Number of common bird species (i.e. the 25% most widespread bird species) per QDS obtained by the Southern African Bird Atlas Project (Harrison *et al*., 1997).
Map 11	Number of rare bird species (i.e. the 25% most narrowly distributed bird species) per QDS obtained by the Southern African Bird Atlas Project (Harrison *et al*., 1997).
Map 12	The percentage area per QDS that is covered by urban build-up (Thompson, 1996).

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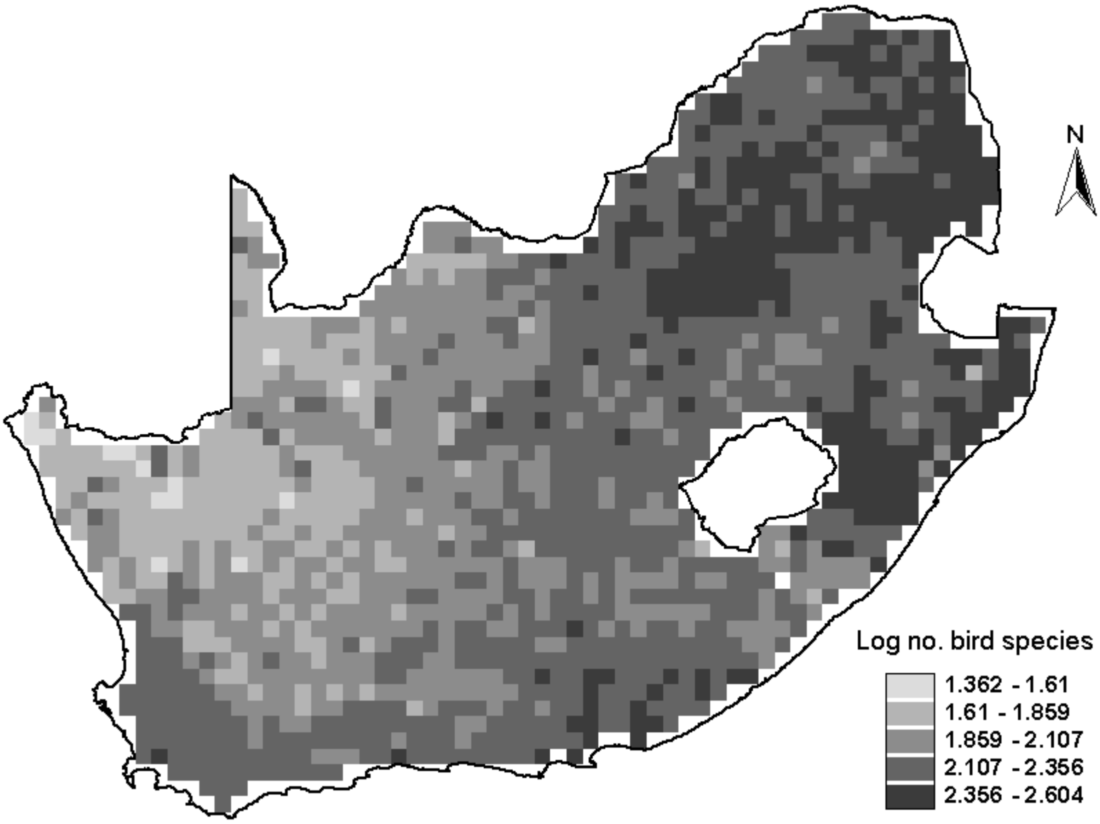
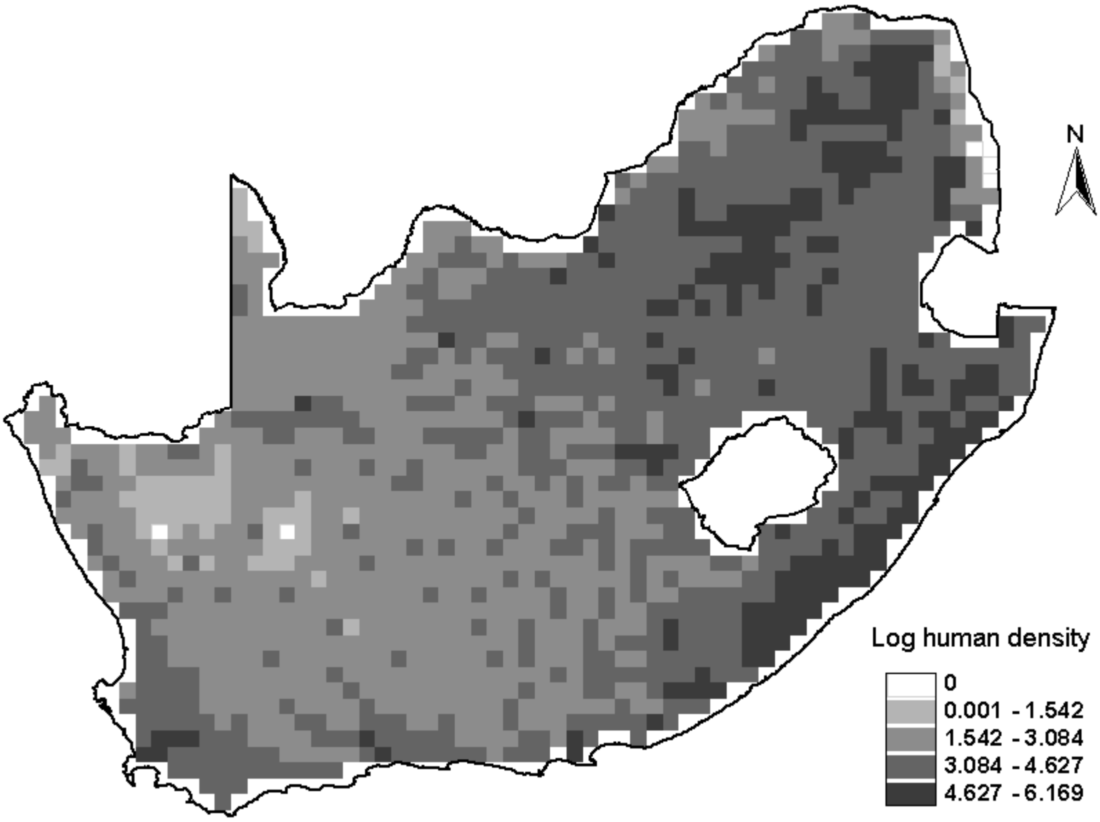
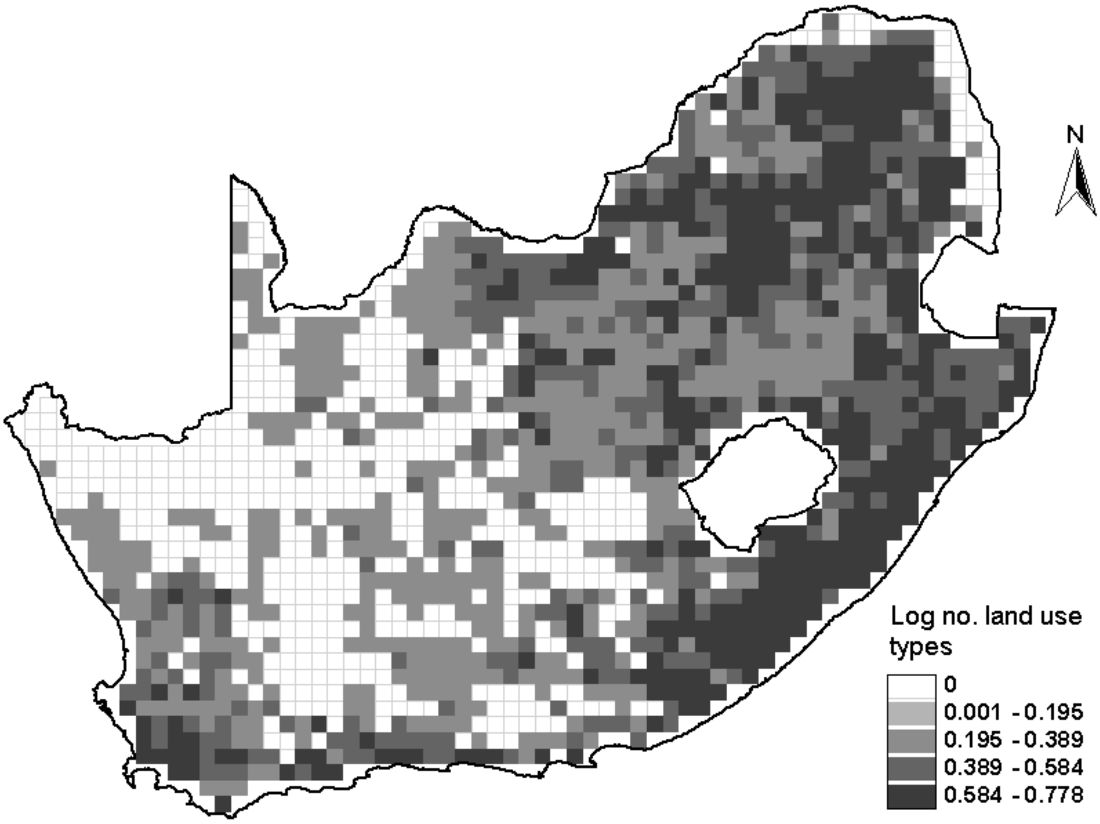
Map 1


N
Log no. bird species
1.362 - 1.61
1.61 - 1.859
1.859 - 2.107
2.107 - 2.356
2.356 - 2.604

