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Adapting Protected Area Networks to the Impacts of Climate Change: Potential Options for the Sub-Saharan Africa Important Bird Area (IBA) Network

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This Thesis is submitted in candidature for the degree of
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Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other University. The research reported within this thesis has been conducted by the author, unless indicated otherwise.

Abstract

Predicted climate change represents a major challenge to conservation over the 21st Century and beyond. Currently, conservation is largely reliant upon static Protected Areas (PAs) to conserve uncommon species. However, evidence from past climate change events suggests that species distributions are dynamic and alter in relation to species' bioclimate envelopes. Adapting PA networks to cope with projected changes in species distributions is a vital role of conservation biology.

The sub-Saharan Africa Important Bird Area (IBA) network is designed to protect sites containing significant proportions of the populations of congregatory species, species which have restricted ranges or species of global conservation concern found on the continent. Here I explore ways in which the IBA network can be adapted to the impacts of climate change. Data of present species ranges and simulations of future range shifts for 1608 bird species for the time periods 2011-2040, 2041-2070, 2071-2100 were used. Initially, using a reserve selection algorithm (RSA), I created optimal PA networks of one- and quarter-degree cells for present and future time periods. I then created near-optimal reserve networks using IBAs alone, or permitting the selection of additional land-areas. Finally, I incorporated economic opportunity costs of land into the RSAs to assess how to adapt the network to climate change in the most economical way.

The results showed that while some areas of Africa will undergo a large reduction in their importance to a complementarity-based PA network (such as West Africa), other areas will increase in importance (East and Southern Africa). Selected PAs often coincided with areas of currently recognised importance to conservation in both present and future projected scenarios. However, the selection of sites in these areas generally increased over the century. The number of additional sites needed to complement the IBA network and reach conservation targets also increased over time. The areas of increased importance were, on the whole, areas of increased economic opportunity costs to conservation and therefore the acquisition costs of PAs selected in the future may be greater than those selected for the present.

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Chapter 1: Predicting the Effects of Climate Change on Species Distributions and Creating Reserve Networks: A Review of Tools and Methods

Introduction

Global climate change is predicted to be an important factor in determining the future distributions of species across the planet (Parmesan & Yohe 2003). During the 20th Century, global average surface temperature increased by approximately 0.74 ± 0.18°C (Trenberth *et al.* 2007), which evidence suggests has already started to disrupt species' former ecological patterns (Hickling *et al*. 2006; McCarty 2001; Root *et al*. 2003; Walther *et al*. 2002). Past global climate change events, such as in the late Pleistocene, have been cited as possible causes of extinction during these time periods (Graham & Grimm 1990), and when coupled with recent anthropogenic land-use transformation, climate change represents a serious threat to global biodiversity (Fischlin *et al.* 2007; Hill *et al*. 1999; Jetz *et al*. 2007).

The Important Bird Area (IBA) programme is a BirdLife International Partnership initiative to select and conserve key sites for bird conservation around the world (Fishpool & Evans 2001). This study focuses on the IBA network of sub-Saharan Africa which covers around 7% of the continent, made up of 863 sites in 42 countries (Hole *et al*. 2009). The sites have been identified as critical for the conservation of bird species as habitat loss and degradation continually increase the chance of species extinction (Fishpool & Evans 2001), however, the IBA network is not designed to cope with the impacts of predicted climate change (Willis *et al*. 2009). Protected Area (PA) networks, such as IBAs, are designed under the false expectation of a stable climate and therefore the efficacies of such networks are likely to be affected by the impacts of climate change (Hannah *et al*. 2007). This thesis looks at how the sub-Saharan IBA network can be adapted to cope with the future threat of climate change.

This literature review aims to evaluate the methods used to forecast the effects of climate change on species distributions and the tools that can be used to design protected area networks that will mitigate the effects of climate change on species assemblages.

Predicting the effects of climate change on species distributions

Palaeoecological Studies

In order to predict the responses of species to present-day and future climate change, it is useful to study the effects of past global climate change (Graham & Grimm 1990). Palaeobiogeographical records provide evidence for a wide range of responses that species have shown to past climate change events, including range shifts, morphological adaptation and evolution (Graham & Grimm 1990; MacDonald *et al*. 2008). Understanding why these observed responses occurred will provide an insight into how to mitigate the effects of climate change effectively (Hannah *et al*. 2002).

Although this study focuses on the effects of species' range shifts, it is important to note that other responses to climate change have been documented. Extensive research carried out on late-Quaternary populations of *Neotoma* (Woodrat *spp.*) in North America have shown strong correlations between climate and body size that closely follow Bergmann's rule (Smith & Betancourt 2006). Furthermore, there is evidence that *Neotoma* has started to exhibit morphological changes relating to present-day climate change (Smith & Betancourt 2006), which is seen as the most basic process of adapting to a changing climate (MacDonald *et al*. 2008). Changes in the distributions of species populations due to climate change have also been detected in the palaeoecological records (Lyons 2003, 2005). It has been shown that in the past, species have shifted their ranges individualistically, leading to novel community-level interactions which are of particular interest to conservationists (Graham & Grimm 1990) as it means that predictions must be made for the outcome of each individual species’ reaction to climate change, rather than looking at the community as a single reactionary entity (Graham *et al*. 1996).

Barnosky *et al.* (2003) referred to morphological and distributional changes as the ‘first-order response’ of a population to climate change, the second-order being extinction, so it is important to understand which response species are currently undertaking, the rate at which they are likely to reach a response, and how to prevent extinction events related to climate change from occurring.

Present-day observations

In order to assess the current effects of climate change on species, observations of organisms must be compared with known climatic data (Harrington *et al*. 1999). Much literature has already noted changes in species’ phenology (Crick *et al*. 1997), geographic distribution, and species interactions (McCarty 2001; Walther *et al*. 2002), and the overall accumulation of evidence indicating biological consequences of climate change removes doubt created by the lack of controlled experiments and differences in the temporal scales among studies (Hughes 2000).

A large proportion of the literature that focuses on the current effects of climate change on species’ distributions has been based on a narrow range of taxa (Hickling *et al*. 2006). Butterflies are a taxonomic group that have well documented records of populations, are sensitive to varying temperatures, are mobile, and therefore are often able to disperse to more climatically suitable locations. Parmesan *et al.* (1996) analysed changes in distributions of European non-migratory butterflies during the 20th Century. By analysing data for Northern and Southern boundary shifts as well as whole range shifts of a variety of different species, they were able to identify trends at a continental scale. The results showed that out of the 52 species analysed for northern boundary shifts, 65% showed northward expansions, with only 2% retracting southwards. Overall, only 4% of the 127 species analysed showed southward shifts of either their northern or southern boundaries.

Parmesan (1999) pointed out that studies that are restricted to local observations run the risk of being compromised by stochastic changes in population. This would therefore lead to expansion of range boundaries that were not primarily caused by climatic alterations. Parmesan (1996) carried out studies on Edith's Checkerspot butterfly (*Euphydryas editha*) at a continental scale so that variation in individual populations would not be a factor in the overall results. *E. editha* has experienced a range of local extinctions in the southern range of its regional-scale metapopulations and a decrease in population extinctions in its northern and high altitude populations indicating an overall response to a changing climate. An important consideration of this study was whether anthropogenic land-use change was responsible for the observed population extinctions. Parmesan (1996) argued that observed trends could not be attributed to habitat degradation because similar rates of degradation were occurring at both latitudinal extremes of *E. editha*'s range. In Hickling *et al*.'s (2006) study of a wide range of taxanomic groups' reactions to climate change, the effects of land-use change were not taken into account. 83% of the species analysed showed northward shifts in distribution, which is notable given that the overall trend was apparently not significantly affected by land-use factors acting independently of climate change.

Birds represent another well documented taxon group that allow analytical studies to be carried out over large areas. Thomas and Lennon (2007) analysed British bird breeding distributions and discovered an average shift of northern boundaries of 18.9 km over a 20 year period between 1968 and 1991. The analysis took account of individual species population expansions and retractions, thereby removing the effects that they would have on range boundaries. As mentioned previously, the effects of anthropogenic land-use change are also important to consider when assessing the impacts of climate on species ranges. La Sorte and Thompson (2007) carried out an extensive analysis of North American bird species' winter ranges over a 30 year period. The study calculated an average northern maximum latitude increase in range of 1.48 km/yr, but the authors were quick to point out that in some cases the observed shift were due to a combination of climate and anthropogenic factors, although the latter only accounted for a small proportion of northward trends.

Modelling future species distributions

Gaining an insight into past and present-day impacts of climate change on species distributions can give us an idea of the potential impacts that climate change will have in the future (Graham & Grimm 1990). However, in order to apply observed trends to future scenarios, modelling techniques that obtain representations of species distributions under climate change must be used. One of the most widely used methods are Bioclimatic Envelope Models (BEM) (Poyry *et al*. 2008).

Bioclimatic Envelope Models

The bioclimatic envelope of a species represents a species' current distribution in relation to the climate found within its realised niche (Pearson & Dawson 2003). Knowledge of these envelopes should allow us to predict the distribution of a species from climate alone, and if applied to projected climate change scenarios, should allow simulation of potential species ranges in the future (Heikkinen *et al*. 2006). BEMs are statistical models that use the current distributions of a species to deduce its climatic requirements (Hijmans & Graham 2006), calculating individualistic responses of species, rather than community responses (Graham *et al*. 1996). There is a variety of different techniques used in bioclimatic modelling (Heikkinen *et al*. 2006). Below I will focus on those that are in regular use in climate change-related population distribution studies and then move attention onto potential alternatives to current approaches.

BIOCLIM

BIOCLIM is one of the most widely used BEMs in climate change ecology (Kadmon *et al*. 2003). It was originally developed to predict areas that maybe suitable for invasive species and therefore allow efficient allocation of preventative measures (Busby 1991). BIOCLIM estimates the value of the bioclimatic envelope of a species as a rectilinear volume, it assumes that a species can exist within the extremes of climate that a species is found

(Beaumont *et al*. 2007; Carpenter *et al*. 1993). BIOCLIM allows equal weighting for all sites where the species is present, this means that no considerations are made for outliers and therefore the technique is sensitive to such anomalies (Beaumont *et al*. 2007). Presence-only data are required for using in BIOCLIM (Heikkinen *et al*. 2006) which is important because most data sets for animal and plant distributions do not have absence data included (Margules & Sarkar 2007; Pearce & Boyce 2006).

Generalised Additive Models (GAMS)

A popular and increasingly used technique in BEMs are GAMs (Heikkinen *et al*. 2006; Thuiller 2003) which are regression based approaches (Elith *et al*. 2006). They are related to general linear models (GLMs), but are non-parametric, and are able to model ecological relationships accurately (Elith *et al*. 2006; Heikkinen *et al*. 2006). This is because the non-parametric smoothing functions which model non-linear trends linking species (dependent) and environmental (independent) data allow species response curves to fit environmental gradients more accurately (Elith *et al*. 2006; Hijmans & Graham 2006; Lehmann *et al*. 2003). GLMs are parametric models and are unable to process complex response curves and as a result, they have been overtaken by GAMs in recent years (Elith *et al*. 2006; Thuiller 2003).

Maximum Entropy Models

Machine learning techniques are able to improve their performance over time, based on previous results, and have been applied to maximum entropy models (Elith *et al*. 2006). MAXENT is one such model that uses incomplete information sets to make predictions by using the distribution of maximum entropy to represent a target distribution, dependent on limiting factors that represent the incomplete information sets available (Phillips *et al*. 2006). Beneficial attributes of MAXENT include its flexibility, ongoing progress within the field of maximum entropy modelling and the requirement of presence-only data (Phillips *et al*. 2006). MAXENT has been shown to out-perform another popular modelling technique; genetic algorithm for rule-set prediction (GARP, an artificial intelligence-based super-algorithm (Heikkinen *et al*. 2006)), proving the predictive power of the machine learning technique (Phillips *et al.* 2006).

GARP

GARP is a modelling technique that utilises a genetic algorithm that searches for non-random associations between presence-only data and climatic factors to design a niche-model for a species (Anderson *et al*. 2002; Heikkinen *et al*. 2006). It uses several different techniques to define the ecological niche of a species by creating sets of rules that lead to the most accurate predictions (Meynard & Quinn 2007; Tsoar *et al*. 2007). The iterative approach leads to the most accurate outcome through evaluating the rule-selection process and then rejecting or accepting the final results (Gomez-Mendoza & Arriaga 2007). The use of several techniques and continuous evaluation of the rule-selection process should always lead to a more accurate result than any single method (Anderson *et al*. 2002; Stockwell & Peters 1999). GARP has been shown not to perform well with extreme data sample sizes, however an updated version, OM-GARP, has been created that can handle different sized data sets. This version has been shown to compete with newer modelling techniques such as MAXENT (Wisz *et al*. 2008), although Elith *et al.* (2006) recorded lower performance levels in OM-GARP.

Artificial Neural Networks (ANNs)

ANNs are computer systems that are based on both the physical and functional structure of the human brain (Pearson *et al*. 2002). They have not been used extensively to model the potential impacts of future climate change on species, but with models such as SPECIES (a Spatial Evaluation of Climate Impact on the Envelope of Species) now available, they are likely to become more popular because of their powerful rule-based modelling techniques (Heikkinen *et al*. 2006) and their ability to deal with ‘noisy’ data (Pearson *et al*. 2002). ANNs have the disadvantage that they require large quantities of data to prepare and validate the network and are unable to initially identify the environmental factors that are affecting species distributions, making them impractical for many studies (Heikkinen *et al*. 2006; Pearson *et al*. 2002).

Climate Response Surfaces (CRSs)

CRSs use gridded presence-absence species data and climate data of the same scale to create a response surface, which is a representation of the areas occupied by a species in multidimensional climate space (Huntley *et al*. 1995). The response surfaces are fitted using locally weighted regression, using several bioclimatic variables such, as mean temperature of the warmest and coldest months (Hole *et al*. 2009; Huntley *et al*. 2008), as predictor variables. CRSs therefore make no assumptions over the form of the relationship between species' probability of occurrence and any of the bioclimatic variables (Huntley *et al*. 2006). Potential future distributions can be simulated by applying the surfaces to different climate scenarios, calculating the probability of occurrence of a species in each cell and then applying a threshold to convert the probabilities to presence-absence data. CRSs have been shown to perform better than rival modelling techniques such as GAMs (Hole *et al.* 2009) and GLMs (Doswald *et al.* 2009) and benefit from user-defined bioclimate variables and the ability to mimic interactions that can occur between bioclimatic variables (Huntley *et al.* 2006; Huntley *et al.* 2008).

Alternatives to Bioclimatic Envelope Models

Unlike BEMs, physiological models attempt to model a species' fundamental niche rather than its realised niche (Morin & Lechowicz 2008), this is seen as an advantage because it removes the influence of biotic interactions from the model so that the envelope created will fully represent the possible distribution of a species in the future (Pearson & Dawson 2003). Correlative models, like BEMs, incorporate the influence of biotic interactions found within species communities into predictions, which means that outcomes from such models rely on these same interactions being present in future communities disturbed by a changed climate (Morin & Lechowicz 2008), which as previously mentioned, has not been the case in the past (Graham & Grimm 1990; Graham *et al*. 1996). Physiologically-based models are not reliant on this, but depict future distributions of species throughout the fundamental niche, which is equally as unlikely as the unchanged continuation of a realised niche into the future, because inter-species interactions often prevent fundamental niches from being filled by a species (Pearson & Dawson 2003). A further consideration is that heterogeneous variation found within species makes it difficult to group a species into a single level of climatic tolerance when considering species that exist in widely scattered subpopulations. Coupled with this is the possibility of evolutionary changes that will make individuals better adapted to new climatic conditions, and makes the stability of the fundamental niche unlikely in the future (Pearson & Dawson 2003).

Despite criticism of BEMs, they are much more widely used than physiological models. This is because they are not reliant on detailed data on the climatic tolerances of species (Heikkinen *et al*. 2006), meaning that they can be applied to a wide range of species and therefore be relevant to broad spatial scales and ecological niches (Morin & Lechowicz 2008), at which BEMs are more accurate (Pearson & Dawson 2003). At finer resolutions, the accuracy of BEMs will decrease because the relative importance of other variables start to become more important (Luoto *et al*. 2007). There are several variables that have been discussed in the literature which are likely to cause inaccuracy within species-climate response surfaces. Poyry *et al.* (2008) showed that traits of individual species can have negative effects on the performance of envelope modelling, with ability to disperse causing a particularly notable effect on modelling accuracy. Kadmon *et al.* (2003) showed that the extent of a species' distribution affected the accuracy of a climatic envelope model. For example, a species that is common within a wide area will be accurately modelled, whereas patchily distributed species that occur over a large area will have a greater inaccuracy associated with the modelling outcomes. Land-use can have a large effect on the distributions of species, especially when considering the ability of a species to shift its range between its present and future distribution (Hill *et al*. 1999). This is an important consideration for this study and therefore will be discussed at greater length.

Araujo *et al.* (2005) caution against using the results from BEMs 'on face value' and other authors have warned that results are often burdened with uncertainty (Dormann *et al*. 2008). However, other studies provide positive results with BEMs. An example is Green *et al.*'s (2008) study which validated climate response surface models through retrodicting recent bird population changes, proving that BEMs can produce reliable results. Applying different envelope models to the same data set will often give different results, which further highlights the potential inaccuracies of the models. One way of combating this is ‘ensemble forecasting’ which uses several models to analyse a data set, and then uses appropriate techniques to examine and combine the alternative outcomes (Araujo 2002). This has become popular in studies that utilise BEMs to predict species range shifts caused by climate change and will potentially increase the understanding of uncertainty of such models.

Other techniques and programs are available to determine the bioclimate envelopes of future species assemblages, but have yet to be applied to such studies. A new concept that has been recently tested is the incorporation of stochastic population models to dynamic bioclimatic habitat models in an attempt to gain greater accuracy in predictions (Keith *et al*. 2008). Keith *et al.* (2008) put forward the novel technique of combining a GAM with a spatially explicit age/stage-based matrix model which incorporated environmental and biotic factors into the scenario. This allows the model to increase its predictive accuracy by incorporating relationships between factors such as range shifts, landscape structure and demographics. This study represents an interface between the BEMs and physiological or mechanistic models that are seen as an alternative for predicting species’ reactions to climate change. Huntley *et al.* (in press) suggest that the next generation of dynamic bioclimatic habitat models will consist of several sub-models; bioclimatic, habitat, population dynamics and dispersal. The creation of even the simplest of integrated models will be a significant step past current BEMs, and the creation of more complex models will highlight shortfalls in existing data sets.

Reserve selection methods

Recent anthropogenic habitat destruction, fragmentation and modification has the potential to deny the existence of continuous areas of habitat that will facilitate the movement of a species from its present-day distribution, to a distribution in the future that is more climatically suitable (Collingham & Huntley 2000; Opdam & Wascher 2004; Travis 2003). If species are unable to modify their distributions, then it is possible that they will face the threat of greatly reduced populations, or extinction (Thomas *et al*. 2004). Therefore, the availability of habitat that a species can utilise for both migration and colonisation is of great concern for conservation efforts in the face of climate change. Protected area networks represent 11.5% of terrestrial habitat across the globe (Rodrigues *et al*. 2004). However, these networks are generally based on present day biogeographical distributions of species, with little consideration for possible changes in the climatic suitability for species that reside within their boundaries (Hannah *et al*. 2007; Hole *et al*. 2009). In order to discover how a protected area network will cope with climate change, BEMs for individual species can be overlaid onto a protected area network in a GIS, giving an idea of how many species will fall within the confines of a protected area in the future (Willis *et al.* 2008). Hole *et al.* (2009) used BEMs to test the ability of the sub-Saharan Africa Important Bird Area (IBA) network to protect species under future climate change scenarios. The results showed that although many protected areas will no longer be suitable for their current species assemblages, they will be capable of protecting different assemblages of species by the end of the 21st Century providing that species can successfully move between protected areas. Hole *et al.* (2009) suggest that one of the greatest challenges in future conservation will be facilitating the movement of species across the landscape to new protected areas.

Reserve Selection Algorithms

Knowing where to place reserves to mitigate the effects of climate change will be very important for future conservation strategies. Reserve Selection Algorithms (RSA) are designed to select optimal sites in a reserve network based on criteria relevant to resources available to a conservation plan

(Cabeza & Moilanen 2001). Here I review several techniques for reserve selection and their capability of being applied to continent-wide strategies for mitigating the effects of climate change on the success of protected area networks.

Designing reserve networks should be done so as to make efficient use of the land available (Possingham 2000). This can be completed with two different representation problems; the minimum area problem and the maximum coverage problem (MCP) (Cabeza & Moilanen 2001). The minimum area problem, also known as the set covering problem (SCP), requires all species to be represented within a reserve network that has the smallest possible area, and the MCP, requires the maximum number of species to be protected in a reserve network that is limited by a cost (Cabeza & Moilanen 2001; Camm *et al*. 1996). There is no simple method for finding an optimal solution for either of these representation problems, because the addition of an optimal site will depend on the current configuration of the protected area network and the remaining areas outside the network (Camm *et al*. 1996).

RSAs select new sites on the basis of several different criteria. Richness algorithms (also known as greedy algorithms) will start by selecting the sites that hold the greatest diversity available and then add sites that provide the largest additional increase in diversity henceforth (McClean *et al*. 2006). Complementarity was first introduced by Vane-Wright *et al.* (1991), and is defined by the addition of sites that complement the previously selected sites by adding the greatest number of new species to the network (Church *et al*. 1996). Complementarity is integral to the richness algorithm, and is often used as an auxiliary selection criterion for when two cells are available which have equal importance to a reserve system, and the choice is made by discerning which site will complement the currently selected network by adding the largest number of novel species (Kelley *et al*. 2002). The rarity approach selects sites depending on their irreplaceability in terms of the rarity of the species, or other factors such as endemism, found within that site (Margules *et al*. 1988; McClean *et al*. 2006). This method helps reduce the total area of a network because essential sites that hold the only population of a species may hold other species that need not be represented again in the network and therefore reduces redundancy. The algorithm will then continue to add sites that contain the most unrepresented species and are therefore irreplaceable (Possingham 2000).

The arguments for the use of different types of algorithm are often based on the optimality of the outcome. Optimality is defined by the representation problem used; if it is an SCP, the optimal solution will be the network that protects all species with the least area, if it is an MCP, the optimal solution will protect the greatest proportion of biodiversity whilst restricted by a set cost. As mentioned above, reserve networks must make efficient use of area in order to be viable (Possingham 2000), as a result, much emphasis has been put on finding optimal reserve networks, and therefore, creating algorithms that produce optimal solutions. Much of the literature states that heuristic methods, which operate through the step-by-step addition of planning units, give suboptimal solutions and only occasionally provide optimality (Cabeza & Moilanen 2001; Church *et al*. 1996; Onal & Briers 2002). By contrast, integer programs (IPs), which determine the way to achieve the optimal outcome, are able to consistently reach optimal solutions for reserve selection problems (Cabeza & Moilanen 2001; Camm *et al*. 1996).

The earliest algorithms selected sites on their intrinsic values. For example, Terborgh and Winter (1983) chose sites that were identified as centres of endemism so as to create a cost-effective reserve network which focused on the most diverse areas for protection. This method is likely to create a large overlap in protected species between reserves, and therefore redundancy within the reserve network (Church *et al*. 1996). To remove this redundancy, Kirkpatrick (1983) used an iterative step-wise approach that recalculated the relative diversity of each remaining site after each stage of selection. This is effectively a greedy heuristic algorithm, which is a richness algorithm that incorporates the principle of complementarity (Pressey *et al*. 1993) and provides simple solutions with fast processing times (Csuti *et al*. 1997). Rarity-based algorithms use a similar step-wise technique in decision making, but generally lead to more efficient solutions (Kershaw *et al*. 1994). Both of these algorithms are classed as heuristics because of their selective step-by-step approach. Heuristic reserve selection algorithms are based on logic designed to achieve efficiency (Church *et al*. 1996). The stepwise approach selects reserves by adding the most efficient site at each stage of the process until all the criteria of the algorithm are met (Vanderkam *et al*. 2007). Although they are designed to achieve efficiency, heuristics rarely reach, or can detect if they have reached an optimal solution (Church *et al*. 1996).

Despite these faults, heuristic algorithms are popular techniques for designing reserve networks, and their efficiency can be improved by using spatial patterns in the data to search for more efficient sites; this approach is called simulated annealing (Csuti *et al*. 1997). Simulated annealing is an iterative optimisation process that starts with a randomly determined reserve network, and then explores trial alternatives by randomly adding or deleting new sites at each iteration (Peralvo *et al*. 2007). The novel modifications are accepted or rejected depending on whether they decrease or increase the value of the cost function, and the algorithm becomes more ‘choosy’ as the process continues because of an annealing schedule that decreases the introduction of ‘bad’ changes over time by decreasing the value of the acceptance function (McDonnell *et al*. 2002; Peralvo *et al*. 2007; Possingham 2000). Simulated annealing algorithms reach optimal solutions more often than heuristic algorithms and are popular as reserve network design tools.

Linear integer programming (IP) algorithms are optimal algorithms and therefore are guaranteed to provide an optimal solution (Onal & Briers 2002). IP algorithms can be modelled as MCP and SCP problems in order to find a reserve network solution; they are difficult optimisation problems and are often cited as having long runtimes (Camm *et al*. 1996; Csuti *et al*. 1997; Vanderkam *et al*. 2007).

Optimality

Despite the obvious advantage of creating optimal reserve networks by using IP algorithms, there is much debate in the literature over what is the most practical type of algorithm. The most commonly used argument against the use of IP algorithms is that they have long computational times that make them a non-viable option for use by conservation planners (Cabeza & Moilanen 2001; Camm *et al*. 1996; Onal & Briers 2002; Pressey *et al*. 1996). Much literature written on the topic of reserve network optimality was written in the mid 1990s (Cabeza & Moilanen 2001) and since then, IPs have become more powerful and are able to process large data sets quickly, making them a more feasible option for conservation planning (Crossman & Bryan 2006; Vanderkam *et al*. 2007). Criticisms about their ability to handle large data sets can also be countered by the application of intelligent pre-processing of data which makes smaller results-sets which are therefore more manageable (Camm *et al*. 1996; Csuti *et al*. 1997; Pressey *et al*. 1996). However, with the increasing use of remote sensing techniques that collect data at continental scales, IPs are still unable to process these vast data sets in acceptable periods of time, and sub-optimal algorithms, which can cope with much larger data set sizes are more favourable as a result (Moilanen 2008; Sarkar *et al*. 2004)

Optimality, although important, is often only practical from a theoretical stand point. Suboptimal solutions can be valid, especially because they are not affected by some of the problems that are often found in optimising algorithms, be they long processing times or possible routes of failure (Pressey *et al*. 1996). Moilanen (2008) points out that because linear IP algorithms cannot process complex non-linear data sets, they lose optimality because of the simplification that occurs when data is linearized during model formulation. This can be especially important when modelling ecosystem processes such as non-stationary species distributions, which is significant when considering the impacts of climate change on species distributions within a reserve network. A further argument for non-optimising algorithms is that an optimal solution is not always necessary because other factors not taken into account by models, such as socioeconomic constraints and current land-use, may need to be considered before a reserve network is accepted and applied (Cowling *et al*. 2003). Reaching optimal solutions may lead to impractical solutions in terms of ecological processes that will affect a reserve network.

Moilanen (2008) points out that creating minimum set reserve networks could increase extinction rates by minimising the number and sizes of individual protected areas, and therefore increasing the effects of habitat fragmentation and habitat loss. Moilanen (2008) cites Vanderkam *et al.* (2007), whose study finds a solution of 39 sites out of an available 89,376 sites that are 25x25m in area, which would cause isolation of reserves and increase the risk of edge effects on protected areas. Finally, when considering the application of reserve selection algorithms in this study, it is important to consider the reliability of the input data. Instead of using observational data to ascertain the presence of a species, the data for the current study will be produced by BEMs, which will have errors associated with the modelling process (Dormann *et al*. 2008). Therefore the detection of a single optimal network may be of lesser importance than detecting networks that are robust to a variety of potential future scenarios.

In this study, optimality and the efficiency of species representation within the selected reserve networks represent a method of measuring the accuracy of the reserve selection methods used. However, it should be acknowledged that as this study is interested in improving the African IBA network, a network selected by conservation planners to efficiently conserve species rather than to use land area efficiently, the use of the term efficiency is not representative of the IBA program’s mission. As a result, optimality is used as an indicator of accuracy within this study, although when applied to a ‘real-life’ scenario, the efficiency of the reserve selection methods used is of decreased significance.