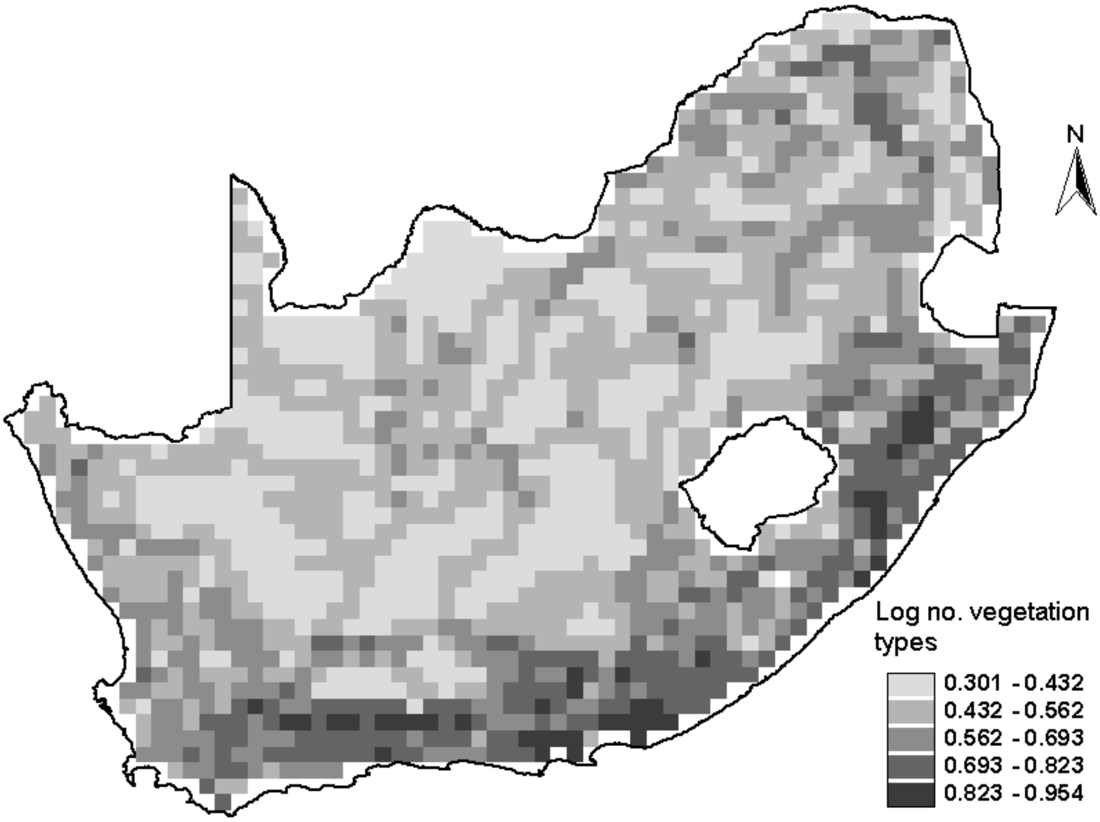
Map 2


N
Log human density
0
0.001 - 1.542
1.542 - 3.084
3.084 - 4.627
4.627 - 6.169

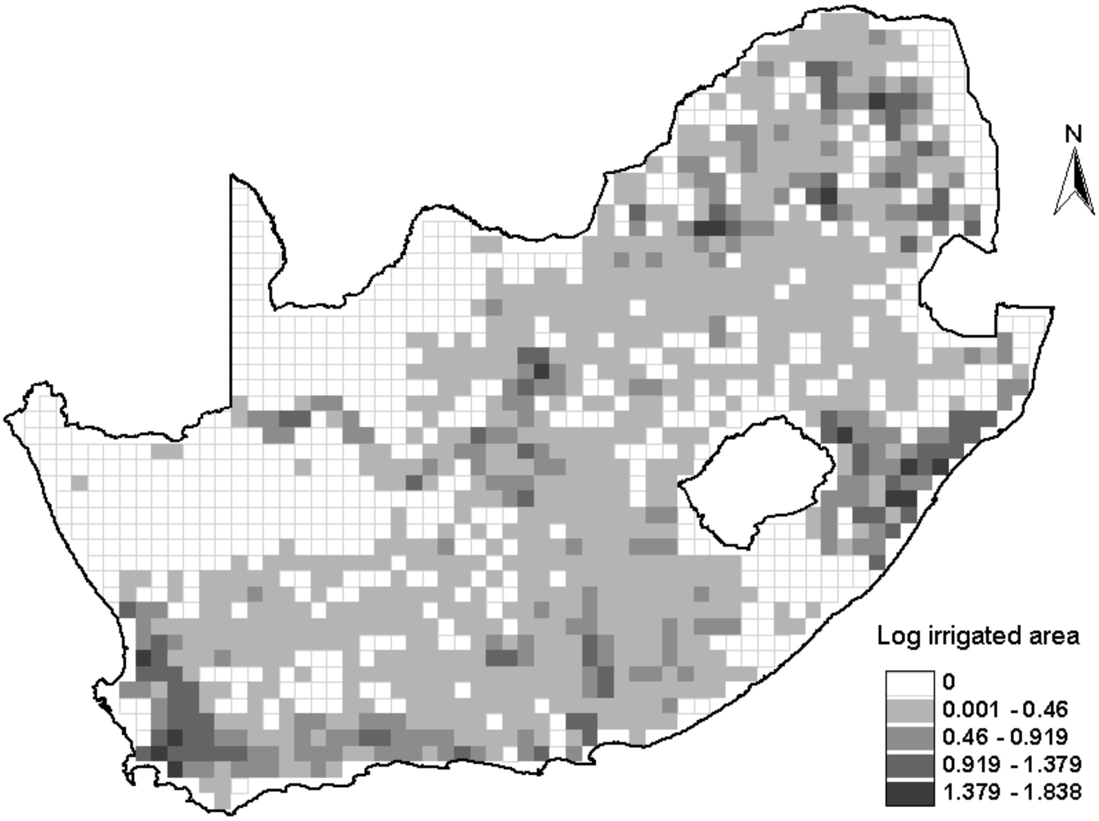
Map 3


N
Log no. land use types
0
0.001 - 0.195
0.195 - 0.389
0.389 - 0.584
0.584 - 0.778

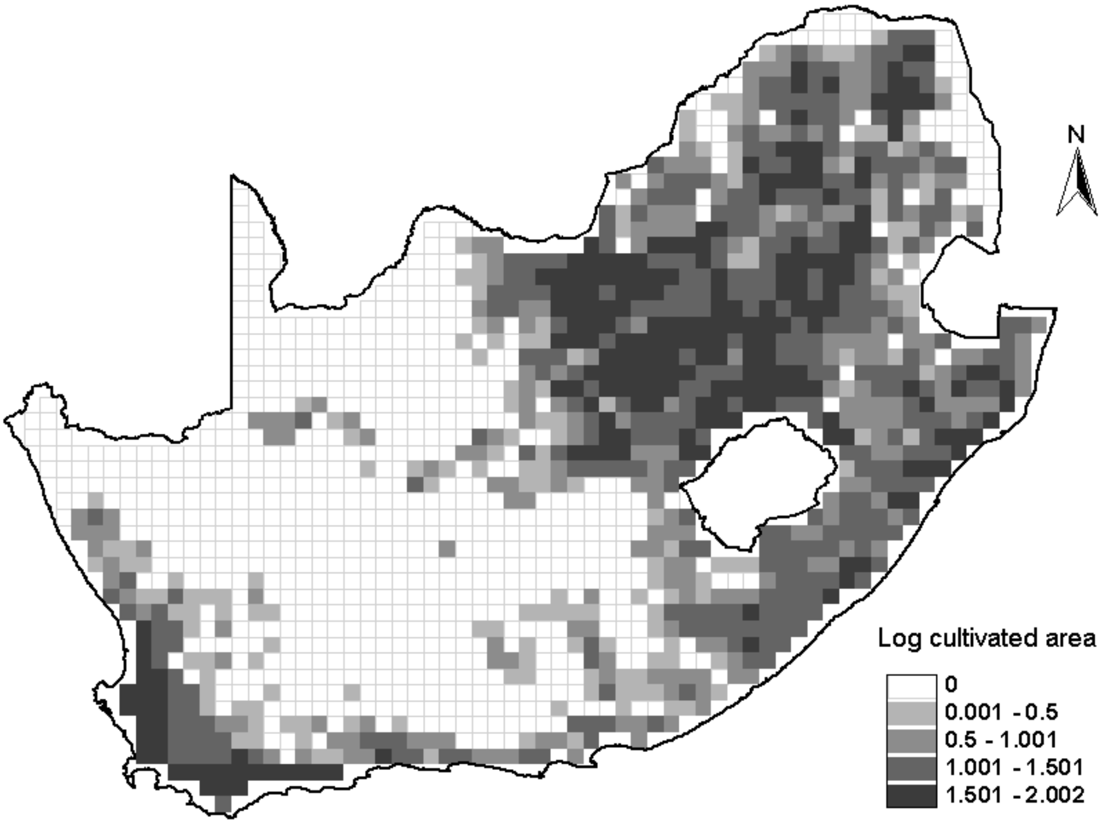
Map 4


N
Log no. vegetation types
0.301 - 0.432
0.432 - 0.562
0.562 - 0.693
0.693 - 0.823
0.823 - 0.954