Cowling *et al.* (2003) compared the choices of conservation planners against those made by systematic reserve selection programs to determine which was the most efficient and how the two methods can be incorporated. The results showed that conservation planners make biased decisions when choosing reserves. These biases are fuelled by considerations that are not important to the selection process of algorithms (such as pre-emption of risk), but which can lead to over-representation of species within a reserve network and under-representation of species that lack protection. The study also highlights a common problem in the literature, which is that reserve selection algorithms are meant to act as a tool for conservation planners, rather than a replacement for them. When considering the use of an ‘off-the-shelf’ selection algorithm, it is important to understand what the program was intended for (optimality, use in meetings, interaction between groups) and then make decisions based on personal requirements. The need for optimality during a meeting between key decision makers is questionable if lengthy computational times are involved, but for the purpose of creating a model network of reserves for decision makers to consider, it would be ideal (Cabeza & Moilanen 2001; Carwardine *et al*. 2007). In the following section I will review some of the popular RSAs that are in use with specific focus in their use as conservation tools.

Marxan

Marxan was created by Ball and Possingham (2000; Possingham *et al.* 2000) of the University of Queensland, Australia, as decision support software for conservation planning. It has been used as a tool for ecoregional conservation planning and uses a simulated annealing algorithm to find a number of solutions, each of which represents a possible set of reserves, and from this, irreplaceability can be calculated to form an efficient reserve network solution (Carwardine *et al*. 2007). The program aims to reduce cost whilst it meets certain biodiversity targets and addresses spatial design goals. The biodiversity targets do not represent a limitation, so if a target can only be met by incurring a large cost, Marxan can disregard it in order to minimise cost. Spatial design objectives can be met with the use of the boundary length modifier (BLM) which determines the relative importance of decreasing the edge-to-area ratio of reserves in the network (Carwardine *et al*. 2007).

C-Plan

C-plan is a greedy heuristic algorithm that uses irreplaceability to add sites in a step-wise fashion (Carwardine *et al*. 2007). The program can be used interactively to create a reserve network, or its heuristic algorithm can create solutions independently. It was designed for use in planned negotiations where it is necessary to obtain quick results that allow users to discuss the outcome of different possible reserve networks (Ferrier *et al*. 2000). The program first calculates an estimate of the number of sites required to reach the targets, followed by an estimation of irreplaceability for each site which allows the algorithm to work out the likelihood of reaching the set targets if a particular site is unavailable as a protected area (Carwardine *et al*. 2007; Ferrier *et al*. 2000). C-plan is not sensitive to spatial patterns and therefore is unable to design spatially compact reserve networks, unless the data are conducive to such a pattern.

ResNet

This is a hierarchically controlled rarity-complementarity-based algorithm that selects an initial site on irreplaceability, complementarity, or a user-defined set of sites (Kelley *et al*. 2002). ResNet will then select cells on the basis of rarity, if two sites are equally irreplaceable within the network, the next site will be added depending on the highest complementarity value. If a decision is still not made, ResNet chooses adjacent sites and failing this will choose the site randomly from the possible alternatives. The algorithm can also be made to check for redundancy within the network, as well as applying cost constraints on the final solution (Kelley *et al*. 2002).

ZONATION

The Zonation algorithm works by iteratively discarding areas of lowest value from the edge of the remaining area, it does this through a reverse iterative heuristic that can reach optimality with a high rate of success (Moilanen 2007). This is done so that the resultant reserve network will have high spatial aggregation, and additionally, the edge removal technique can reduce processing time, allowing Zonation to be used on very large data sets (Moilanen 2007; Moilanen *et al*. 2005). The result of the algorithm is a nested ranking of reserve sites which is easily interpreted for conservation planning (Kremen *et al*. 2008; Moilanen *et al*. 2005).

CPLEX

CPLEX is an optimising program that uses a branch and bound algorithm which solves mixed integer problems (Ohman & Wikstrom 2008). A branch and bound algorithm works by initially solving the linear programming relaxation which is applied to preliminary solutions that are created by a number of heuristics (Pyke & Fischer 2005). If the value of the solution is an integer, then the optimal solution has been found, if not, branching occurs and two new problems are created. These two solutions are then solved and the process continues until all the possible alternatives have been determined and the optimal solution is created (Csuti *et al*. 1997).

Applying RSAs to large datasets

Some reserve selection algorithms have already been applied to similar tasks and scales that will be relevant for this project and could potentially give an indication as to which algorithms are able to create continental-scale reserve networks for a large species assemblage. McClean *et al.* (2006) used a rarity and a richness heuristic algorithm to select protected areas that will aid the Sub-Saharan Africa Important Plant Area network in mitigating the effects of climate change on plant conservation areas. The heuristic algorithms were capable of processing data at the same scale that this study will use, although McClean *et al.* (2006) did not fully discuss the computational times or sub-optimality of the algorithms used. Pyke and Fischer (2005) used CPLEX to create a reserve network that will cope with climate change at a smaller scale (Central Valley Ecoregion, California, USA). CPLEX was only run to find a solution within 0.01% of the optimum to reduce computational time, whilst still giving a near optimal solution. MARXAN has been applied to a continental scale by Rondinini *et al.* (2006) who used it to determine irreplaceability among African protected areas and their vulnerability to human population. Although this study did not involve climate change, it proves the ability of MARXAN, and therefore simulated annealing algorithms, to model at appropriate scales.

Habitat connectivity

Habitat corridors

Facilitating the dispersal of species from their present distributions to potential future distributions will be a major task for conservationists in the future. There has been much debate in the literature over the best ways of achieving this, with particular focus on the practicality of habitat corridors which link habitats together so that species can move freely between metapopulations (Vandermeer & Carvajal 2001). Habitat corridors represent a feasible solution to the problem of connectivity between reserves that hold certain species presently, and reserves that could potentially hold these species in a future climate scenario (Vos *et al*. 2008). In this section I review a selection of relevant literature based on the topic of habitat corridors, and outline some of the software that is available for designing corridor systems.

The theoretical support for habitat corridors is based around the theory of island biogeography and metapopulation dynamics. Isolation of a habitat will decrease immigration of individuals and local stochastic extinction events will reduce the diversity of species found within that habitat (Kupfer *et al*. 2006). However, in a metapopulation, repopulation through the immigration of new species will keep the number of species at a dynamic equilibrium (Moilanen & Hanski 1998). When considering the effects of climate change on a reserve network with poor biological connectivity between reserves, increased extinction rates caused by a decrease in climatic suitability will not be counteracted by increased immigration from other protected areas, and therefore, the dynamic equilibrium will cause an overall decrease in biodiversity within that reserve. Facilitating the immigration of species across climatic gradients will allow individuals to colonise new habitats that may become climatically suitable in the future, and therefore decrease extinction risk. Parmesan (1996) showed that *E. editha* experienced local population extinctions at the southern margin of its distribution, and colonisations at the northern margin which were causing an overall northward shift in the species' distribution. This provides some evidence for the fact that species can respond to climate change through metapopulation dynamics. If new colonisations were unable to take place at the northern boundary of *E. editha*'s range, then the species' range would have decreased.

Habitat corridors are often criticised because their simplicity of design represents a disregard for other forms of connectivity, such as movement between habitat patches within the environment (Hannon & Schmiegelow

2002; Lindenmayer *et al*. 2008). When applied to climate change, there are several other important criteria that must be considered. One of the most important is calculating the correct orientation of the corridors. Halpin (1997) recognised that creating corridors that were orientated in a north-south direction to facilitate climate forcing due to temperature gradients alone would fail to incorporate the additional effects of changes in climate moisture levels. Other such factors make predicting appropriate paths of potential migration difficult and therefore makes the application of resources to such projects hazardous. Not enough is understood about the ecology of habitat corridors to guide landscape managers in their application, with knowledge of corridor dimensions and which species are likely to utilise corridors, being of particular importance to conservationists (Halpin 1997).

Connectivity software

There are several programs available that can design conservation corridors through a landscape for species dispersal. The least cost paths algorithm (LCPA) is one of the simplest methods of creating habitat corridors. LCPA finds the path of least resistance through a habitat using a simple algorithm that has fast run times. The simplicity of LCPA has been criticised because the program relies on only finding one corridor for dispersal, which may not be ecologically effective (Drielsma *et al*. 2007). Hargrove *et al.* (2005) created PATH (Pathway Analysis Through Habitat) which uses a virtual walker to simulate the movement of a species through a landscape. The walkers can be assigned attributes so that they match the decision making of different species, and as they disperse from a habitat site, they search for the most desirable path through the landscape. The algorithm requires large computational power due to its complexity and decision-making ability. Drielsma *et al.* (2007) introduced the spatial links tool which creates corridors by mapping link values based on the contribution of ecologically efficient paths to overall region-wide connectivity.

To my knowledge, these tools have not been used to model connectivity at the continent-wide scales, of this project, and as a result it is unclear whether such programs could be applied. A further consideration is whether the programs are able to identify corridors that are specifically oriented along climatic gradients, if not, they will be impractical for their desired use. There are possible alternatives to habitat corridors which are often cited in the literature. McClean *et al.* (2006) recommended maximising reserve area in order to maintain plant diversity in the future. Other authors simply recommend improving aspects of the matrix which would create a more hospitable environment for species dispersal, therefore allowing colonisation of reserves in new climate space to take place (Blaum & Wichmann 2007; Fahrig 2001; Vos *et al*. 2008).

Conclusions

This literature review has covered some of the evidence that suggests species are likely to respond to impending climate change through individualistic range shifts. There is evidence that other forms of adaptation will also occur, but evidence of range shifts that have occurred because of climate change in recent years increases the importance of finding ways to assist natural systems in coping with changes in distribution, especially when considering the combined effects of climate change and anthropogenic habitat change processes.

There are a number of caveats in the use of BEMs to predict future species distributions. However, BEMs represent the most effective way of carrying out such predictions to date. It is important to realise that these errors are likely to be present, so that outcomes from these models are not used without considerations for such inaccuracies. However, these predictions are important to assess risks and to create conservation plans that can be applied if the predicted scenarios are realised

I looked at potential ways of spatially designing reserve networks that could mitigate the effects of climate change. When considering the tools that are available to design potential alterations to a protected area network at the continental-scale, most literature cautions against the use of optimising algorithms, such as branch-and-bound algorithms, that are unable to cope with the volume of data that is necessary for modelling at these scales. Heuristic algorithms are able to cope with large data sets, but are criticised because of their often sub-optimal results. Simulated annealing methods, however, offer a middle ground between optimality and ability to cope with large data sets, and programs such as Marxan are freely available and widely used. Marxan also provides the useful function of starting with a user-defined set of reserve sites, which means that modifications can be made to an existing reserve network. This is especially useful when considering additional sites that will complement a reserve network in a future climate scenario.

Modelling possible ways to facilitate migration caused by climate forcing may not be possible because of the lack of appropriate programs that can model at a large enough scale or model in an orientation that is relevant in relation to climatic gradients. Application of these programs to such a task will be a novel area of study and is worth further consideration.

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Chapter 2: Key regions of current and projected future avian biodiversity across Sub-Saharan Africa

Abstract

Protected areas are a crucial tool used to protect species from the encroachment of human development (Gaston *et al.* 2008). However, with a changing climate some protected areas may become redundant if the climate becomes unsuitable for key species (Rodrigues *et al.* 2000). Here I produce an ideal minimum network to protect bird species based on gridded cells across sub-Saharan Africa for the recent period and contrast this to similar networks designed to protect species under future climate scenarios. I chose the birds of Sub-Saharan Africa, a well documented group for which data sets are available at the continental scale. Using a reserve selection algorithm to select one and quarter-degree cells, reserve networks were designed which represented all species across the continent. I demonstrate that cells in upland areas will become increasingly important in protecting species through the current Century and highlight key sites that are selected during all time periods considered.

Introduction

Future changes in climate could have both positive and negative effects on the performance of protected areas (PAs). To date, PAs have been designated under the assumption that climate will remain unchanged and hence PAs will continue to protect current species assemblages in the future (Burns *et al.* 2003; Hannah *et al*. 2007). As climate changes, current PAs may become redundant as the local climate changes, altering the species assemblages found within them. This will have a large impact on biological conservation because of its reliance on the presumed continuing performance of PAs throughout the world (Rodrigues *et al*. 2004).

The allocation of land for protection is often due to chance historical events, a lack of utility, or due to landscape aesthetics, which appeal to human nature (Pressey 1994). This form of *ad hoc* reservation is responsible for a large proportion of protected areas worldwide, but it is a very inefficient method, in terms of available space, of preserving biodiversity (De Klerk *et al*. 2004). Recent methods for selecting PAs to protect biodiversity include the identification of biodiversity hotspots (Myers *et al*. 2000) and systematic reserve selection; the latter calculates the most efficient allocation of land for protection, in terms of species coverage (Rondinini *et al*. 2005). This allows resources to be focused in areas where biodiversity is highest, and therefore the efficiency of reservation over a large scale can be increased. Both *ad hoc* and hotspot reservation have been criticised because they can lead to under-representation of biodiversity in areas with low levels of endemism or because of discrimination in the historical selection of PAs (Pressey 1994). The combination of inefficiently located reserves and a lack of consideration for the effects of changing climates, suggests that a re-evaluation of key PA networks is urgently required. Understanding how species distributions will be affected by climate change will be a priority for conservation biology over the coming Century and will allow conservation organisations to focus attention on where to locate PAs in the future (Heller & Zavaleta 2009).

Research into the potential impacts of climate change on the distributions of species and consequently on the future effectiveness of reserves is a relatively recent area of study (Heikkinen *et al*. 2006). Palaeoecological studies have demonstrated how species ranges have altered in response to climatic change in the past and indicate how species may respond to projected future changes (MacDonald *et al*. 2008). They show that species respond individualistically to changing climate, highlighting the importance of projecting responses for individual species rather than for communities as a whole and that changes in climate will cause changes in the composition of species communities in the future (Graham & Grimm 1990). Although a large number of studies have projected the future distributions of species, few have attempted to use predicted future assemblages of species in an applied way to explore the robust nature of current conservation strategies. Several studies have used reserve selection algorithms (RSAs) both to create potential reserve systems that can cope with the effects of climate change and to test the resilience of reserve systems to cope with such changes. Heuristic algorithms have been used to create a reserve system to test the effectiveness of the sub-Saharan Africa Important Plant Area (IPA) network under future climate scenarios (McClean *et al*. 2006). At a local scale, integer programming (IP) algorithms have been used to determine an optimal reserve network for fairy shrimp (*Anostraca*) in California, USA, capable of withstanding projected climate change (Pyke and Fischer 2005). The latter study highlighted that making bioclimatically representative reserve networks does not necessarily require a large addition of resources, but rather a greater understanding of how climate will impact such networks. RSAs have been coupled with distribution models to determine the effectiveness of protected areas under differing climate scenarios (Hannah *et al.* 2007). Hannah *et al.* (2007) concluded that creating new protected areas would help to reduce the negative impacts of climate change and that the 'cost of waiting' often increased the additional area required to represent all species under climate change. To date, there have been no attempts to create potential future reserve networks for avifauna at a continental-scale, which is likely to be of great importance for conservation in the future. This study will use Marxan, an RSA which uses the process of simulated annealing to calculate optimal reserve networks. Marxan provides a compromise between accuracy and processing times which is ideal for the datasets used in the study.

The 'bioclimate envelope' of a species represents a species' distribution at one time period in relation to the climatic conditions within its realised niche at that time (Pearson & Dawson 2003). There are a wide diversity of techniques for relating a species distribution to climate and whose use is partly dependent upon the type of data available or the statistical framework of choice. Simulations from several models are often combined to produce an 'ensemble forecast' (Araujo & New 2007). Bioclimatic Envelope Models (BEMs) have the potential to simulate the distribution of a species based solely on climatic data, and if applied to projected climate change scenarios, allow simulation of potential species ranges in the future (Heikkinen *et al*. 2006). However, there are numerous other factors that may prevent the modelled response from occurring such as biological interactions between species (Araujo and Luoto 2007). BEMs are statistical models that use the current distributions of a species to deduce its climatic requirements (Hijmans & Graham 2006), calculating individualistic responses of species rather than whole-community responses. These climatic requirements can then be applied to future climate scenarios to provide predictions of the distributions of species.

Using simulated avifaunal range data from BEMs, reserve networks can be designed using reserve selection programs which select protected areas on the basis of how their species assemblages will contribute to the overall species coverage of the network. Here I apply RSAs to gridded data simulating avian diversity for the recent period and for three future time periods across sub-Saharan Africa. By producing a theoretical network of key grid cells for different time periods and under several future climate projections I aim to identify key regions that remain important for avian diversity through the current Century or whose importance is evident for varying future climate scenarios.

Methods

Data for one-degree and quarter-degree cells across sub-Saharan Africa were used to create theoretical reserve networks using planning units sized at those same resolutions. This was done for recent (referred to as present) species assemblages as well as for predicted species assemblage data obtained from three different climate scenarios for 2025, 2055 and 2085 that were created using climatic response surface (CRS) models.

Sub-Saharan Africa is defined as the region of mainland African south of 20°N. Here I apply an RSA and bioclimate envelope models (BEMs) to gridded data at a one-degree (latitude-longitude) and a quarter-degree resolution across sub-Saharan Africa. The area is represented as 1,963 one-degree cells (which are approximately 111 km^2) at the equator and 29,575 quarter degree cells (which are approximately 25 km^2). Approximately 2,000 bird species occur in this region of these 1,608 have been successfully modelled using BEMs as part of a previous project (Hole *et al*. 2009 – see below).

Bioclimate and species data

Birds are a well used and appropriate taxon group for such studies for several reasons, the most important being the extensive presence/absence data sets that are available over continent-wide scales (Pearson 1994). It has also been shown that birds can act as good indicators of endemism for other taxonomic groups, illustrating the value of their conservation in a broader context (Brooks *et al*. 2001b; Gregory *et al*. 2009).

The models simulating future distributions of bird species across sub-Saharan Africa, were produced by Hole *et al*. (2009) from recent species distribution data (1980-2000; (Brooks *et al.* 2001a)) from the Zoological Museum of the University of Copenhagen (Jetz & Rahbek 2002). Presence-absence data for 1608 species were available for the 1963 one-degree cells that make up sub-Saharan Africa. Mean bioclimatic data for the one-degree cells were created from mean monthly temperature and precipitation data available for quarter-degree cells for the period 1950-2000 (Hijmans *et al.* 2005). Seven bioclimatic variables were chosen for modelling the bioclimatic envelopes of each species; mean temperature of the coldest month; mean temperature of the warmest month; an estimate of the ratio of actual to potential evapotranspiration; wet season duration; wet season intensity; dry season duration; and dry season intensity (Willis *et al*. 2009). They were selected for their previously confirmed ability in modelling the bioclimate envelopes of a wide range of European and African bird species (Huntley *et al*. 2006). The first three variables were used as standard variables in all models, but only one of the four seasonality variables, wet season and dry season duration and intensity were used (the procedure for selecting the fourth variable is explained by Huntley *et al.* 2006).

The climate data for the future time periods were obtained from three general circulation models (GCMs); HadCM3 (Gordon *et al.* 2000), ECHAM4 (Roeckner *et al.* 1996) and GFDL-R30 (Knutson *et al*. 1999). The simulations used were based on the Special Report on Emissions Scenarios' (SRES) B2a scenario for three time periods, which represent 30 year averages for 2011-2040 (abbreviated from here-on-in to the central year of the series; 2025), 2041-2070 (2055) and 2071-2100 (2085). The SRES B2a scenario describes a world in which the emphasis is on local solutions to economic, social and environmental problems. There is intermediate economic development compared with other scenarios, as well as less rapid land-use changes and more diverse technological change. The scenario represents increased environmental protection and social equity at local and regional scales. This leads to a scenario which predicts mid- to low- green house gas emissions over the 21st Century (Nakicenovic & Swart 2000). The GCMs used are representative of the mean for the nine models included in the Intergovernmental Panel on Climate Change (IPCC) Third Assessment Report (Cubasch *et al*. 2001) and range in simulated precipitation regimes from relatively wet (GFDL-R30) through to the mean (HadCM3) and relatively dry (ECHAM4). Since the data have been created using climate models from the Third Assessment Report, the IPCC Fourth Assessment report has been published. The models used have therefore since been improved by the reduction of error in the prediction of precipitation, mean sea-level rise and surface air temperature (Randall *et al.* 2007). Nonetheless, it is expected that the projected range shifts to be broadly similar.

The bioclimatic envelope of each species was estimated using a CRS, which uses locally weighted regression to fit a response surface to a species' presence-absence data. This method was chosen over alternative approaches such as generalised additive models (GAM) after paired t-tests on sensitivity and true skill statistic (the assessment metrics used) indicated that CRSs performed better than GAM (see Hole *et al.* 2009). The CRS models were validated using two techniques; firstly, for species which were recorded in > 20 one-degree cells, *K*-fold partitioning was used. *K*-fold partitioning is a procedure which generates *K* models by partitioning the data into *K* equal-sized sets apart from the *i*-th set which is used as training data. This process is carried out *K* times with each *K* subsample used once as the training data, this has the advantage of using all data for both validation and training (Ali &

Pazzani 1996). This method has advantages over the often applied 70:30 data splitting approach for model creation and validation (Thuiller *et al*. 2009) as it reduces potential issues of spatial autocorrelation.

Predictive performance was assessed using values obtained for the area under the curve (AUC) of a receiver-operated characteristic plot (Fielding & Bell 1997). This was carried out for 1401 species, 89% of which exhibited *K*-fold partitioned AUCs of ≥ 0.9 (no species had a *K*-fold partitioned AUC < 0.7), indicating high-model performance (Swets 1988). Model fit for the remaining 207 species, recorded in fewer than 20 one-degree cells, was assessed using a jack-knifing approach. This process calculates the probability of a species' occurrence in a single one-degree cell, using a model built using all of the data except for the cell for which I wish to obtain a simulation of occurrence. This is repeated for all 1,963 cells of sub-Saharan Africa, for each species, and essentially produces simulations independent of the data used to create the CRS. Although this is more prone to issues of spatial autocorrelation than K-fold partitioning, the latter procedure cannot be used on restricted range species as large proportions of their entire range often fall within a single excluded panel. The projection accuracy was assessed using the same AUC process as applied to the more widespread species. 83% of the 207 species displayed a jack-knifed AUC ≥ 0.9, which again indicates a high-model performance (for more details, see Hole *et al*. 2009).

Reserve selection

To create reserve networks, a simulated annealing reserve selection algorithm, Marxan version 1.8.10 (Ball & Possingham, 2000; Possingham *et al*. 2000), was used to create near optimal solutions using a set-covering problem. Simulated annealing operates through a process of random addition and removal of planning units from a preliminary set of units using stepwise iterations until an optimal solution is produced. Optimality for this study was defined as the representation of all species within a reserve network using the minimum number of planning units possible. Simulated annealing is not guaranteed to reach an optimal solution unlike algorithms such as integer programs (IPs), which will do so routinely (Onal & Briers 2002). However, unlike IPs (Moilanen 2008), simulated annealing algorithms will reach near optimal solutions over a relatively short timescale, an important consideration given the large data sets being processed in this study. Other heuristic approaches have been criticised in the literature for reaching sub-optimal solutions (Church *et al*. 1996). Heuristic algorithms reach solutions faster than both IPs and simulated annealing methods, however, the middle-ground between speed and optimality provided by simulated annealing meant that it was seen as the most appropriate choice for this study.

Reserve selection simulations were run for one-degree cells using the present and 2085 data and using the present, 2025, 2055 and 2085 data for the quarter-degree cells. This was carried out for two separate species coverage targets of one and five representations per species across the reserve network. A target of one was chosen to give an indication of where reserves would need to be placed in order to represent every species once. A target of five is more biologically useful in a reserve network where separate populations are preserved, protecting species from local extinction events and is therefore presented in the results. Other studies at similar scales have used representation targets of one (McClean *et al*. 2006) and three (Fjeldsa 2007) units, whereas other studies have used variable targets depending on factors such as the conservation status of a species or to protect a percentage of a species' range (Illoldi-Rangel *et al*. 2008; Rouget 2003).

Marxan was set to perform 1,000,000 iterations per run. Iterations are the individual steps that Marxan performs when adding or removing PAs from the reserve network in each run. 10,000 temperature decreases were performed in each run, temperature decreases are the procedure that initially allows negative additions to the network as well as positive ones which prevents each run from reaching local optimums instead of a global optimum. Some studies using Marxan (e.g. Rondinini *et al.* 2005), have used 1000 runs per simulation whilst other have used 100 runs per simulation (e.g. Zielinski *et al*. 2006). For this study preliminary simulations were carried out using 1000 runs but these were found to yield similar results to simulations using only 100 runs.

Therefore, I followed Zielinski *et al*. (2006) in using 100 runs for each simulation. The significance of optimality in this study is questionable as there are many other factors that would need to be taken into account before the results could be applied practically, especially when considering the scale and potential caveats of the data (Cowling *et al*. 2003; Knight *et al*. 2008; Knight *et al*. 2006). The cost of the planning units was fixed because on average the cells are the same size (there are small variations in size and shape depending on their latitude relative to the equator).

Each run produced a network comprised of a number of planning units and listed the shortfall, in terms of the number of species not represented by the network (or the under-representation of species, in terms of the number of planning units in which they were protected in the network). The optimal solution was saved as a list of planning units.

Results

The results shown presented as maps (Figs. 1.1 & 1.2) with the cells selected by Marxan identified. For the future scenarios, because there were three different climate scenarios for each time period, all selected cells are shown on the map, with those cells selected in more than one climate scenario highlighted by a different colour and size. The selection of a cell in more than one climate scenario does not strictly represent the importance of a cell, but acts as a proxy of importance whereby the cell is more resilient to different predicted climate scenarios.

The species shortfall and the number of cells in each reserve network selected by Marxan is shown in table 1.1(selected quarter-degree cells, as well as species shortfalls are listed in supplementary material S1). The shortfall is the number of species that were not represented within the network. Depending on the Conservation Unit (CU) target for the reserve network, the shortfall will represent different circumstances. For a CU target of 1, the shortfall shows the number of species that were not represented within the network and therefore shows that according to the data, the species does not have any remaining suitable bioclimate in sub-Saharan Africa. For a CU target of 5, the shortfall shows the number of species that are not represented in five or more cells in the network.

One-degree data

The reserve networks created from the one-degree data show similar patterns of distribution across sub-Saharan Africa between the current period and the projected 2085 scenarios (Fig.1.1a-b). Noticeable groupings of selected cells are found in Fig.1.1a-b in areas such as the Albertine Rift, Eastern Arc Mountains, Kenyan Mountains, Ethiopian Highlands, Cameroon Mountains and the Cameroon and Gabon Lowlands. There are also smaller, more isolated, groupings in the Upper-Guinea Forests, Western Angola and Namibia. These groupings become more prominent in Fig. 1.1b, in particular, the Ethiopian Highlands, Drakensberg Mountains, Highveld, and the Cape floristic region appear to show an increase in the number of selected cells. This is highlighted in Fig. 1.1b, by the increased representation of cells in more than one climate scenario, indicating the importance of these cells over a range of differing future climates.