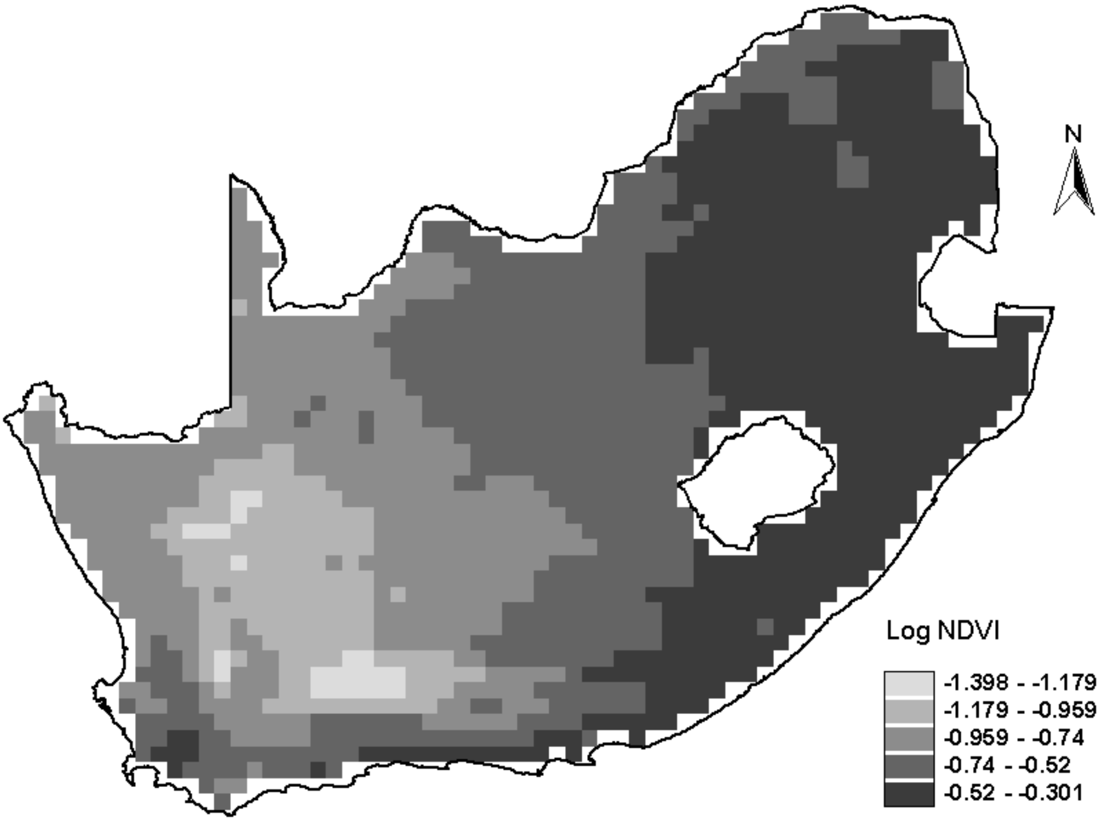
Map 5


N
Log irrigated area
0
0.001 - 0.46
0.46 - 0.919
0.919 - 1.379
1.379 - 1.838

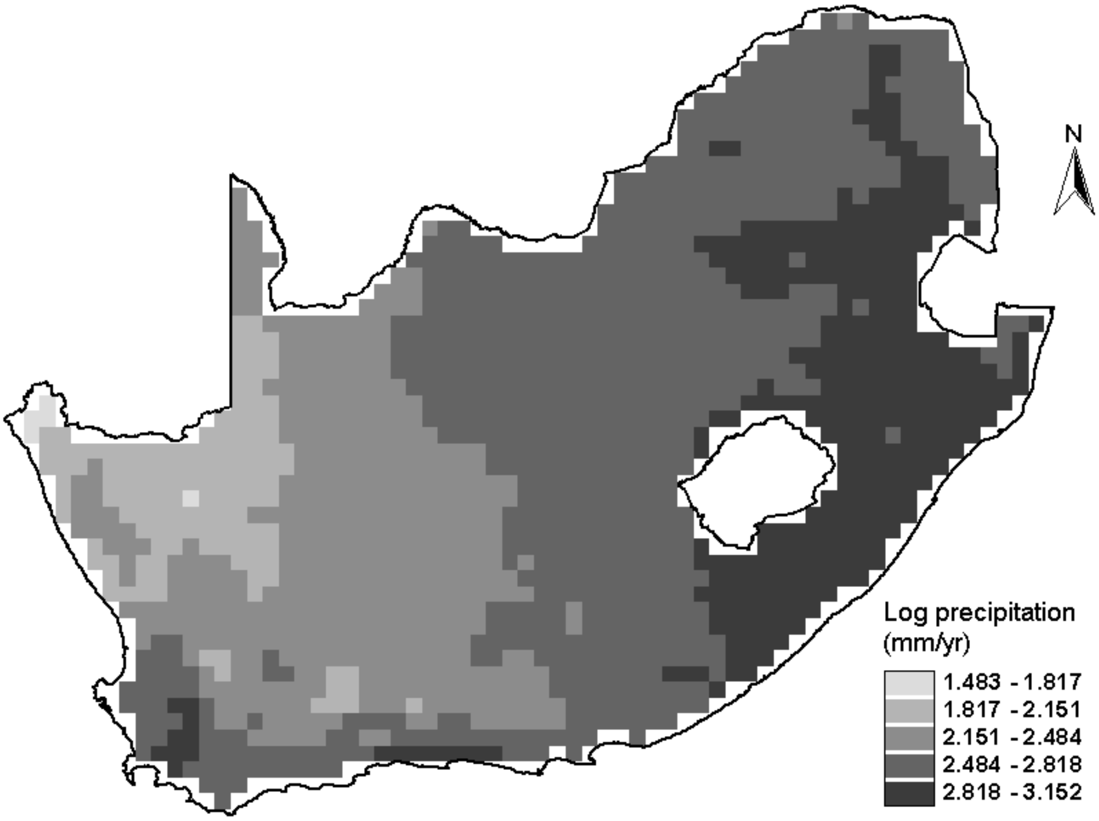
Map 6


N
Log cultivated area
0
0.001 - 0.5
0.5 - 1.001
1.001 - 1.501
1.501 - 2.002

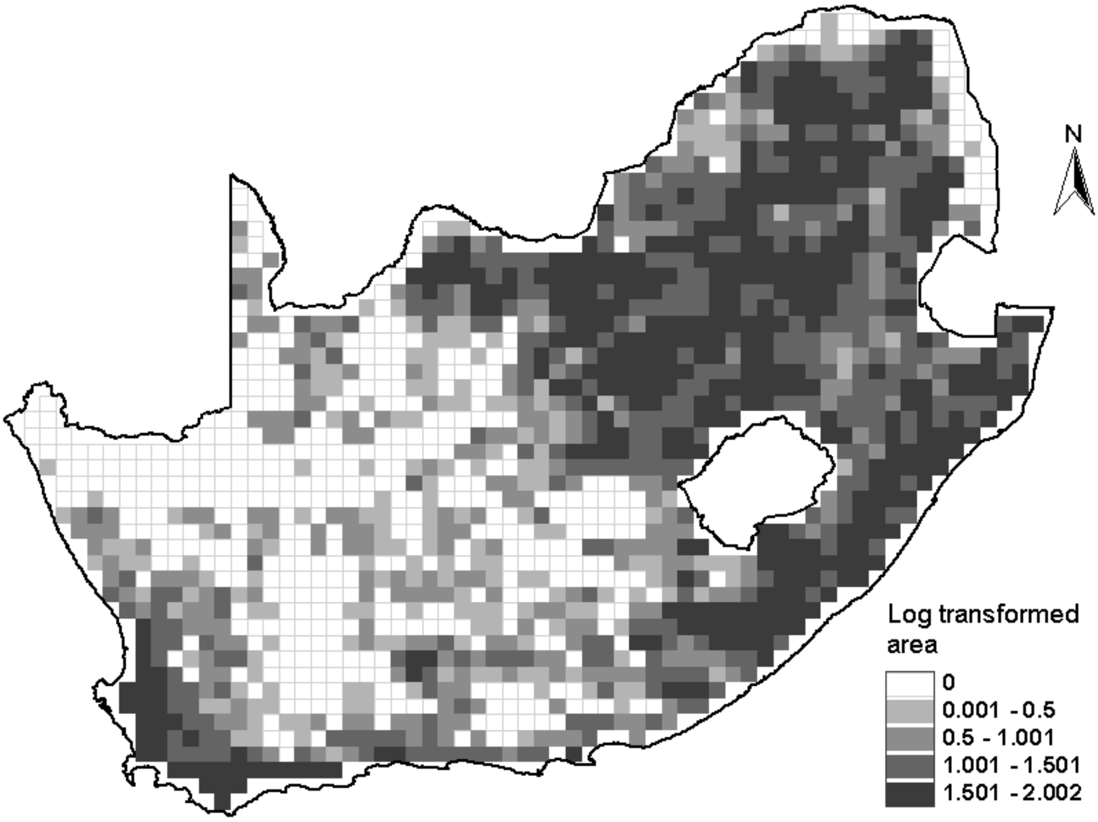
Map 7


N
Log NDVI
-1.398 - -1.179
-1.179 - -0.959
-0.959 - -0.74
-0.74 - -0.52
-0.52 - -0.301