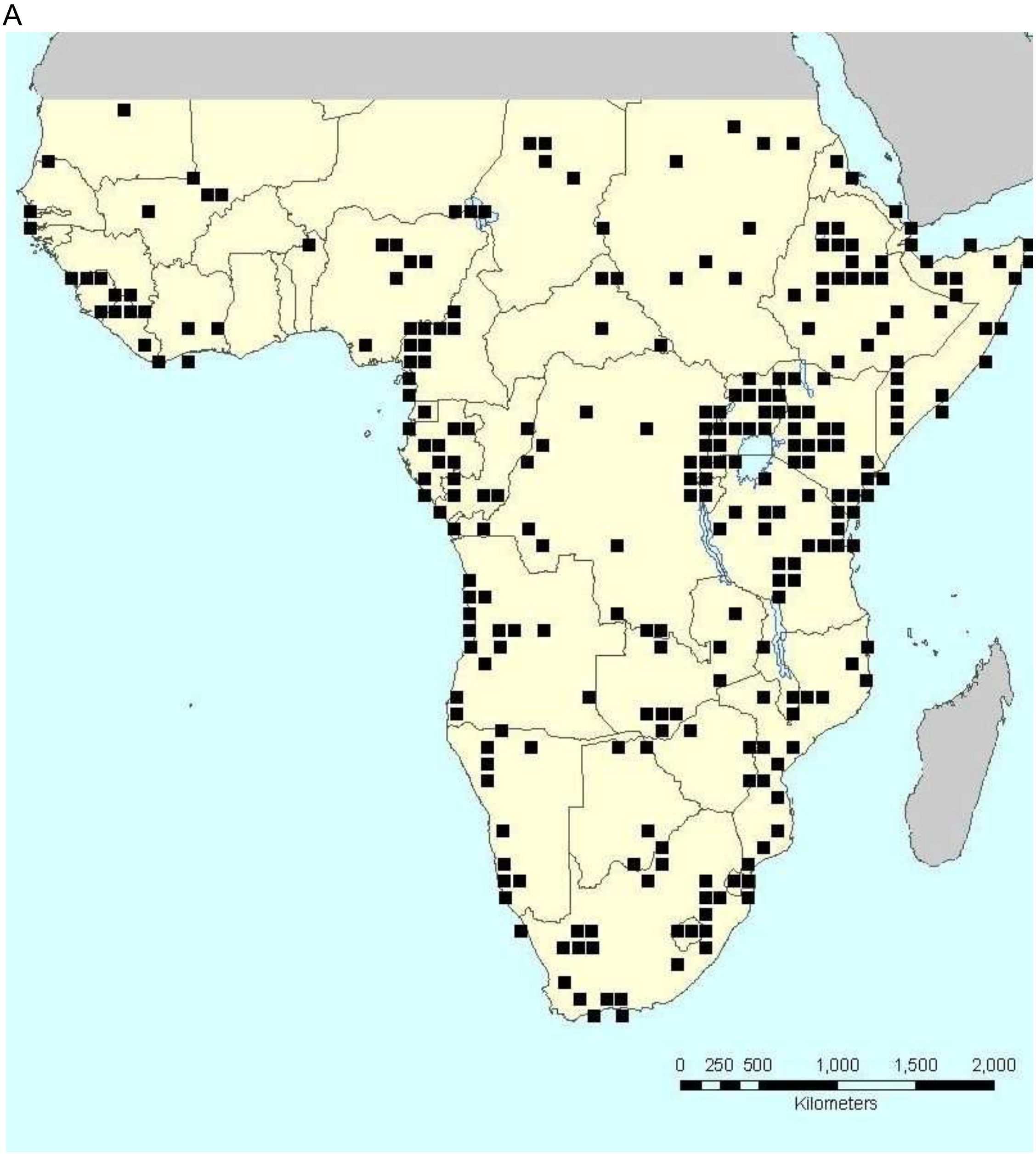

Figure 1.1 *(A) One degree cells selected by Marxan to protect bird species in sub-Saharan Africa for current species distributions. Cells represented in black.*

B

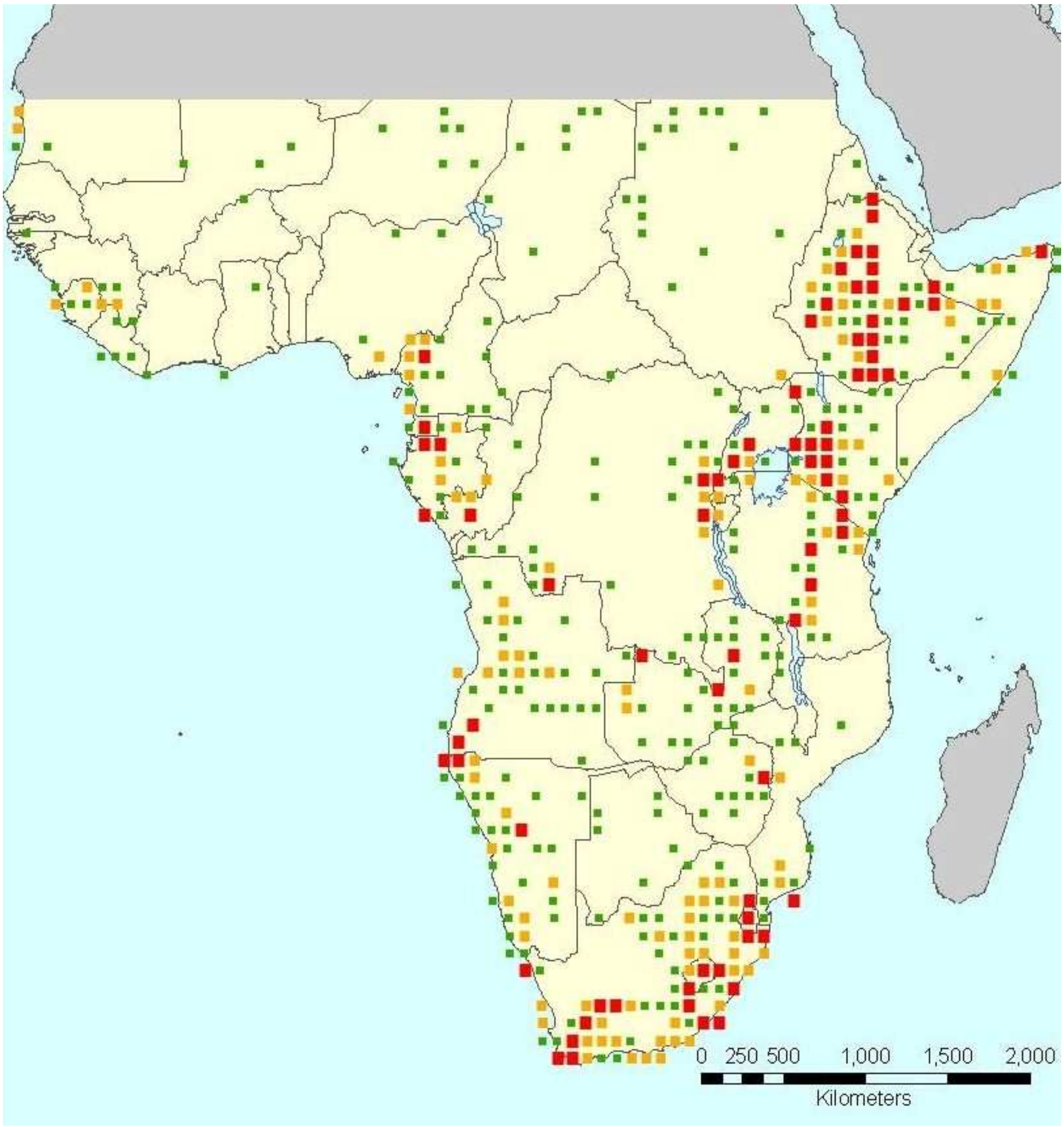

Figure 1.1 *(B) Map of selected one-degree cells selected by Marxan to protect sub-Saharan African bird species for projected 2085 species distributions coloured depending on the how many future scenarios (ECHAM4 / OPYC, GFDL-R30, HadCM3) they are selected in. Red = 3 times, Orange = 2 times, Green = 1 time.*

Quarter-degree data

The selected quarter-degree reserve networks show a clear and progressive change in distribution over the four time periods used (Fig. 1.2a-d). The areas in which the quarter-degree cells are grouped are the same as those selected for the one-degree reserve networks, but show a higher degree of detail, owing to the finer scale. There are few major differences between the selections made by Marxan for the present and for 2025 with selection in the Ethiopian Highlands, North Somali Mountains, Albertine Rift, Cameroon and Gabon Lowlands, Cameroon Mountains and Upper Guinea Forests. Fig. 1.2b has more concentrated clusters in areas such as the Kenyan Mountains, Eastern Zimbabwe Mountains, Tanzania-Malawi Mountains, Cape Floristic Region (CFR), South African Grasslands and Highveld, and in the West of Namibia and Angola. Many of these areas are defined as Endemic Bird Areas (EBAs (Stattersfield *et al.* 1998)).

The pattern of selected cells in the 2055 and 2085 is the same as that of 2025 but with a greater degree of clustering. This is highlighted by larger number of cells selected in two or more of the GCM scenarios for each time period (Fig. 1.2c-d). These areas of increased selection are all highland areas which are also selected for the present-day distributions, however, the reserve networks for 2055 and 2085 avifauna distributions have more cells selected within these areas (e.g. South Africa and Ethiopia; Fig. 1.3). Lowland areas such as in the Demorcratic Republic of Congo experience a decrease in selection from the present compared with end of Century simulations. (Fig. 1.3).

A

Figure 1.2 *(A) Quarter-degree cells selected by Marxan to represent sub-Saharan African bird species in their current distributions. Cells are represented in black and are not shown to scale.*

B

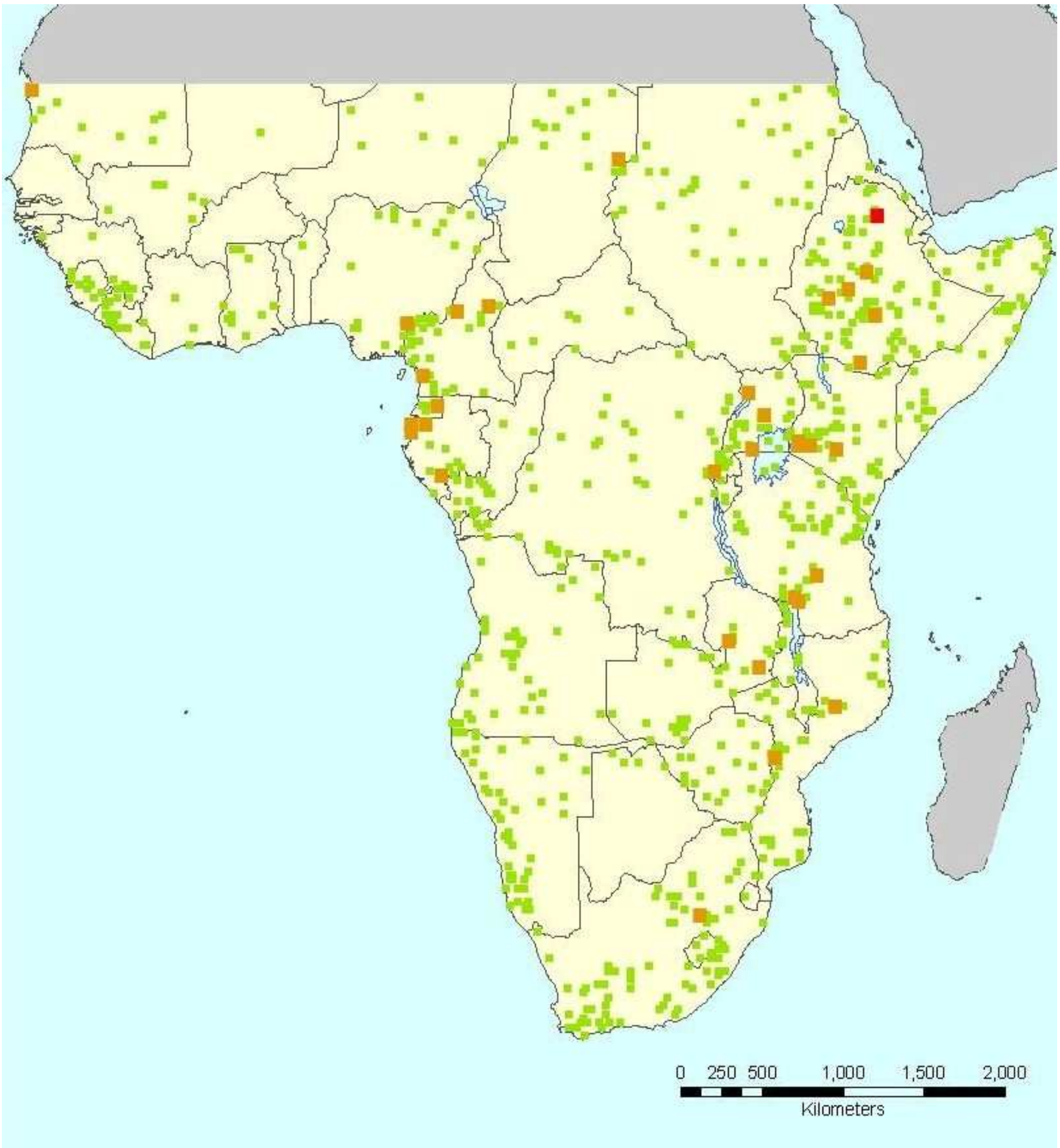

Figure 1.2 *(B) Map of quarter-degree cells selected by Marxan to protect sub-Saharan African bird species for projected 2025 species distributions coloured depending on the how many future scenarios (ECHAM4 / OPYC, GFDL-R30, HadCM3) they are selected in. Red = 3 times, Orange = 2 times, Green = 1 time. Cells are not shown to scale.*

C

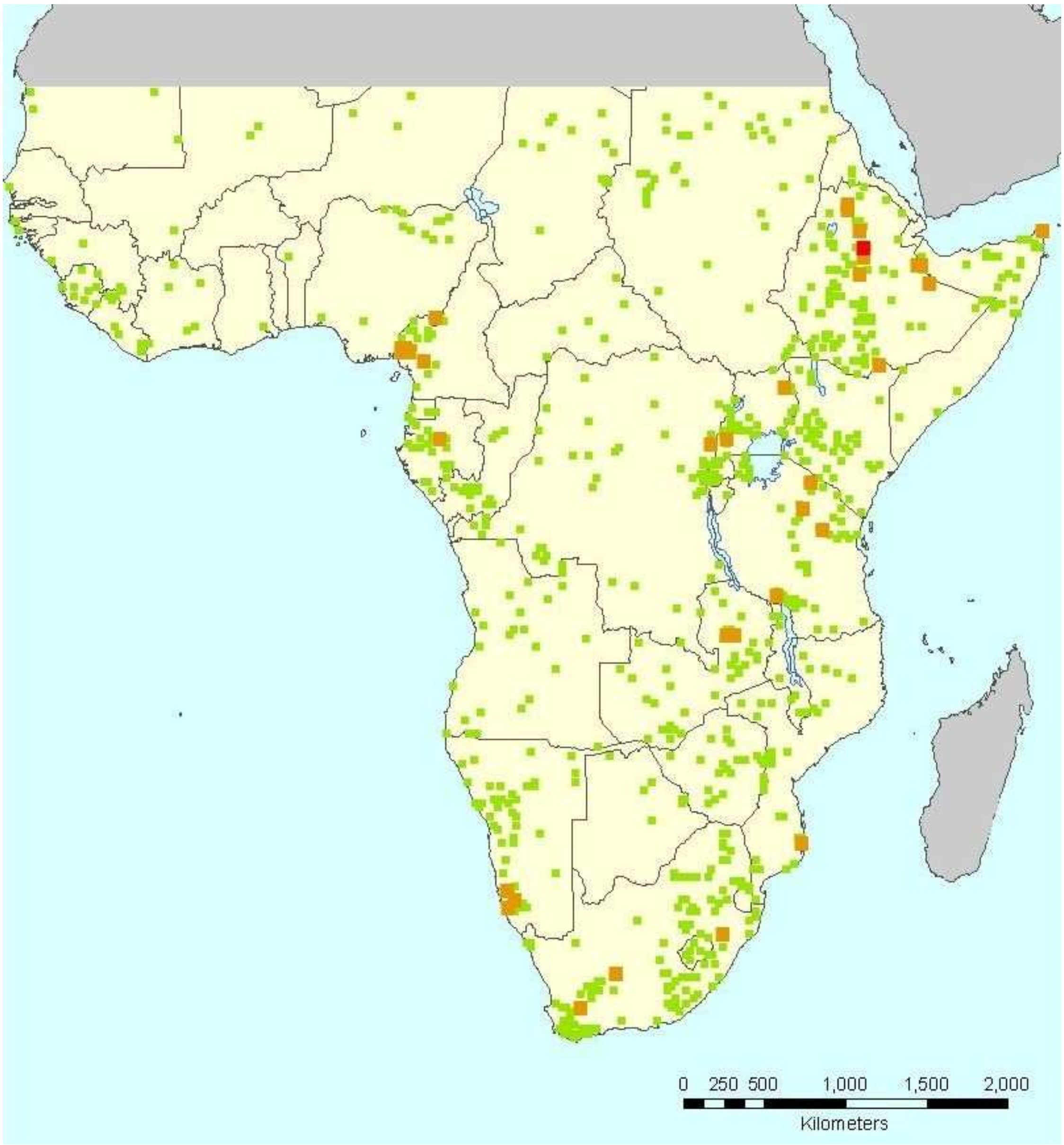

Figure 1.2 *(C) Map of quarter-degree cells selected by Marxan to protect sub-Saharan African bird species for projected 2055 species distributions coloured depending on the how many future scenarios (ECHAM4 / OPYC, GFDL-R30, HadCM3) they are selected in. Red = 3 times, Orange = 2 times, Green = 1 time. Cells are not shown to scale.*

D

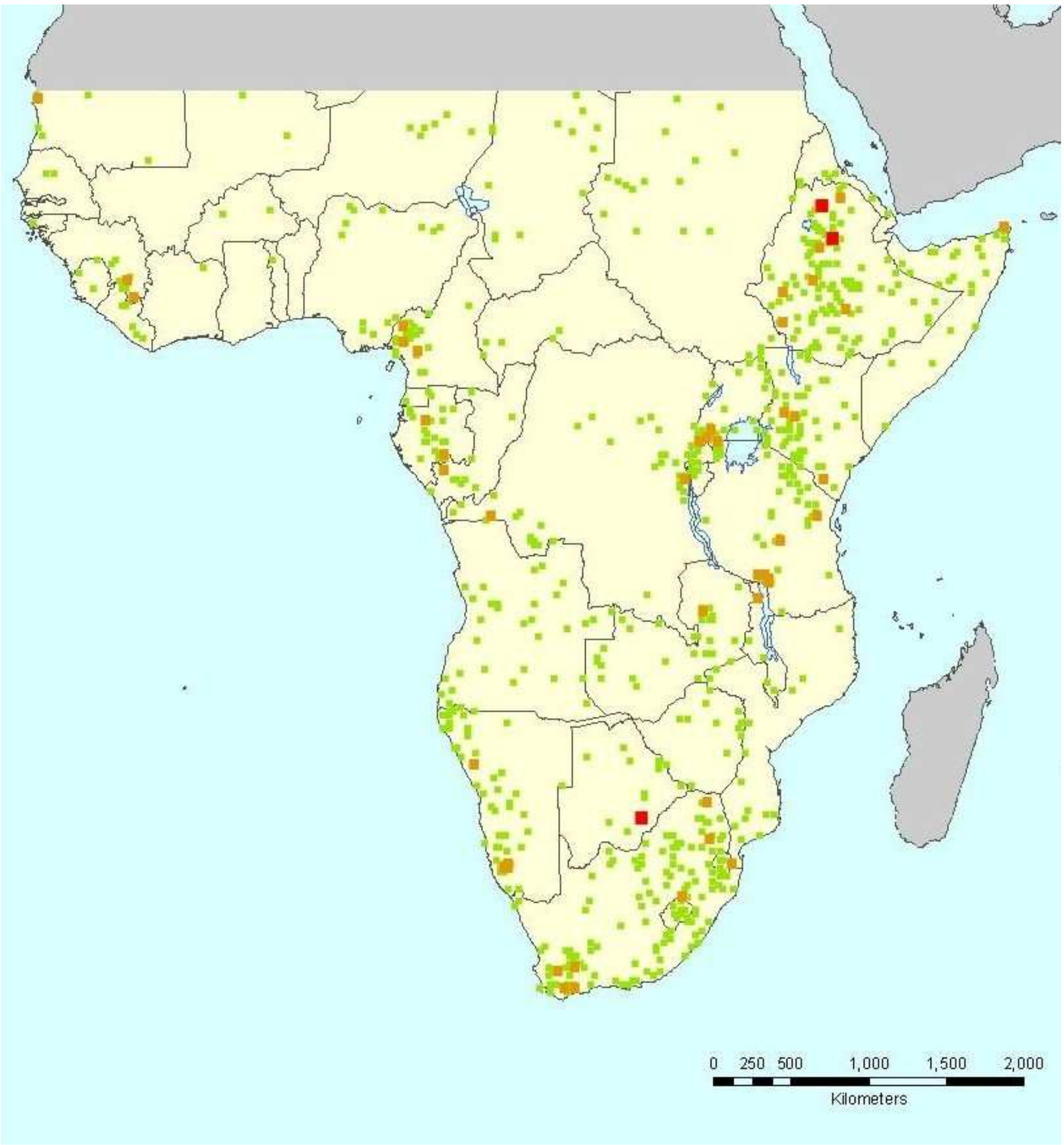

Figure 1.2 *(D) Map of quarter-degree cells selected by Marxan to protect sub-Saharan African bird species for projected 2085 species distributions coloured depending on the how many future scenarios (ECHAM4 / OPYC, GFDL-R30, HadCM3) they are selected in. Red = 3 times, Orange = 2 times, Green = 1 time. Cells are not shown to scale.*

Climate data

There are in some cases, as would be expected, noticeable differences between the three GCM scenarios, in terms of how concentrated the groupings of cells are in specific areas (Fig. 1.4). The three different climate scenarios mostly differ because of precipitation levels (Wichmann *et al*. 2003). The relatively ‘wet’ GFDL-R30 scenario has less clustering in the two peak areas of Ethiopia and South Africa, as opposed to the ‘dry’ ECHAM4 / OPYC scenario, potentially showing less upslope migration due to climate forcing in these areas. Additionally, GFDL-R30 has fewer shortfall species than the other scenarios in the one-degree data, again indicating a more optimistic outcome due to differences in precipitation (Table 1.1). These differences are highlighted in Fig. 1.4, which shows the number of cells selected in each country for the present and three 2085 GCM scenarios. These differences can be seen in areas such as Ethiopia and South Africa where a greater number of cells are selected for the ‘dry’ ECHAM scenario compared with the ‘wet’ GFDL-R30 scenario.

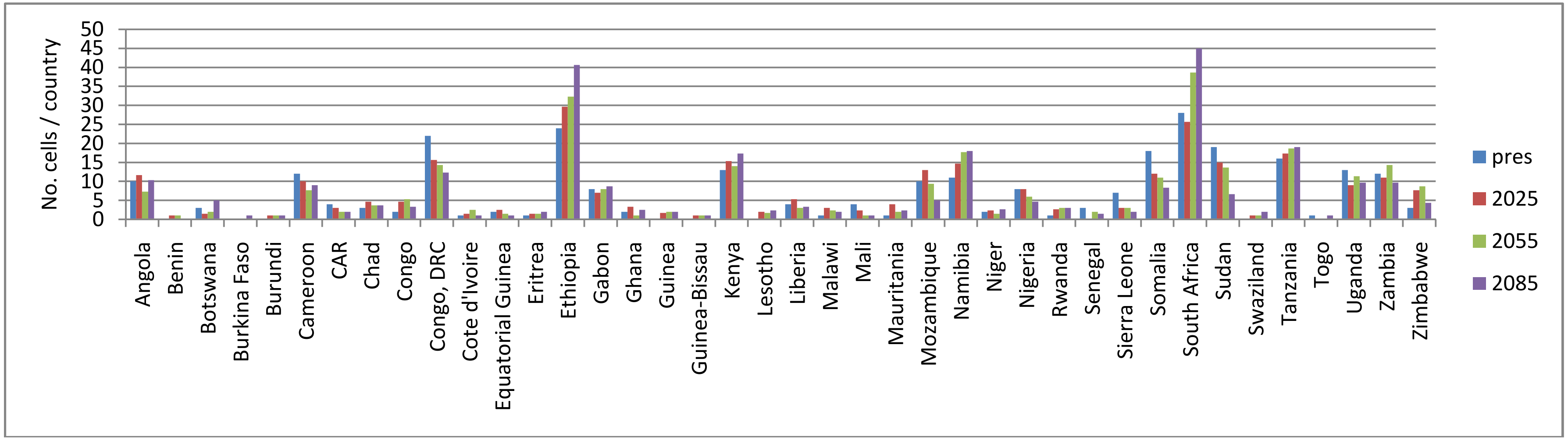

Figure 1.3: *The average number of quarter-degree cells selected by Marxan in each country for the three GCM scenarios for the present, 2025, 2055 and 2085.*

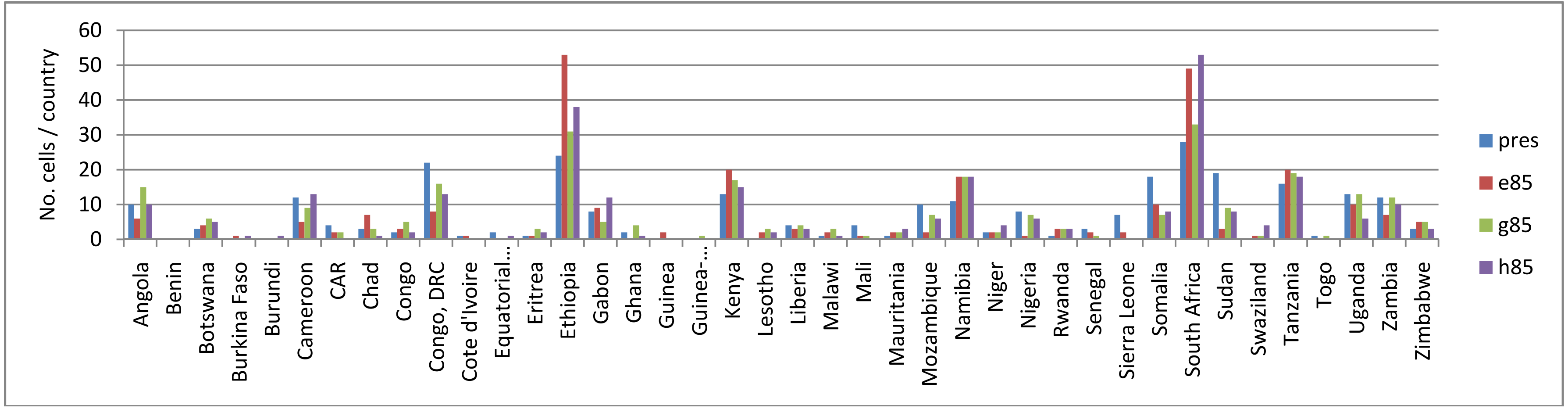

Figure 1.4: *The total number of quarter-degree cells selected by Marxan in each country for the present and the three end of Century (2085) GCM scenarios, ECHAM4, GFDL and HadCM3.*

Table 1.1: *Results from reserve selection for the one and quarter-degree data. PU represent the planning units which are single cells. The different climate simulations; ECHAM4 /OPYC , GFDL-R30 and HadCM3 are represented as E, G and H respectively.*

One-degree	CU target - 1		CU target - 5	
	Total PUs	Spp.	Total PUs	Spp. shortfall
Present	55	0	278	10
E80	59	21	242	141 (21 unrepresented)
G80	55	9	244	114 (9 unrepresented)
H80	62	21	245	133 (21 unrepresented)
Quarter-degree				
Present	59	0	269	0
E20	58	0	268	0
G20	59	0	268	0
H20	58	0	272	0
E50	59	0	263	0
G50	61	0	274	0
H50	61	0	272	0
E80	58	0	295	4
G80	59	1	270	2(1unrepresented)
H80	59	0	271	4

Discussion

The networks produced by Marxan comprise those sites that are required to meet the conservation targets whilst minimising the area of the reserve network. Selected cells are likely to contain rare and endangered species (Reyers *et al*. 2000) which without protection may be at risk from local population extinctions from processes such as habitat degradation and fragmentation. Variation in the selection of cells among the four time periods suggests a changing importance in many areas over time. The cells selected for the current period are reasonably well distributed across Africa, though with some obvious groupings. The localities of grouped cells tend to coincide with known biodiversity hotspots and EBAs (Stattersfield *et al.* 1998). Such regions are likely to be selected by Marxan because they contain range-restricted species (Azeria *et al*. 2007; De Klerk *et al*. 2004).

Highland areas are hotspots for endemism because of frequent changes in climatic zones over relatively short elevation ranges (Williams *et al*. 2003), which causes speciation over short distances and explains the selection of such cells for present-day bird species distributions. However, climate change is expected to force some non-montane species to seek areas of higher altitude in order to remain within their current bioclimatic envelopes in the future, increasing the importance of highland areas for conservation (Pounds *et al*. 1999; Sekercioglu *et al*. 2008). Due to the fact that land area decreases with elevation, as species are forced to higher altitudes, they will experience decreases in range size (Gage *et al*. 2004). Small range sizes are correlated with increasing extinction risk (Harris & Pimm 2008), therefore species that experience decreases in range due to up-slope climate forcing will be under increasing risk of extinction (Sekercioglu *et al*. 2008). The extinction risk posed by climate-induced decrease in range can be exacerbated by factors such as habitat fragmentation which will impede dispersal to more suitable habitats and microclimates, and increases the importance of well planned reserve networks (Raxworthy *et al*. 2008). The areas that are highlighted as being important for conservation in the future are also areas that tend to currently lack protection as reserves (De Klerk *et al*. 2004) and are under threat from large human populations (Rondinini *et al*. 2006). Increasing importance because of climate change coupled with the lack of protection due to the past '*ad hoc'* selection of reserves and the threat of human encroachment means that these areas should be of the highest priority for conservation in Africa so as to ensure their protection in the future. The priority areas for conservation identified in this study should be considered in terms of the reliability and scale of the bird data and the scale of the planning units.

There are several caveats in generating the simulated range data for this study, starting firstly with the climate scenarios used. The three simulations were chosen because they represented the mean for the nine models included in the IPCC Third Assessment Report (Cubasch *et al*. 2001). As mentioned in the Third Assessment Report, these models are affected by three different forms of uncertainty; uncertainty in forcing scenarios, uncertainty in modelled reponses to given forcing scenarios and missing or misrepresented physical processes in models (Cubasch *et al*. 2001).The 'complex, chaotic, non-linear dynamics' in climate systems are also a limiting factor to the accuracy of any climate model (Moore *et al.* 2001). These potential sources of error should be acknowledged when inferring applications of the results of this study to real life situations, but are unavoidable due to the predictive nature of the research.

Another potential limitation in the accuracy of this study is the use of a BEM to predict the distributions of species from their bioclimatic envelopes. This method of predicting species distributions has been criticised for its simplicity in terms of using climate as the sole influencing factor of species ranges (Hampe 2004). Despite these criticisms, BEMs are widely used because they are not reliant on detailed climatic tolerance data of individual species (Heikkinen *et al*. 2006). Scale is an important factor when interpreting the results of BEMs because they are more accurate at large scales (Pearson & Dawson 2003; Morin & Lechowicz 2008). At smaller scales other factors become more important in determining a species' niche (Luoto *et al*. 2007).

The effects of scale are evident in the results as there are obvious differences in the shortfalls of species at the two different scales of this study. The one-degree cell simulations show much greater numbers of species as un- or under-represented within the selected reserve networks than the quarter-degree simulations do. Both sets of data are derived from the same source so the differences observed are caused by scale. The one-degree data are the average climate over a larger area than the quarter-degree data and therefore fewer species will be compatible with the bioclimate. For the quarter-degree data, over the distance of 100 km, there could potentially be several different bioclimates represented that would not be identified at the one-degree scale and therefore the species that exist in these bioclimates would be included. This is particularly true in highland areas where a distance of 100 km can constitute large elevational ranges and consequently bioclimates. Therefore, the quarter-degree data will identify climatically suitable areas for species which were not highlighted by the one-degree data, decreasing the shortfall of species in the results.

The regions that have large numbers of selected planning units are likely to be of importance in the future due to their current biodiversity and endemism as well as their high altitude compared with surrounding areas. Notwithstanding issues of species' ability to respond to climate in a fragmented landscape, these simulations could be used to identify those countries or regions of greatest importance for conservation in the future.

African countries differ greatly in their ability to protect biodiversity, but as a continent, Africa suffers from many factors that impede conservation such as poverty, population growth and political instability (Hackel 1999; Kanyamibwa 1998). Being aware of which countries will be of the greatest importance to conservation in the future will allow conservation managers to develop strategies that are specific to the current and potential future state of those countries. Using examples of the two countries that contain the greatest number of selected planning units in the future, South Africa and Ethiopia, potential issues in creating conservation strategies that are robust to climate change can be identified. South Africa has a well developed and funded conservation infrastructure (Knight *et al*. 2006), so when faced with the task of mitigating the impacts of climate change, conservation planners will have an organised and clearly defined PA network with which to work. By contrast, Ethiopia has been severely affected by civil war and as a result, wildlife conservation is not a priority for the country's meagre resources (Gebre-Michael 1992). In Ethiopia's case, community-based conservation strategies may be more successful than 'fortress conservation' strategies previously used there (Gebre-Michael *et al*. 1992).

More data are required before conservation organisations can start to take action on predicted future impacts of climate change on bird assemblages in Africa. Hannah *et al.* (2007) caution about the 'cost of waiting' to take action against the impacts of climate change, however, allocating conservation resources to areas predicted to increase in importance could create inefficiency costs if those predictions fail to come true. How accurate data are required to be before action is taken will be an important question for conservation planners (Grantham *et al*. 2009). However, since many of the areas that have been highlighted by this study as potential priority areas in the future are already recognised as important to avian conservation efforts in the present-day, then conservation efforts focused on these areas will represent an investment in the present as well as the future (McClean *et al*. 2006).

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Chapter 3: Impacts of Climate Change on the African Important Bird Area Network: Potential Options for Adaptation

Abstract

Climate change, in collaboration with habitat destruction, is likely to be one of the greatest threats to the persistence of avifauna species in the foreseeable future. Although Protected Areas are assigned to preserve key species' habitats, they have, to date, been designed to function in a stable climate. As climate change alters the distributions of species' ranges, Protected Areas may become redundant as the species they currently protect are climatically forced into other areas. This study explores climate change effects on a continent-wide protected area network and, using a reserve selection algorithm, attempts to determine ways to mitigate and adapt to such impacts. I find that climate change has a large effect on the continent-wide distribution of those Protected Areas selected to efficiently represent the bird species of sub-Saharan Africa.

Introduction

Protected Areas (PAs) are vital for the protection of species from extinction (Gaston *et al.* 2008). However, the performance of PAs is vulnerable to the effects of climate change because of changes in species assemblages that can be caused by a changing climate (Hannah *et al.* 2007). As the climate found in a PA changes, the species that are present within the reserve may become locally extinct, either because of direct effects of unsuitable climate, or because species that are better adapted to the new climate colonise and alter the present species assemblages (Burns *et al*. 2003). Predicting those changes that are likely to impact the efficacy of PAs will allow conservation practitioners to put into place methods for mitigating the effects of climate change as well as concentrating resources on areas which will be of great importance for conservation over the coming Century (Heller & Zavaleta 2009).

The African Important Bird Areas (IBA) network has been designed to monitor and protect areas of conservation importance for range- and biome-restricted bird species as well as areas that hold significant congregations of single or multiple species. Each IBA was chosen on four selection criteria; (1) significant numbers of one or more species which are of global concern to conservation, (2) significant component of populations of one or more species with restricted ranges, (3) a significant component of a group of species which are largely or wholly confined to one biome, or (4) significant numbers (>1%) of the biogeographical populations of one or more congregatory species (Fishpool & Evans 2001). Over the whole continent, there are more than 1230 IBAs in 58 countries which cover approximately 7% of the land area (Fishpool and Evans 2001). Although the IBA network is comprised of PAs, it is not the goal of the IBA program to make all IBAs into PAs. Instead, in areas defined as IBAs, policies that halt the further disruption to bird species would be favoured over the costly task of protection under the IUCN PA categories 1-6. If all IBAs received such protection, the risk of extinction of many bird species would surely be greatly decreased in Africa. However, the IBA network was designed to protect species under the scenario of relatively stable climatic conditions (Willis *et al*. 2009b). With the looming threat of climate change now well documented, attention must be focused on how climate change will affect the performance of PA networks such as the IBA program (Burns *et al*. 2003). This study aims to identify ways to increase the IBA network's resilience to the impacts of climate change through adaptation.

The study utilises projections of species current and projected future occurrence in protected areas from a study undertaken by Hole *et al.* (2009), which forecasts the turnover of bird species in IBAs in sub-Saharan Africa during the 21st Century. Hole *et al.* (2009) showed that the African IBA network will provide climate space for the majority of species throughout the 21st Century although there is the potential for high turnover of species in many IBAs. By applying a reserve selection algorithm (RSA) to their simulations of current and projected future assemblages of birds in African IBAs, the importance of protected areas within the network can be gauged by complementarity (Latta 2005). RSAs are programs which calculate efficient reserve networks through the systematic selection of planning units based on species distribution data. Applying such RSAs to the future IBA projections will provide an indication of those reserves that will be of particular importance to avifauna conservation in the future. Negative impacts on the network can then be potentially mitigated against by identifying ways in which to improve the resilience of the network to climatic change.

This study explores how the IBA network could be improved in the future through the addition of new sites, selected by an RSA, that are currently unprotected, yet have the potential to become very important in the future for those components of avian biodiversity that are projected to become underrepresented in the network. An alternative approach to mitigating the impacts of climate change is through the identification of IBAs which maintain populations of the same species throughout the upcoming Century. Such IBAs therefore will protect populations that are not at risk from having to shift their ranges as climate changes. This study demonstrates a case-study approach to adapt and mitigate against future projected changes as a result of climate change. Such approaches can help to direct conservation efforts most efficiently in the future and suggest alterations that could be made to existent continent-wide PA networks.

Methods

This study focuses on IBAs located on mainland Africa south of 20^{o} North (sub-Saharan). In this region there are 803 IBAs and 1679 bird species, although only 1608 species have sufficient data to be modelled. The data for the future distributions of species were obtained from modelling work undertaken as part of a previous project (Hole *et al*. 2009).

Bioclimate and Species Data

The models simulating future distributions of bird species across sub-Saharan Africa, were produced by Hole *et al*. (2009) from recent species distribution data (1980-2000; Brooks *et al.* 2001) from the Zoological Museum of the University of Copenhagen (Jetz and Rahbek 2002). Presence-absence data for 1608 species were available for the 1963 one-degree cells that make up sub-Saharan Africa. Mean bioclimatic data for the one-degree cells were created from mean monthly temperature and precipitation data available for quarter-degree cells for the period 1950-2000 (Hijmans *et al* 2005; http://www.worldclim.org). Seven bioclimatic variables were chosen for modelling the bioclimatic envelopes of each species; mean temperature of the coldest month; mean temperature of the warmest month; an estimate of the ratio of actual to potential evapotranspiration; wet season duration; wet season intensity; dry season duration; and dry season intensity (Willis *et al*. 2009b). They were selected for their previously confirmed ability in modelling the bioclimate envelopes of a wide range of European and African bird species (Huntley *et al.* 2006). The first three variables were used as standard variables in all models, but only one of the four seasonality variables, wet season and dry season duration and intensity were used (the procedure for selecting the fourth variable is explained by Huntley *et al.* 2006).

The climate data for the future time periods were obtained from three general circulation models (GCMs); HadCM3 (Gordon *et al.* 2000), ECHAM4 (Roeckner *et al.* 1996) and GFDL-R30 (Knutson *et al.* 1999). The simulations used were based on the SRES B2a emissions scenarios for three time periods, which represent 30 year averages for 2011-2040 (abbreviated from here-on-in to the central year of the series; 2025), 2041-2070 (2055) and 2071-2100 (2085). The GCMs used are representative of the mean for the nine models included in the Intergovernmental Panel on Climate Change (IPCC) Third Assessment Report (Cubasch *et al.* 2001) and range in simulated precipitation regimes from relatively wet (GFDL-R30) through to the mean (HadCM3) and relatively dry (ECHAM4). Since the data have been created using climate models from the Third Assessment Report, the IPCC Fourth Assessment report has been published. The models used have therefore since been improved by the reduction of error in the prediction of precipitation, mean sea-level rise and surface air temperature (Randall *et al*. 2007).

The bioclimatic envelope of each species was estimated using a Climate Response Surface (CRS), which uses locally weighted regression to fit a response surface to a species' presence-absence data. This method was chosen over alternative approaches such as generalised additive models (GAM) after paired t-tests on sensitivity and true skill statistic (the assessment metrics used) indicated that CRS performed better than GAM (see Hole *et al.* 2009). The CRS models were validated using two techniques; firstly, for species which were recorded in > 20 one-degree cells, *K*-fold partitioning was used. *K*-fold partitioning is a procedure which generates *K* models by partitioning the data into *K* equal-sized sets apart from the *i*-th set which is used as training data. This process is carried out *K* times with each *K* subsample used once as the training data, this has the advantage of using all data for both validation and training (Ali & Pazzani 1996). This method has advantages over the often applied 70:30 data splitting approach for model creation and validation (Thuiller *et al*. 2009) as it reduces potential issues of spatial autocorrelation.

Predictive performance was assessed using values obtained for the area under the curve (AUC) of a receiver-operated characteristic plot (Fielding and Bell 1997). This was carried out for 1401 species, 89% of which exhibited *K*-fold partitioned AUCs of ≥ 0.9 (no species had a *K*-fold partitioned AUC < 0.7), indicating high-model performance (Swets 1988). Model fit for the remaining 207 species, recorded in fewer than 20 one-degree cells, was assessed using a jack-knifing approach. This process calculates the probability of a species' occurrence in a single one-degree cell, using a model built using all of the data except for the cell for which I wish to obtain a simulation of occurrence. This is repeated for all 1963 cells of sub-Saharan Africa, for each species, and essentially produces simulations independent of the data used to create the CRS. Although this is more prone to issues of spatial autocorrelation than K-fold partitioning, the latter procedure cannot be used on restricted range species as large proportions of their entire range often fall within a single excluded panel. The projection accuracy was assessed using the same AUC process as applied to the more widespread species. 83% of the 207 species displayed a jack-knifed AUC ≥ 0.9, which again indicates a high-model performance (for more details, see Hole *et al*. 2009).

Species simulated presence/absence for each IBA were calculated by characterising one or more bioclimates in each IBA and then applying the CRS model for each species to the bioclimate(s) for each IBA. This was accomplished using a spatial intersection, within a GIS, of the IBA polygons, a one-degree grid to determine the broad spatial extent of each IBA, and a quarter-degree grid for each of the seven bioclimatic variable grids and for elevation. To produce a probability of occurrence for each species in each IBA, single or multiple bioclimates were assigned to each IBA. This was done by firstly assessing the size of the IBAs using the one-degree grid, if an IBA spanned more than a single one-degree cell, the polygon was split into a number of sub-polygons, by intersecting the one degree cells and the IBA polygon. The polygons or sub-polygons were then assigned bioclimates according to the associated quarter-degree climate data. Similarly, if the elevational range of a polygon or sub-polygon was >600 m, the component quarter-degree cells were stratified into two or more elevation bands and a separate bioclimate was calculated for each band. Finally, the one-degree models for all species were projected onto each IBA's bioclimate(s) for all time periods and climate scenarios. The probabilities of occurrence were converted to presence or absence data by applying the threshold probability that maximised Cohen's κ for the one-degree model (Huntley *et al.* 2006). Therefore, if a species' probability of occurrence exceeded the threshold probability in any of the sub-polygons of an IBA, it was regarded as present.

Reserve Selection

The RSA Marxan was used to select the combination of IBAs which protects all species most efficiently (Ball & Possingham 2000; Possingham *et al.* 2000). This program uses simulated annealing to select planning units that represent all target species whilst minimising the cost of the reserve network (Carwardine *et al*. 2007). Cost, in this context, refers to the size of the reserve network which can be used to calculate other costs such as the economic costs of protecting the selected areas. Marxan was used because of the combination of speed and reliability when using large data sets, and because results reach a high degree of optimality; traits which are not found together in simpler heuristic or more complex integer programming algorithms (Nicholson *et al*. 2006; Oetting *et al*. 2006). In selecting IBAs, the cost of each IBA was kept equal despite the large variation in size that exists among the different reserves. This was done partly because costing the reserves is a complex procedure that is beyond the scope of this particular study and the inclusion of cost in selection may have removed the importance of climate as the major selection factor in the simulations.

Marxan uses the process of simulated annealing to select the most efficient sites for a network. This process works through the random addition and removal of planning units (PU) from an initial reserve network that is either selected randomly by Marxan or by the user (Peralvo *et al.* 2007). Once a site is added or removed, Marxan re-evaluates the performance of the network and will accept the alteration if it has a positive effect on solving the set-covering problem. Initially, additions to the network which have a negative effect are retained so as to prevent the simulation reaching local optima, but as the simulation continues, more negative additions are rejected because of the decreasing value of the cost functions within the program (McDonnell *et al*. 2002; Peralvo *et al*. 2007; Possingham 2000). The selection of PUs is based on complementarity, which selects PUs depending on how a newly added site complements the species that are already protected within the network (Church *et al*. 1996). By doing this, the efficiency of the network is increased because PUs are added in the order of sites which append the greatest number of novel species to the existing network. In this way, the best reserve network will indicate the most efficient way in which to protect all species with the available PUs. This can therefore indicate to planners areas that are of high importance to conservation.

A species representation target of conserving five separate populations was used when running Marxan. This target was chosen in order to create a network that would be robust to local population extinctions. As this study deals with a large number of species that inevitably vary in their range and population sizes, as well as their threat of extinction, along with uncertainty in future climate projections, choosing a single representation target for all species is marred by uncertainty (Justus *et al*. 2008). Assigning numerical representation targets for species has been criticised as a purely arbitrary exercise (Wiersma & Nudds 2006). However, at the scale of this study, defining realistic targets for each species would be a challenging task, requiring knowledge of population sizes and the degree of threat for species at local, regional and continental scales. With this in mind, the targets were chosen as a simple first-step approach to a complex problem.

Reserve selection for present and future species distributions

Species simulated occurrence data for the four different time periods (present, 2025, 2055 and 2085) were used in MARXAN to create optimal reserve networks based on each IBA's simulated species communities. This gives a unique view of how climate will affect the importance of the different IBAs across the Century and indicates patterns which could occur as the effects of climate change increase.

In order to show differences between those IBAs that were selected for present-day distributions and those selected for the future simulations, one-way ANOVA and paired samples T-tests were used to compare the elevation characteristics of the different sites. The characteristics used for comparison were the maximum elevation and the elevational range found within the IBA. For the ANOVA analyses, comparison was made between those IBAs selected for the present-day and the IBAs that were selected for the future, with different categories depending on how many of the three climate scenarios the IBAs were chosen in.

Combining IBAs and quarter-degree cells to produce networks for the future

Since IBAs have been chosen to protect sites of significant importance to avifauna species of conservation concern in Africa under current climatic conditions, few additions to the network should be necessary at present to increase the representation of species within the network. However, under future climate change scenarios, the ability of the network to represent all species may be compromised. Therefore, by permanently fixing the IBAs into the network within Marxan, by changing their planning unit status (Game & Grantham 2008), Marxan can be made to select additional areas around the IBAs to increase species representation in the network under future climate scenarios. Therefore, as potential additions to the IBA network, the quarter-degree cells across sub-Saharan Africa were made available for the relevant time periods; their simulated species assemblages being derived from applying the CRS models to the mean climate for each cell. Those quarter-degree cells that fell within the boundaries of an IBA were removed, allowing Marxan to select the cells that provided additional coverage outside of the current network in order to reach total representation of species alongside the existent reserves. This approach helps to counter potential shortfalls in the IBA network in the future by suggesting potential localities for additions to the network.

Key Stable Sites (KSSs)

IBAs that are simulated to be suitable for a species throughout the current Century (which I term key stable sites, KSSs) could be of great importance to conservation because they provide such species with permanent sanctuaries over time in a changing climate (Vos *et al*. 2008). This removes the need for such species to undergo range shifts caused by climate forcing. Such shifts could necessitate the movement of species across unprotected land, which is often associated with increased risk to individuals (McInerny *et al*. 2007). By identifying KSSs, conservation can determine those species that are likely to remain protected throughout the Century within the IBAs they currently occupy. In this way, extra effort can be made to maintain healthy populations of such species within these PAs.

KSSs were identified by collating simulated occurrences for each species in every IBA across the Century. In essence the KSS network is a scenario which assumes that species will be unable to disperse to new IBAs. Marxan was then used to select a network of reserves that most efficiently represented all species found within KSSs. Through this method, those KSSs which protect the most species throughout the Century will be included into the network.

For the basic reserve selection and KSS simulations, 100 runs were completed for each climate scenario. Although other studies that have used Marxan used more than 100 runs per simulation (e.g. Rondinini *et al*. 2005), 100 runs was viewed as adequate for this study because initial trials showed that increasing the number of runs performed by Marxan in each simulation had little effect on the efficiency of the network created. Additionally, creating an optimal network was not considered vital because of other factors that may limit the accuracy of the results within this study (Cowling *et al*. 2003; Dormann *et al*. 2008; Knight *et al*. 2008; Knight *et al*. 2006). When adding quarter-degree cells to the IBA network, 200 runs were performed per simulation because of the larger number of PUs used.

Results

The number of climate scenarios an IBA was selected in is used as an indicator of the importance of selected planning units. Although the number of climate scenarios an IBA was selected in does not necessarily denote importance to conservation, it does indicate that even under different future climate scenarios, the site was repeatedly selected and therefore symbolizes resilience of that site to climatic change. The identification of sites that operate over a range of different climate scenarios is potentially of great importance for conservation, due to the uncertainty involved in the prediction of climate change.

Data on the selected planning units and unrepresented species are listed in the supplementary material (S2).

Reserve selection for present and future species distributions

There is a clear change over the Century in the pattern of distribution of IBAs selected to best protect species (Fig. 2.1a-d). In the present time period, IBAs selected are well dispersed across the sub-continent and represent all major biomes and endemic bird areas (Fig. 2.1a). The pattern for 2025 is similar, though with increased sites selected in East Africa and fewer in West Africa (Fig. 2.1b). The results from 2055 and 2085 also show this trend of reduced selection in the west and increased selection in the east, as well as an increase in IBAs selected in southern Africa (Fig 2.1c-d). The changes in the distribution of chosen IBAs is gradual over time, but a comparison of the present-day distributions with those for 2085 (Figs 2.1a & 2.1d), demonstrates a marked change in selection over the Century. Data on which IBAs were selected for the difference scenarios and for the shortfall species is provided in the supplementary material (S2)

Those IBAs selected for the present-day were compared with the IBAs selected for future scenarios. A significant difference in the maximum elevation found within the selected IBAs was shown between present-day and end of Century predictions (ANOVA; $F_{3,799}=12.031$, $P<0.001$). This difference was also shown for the elevational range found within the IBAs (One-Sample T-test; d.f. = 358, Sig.2-tailed P=.025), providing evidence that IBAs with large elevational ranges and high maximum elevations will be efficient at protecting bird species in Africa in the future.

A

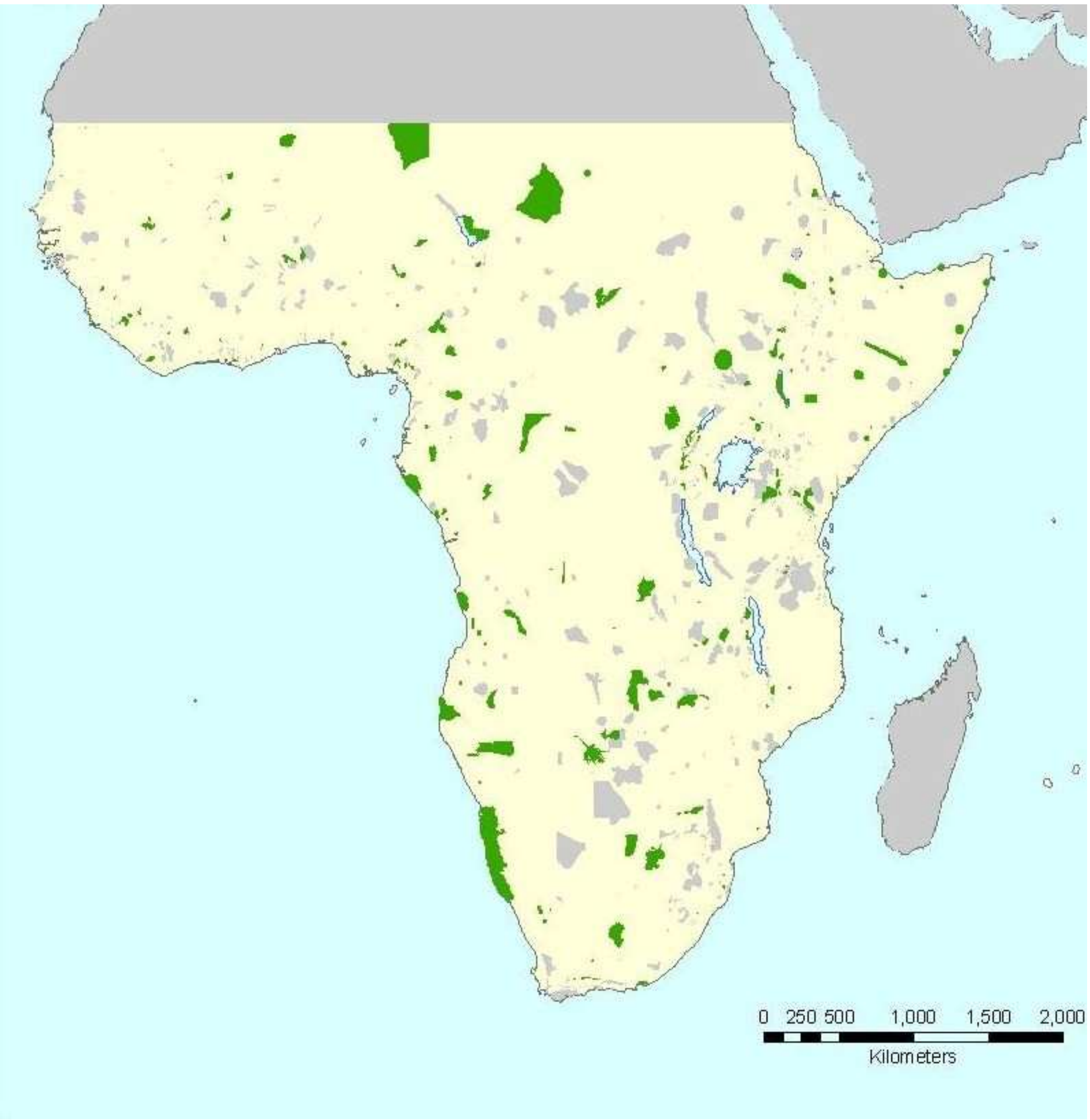

Figure 2.1 *(A) Optimal reserve networks of IBAs selected using Marxan to protect sub-Saharan African bird species for current species distributions. Note for the present period, there is only one, i.e. observed 'scenario'. Selected IBAs are shaded in green, unselected IBAs are shaded in grey.*

B

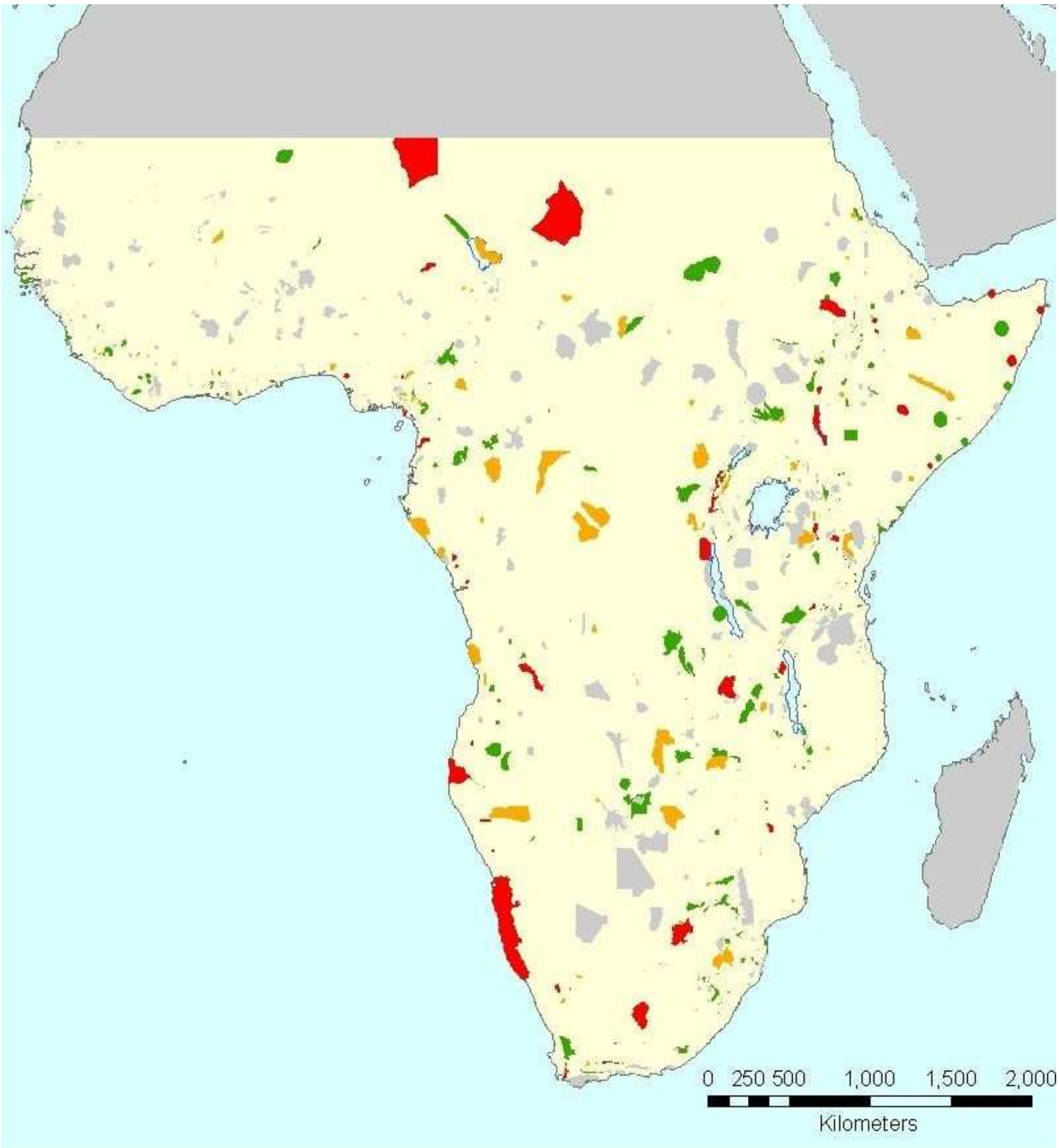

Figure 2.1 *(B) Optimal reserve networks of IBAs selected using Marxan to protect sub-Saharan African bird species for projected 2025 species distributions. The colour scheme represents how many of the three different climate scenarios the IBA was selected in; Green = 1, Orange = 2, Red = 3. Unselected IBAs are shaded in grey.*