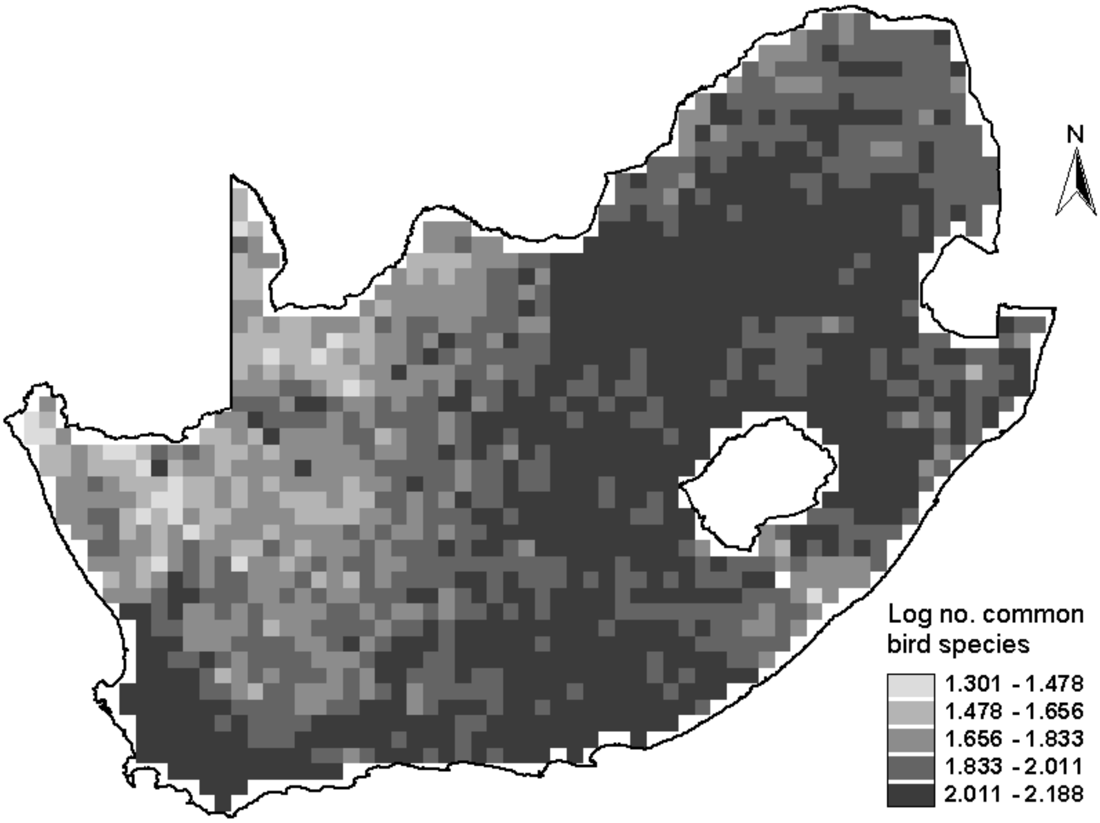
Map 8


N
Log precipitation (mm/yr)
1.483 - 1.817
1.817 - 2.151
2.151 - 2.484
2.484 - 2.818
2.818 - 3.152