C

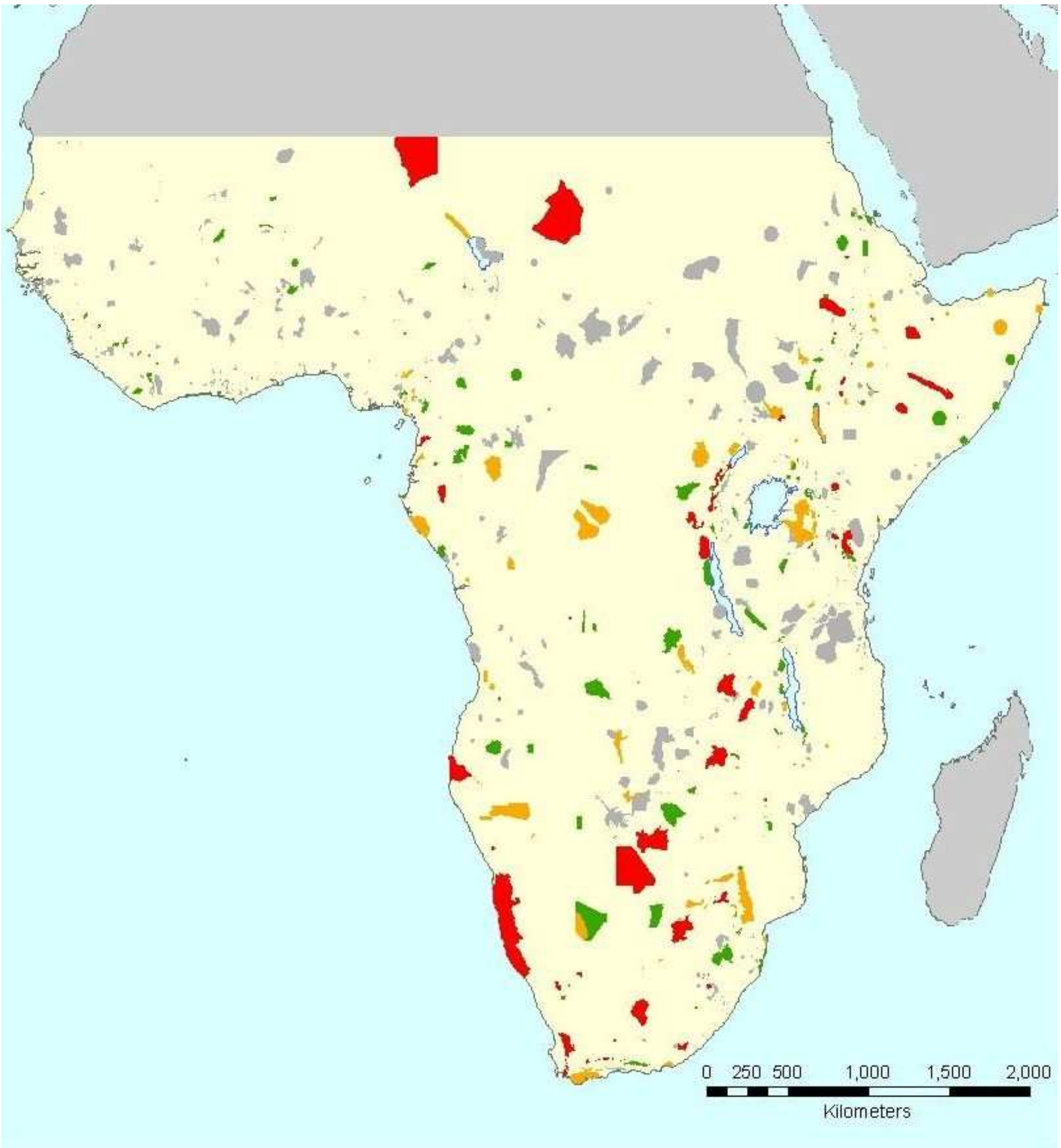

Figure 2.1 *(C) Optimal reserve networks of IBAs selected using Marxan to protect sub-Saharan African bird species for projected 2055 species distributions. The colour scheme represents how many of the three different climate scenarios the IBA was selected in; Green = 1, Orange = 2, Red = 3. Unselected IBAs are shaded in grey.*

D

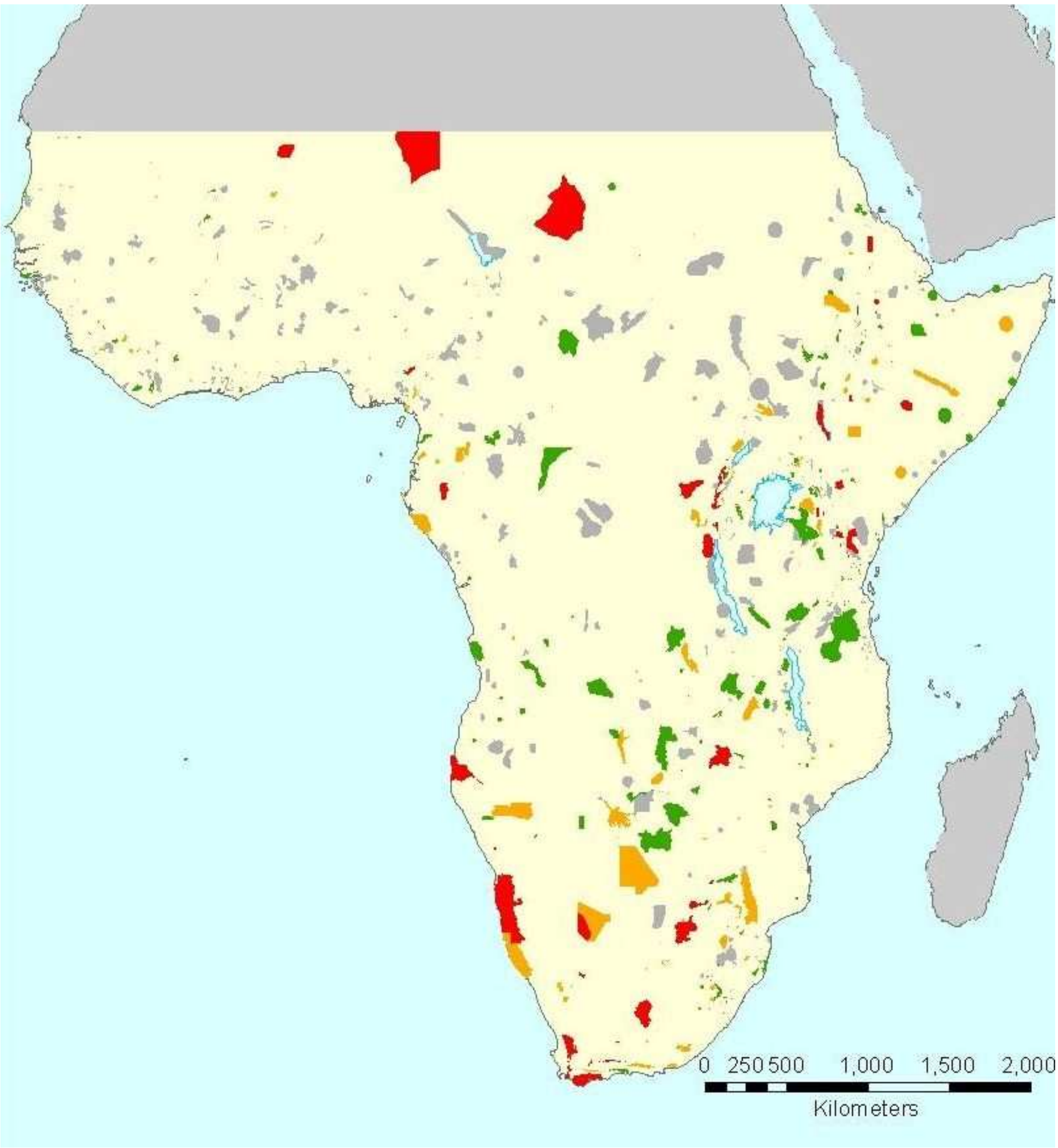

Figure 2.1 *(D) Optimal reserve networks of IBAs selected using Marxan to protect sub-Saharan African bird species for projected 2085 species distributions. The colour scheme represents how many of the three different climate scenarios the IBA was selected in; Green = 1, Orange = 2, Red = 3. Unselected IBAs are shaded in grey.*

Additional quarter-degree cells assuming species dispersal

The analyses to determine locations for additional sites that could strengthen the IBA network produced similar results for the future time period scenarios. These analyses assume that species for which projected IBAs are simulated to be suitable will be capable of reaching these locations, and therefore assume no limitations in dispersal to newly suitable IBAs. Additional localities selected under the end of Century climate change scenarios were much more numerous than those selected to more fully protect species in the present period.

For the present period, 40 additional sites were needed to obtain full representation. These sites occur on the Horn of Africa (10 sites) and in Ethiopia, in scattered sites in north and west Africa, three equatorial locations in Gabon/Congo, seven sites spanning 15-18 degrees south in Mozambique, Malawi, Zambia and Namibia, and four sites in the Namib-Karroo region of South Africa (Fig. 2.2a). The major species under-represented in the current IBAs which are protected in these 40 sites are summarised in the supplementary material (S2.2).

The average number of additional sites for each time period increased over the Century (2025 – 58, 2055 – 71, 2085 – 75) summarised in table 2.1.

The additional sites selected for 2025 have a similar distribution to the present with clusters occurring in the same areas (fig. 2.2b). There is a linear group of additional cells that have been selected along the Atlantic coast from Namibia to Angola. Clusters on the Atlantic coast are also found in Equatorial Guinea and the du Chaillu Mountains of Gabon where three sites have been selected in two GCM scenarios.

The additional cells selected for 2055 and 2085 differ from those selected in the first half of the Century mainly because of the selection of sites in the Ethiopian Highlands in Northern Ethiopia, the Eastern Arc Mountains and in North-East Tanzania. Particular clusters selected for 2055 and 2085 are seen in Northern Ethiopia and the Horn of Africa, the Eastern Arc Mountains, South African Highveld and Namib-Karroo regions, and northern lowland regions and du Chaillu mountains of Gabon. There is also an almost continuous strip of additional sites selected that run along the Atlantic coast from South Africa, through Namibia to the North-west of Angola. There is also a cluster of additional cells in the Drakensberg Mountains present in the 2085 network which is not found in the 2055 network.

It must be made clear that because this study uses a numerical representation target, additional sites do not necessarily indicate a shortfall in the IBA network's coverage and protection of a species, but could highlight areas where the protection offered to species is not extensive.

A

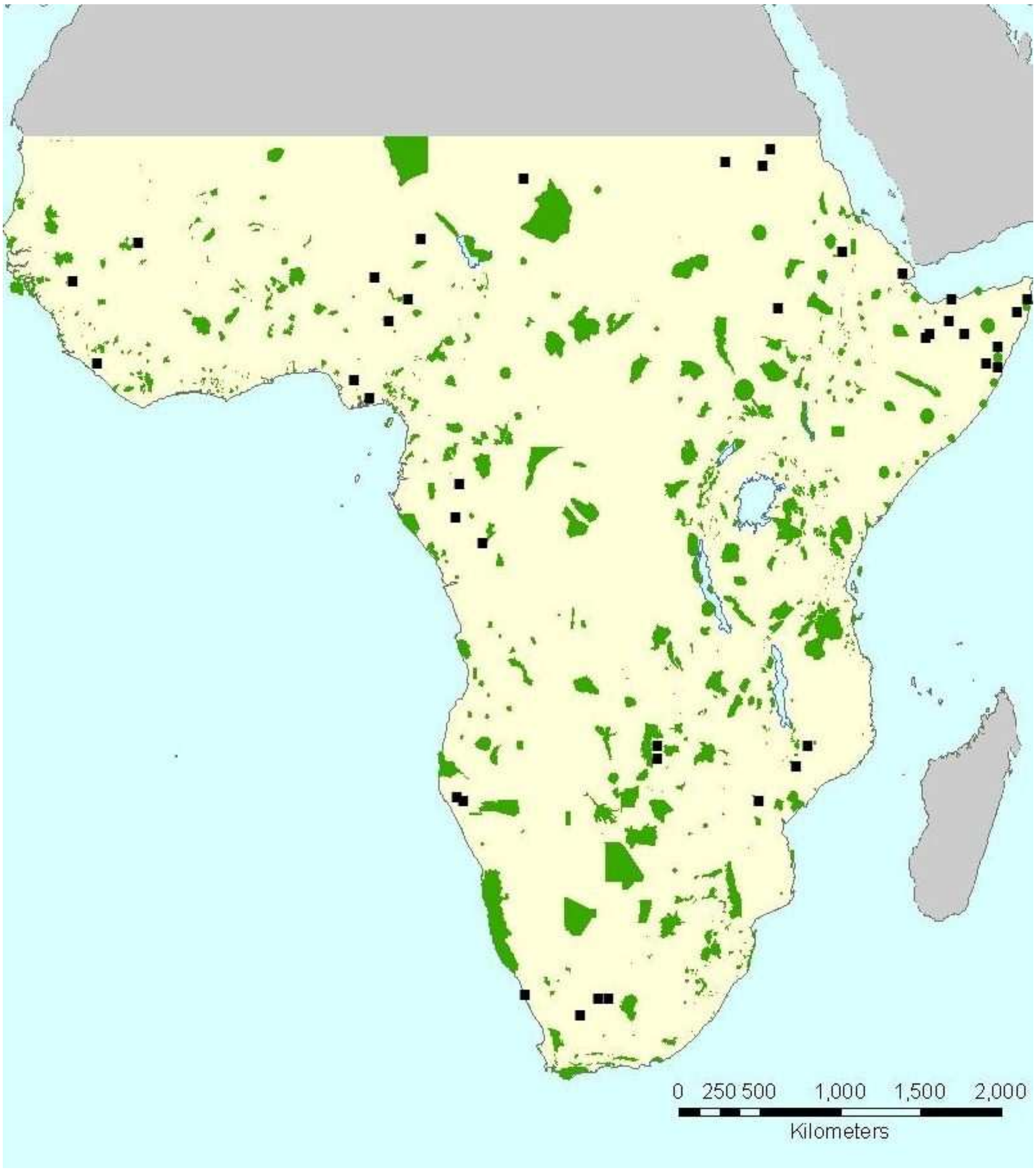

Figure2.2 *(A) Quarter-degree cells selected by Marxan in addition to the IBAs of sub-Saharan Africa to increase species representation in the network for current species distributions. The IBA network is represented in green. The Quarter-degree cells are represented as black. The cells are not shown to scale.*

B

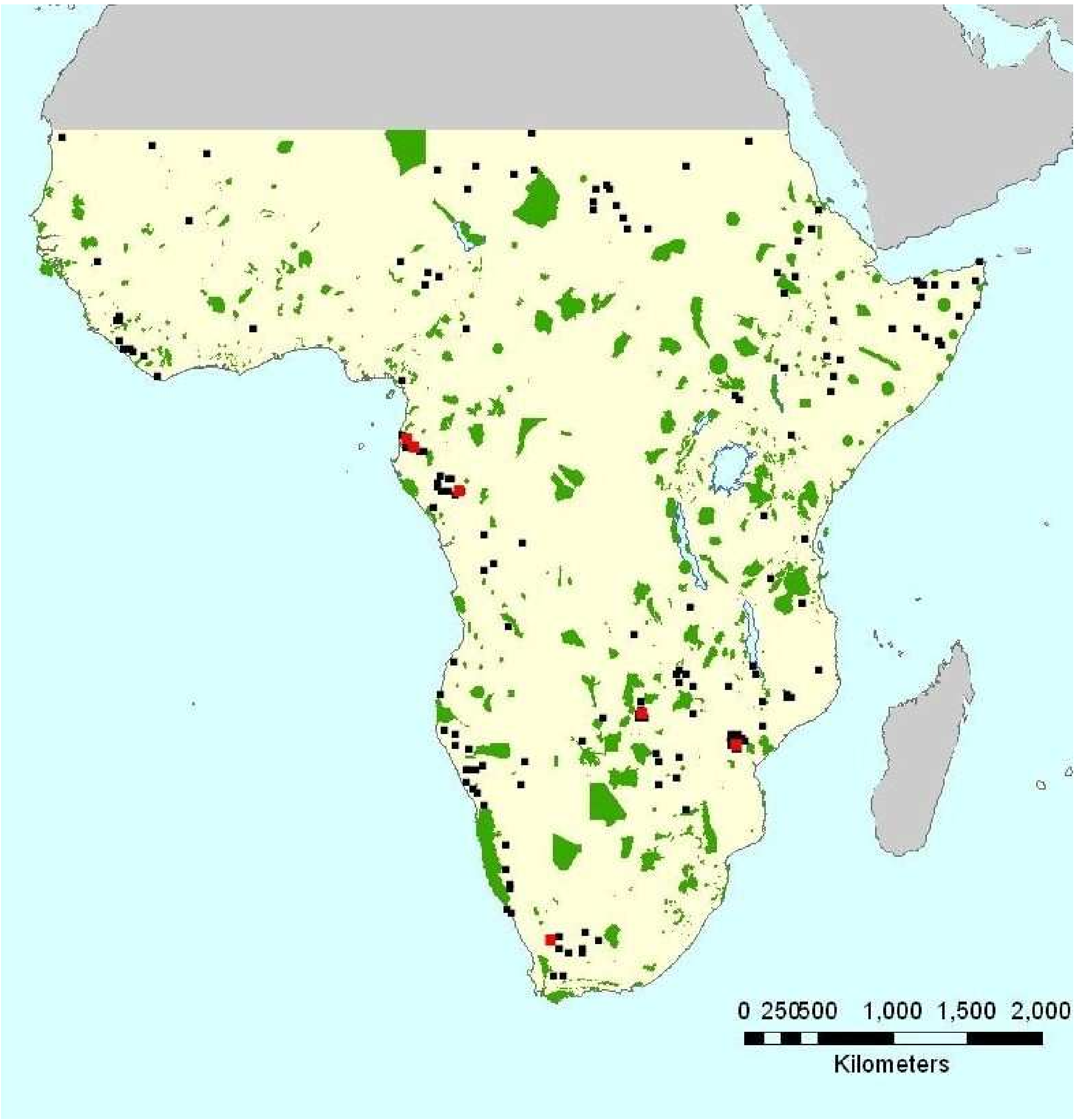

Figure2.2 *(B) Quarter-degree Cells selected by Marxan in addition to the IBAs of sub-Saharan Africa to increase species representation in the network for projected 2025 species distributions. The IBA network is represented in green. The Quarter-degree cells are represented as black for those that are selected in one future climate scenario and red for those selected in two. No cells were selected for all three scenarios. The cells are not shown to scale.*

C

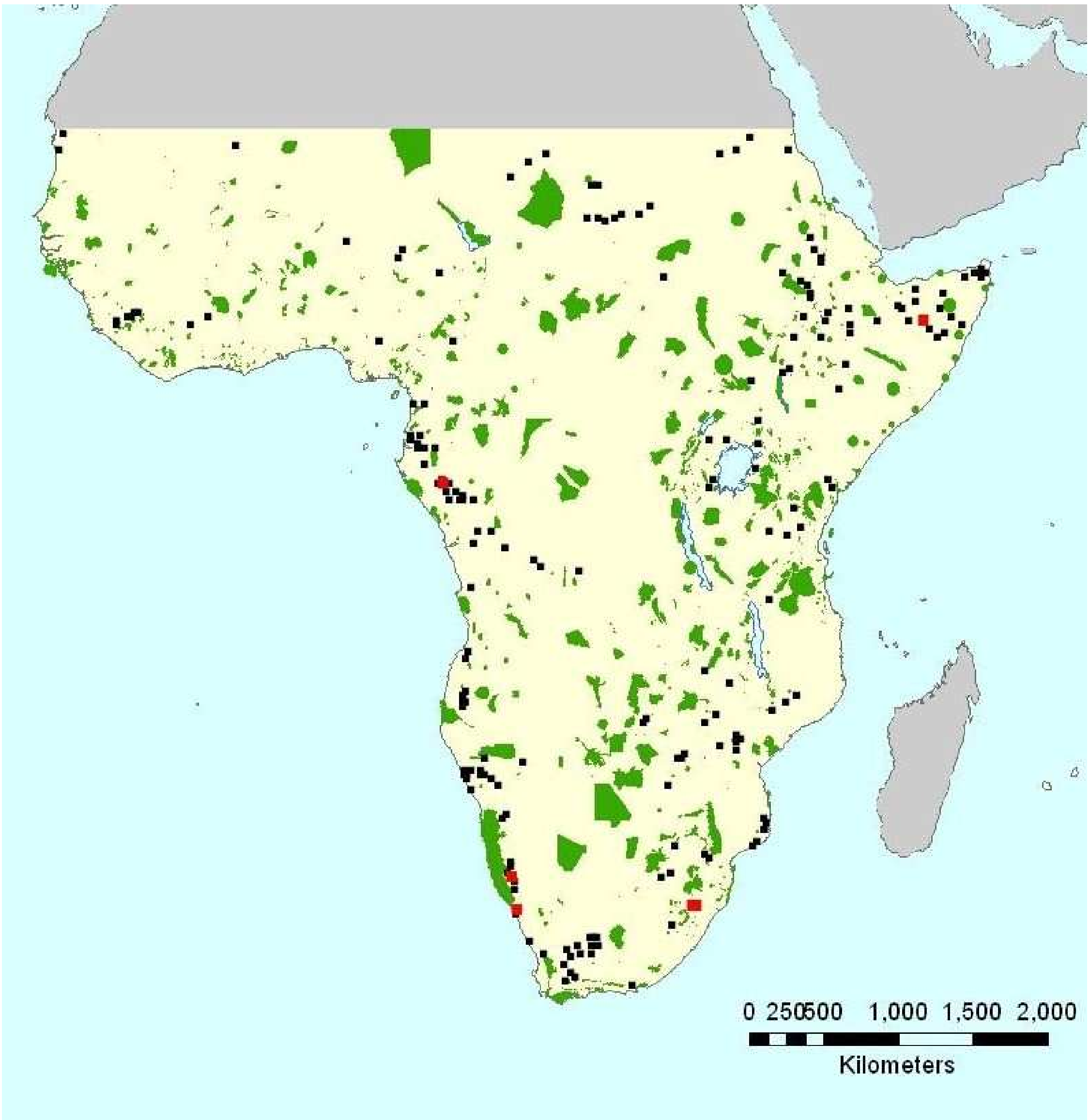

Figure2.2 *(C) Quarter-degree Cells selected by Marxan in addition to the IBAs of sub-Saharan Africa to increase species representation in the network for projected 2055 species distributions. The IBA network is represented in green. The Quarter-degree cells are represented as black for those that are selected in one future climate scenario and red for those selected in two. No cells were selected for all three scenarios. The cells are not shown to scale.*

D

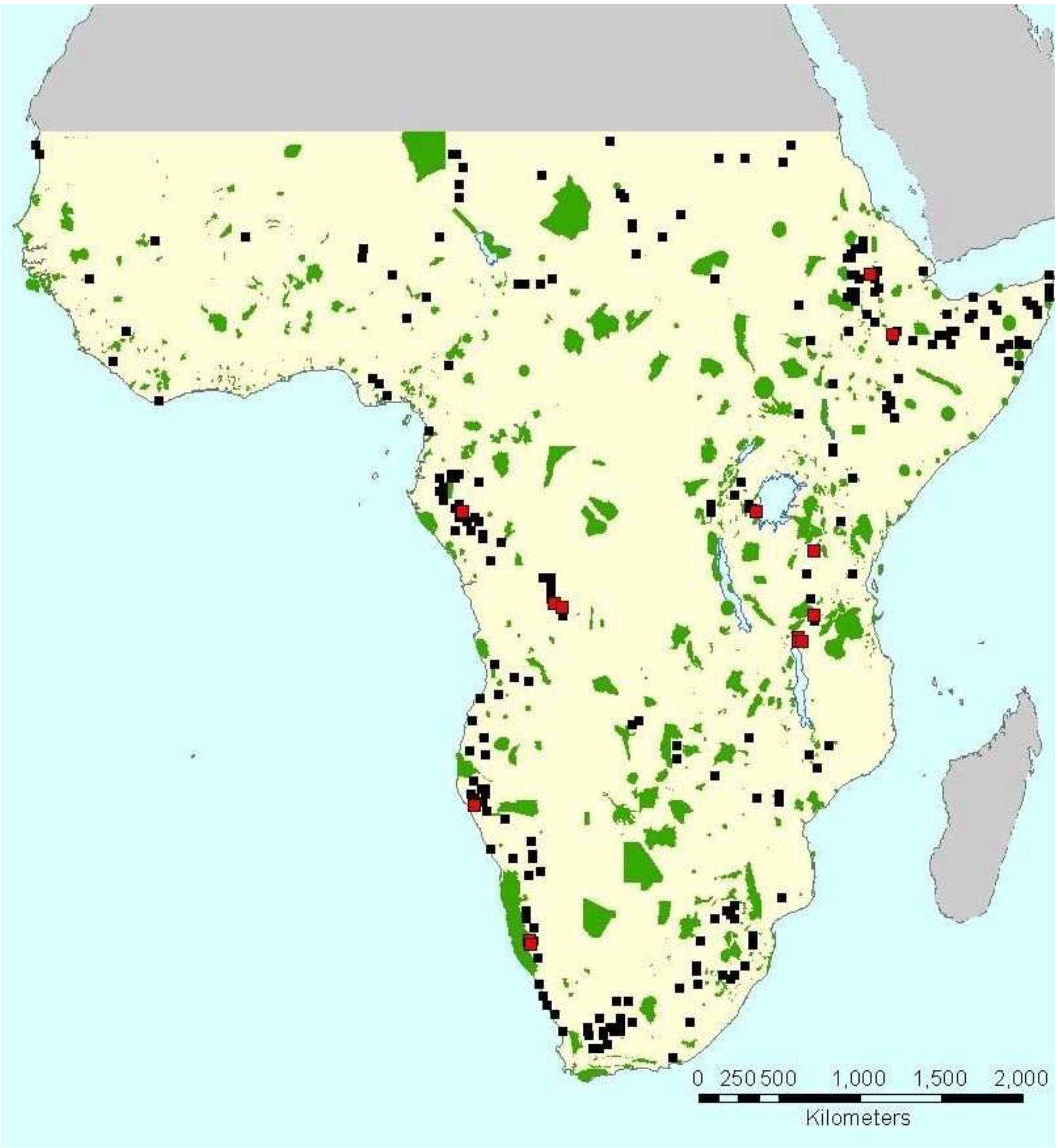

Figure2.2 *(D) Quarter-degree Cells selected by Marxan in addition to the IBAs of sub-Saharan Africa to increase species representation in the network for projected 2085 species distributions. The IBA network is represented in green. The Quarter-degree cells are represented as black for those that are selected in one future climate scenario and red for those selected in two. No cells were selected for all three scenarios. The cells are not shown to scale.*

Table 2.1: *Number of additionally selected cells selected for each time period and GCM scenario, as well as the number of un- and underrepresented species in each of the scenarios. GCM scenarios are represented as E (ECHAM4); G (GFDL R30); H (Had CM3), with the time period represented by the number.*

Scenario	No. Additional PUs	No. underrepresented Spp.	No. Unrepresented Spp.
Present	40	0	0
E25	58	1	0
G25	62	0	0
H25	54	0	0
E55	72	0	1
G55	69	1	1
H55	71	2	0
E85	80	3	1
G85	60	2	2
H85	84	6	0

Key Stable Sites (KSS)

The KSS network that was selected shows a different pattern from that seen for the previous analyses, which assumed species colonisation of newly suitable sites (Fig. 2.3). The recurrent theme of selection of IBAs in Eastern and Southern Africa (Fig. 2.1-2.2) for end of Century species distributions is not evident with the KSS analysis. There is a reasonably well-distributed selection of IBAs across sub-Saharan Africa. Special attention must be paid to those KSSs that are selected for all three climate scenarios as these represent the most stable IBAs, regardless of the direction of future climate change. Such KSSs are clustered in the Ethiopian Highlands, Horn of Africa, Eastern Arc mountains, Albertine Rift, the Cameroon Highlands, Congo and a concentration across Southern Africa. There is a noticeable absence of large KSSs from West Africa, with few being selected in the region overall.

The selected KSSs show significant correlations between maximum altitude found within the KSS and selection by Marxan (Paired Samples T-test; d.f.=389, sig.2-tailed P <.001). There is also a significant difference between the elevational ranges of those IBAs selected as KSSs in the network and all other IBAs (ANOVA; $F_{3,799}$=47.325, P<0.001; Paired Samples T-test; d.f.=389, sig.2-tailed P <.001). There was a significant relationship between the size of the KSSs and how many climate scenarios they were selected in (ANOVA $F_{3,799}$=13.573, P <.001; d.f.=389, Paired Samples T-test sig.2-tailed P=.033), with IBAs selected in all three scenarios being significantly larger than those that were not (ANOVA; LSD and Bonferroni multiple comparisons; P <.001; See Table 2.2) indicating that the climatic stability of a PA is related to its size.

Selecting IBAs based solely on sites that retain suitable climate for species during the whole of the current Century inevitably results in some species not being represented at all in the network. Under the GFDL-R30 climate scenario 55 species are not represented in key stable sites, under the HADCM3 scenario 61 species are not represented and under the ECHAM 4 scenario 71 are not represented (Table 2.3).

Table 2.2: *LSD and Bonferroni ANOVA Post Hoc tests showing the significance of variance between the size of KSSs selected in all three GCM scenarios and those that were not. The group numbers represent the number of GCMs a KSS was selected in.*

Post Hoc Test	No. of GCM scenarios IBA was selected in		Sig.
LSD	0	1	0.988
		2	0.413
		3	<0.001
	1	0	0.988
		2	0.476
		3	<0.001
	2	0	0.413
		1	0.476
		3	<0.001
	3	0	<0.001
		1	<0.001
		2	<0.001
Bonferroni	0	1	1
		2	1
		3	<0.001
	1	0	1
		2	1
		3	<0.001
	2	0	1
		1	1
		3	<0.001
	3	0	<0.001
		1	<0.001
		2	<0.001

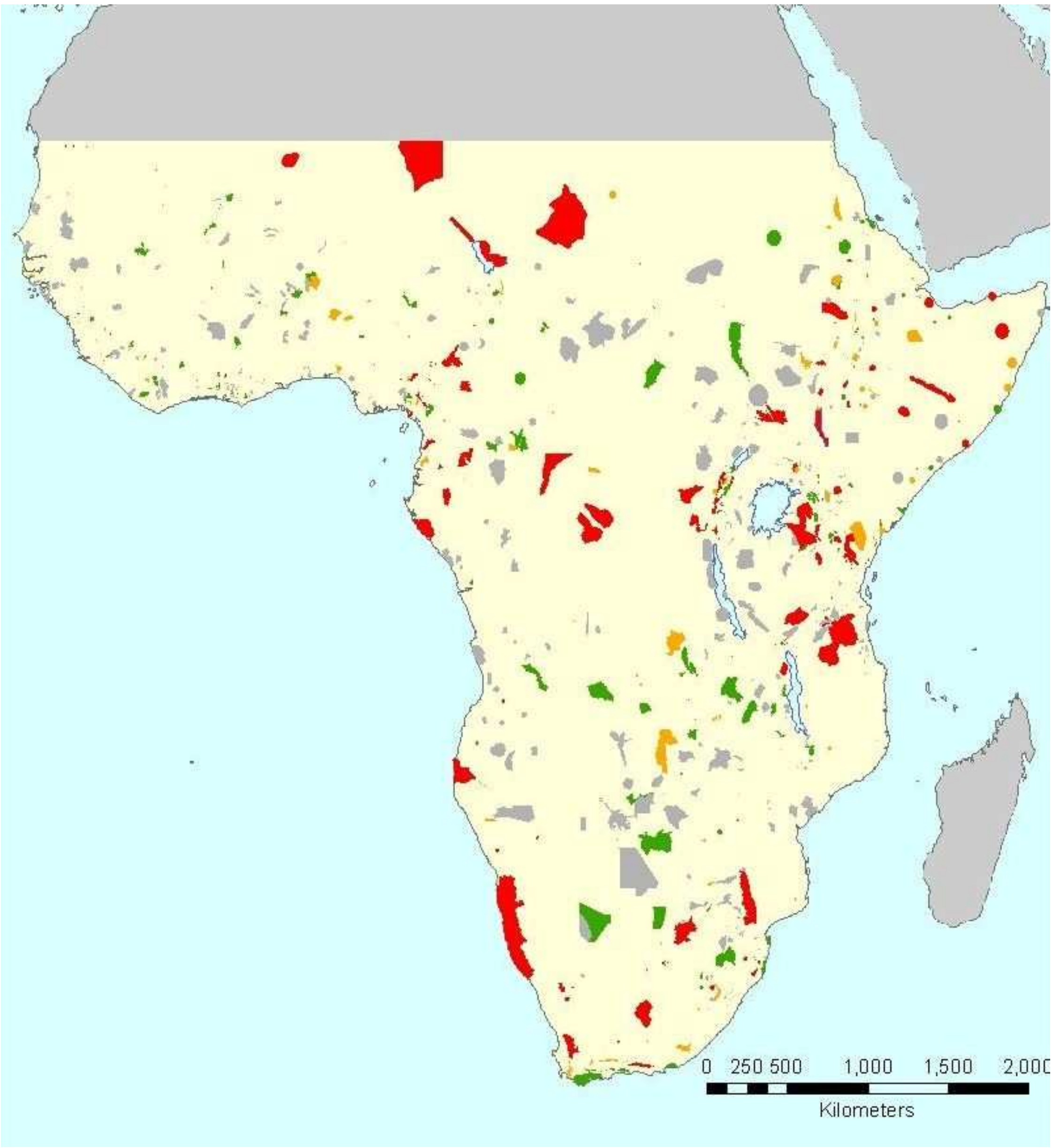

Figure 2.3 *KSSs* for all three future time periods (2025, 2055, 2075) and climate scenarios (GFDL-R30, HadCM3, ECHAM4) selected by Marxan to represent sub-Saharan African bird species. *Colour scheme represents the number of climate scenarios the KSS was selected for; Green = 1, Orange = 2, Red = 3. Unselected IBAs shaded grey.*

Table 2.3: *List of species unrepresented in the KSS network for the three GCM scenarios.*

Species' Scientific name	HADCM3	ECHAM4	GFDL-R30
Agapornis lilianae	*	*	*
Agapornis nigrigenis	*	*	*
Agapornis personatus	*	*	
Alethe choloensis	*	*	*
Alethe fuelleborni		*	
Andropadus chlorigula		*	
Anthreptes rubritorques		*	
Anthus melindae	*		
Apalis binotata	*	*	*
Apalis chapini		*	*
Apalis chariessa	*	*	*
Apalis chirindensis	*	*	*
Bathmocercus winifredae		*	*
Batis margaritae	*	*	
Batis minima	*	*	*
Batis minulla	*	*	*
Bradypterus grandis	*	*	*
Bubo shelleyi			*
Bubo vosseleri	*	*	*
Campethera mombassica	*	*	
Caprimulgus binotatus			*
Cercomela dubia	*		
Certhilauda barlowi	*	*	*
Certhilauda burra	*	*	*
Certhilauda erythrochlamys			*
Cisticola dambo	*	*	*
Cisticola melanurus		*	*
Colius castanotus	*	*	
Columba oliviae	*	*	*
Dendropicos stierlingi	*		
Drymocichla incana		*	*
Egretta dimorpha	*	*	*
Egretta vinaceigula	*	*	
Estrilda thomensis	*		
Euplectes aureus	*	*	*
Francolinus griseostriatus	*	*	*
Francolinus harwoodi	*	*	
Hirundo fuliginosa			*
Lagonosticta sanguinodorsalis	*	*	*
Lagonosticta virata	*	*	*
Laniarius fuelleborni		*	

Lanius gubernator		*	
Lanius marwitzi		*	*
Lybius chaplini	*	*	*
Macronyx grimwoodi		*	
Malaconotus monteiri	*		
Malimbus ballmanni	*		*
Melignomon eisentrauti	*		*
Mirafra alopex	*		*
Mirafra angolensis		*	
Mirafra collaris	*		
Mirafra rufa	*	*	
Mirafra somalica	*	*	*
Modulatrix orostruthus			*
Nectarinia moreaui		*	*
Nectarinia osea	*	*	*
Neocichla gutturalis	*	*	
Oenanthe phillipsi	*		
Oriolus chlorocephalus	*		
Orthotomus metopias		*	
Phedina brazzae	*	*	*
Phyllastrephus alfredi	*	*	*
Phylloscopus laurae	*	*	
Platysteira albifrons	*	*	*
Plocepasser donaldsoni	*	*	*
Ploceus angolensis	*	*	
Ploceus batesi		*	*
Ploceus dicrocephalus	*	*	
Ploceus katangae		*	
Ploceus nicolli		*	
Ploceus spekeoides	*	*	*
Ploceus temporalis		*	
Poicephalus crassus	*	*	*
Prinia fluviatilis	*	*	*
Prinia leontica		*	*
Sarothrura lugens		*	
Serinus ankoberensis		*	
Serinus xantholaemus	*	*	
Sheppardia sharpei		*	
Spizocorys obbiensis	*	*	*
Spizocorys personata	*	*	*
Spizocorys sclateri			*
Swynnertonia swynnertoni		*	*
Tauraco erythrolophus	*	*	
Turdoides hindei		*	*
Turdoides melanops	*	*	*

Turdoides sharpei	*		*
Vidua codringtoni	*		*
Vidua larvaticola	*	*	*
Xenocopsychus ansorgei	*		
Zoothera cameronensis			*
Zoothera crossleyi	*	*	

Discussion

Our results indicate that future changes in climate are likely to have an impact on the performance of the current African IBA network. Compared with the results from Hole *et al.* (2009), this study suggests a more pessimistic outcome because where Hole *et al.* (2009) show that species turn over will be high within PAs, they do not show the extent of species distribution change across sub-Saharan Africa. The network as a whole, however, copes well in terms of species representation. Identifying those areas and IBAs that are predicted to gain species in the future will be of great importance to conservation and the results from this study provide some evidence to the identity of these areas.

Selection in Present and Future Time Periods

The predominant shift of importance to IBAs in Southern and Eastern locations can be explained in two ways which are not mutually exclusive. Firstly, climate is predicted to undergo changes in West Africa that will be detrimental to the current assemblage of species, affecting the ability of species to maintain viable populations within these areas. Climate in West Africa is expected to cause negative changes in plant communities under certain climate scenarios (Dixon *et al*. 1996; Delire *et al*. 2008) and has been identified as a possible cause of change in flora and avifauna distributions in the past (Thiollay 1998; Wittig *et al*. 2007). This is further supported by the East-West aridity gradient in Southern Africa that is predicted to become amplified in the future (Erasmus *et al*. 2002). The bioclimate models will therefore show an exodus of species from these areas as the climates they were initially matched to are no longer found within the region.

Alternatively, Eastern and Southern Africa have many highland areas which will provide areas which maintain hospitable climates for many species as climate changes (Sekercioglu *et al*. 2008). This would explain the increases in IBA selection in Eastern Africa where highland areas such as the Ethiopian highlands, Eastern Arc Mountains, Highveld and Albertine Rift are found. This is supported by the significantly larger maximum elevation and elevational ranges found in IBAs selected in future time periods. Upslope movement of species in response to changing climate has been shown both theoretically (Colwell *et al*. 2008) and empirically (Nogue *et al*. 2009; Wilson *et al*. 2005;

Wilson *et al*. 2007) by studies focussing on climate change. It is likely that highland regions will be of increasing importance in the future as they provide species with suitable climate space through upslope migration. Erasmus *et al.* (2002) predicted similar East-West shifts in species distributions across South Africa, attributing this to both climate and topography. These two processes acting in unison will surely have a significant impact on an East-West migration pattern of avifauna species over the coming Century.

Additional quarter-degree sites

The cells selected in addition to the IBA network were often clustered into certain regions, often in areas of high elevation. As previously mentioned, highland areas may become particularly important with climate change which would explain such selections. In these areas, although there may be sufficient numbers of IBAs, the increase in diversity predicted by the CRS models will mean that even an extensive reserve network would be unlikely to represent every species in five different PAs. Therefore, although the results would suggest the need for a dramatic increase in PA coverage in these regions, this may be an exaggerated conclusion. However, it further stresses the conclusions from the previous analyses that highland areas will be of increasing importance to conservation in the future and sufficient resources should be focused in such areas.

The apparent increased requirement for protection along the Atlantic Coast from South Africa to Angola cannot be explained through the need for protection in highland areas because these additional PAs are predominately lowland. A study by Thuiller *et al.* (2006) showed that protected areas near the Namibian coast, which form a large proportion of additional cells along the Atlantic coast, are likely to experience an overall increase in plant species over the same time period as this study. Although the study focuses on plant taxa, it does suggest that climate change may not cause decreases in species numbers in this area and therefore provides some support that additional protection is required in this region. It must be noted that Thuiller *et al.* (2006) performed their simulations under a different emissions scenario and therefore results must be compared with caution.

The predominant selection of cells in highland areas can also, to a certain extent, be attributed to the endemic bird areas found in these areas, which contain species which cannot be protected anywhere else and are therefore a priority for conservation (Stattersfield *et al.*1998). This will cause increased selection in these areas, which, in combination with upslope migration over the Century, will contribute to the clusters of additional cells across Africa.

Further research could be carried out to show whether the selection of additional sites for current species distributions has an effect on the number of additional sites required for future species distributions. This would then identify whether sites selected in the present would be of continued conservation importance throughout the century and therefore identify additional KSSs to the network.

Key Stable Sites

A major caveat of using BEMs to predict the effects of climate change on species' distributions is that it uses the correlation between climate and species distribution to predict future distributions (Morin & Lechowicz 2008). Therefore, if the ideal climate for a species was found to be in an area that would be impossible for that population to migrate to, the model would still identify this as its future distribution (Morin & Thuiller 2009). In addition to this, even if migratory distances represented only small physical distances, the negative impacts of habitat fragmentation on a landscape could make such migration an unfeasible task (McInerny *et al*. 2007; Opdam & Wascher 2004; Travis 2003). For this reason, the concept of a KSS is important because it allows conservation to focus on areas that are predicted to maintain a similar species assemblage in the future. This will allow PAs to protect a species without the risk of long distance dispersal between habitats or across a potentially hazardous matrix. It also removes a degree of inaccuracy from the analyses because the uncertainties of dispersal created by bioclimatic envelope models are nullified.

Particular attention can be paid to how many of the GCM scenarios a KSS was selected in because, in KSSs, stability is vital due to the uncertainty that surrounds predicting climate change (Moore *et al.* 2001). If a site is able to maintain stable populations of species in three different modelled climate scenarios, then it is likely that it will be robust to actual climate change events. The wide distribution of KSSs over Sub-Saharan Africa is encouraging in that such sites are not confined to a single region and therefore provides some hope for the persistence of species in all parts of the continent.

KSSs are functionally very similar to climate refugia which provide stable climates for species in times of harsh climatic conditions (Klein *et al*. 2009), although they are identified in different ways. Klein *et al*. (2009) identified climate refugia as areas of high and regular plant production in a semiarid environment using estimates of gross primary productivity. This study, however, identified KSSs from predicted future species distributions throughout the Century and therefore, depending on the accuracy of the modelling techniques, will provide an accurate assessment of that site's ability to maintain homogenous species populations in the future. The discovery that topographical features can increase the likelihood of an IBA being a KSS has important implications for the identification of climate refugia across Africa. The effect that area had on the selection of KSSs in all GCM scenarios is also of great interest, especially for any SLOSS debates that arise over the best adaptation strategies for climate change.

Adaption and Mitigation of the IBA network

What does this study suggest for future and present conservation measures that aim to address the impacts of climate change? Answers to this question can be addressed at varying scales, as not all solutions are relevant to the continent as a whole. At the continental scale, some regions have been identified as increasingly important over the coming Century. Although the majority of these are in highland areas, some are located in lowland areas such as the West coast of Southern Africa. It is vital that areas such as these receive sufficient resources to start and maintain viable reserve networks that not only provide adequate habitat for climate migrants, but also facilitate the dispersal of migrating species across the landscape to areas with suitable climate. This may include investment in increasing the quality of the landscape matrix as well as into habitat quality within PAs (Fahrig 2001; Huntley *et al*. 2006).

At the regional scale, additions that could be made to the IBA network have been highlighted in this study which would allow the network to better represent avifauna species across Sub-Saharan Africa. However, as the African IBA network includes areas that are currently unprotected (Approx. 43% (Buchanan *et al*. 2009)), it is vital that these areas continue to be monitored and acquire either protection or conservation management in the future so that the habitats remain intact. This will help to facilitate species migration and resettlement caused by climate change. Increasing the area of land under protection is cited as being one of the best ways to prepare for the effects of climate change on a species community (Hannah *et al*. 2007; McClean *et al*. 2006).

Although directing resources to areas that will be of increasing importance in the future will, to a certain extent, guarantee protection of species that migrate to areas of more suitable climate, attention must also be paid to areas that are predicted to suffer greatly from the effects of climate change. Dividing resources between areas that are considered to be ‘low risk’ as opposed to ‘high risk’ is a complex problem that depends on the levels of risk threatening different areas, the ratio of areas under different threat levels and the quality of the PAs (Game *et al*. 2008). How to divide conservation resources between areas with different levels of risk from climate change will be an important area of study in the future and may involve conservation triage (Willis *et al*. In Press).

In this study, West African IBAs were generally selected less frequently in future climate scenarios indicating a decrease in rare and range restricted species. This region may therefore require local efforts to decrease the negative impacts that climate change may have on such an area. However, the options that are available to mitigate such effects are few because climate is the overriding factor that determines a species’ persistence in a habitat (Rahbek & Graves 2001; Thuiller *et al*. 2004). Killeen and Solozarno (2008) provide ideas for mitigating the impacts of climate change in the Amazon rainforest, which are based on the strategic location of reserves and corridors so as to maximise the movement of species in the event of climate change. The protection of habitat corridors that run along environmental or elevational gradients would provide opportunities for species to migrate to more suitable climates. Killeen and Solozarno (2008) also point out that the Intelligent location of PAs in ecotones and areas which are predicted to have stable precipitation regimes would maximise their impact by increasing stability within the PA network, a strategy similar to the use of KSSs.

At a more local scale, actions can be taken within PAs to mitigate against the impacts of climate change. Maintaining a high quality of habitat within PAs by promoting structural complexity within the system is an important task for conservation managers (MacNally *et al*. 2009). By maintaining healthy ecosystems through good management practices, species are more likely to avoid drastic population declines that could lead to local extinctions. In addition to maintaining ecosystems as a whole, intensive management of particular species that are predicted to be at risk from climate change will promote population persistence over time (Williams *et al.* 2005).

In the event that climate change degrades habitats in West Africa to an extent that species are unlikely to survive in the region, one of the most documented options available to conservation is assisted migration which will allow species to be placed in areas that are of suitable climate and habitat (Hayward 2009; Mueller & Hellmann 2008). This method is notoriously disputed, and although it has recently been proven to work (Willis *et al*. 2009a), damage created by the introduction of alien species across the planet has caused extensive harm to ecosystems and has resulted in numerous species extinctions (Mueller & Hellmann 2008). The application of assisted migration as a conservation tool would have to be used only as a last resort, with detailed study on the possible impacts of such actions having taken place and the relevant cost-benefit analyses completed.

Conclusions

The future of avifauna conservation in Africa is reliant on the IBA network's ability to both preserve suitable habitat and to adapt to the increasing threat of climate change. This study identifies areas which will be of increasing importance to conservation over the coming Century because of both increasing and decreasing species occurrences in these areas. How to mitigate against and adapt to changes in climate will vary depending on how climate impacts these areas and an important theme of future research is how to divide resources between these two defined areas. From a basic view point, increasing the area of land under legal protection will increase a PA network's ability to cope with climate change (Hannah *et al.* 2007), therefore, it must be a key goal of conservation to increase the proportion of IBAs under official protection. The recognition of KSSs as climate refugia for species will allow the persistence of populations in habitats isolated by both human development and climate change. Climate refugia have been identified as a key tool in adaptation of conservation networks in the future (Noss 2001).

In order to keep track of the impacts caused by climate change across Africa, it is vital that monitoring of species assemblages is carried out within IBAs and schemes are currently underway to do this (Bennun *et al*. 2005; Tushabe *et al*. 2006). These data will allow conservationists to observe how climate is altering species' distributions and will allow better informed decisions to be made on how to mitigate and adapt to these changes. Up-to-date information will also allow more accurate predictive modelling which will further improve conservation planners' abilities to 'pre-empt' climate change. It also must be mentioned that as biodiversity is at risk from both climate change as well as direct human-induced habitat change (Pyke 2004), studies that factor in both of these issues will model the threats to biodiversity more accurately (Buchanan *et al*. 2009; de Chazal & Rounsevell 2009).

Although increasing the percentage of officially protected IBAs in Africa will undoubtedly help conservation in preserving habitat for species in an uncertain future, it is still within our power to cap a global increase in temperature at below 2 Celsius. Influencing policy to achieve this must also be a vital role of conservation biology (Huntley *et al*. 2006; Thomas *et al*. 2004).

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Chapter 4: Incorporating economic costs into reserve selection for present and projected future bird species distributions

Abstract

The impacts that climate change will have on species assemblages have been widely researched and are an increasingly important consideration for conservation organisations. Existing methods of conservation revolve around static Protected Area networks which will be put under strain by the dynamicity of species' distribution shifts caused by changes in climate. Adaptation of these networks to climate change is essential for their continued success in the future, however, economic costs of such endeavours are an important issue for the already stretched resources of conservation. In this study, a Reserve Selection Algorithm is used to adapt the Important Bird Areas network in sub-Saharan Africa to future climate scenarios using predicted species distributions from Climate Response Surfaces for the 21st Century. Opportunity costs were included into the reserve selection process so that the spatial heterogeneity of land prices could be taken into account. The results showed that the costs of adapting the network to climate change may increase over the Century as a result of changes to species distributions.

Introduction

Protected Areas (PAs) are integral to the global effort in preventing species extinction (Gaston *et al.* 2008; Heller & Zavaleta 2009). However, although PAs protect species from the destruction and fragmentation of natural habitats, when these anthropogenic forces are combined with the impacts of climate change, current PA systems are likely to come under strain as species' distributions are shifted by changing climate (McInerny *et al.* 2007; Travis 2003). Changes in climate could lead to an exodus of species from PAs, potentially shifting species' bioclimates into unprotected land, unless their altered distributions fall within other PAs (Hole *et al.* 2009). Designing PA networks that take these projected changes in species' distributions into account will increase their potential to protect species as climate changes throughout the coming Century.

This study focuses on the African Important Bird Areas (IBAs) network which is part of a Birdlife International program to identify a network of sites that are essential for the long-term survival of bird species (Buchanan *et al.* 2009). Each IBA was chosen on four selection criteria; (1) significant numbers of one or more species which are of global concern to conservation, (2) significant component of populations of one or more species with restricted ranges, (3) a significant component of a group of species which are largely or wholly confined to one biome, or (4) significant numbers (>1%) of the biogeographical populations of one or more congregatory species (Fishpool & Evans 2001). The network is comprised of sites of varying protection status as well as a number of unprotected sites, the protection of which would undoubtedly lead to a decreased risk of extinction of many bird species in Africa as well as acting as an umbrella for other taxonomic groups across the continent (Brooks *et al*. 2001; Tushabe *et al*. 2006). However, the management of new sites must be considered with three factors in mind; how the species a site protects complements the network's current species assemblage, whether the site could lose species in the future due to climate change, and the economic cost of the reserve relative to its importance, measured by complementarity, within the network.

In a previous study I modelled idealised reserve networks to account for recent and predicted future distributions of bird species in sub-Saharan Africa using quarter-degree cells and IBAs as selection units in a reserve selection algorithm (RSA; Chapters 2&3). Using RSAs to create networks based on species' simulated future distributions allows the identification of areas which will be of particular importance to conservation in the future. RSAs are a popular method of creating reserve networks because they systematically select reserves so that species are protected with the most efficient use of space, therefore theoretically reducing the cost of the reserve network (Margules & Pressey 2000; Naidoo & Ricketts 2006). Compared with *ad hoc* reserve selection or the use of species hotspots (Pressey 1994), RSAs guarantee protection of all selected species whilst minimising the number of PAs required. However, selecting sites that provide protection for species in the smallest possible area does not ensure that network costs are minimised because spatial variation in land prices is not taken into account (Ando *et al.* 1998). Biological diversity has been spatially correlated with human population densities (Balmford *et al.* 2001; Chown *et al*. 2003; Rondinini *et al*. 2006), so as a result, protecting the most biologically diverse areas may be an expensive option because competition with human land uses increases land prices despite the efficient use of land. Therefore, in order to design the most economical reserve networks, it is necessary to take into account the spatial variation that occurs in land prices so that conservation resources can be spent efficiently (Ando *et al.* 1998; Perhans *et al.* 2008).

The costs of conservation activities fall into several categories which include fixed and dynamic costs, and both direct and indirect costs to conservation. Acquisition costs are the costs of gaining property rights for an area (Naidoo *et al.* 2006) and represent the direct financial expenditure for purchasing an area of land for conservation. Land prices can be as spatially heterogeneous as biodiversity and therefore can be incorporated into RSAs in order to create resource efficient reserve networks. Data for land prices are available to a certain extent in developed countries and has been used in several studies to create budget-restrained reserve networks (Ando *et al.* 1998; Polasky *et al.* 2001; Strange *et al.* 2006), but such data are not as widely available for less economically developed countries and regions (Naidoo *et al.* 2006). This study uses land acquisition costs across sub-Saharan Africa where data for land prices is not widely available (Moore *et al.* 2004); instead the cost of land was calculated from the estimated value of the land if it were used for activities other than conservation (i.e. an opportunity cost). Opportunity costs are the costs that are foregone by committing land to conservation and not to commercial land uses (James *et al.* 1999; Wilkie *et al.* 2001). Instead of being merely a value for the cost of an area of land, they take into account the fact that commercial endeavours, such as agriculture, generate revenue from the land and therefore conservation must provide funds that offset and compete with the ongoing financial benefits that such activities provide.

By incorporating economic costs into the reserve selection methods used in an earlier study (Chapter 3), the impacts of climate change on the African IBA network can be mitigated against whilst decreasing the overall cost of the network. To do this, an appropriate land-cost data set, available at a suitable scale, must be used. Naidoo & Iwamura (2007) calculated opportunity costs by estimating the economic value of crops and livestock produced across the globe. It was assumed that the annual rental value of an area of land was equivalent to the total annual net revenue generated through agricultural activities. Using this data set, it is possible to assign economic value to all of sub-Saharan Africa and therefore cost can be used in reserve selection. These data however, do not take into account revenue derived from the logging industry in Central Africa and therefore some areas of high economic value to logging are not identified by Naidoo & Iwamura (2007). Additionally, these calculations do not value land for the ecosystem services they provide, which may become important in valuing land in the future as schemes such as the United Nations REDD programme (Reducing Emissions from Deforestation and Forest Degradation in Developing Countries) are implemented (Angelsen 2008; Kindermann *et al.* 2008).

Here I use an RSA to select parcels of land that could operate, alongside the current protected area networks, to ensure long-term future protection of avian biodiversity across sub-Saharan Africa under future climate change projections. I use opportunity costs to permit the most economical selection of land required to augment the current network.

Methods

Opportunity costs

The opportunity costs of quarter degree cells (of area approximately 25 km x 25 km) across sub-Saharan Africa were calculated using estimates of both crop and livestock productivity derived from Naidoo and Iwamura (2007) (Fig.

3.1). The text below, based on Naidoo and Iwamura (2007), provides further details on how these opportunity costs were produced.

Crops

Eighteen globally important major crops were considered in calculating crop productivity, as well as a number of regionally important minor crops. Potential crop suitability was calculated for each major crop. This was done on a global map of 5’ resolution with suitability defined as the fraction of the maximum agro-climatically attainable yield for each grid cell. This was dependent on five factors: climatic zone, soil conditions, the technical level of the farming practice, crop- and climatic-specific response to irrigation and the possibility of irrigation in each cell. From the potential crop suitability, maps of potential global crop yield were developed for each crop (in tonnes per hectare). Data were not available for the minor crops at equivalent geographic detail and therefore actual yields for the 25 minor crops were calculated for 22 defined regional divisions. This was done based on total production and total area under cultivation for each region.