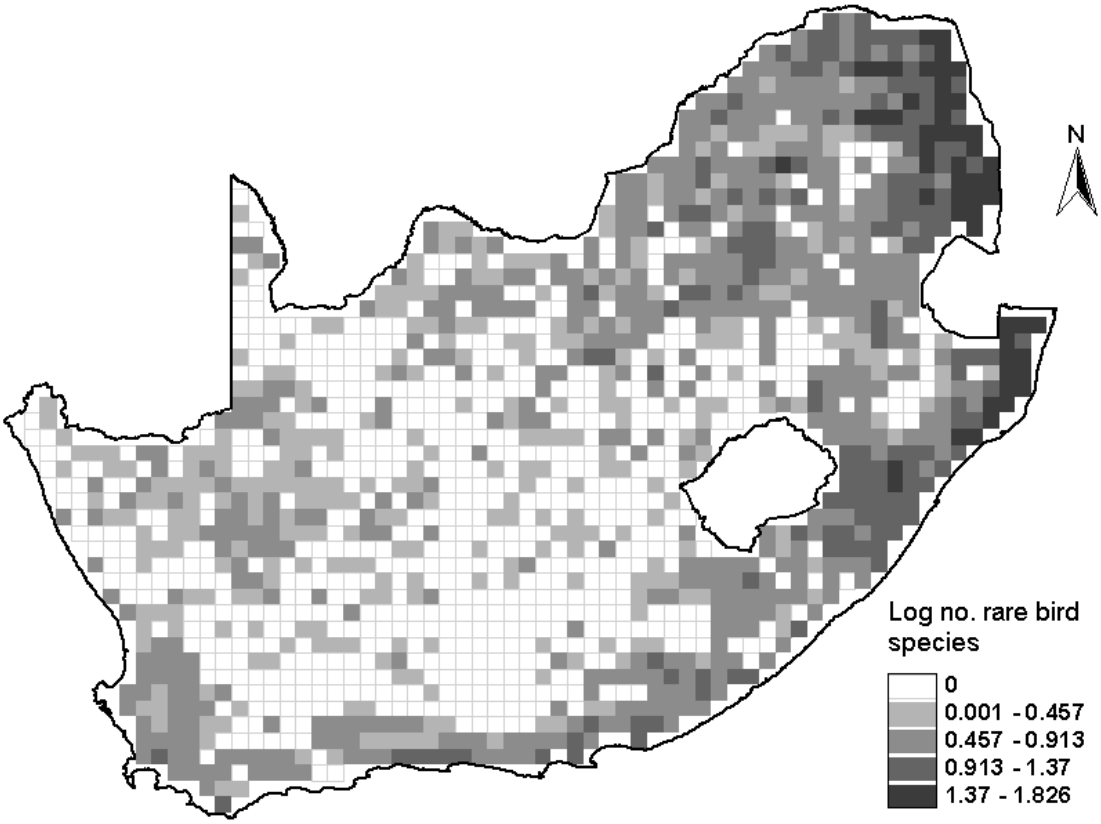
Map 9


N
Log transformed area
0
0.001 - 0.5
0.5 - 1.001
1.001 - 1.501
1.501 - 2.002

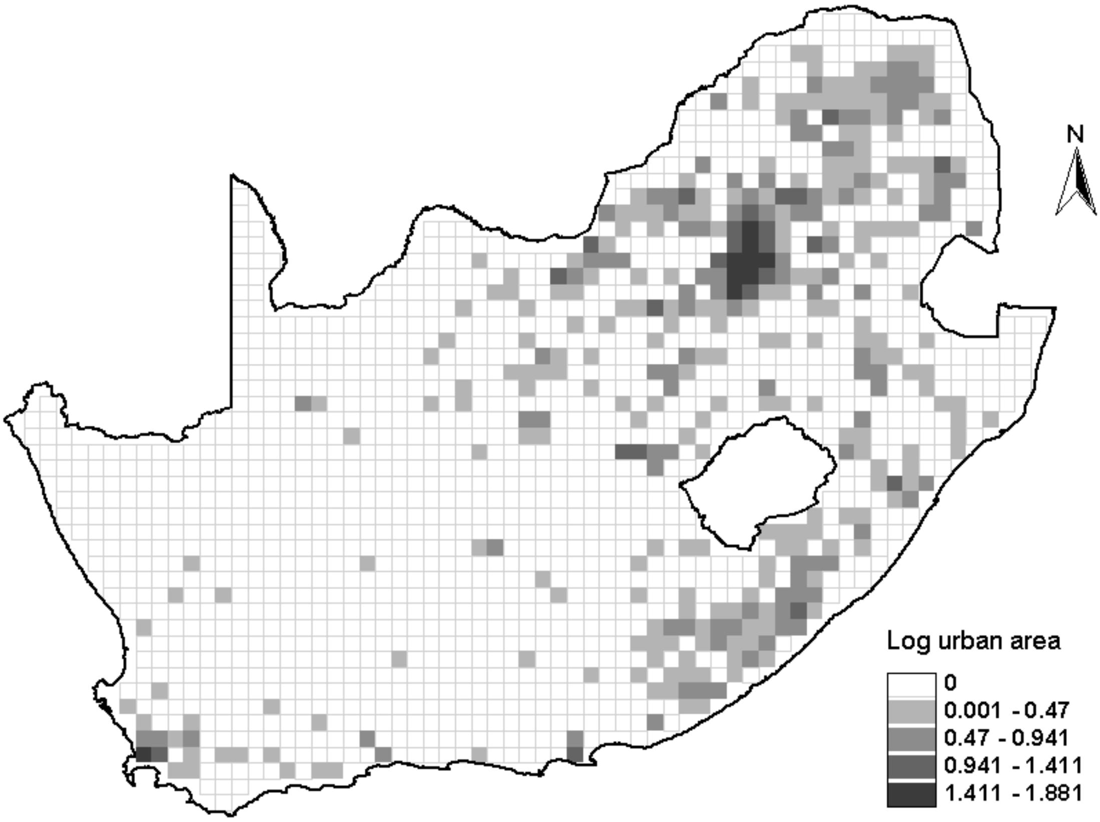
Map 10


N
Log no. common bird species
1.301 - 1.478
1.478 - 1.656
1.656 - 1.833
1.833 - 2.011
2.011 - 2.188

Map 11


N
Log no. rare bird species
0
0.001 - 0.457
0.457 - 0.913
0.913 - 1.37
1.37 - 1.826

Map 12


N
Log urban area
0
0.001 - 0.47
0.47 - 0.941
0.941 - 1.411
1.411 - 1.881