Each potential major crop yield was multiplied to the corresponding global producer price for each grid cell to create a potential rent. The producer price for each crop type was calculated as a global producer price which decreased the potential error created by variation in the quality of data for some crop-producing areas. The global producer price therefore represented the prices that would be expected by most farmers across the world which, so as to reduce the effect of annual deviations in producer prices, were represented as a 12 year average (1991-2002) of producer prices taken from the top-5 producing countries. The potential rent calculated from this was then multiplied by the fraction of that cell estimated to hold the crop, which was obtained from global crop distribution data. The global crop distributions were taken from Leff *et al.* (2004) who defined 17 separate crop types used in the global cropland dataset of Ramankutty and Foley (1998) over a six year period which centres around 1992. This led to an estimation of gross rents so a weighted average could be taken for each 5’ cell. For the minor crops, the same process was undertaken but a region-wide average yield was taken for each region of the world (Leff *et al.* 2004). A weighted average was then taken to obtain a region-wide per-hectare gross rent which was then spatially assigned the per-hectare rents by the fraction of the grid cell occupied by the minor crop using global distribution maps (Leff *et al.* 2004). The gross economic rents for both major and minor crops were then summed to give a gross economic rent for crops in each cell.

Livestock

To estimate the gross economic rents of livestock, recently developed fine-scale global livestock distribution maps were used (Wint and Robinson 2006). Expected global densities of cattle, sheep, goats, pigs, poultry and buffalo were estimated using regression-based methods at a 3' resolution. The average mass of edible meat (derived from estimates of average carcass weights for 5 broad regions across the globe) was used to estimate the total number of tons of meat produced in each cell. Global producer prices were then calculated for each livestock type and multiplied by the meat yield per hectare to create a gross potential rent from livestock. This was then multiplied by the fraction of each cell estimated to be occupied by pastures (Foley *et al*. 2005).

To calculate the total opportunity cost of each cell, the highest value of either the crop or livestock rent was taken as the rent for that cell. Although this removed the likely possibility that land within each cell could be used for both crop and livestock production, intra-cell differences could not be defined with the methodologies used.

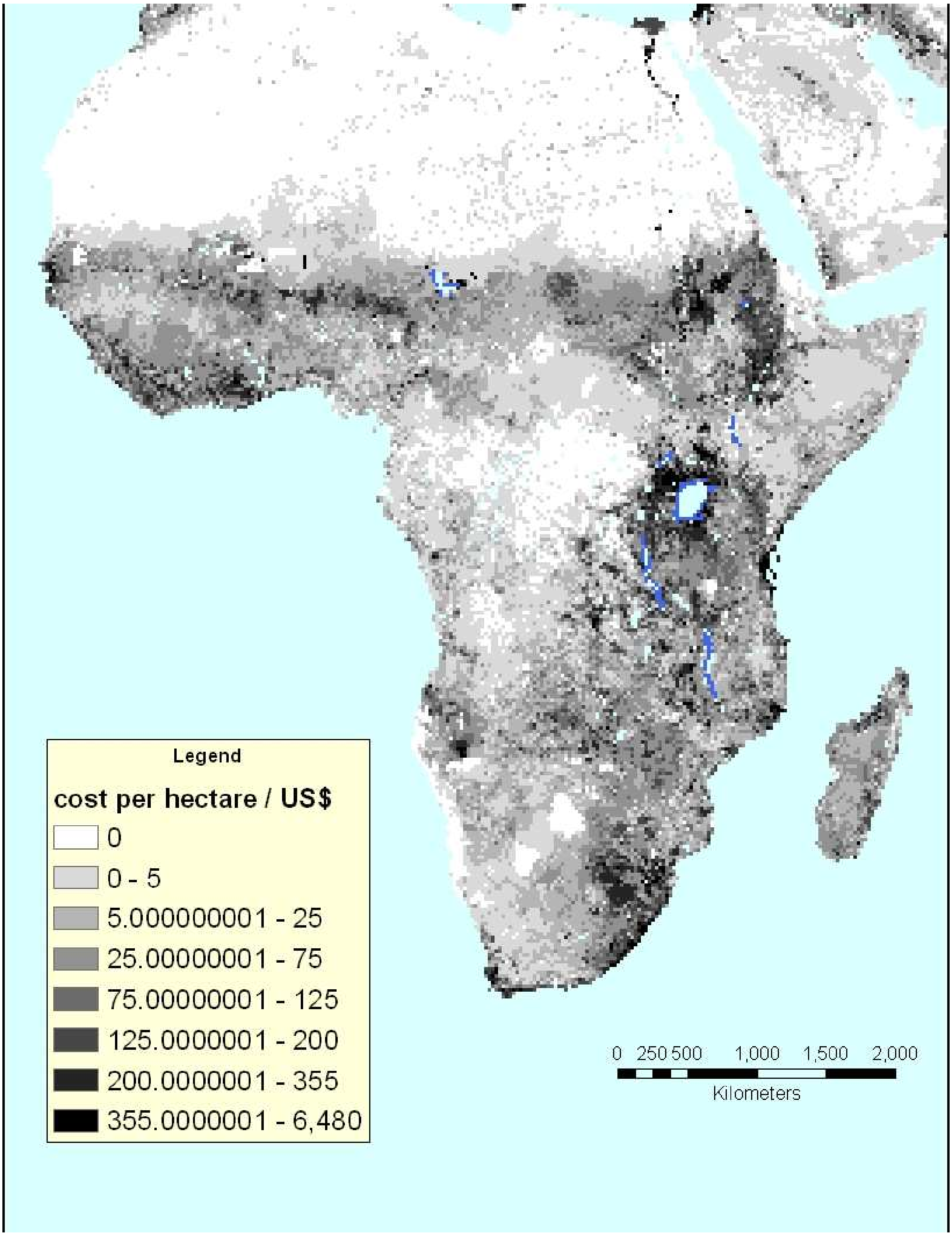

Figure 3.1. *Agricultural opportunity costs per hectare for quarter-degree cells across Africa based on data from Naidoo & Iwamura (2007).*

Bioclimate and Species Data

The models simulating future distributions of bird species across sub-Saharan Africa were produced by Hole *et al*. (2009) from recent (from here-on-in referred to as current; 1980-2000) species distribution data (Brooks *et al.* 2001) from the Zoological Museum of the University of Copenhagen (Jetz & Rahbek 2002). Presence-absence data for 1608 species for which reliable models could be constructed were available for the 1963 one-degree cells that make up sub-Saharan Africa. Mean bioclimatic data for the one-degree cells were created from mean monthly temperature and precipitation data available for quarter-degree cells for the period 1950-2000 (Hijmans *et al*. 2005; http://www.worldclim.org). Seven bioclimatic variables were chosen for modelling the bioclimatic envelopes of each species; mean temperature of the coldest month; mean temperature of the warmest month; an estimate of the ratio of actual to potential evapotranspiration; wet season duration; wet season intensity; dry season duration; and dry season intensity (Willis *et al.* 2009). These were selected for their previously confirmed ability in modelling the bioclimate envelopes of a wide range of European and African bird species (Huntley *et al.* 2006). The first three variables were used as standard variables in all models, but only one of the four seasonality variables, wet season and dry season duration and intensity were used (the procedure for selecting the fourth variable is explained by Huntley *et al.* 2006).

The climate data for the future time periods were obtained from three general circulation models (GCMs); HadCM3 (Gordon *et al.* 2000), ECHAM4 (Roeckner *et al*. 1996)and GFDL-R30 (GFDL) (Knutson *et al.* 1999). The simulations used were based on the SRES B2a emissions scenarios for three time periods, which represent 30 year averages for 2011-2040 (abbreviated from hereon in to the central year of the series; 2025), 2041-2070 (2055) and 2071-2100 (2085). The GCMs used are representative of the mean for the nine models included in the Intergovernmental Panel on Climate Change (IPCC) Third Assessment Report (TAR) (Cubasch *et al*. 2001) and range in simulated precipitation regimes from relatively wet (GFDL-R30) through to the mean (HadCM3) and relatively dry (ECHAM4). The future projections used future climate simulations from the TAR, however recently the IPCC Fourth

Assessment Report (FAR) has been published (Randall *et al.* 2007). The projections from the TAR are broadly consistent with those from the FAR, although the FAR is more advanced. The new assessment of *likely* ranges now relies on more climate models than the TAR, models which have increased complexity and realism and increased understanding of the processes and feedbacks involved in the global carbon cycle (Soloman *et al.* 2007). Nonetheless, I expect the projected range shifts to be broadly similar.

The bioclimatic envelope of each species was estimated using a Climate Response Surface (CRS) modelling approach, which uses locally-weighted regression to fit a response surface to a species' presence-absence data. This method was chosen over alternative approaches such as generalised additive models (GAM) after paired t-tests on sensitivity and true skill statistic (the assessment metrics used) indicated that CRS performed better than GAM (see Hole *et al*. 2009). The CRS models were validated using two techniques; firstly, for species which were recorded in > 20 one-degree cells, *K*-fold partitioning was used. *K*-fold partitioning is a procedure which generates *K* models by partitioning the data into *K* equal-sized sets apart from the *i*-th set which is used as training data. This process is carried out *K* times with each *K* subsample used once as the training data. This has the advantage of using all data for both validation and training (Ali & Pazzani 1996) and has advantages over the often applied 70:30 data splitting approach for model creation and validation (Thuiller *et al*. 2009) as it reduces potential issues of spatial autocorrelation. Predictive performance was assessed using values obtained for the area under the curve (AUC) of a receiver-operated characteristic plot (Fielding & Bell 1997). This was carried out for 1401 species, 89% of which exhibited *K*-fold partitioned AUCs of ≥ 0.9 (no species had a *K*-fold partitioned AUC < 0.7), indicating high-model performance (Swets 1988). Model fit for the remaining 207 species, recorded in fewer than 20 one-degree cells, was assessed using a jack-knifing approach. This process calculates the probability of a species' occurrence in a single one-degree cell, using a model built using all of the data except for the cell for which we wish obtain a simulation of occurrence. This is repeated for all 1963 cells of sub-Saharan Africa, for each species, and essentially produces simulations independent of the data used to create the CRS. Although this is more prone to issues of spatial autocorrelation than K-fold partitioning, the latter procedure cannot be used on restricted range species as large proportions of their entire range often fall within a single excluded panel. The projection accuracy was assessed using the same AUC process as applied to the more widespread species. 83% of the 207 species displayed a jack-knifed AUC ≥ 0.9, which again indicates a high-model model performance (for more details, see Hole *et al*. 2009).

Species simulated presence/absence for each IBA were calculated by characterising one or more bioclimates in each IBA and then applying the CRS model for each species to the bioclimate(s) for each IBA (see Hole *et al*. 2009). This was accomplished using a spatial intersection, within a GIS, of the IBA polygons, a one-degree grid to determine the broad spatial extent of each IBA, and a quarter-degree grid for each of the seven bioclimatic variable grids and for elevation. To produce a probability of occurrence for each species in each IBA, single or multiple bioclimates were assigned to each IBA. This was done by firstly assessing the size of the IBAs using the one-degree grid, if an IBA spanned more than a single one-degree cell, the polygon was split into a number of sub-polygons, by intersecting the one degree cells and the IBA polygon. The polygons or sub-polygons were then assigned bioclimates according to the associated quarter-degree climate data. Similarly, if the elevational range of a polygon or sub-polygon was >600 m, the component quarter-degree cells were stratified into two or more elevation bands and a separate bioclimate calculated for each band. Finally, the one-degree models for all species were projected onto each IBA's bioclimate(s) for all time periods and climate scenarios. The probabilities of occurrence were converted to presence or absence data by applying the threshold probability that maximised Cohen's κ for the one-degree model (Huntley *et al*. 2006). Therefore, if a species' probability of occurrence exceeded the threshold probability in any of the sub-polygons of an IBA, it was regarded as present.

Incorporating Costs into Reserve Selection

To match the resolutions of the cost and bioclimate data the cost data was converted from 5’ cells to quarter-degree cells. To carry out this conversion, the nine 5’ cells that make up each quarter-degree cell were added together to calculate the overall cost of the cell. In order to calculate the value for each IBA, the 5’ cost cells were clipped by the IBA polygon shape files within a GIS. The cells that were clipped were then used to create a mean average of cost within the IBA which was then multiplied by the area of the IBA to calculate the total cost.

The RSA Marxan was used for the reserve selection process (Ball & Possingham 2000; Possingham *et al.* 2000). Marxan uses a process called simulated annealing to create near-optimal reserve networks, the process starts with a random or user assigned network which is iteratively changed by the addition or removal of planning units (PUs) until the most efficient network is reached. The acceptance of an addition or removal from the network is determined by complementarity, which is a process whereby the PU is assessed by its ability to complement the species assembly protected within the reserve network. If a PU does not protect species that will contribute to reaching specific targets, then it will not be accepted. Initially, additions to the network which have a negative effect on reaching representation targets are retained so as to prevent the simulation reaching local optima within the network, but as the simulation continues, more negative additions are rejected because of the decreasing value of the cost functions within the program (McDonnell *et al*. 2002; Peralvo *et al*. 2007; Possingham 2000).

If a cost is included with a PU within Marxan, the cost is added to the objective function. Marxan’s goal is to reduce the value of the reserve network’s objective function which consists of the costs of each PU and a penalty for unmet species targets (Game & Grantham 2008). Through this function, Marxan can balance the total economic costs of the reserve network with reaching specified targets, therefore reaching a solution which is sympathetic to both needs. If a PU has no cost, Marxan will automatically select it because the objective function is not increased by its addition. Therefore, if a PU in this study had an opportunity cost of zero, it was assigned an arbitrary cost so that it was not automatically included in the selected network.

Building on past work on the impacts of climate change on the African IBA network (Chapter 3), several different scenarios were used in the reserve selection process. Marxan was run for all time periods and climate scenarios using several different approaches that incorporated opportunity costs. Initial RSAs were run on (1) IBA polygons and (2) individual quarter-degree cells each one of which was attributed a potential species component and an opportunity cost. In addition to this, the two data sets were combined so that selected sites could potentially include both IBAs in the current network and quarter degree cells (that did not intersect an existing IBA). This was done in two ways; (1) all the IBAs were permanently fixed into the network (i.e. they could not be removed from the initial network) within Marxan and the quarter-degree cells were selected additionally, (2) those IBAs which are officially protected by law (IUCN Protected Area category I to VI – as of 2008) were permanently fixed within the network whilst quarter-degree cells were available for being selected additionally.

For each reserve selection simulation, a representation target of occurrence within five planning units (IBAs or quarter degree cells) was used for each species.

Results

IBA network selected with cost

The inclusion of cost data substantially altered the selection of IBAs in a protection network, in comparison to the networks selected when opportunity cost data was not included as a selection factor (Fig. 2.1; Chapter 3). Substantially more IBAs were selected when cost was included, however, the areal extent of the network was greatly reduced. In particular, some of the larger IBAs from parts of the continent which have high opportunity costs (e.g. TZ009, ET002, ZA044 (Fishpool & Evans 2001)); Fig. 3.1). For the present period, a significant part of southern Africa, including the Cape Floristic Region (CFR) and the Highveld of South Africa, had no IBAs selected within them when opportunity costs were considered, despite reasonably extensive representation when costs were excluded. In addition, Ethiopia, southern Sudan and West Africa had relatively few of the current IBAs selected within them (Fig. 3.2a). The region around Lake Victoria, which includes the Eastern Arc Mountain range, North-East Tanzania, Uganda and Rwanda, is also a notable area in which opportunity costs are high and, as a result, few IBAs have been selected.

The reserve networks designed for the 2025 period select fewer sites than for the present time period (Fig. 3.2b; Table 3.1), although there is greater selection in areas such as the Highveld and Karoo in Southern Africa, Sudan and the Ethiopian Highlands. However, overall many IBAs selected in all three 2025 climate scenarios were also selected for the present, suggesting a similar suite of IBAs would protect species across both periods.

The networks selected for 2055 show an increase in the number of IBAs selected in areas of high opportunity costs, in comparision to the present and 2025 networks (Fig. 3.2c). Most notable are the increases in sites selected in southern Africa, including the CFR and in countries such as Botswana, where IBAs are included in all three GCM scenarios. There are increases in the number of IBAs selected around Lake Victoria. The networks selected for 2085 select even more IBAs in Southern Africa and the region surrounding Lake Victoria (Fig. 3.2d) than do the earlier networks, highlighting that although these IBAs may appear relatively unimportant across the network as a whole at present, they will become of much greater importance through the current Century. The CFR has several IBAs within it which are represented in all three GCM scenarios for 2085 and there is an increase in representation in the Highveld. There is also a decrease in the number of IBAs selected in all three of the GCM scenarios in the Ethiopian Highlands and Somalia (from 5 in 2055 to 2 in 2085) and the Congo basin (from 7 in 2055 to 3 in 2085).

The total opportunity costs of the networks are highly variable among the three climate scenarios for each future period and across the time periods, but are consistently less expensive than networks selected without the use of cost (Table 3.1). On average, however, there were similar numbers of IBAs selected for the best network in each of the time periods and GCM scenarios (253 for present, and on average 234, 235 and 225 for the periods 2025, 2055 and 2085 respectively). However, the numbers of both unrepresented species and underrepresented species increased over time.

A list of selected IBAs and unrepresented species from the optimal IBA networks are supplied in the supplementary material (S3.1).

A

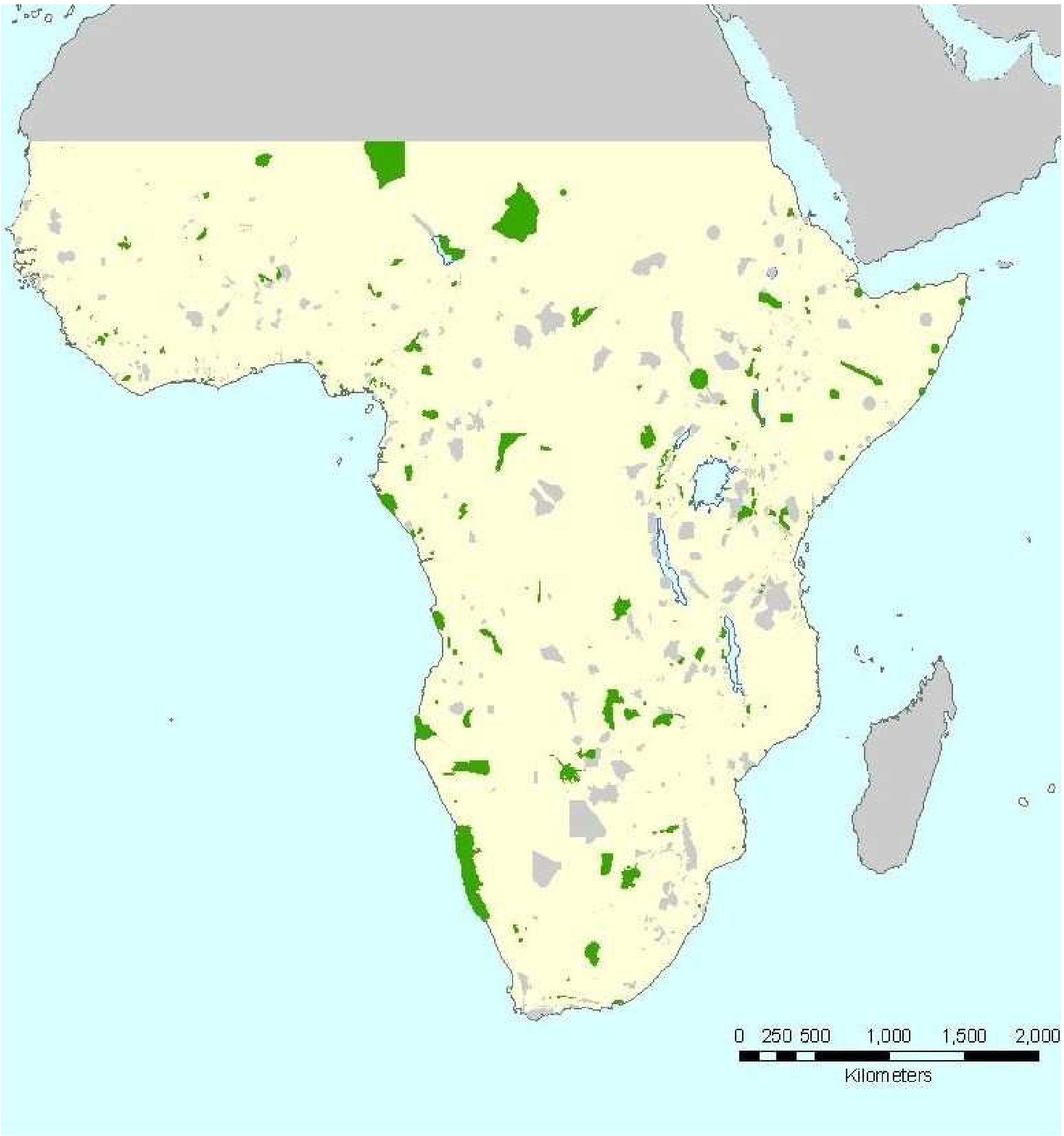

Figure 3.2 *(A) Optimal networks of IBAs selected by Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for current species distributions. Selected IBAs are shaded green. Unselected IBAs are shaded grey.*

B

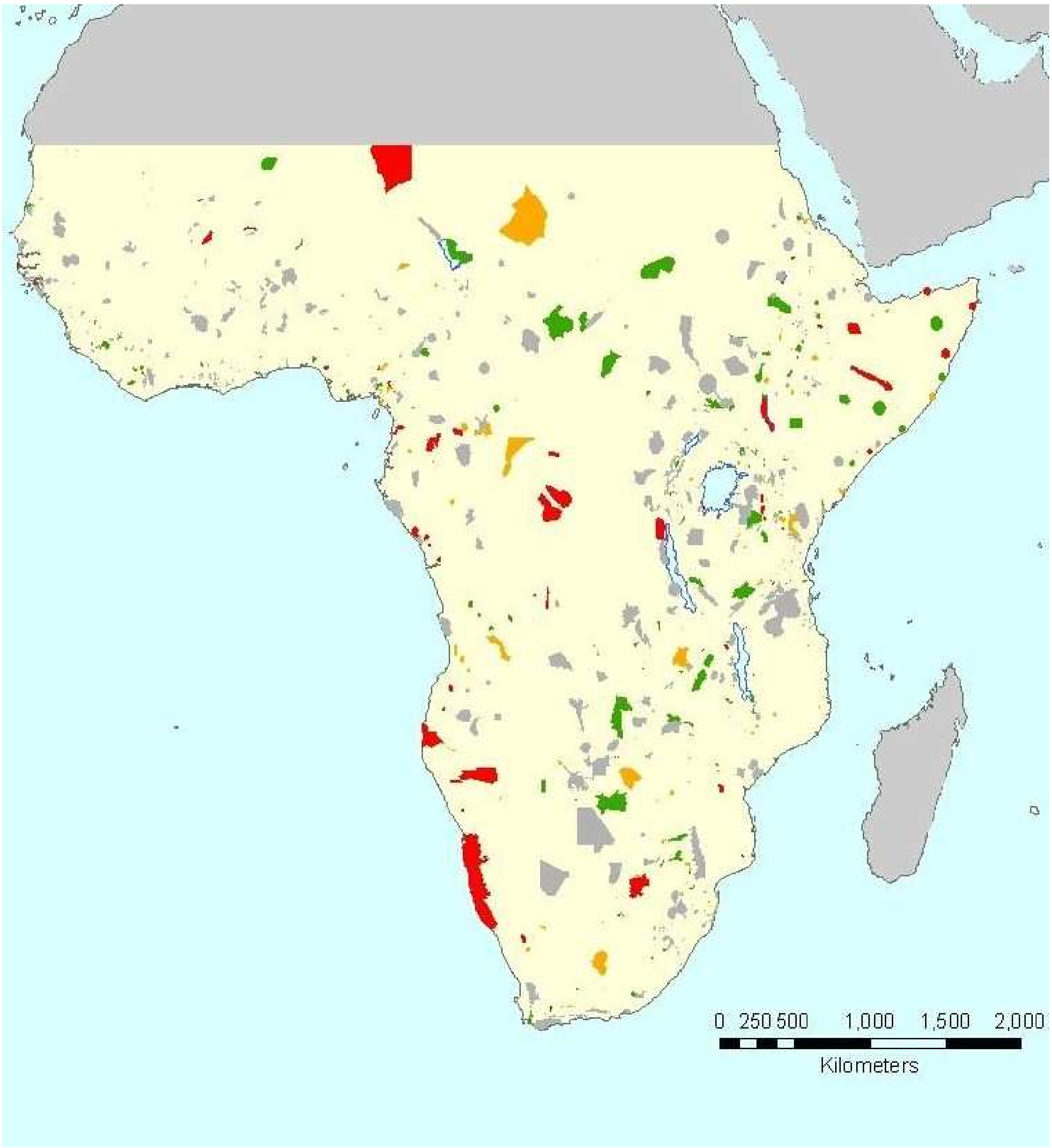

Figure 3.2 *(B) Optimal networks of IBAs selected by Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for projected 2025 species distributions. IBAs selected in one or more climate scenario are represented by different colours; one – green, two – orange, three – red. Unselected IBAs are shaded grey.*

C

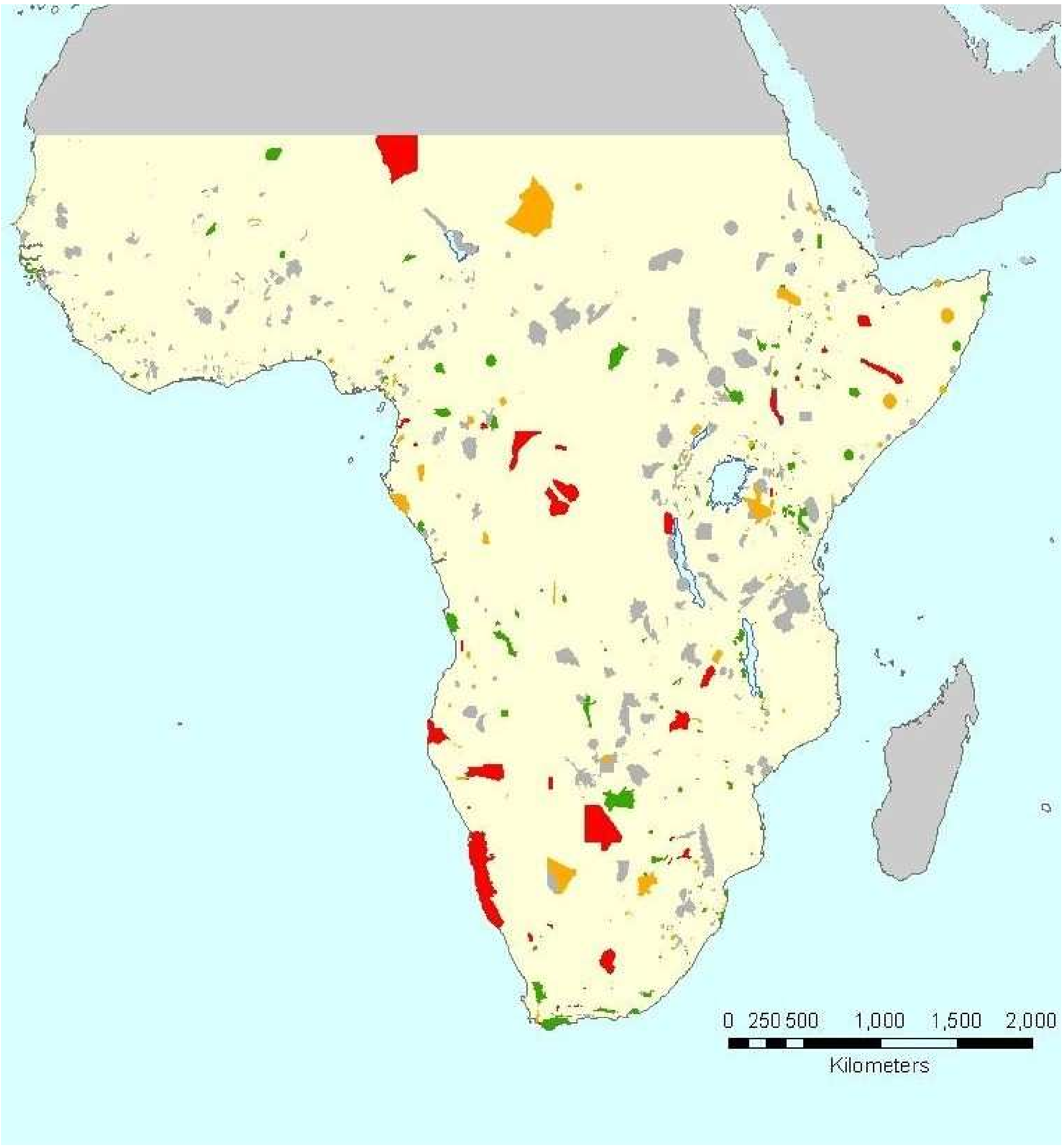

Figure 3.2 *(C) Optimal networks of IBAs selected by Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for projected 2055 species distributions. IBAs selected in one or more climate scenario are represented by different colours; one – green, two – orange, three – red. Unselected IBAs are shaded grey.*

D

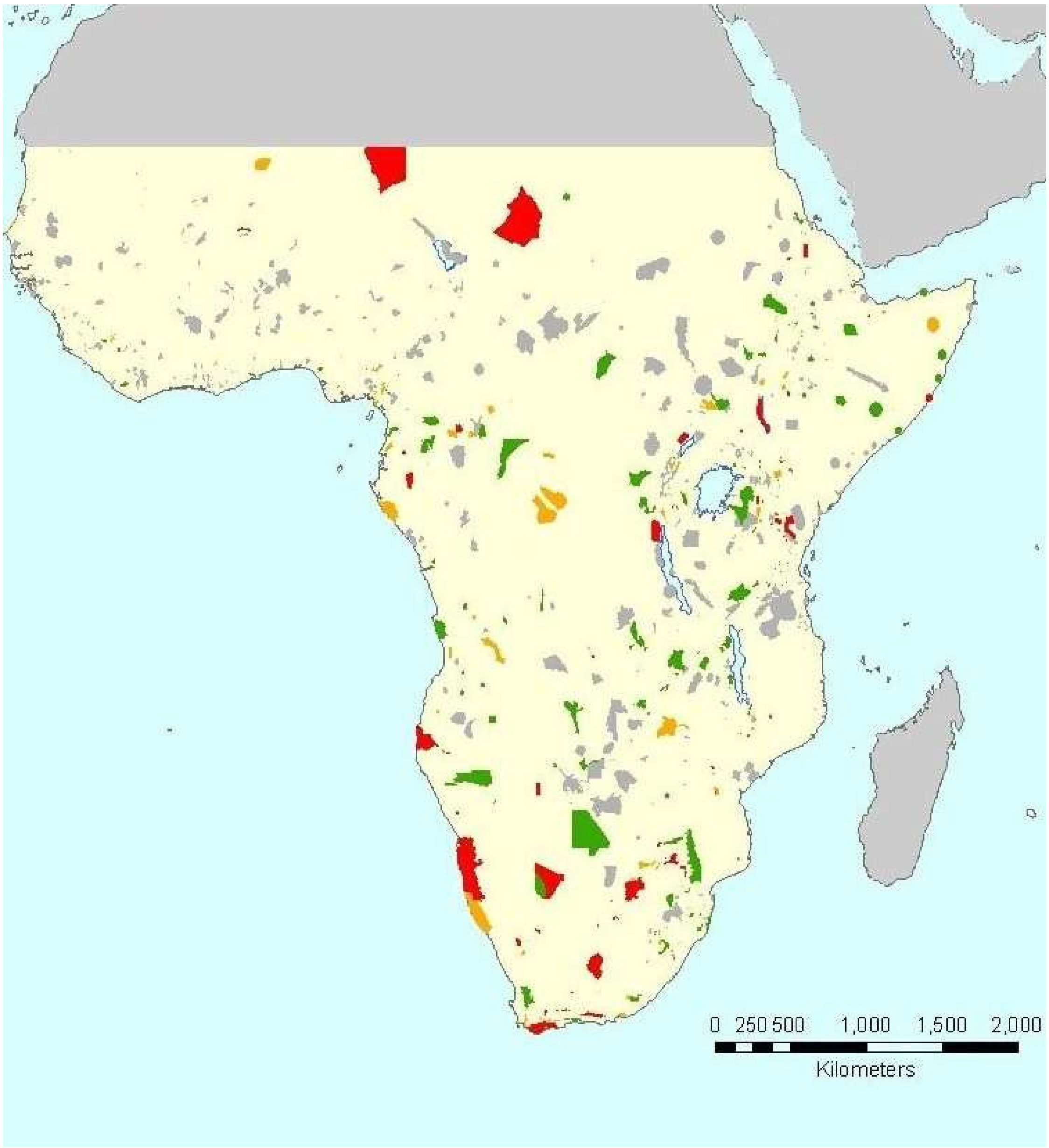

Figure 3.2 *(D) Optimal networks of IBAs selected by Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for projected 2085 species distributions. IBAs selected in one or more climate scenario are represented by different colours; one – green, two – orange, three – red. Unselected IBAs are shaded grey.*

Quarter-degree network selected with cost

The network of quarter-degree cells selected to protect species for the present-day period has a widely dispersed distribution, though with some clustering regionally (Fig. 3.3a). There is an interesting near-linear transect of cells crossing the centre of the Congo Basin. Many selected cells, as might be expected, cluster in Endemic Bird Areas (EBAs, Stattersfield *et al.* 1998) of particularly high endemism such as the Cameroon Highlands, the Eastern Zimbabwe Mountains, the Albertine Rift Mountains, the Central Ethiopian Highlands and Tanzanian-Malawi Mountains. However, some EBAs are relatively poorly represented despite harbouring many endemics, e.g., Upper-Guinea Forests. By contrast there are also clusters of cells selected in regions that contain no endemic bird areas. Examples of the latter include the region of northern Chad, a strip of cells on the border between Somalia and SE Ethiopia and a strip of cells from Mali down to Guinea.

The networks selected for 2025 (Fig. 3.3b) have clusters of cells in areas such as the Ethiopian Highlands, the Cameroon Highlands, Gabon, Lake Victoria, the Albertine Rift, Eastern Arc Mountains and clusters of cells that run close to the coast of Southern Africa up the Atlantic coast to Gabon. The 2055 network shows similar patterns with an increase in the occurrence of cells in different climate scenarios (Fig. 3.3c). There is a noticeable increase in selection of cells in the Cape Floristic Region (CFR) of South Africa and a decrease in the selection of cells in large parts of West Africa as well as in Lake Victoria. The 2085 networks have a similar pattern of selection to the 2055 networks, but they show an increase in selection of cells along the Atlantic coast of Southern Africa (Fig. 3.3d). The number of cells selected for the best network does not differ substantially among the time periods or scenarios (344 cells for the present period and on average, 329, 339 and 324 cells selected for the timer period 2025, 2055 and 2085 respectively; Table 3.1)

The cost of the networks increase in a near-linear fashion over the course of the Century (Table 3.1 & Fig. 3.4) from around US$282 million for the present up to around US$658 million for the HadCM3 2085 network, with the network required to protect species under the GFDL scenario of climate change being consistently the cheapest of the three. The inclusion of cost as a selection factor created cheaper networks than when cost was not included (Table 3.1), while at the same time, increasing the number of cells selected (Table 1.1; Chapter 2). Comparing Fig. 3.3 with Fig. 1.2 (Chapter 2; included alongside the corresponding time period for Fig. 3.3) reveals a marked difference in the distribution of cells between the two simulations. The distribution of cells in Fig 3.3 is more concentrated, with a larger number of cells being selected in two or more of the GCM scenarios in each of the time periods.

For all the present and future climate scenarios the optimal networks produced from quarter degree cells were substantially cheaper than the IBA networks (cell networks for the various time periods/scenarios ranged in costs from 4% to 44% of the costs of the equivalent IBA network). Therefore, ignoring the logistics and costs of creating such a PA network, it appears from this simple comparison that selecting a network derived anew from quarter degree cells would be substantially less expensive, in terms of opportunity costs, than a network that utilised IBAs to achieve the same goals.

Many of the cells selected in a network for all of GCM scenarios for a single future time period coincide with EBAs. For example, in 2085 cells selected in the network under all three GCM scenarios (shaded red in Figure 3.3d) cover areas of the Cameroon Mountains (EBA 085), the Cameroon and Gabon Lowlands (EBA 086), Lesotho Highlands (EBA 090), Eastern Zimbabwe Mountains (EBA 104), Albertine Rift Mountains (EBA 106), Serengeti Plains (EBA 108), South Ethiopian Highlands (EBA 114) and the Central Ethiopian Highlands (EBA 115). Key cells selected under all three GCM scenarios but not in EBAs include two on the Atlantic coast of Namibia and South Africa, six cells in northern Chad, and one cell each in Mali and Niger.

Figure 1.2 *(A)* ***From Chapter 2, p48*** *Quarter-degree cells selected by Marxan to represent sub-Saharan African bird species in their current distributions, Cells represented in black.*

A

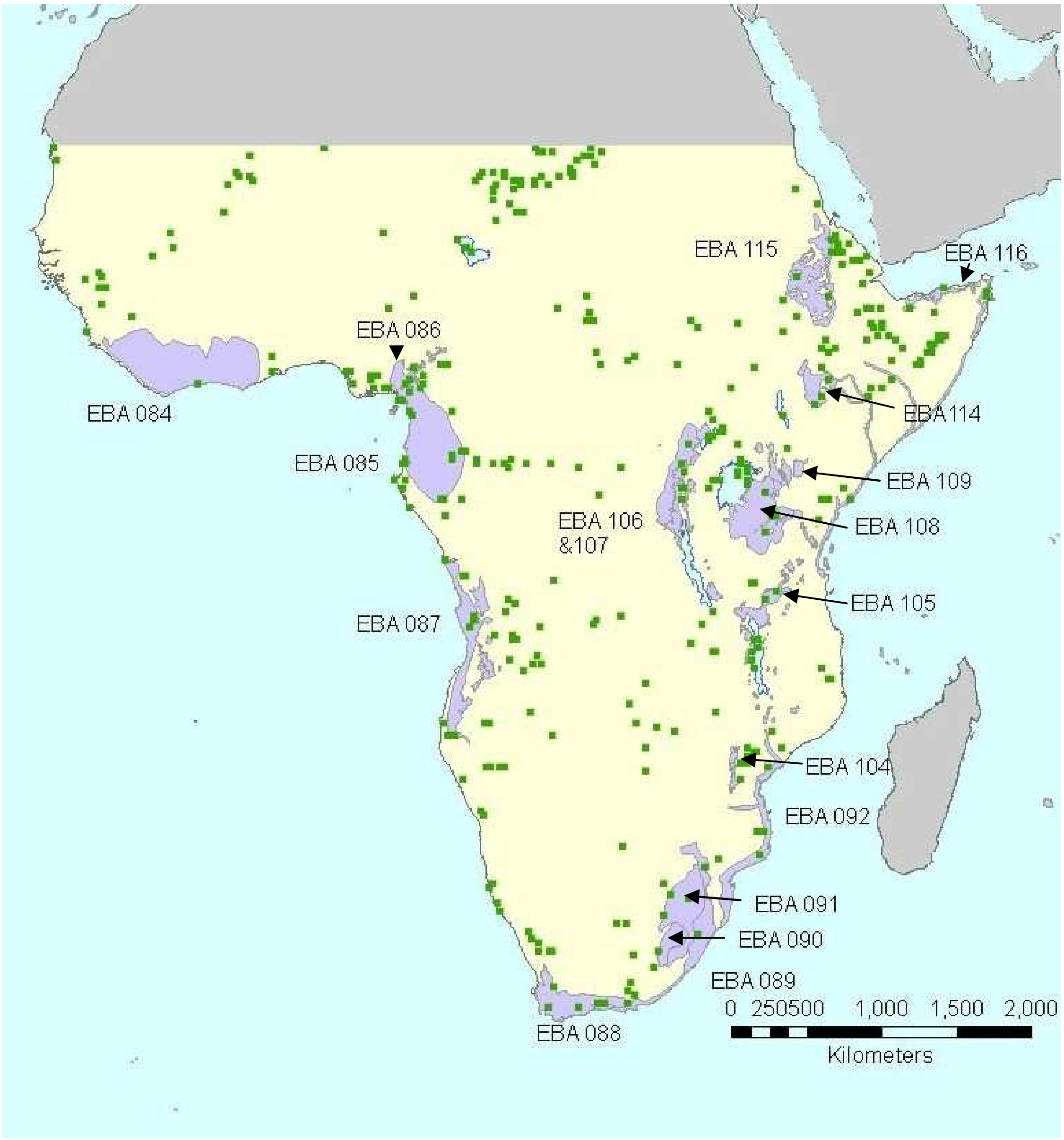

Figure 3.3 *(A)Optimum networks of quarter-degree cells created by Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for current species distributions. The cells are shaded green and are not shown to scale. EBAs are shaded in grey and labelled.*

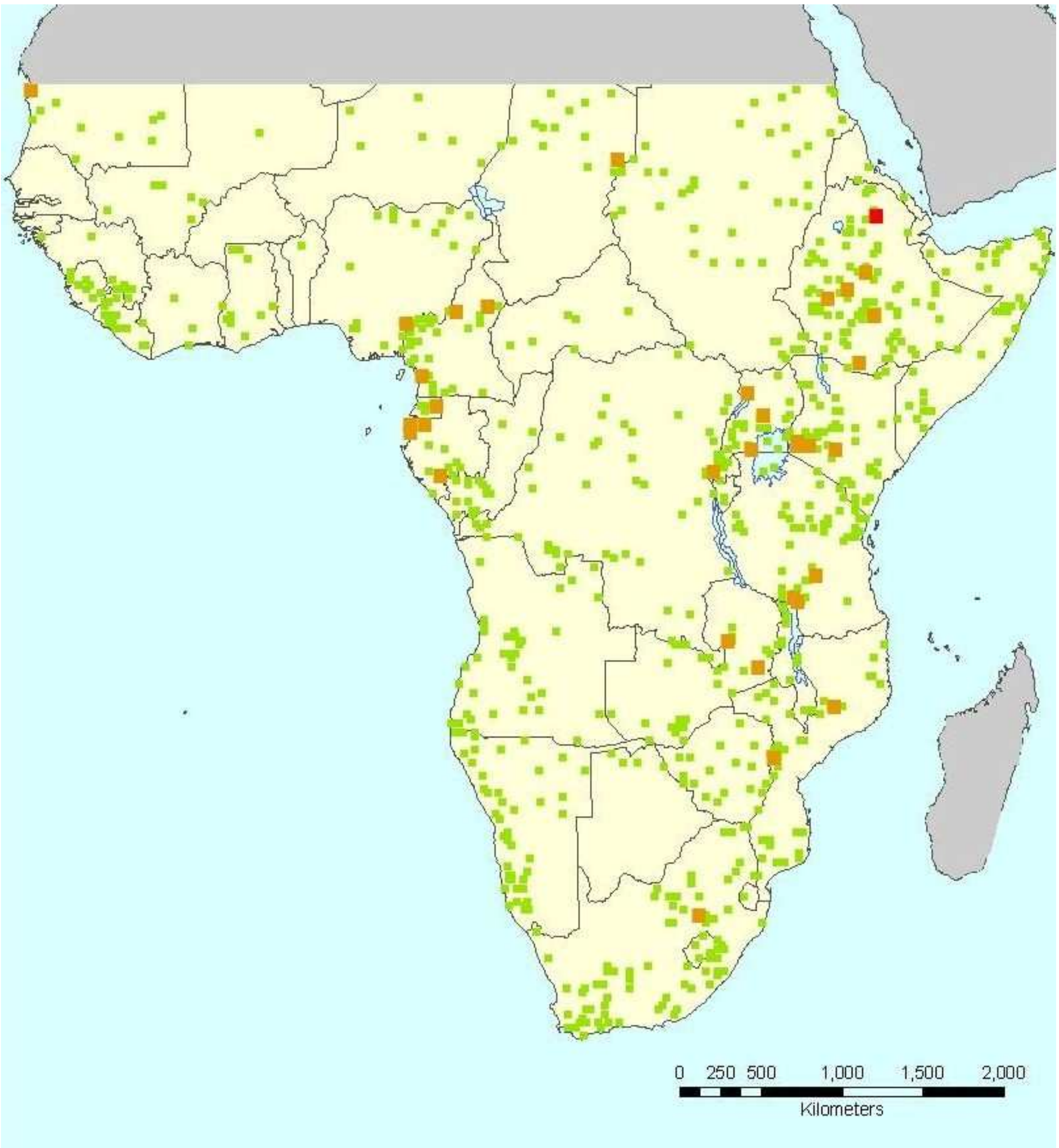

Figure 1.2 *(B)* ***From Chapter 2, p49.*** *Map of quarter-degree cells selected by Marxan to protect sub-Saharan African bird species for projected 2025 species distributions coloured depending on the how many future scenarios (ECHAM4 / OPYC, GFDL-R30, HadCM3) they are selected in. Red = 3 times, Orange = 2 times, Green = 1 time.*

B

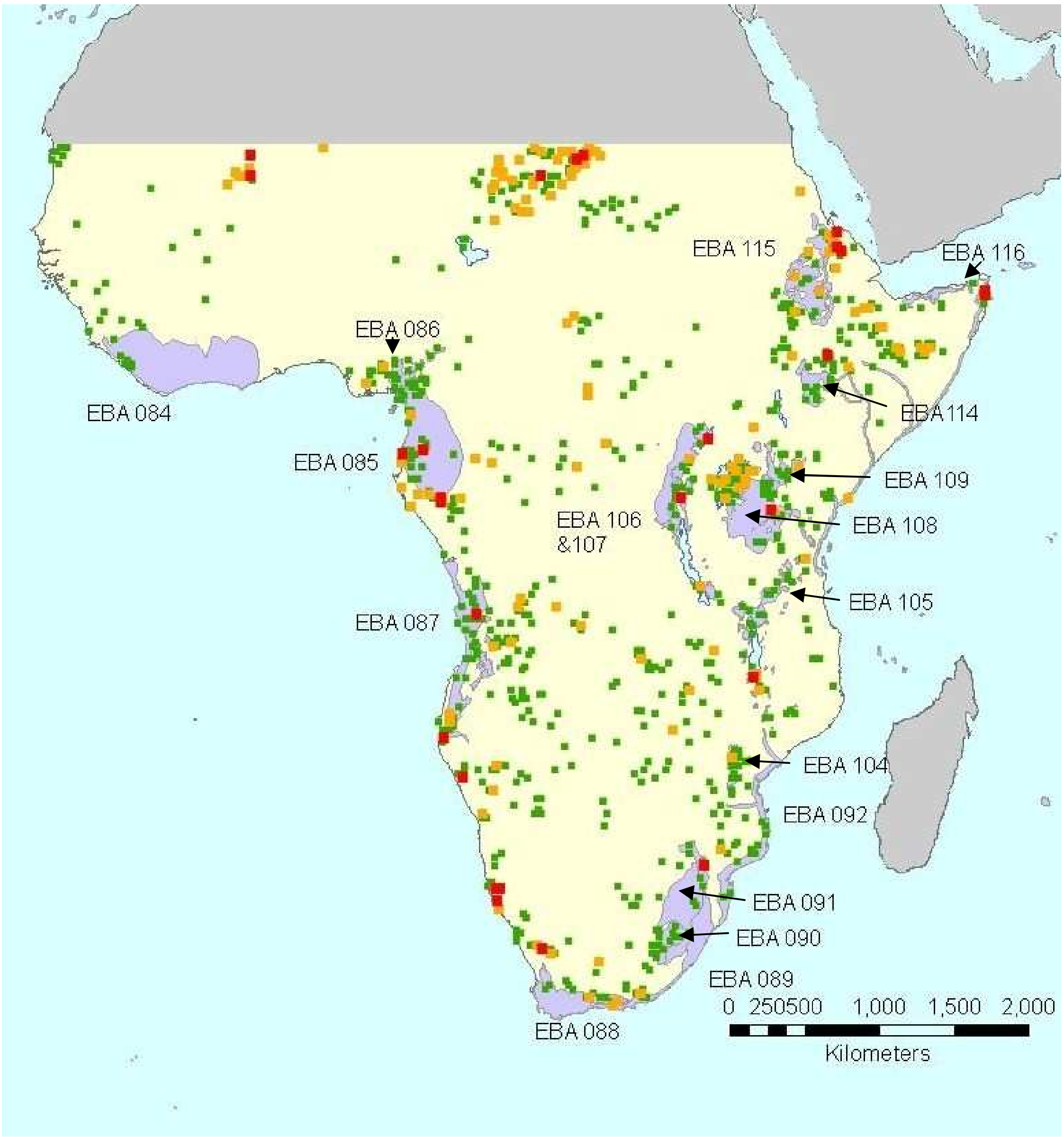

Figure 3.3 *(B)Optimum networks of quarter-degree cells created by Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for projected species distributions in 2025. Quarter-degree cells selected in one or more climate scenario are represented by different colours; one – green, two – orange, three – red. The cells are not shown to scale. EBAs are shaded in grey and labelled.*

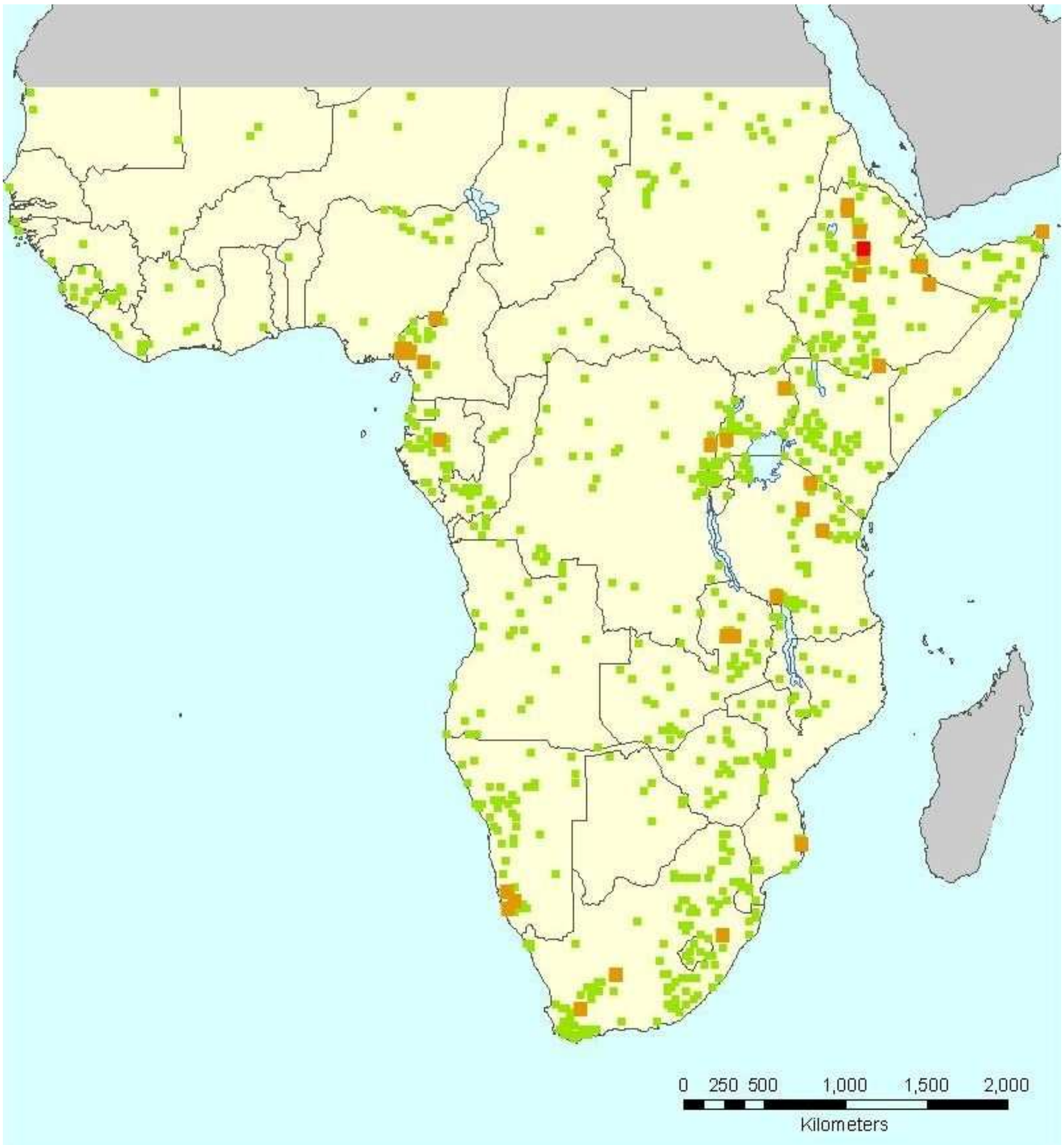

Figure 1.2 *(C)* ***From Chapter 2, p50.*** *Map of quarter-degree cells selected by Marxan to protect sub-Saharan African bird species for projected 2055 species distributions coloured depending on the how many future scenarios (ECHAM4 / OPYC, GFDL-R30, HadCM3) they are selected in. Red = 3 times, Orange = 2 times, Green = 1 time.*

C

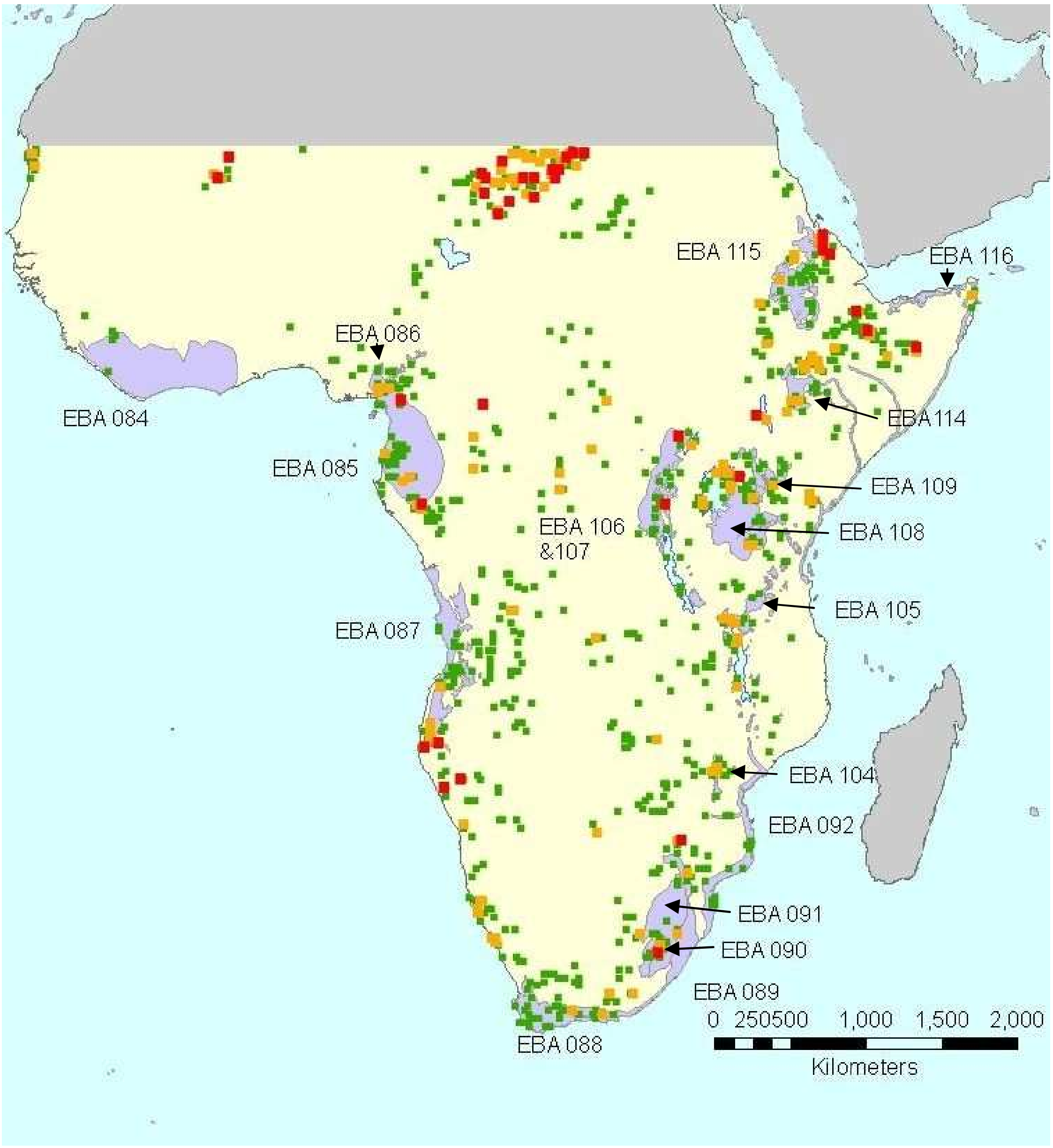

Figure 3.3 *(C)Optimum networks of quarter-degree cells created by Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for projected species distributions in 2055. Quarter-degree cells selected in one or more climate scenario are represented by different colours; one – green, two – orange, three – red. The cells are not shown to scale. EBAs are shaded in grey and labelled.*

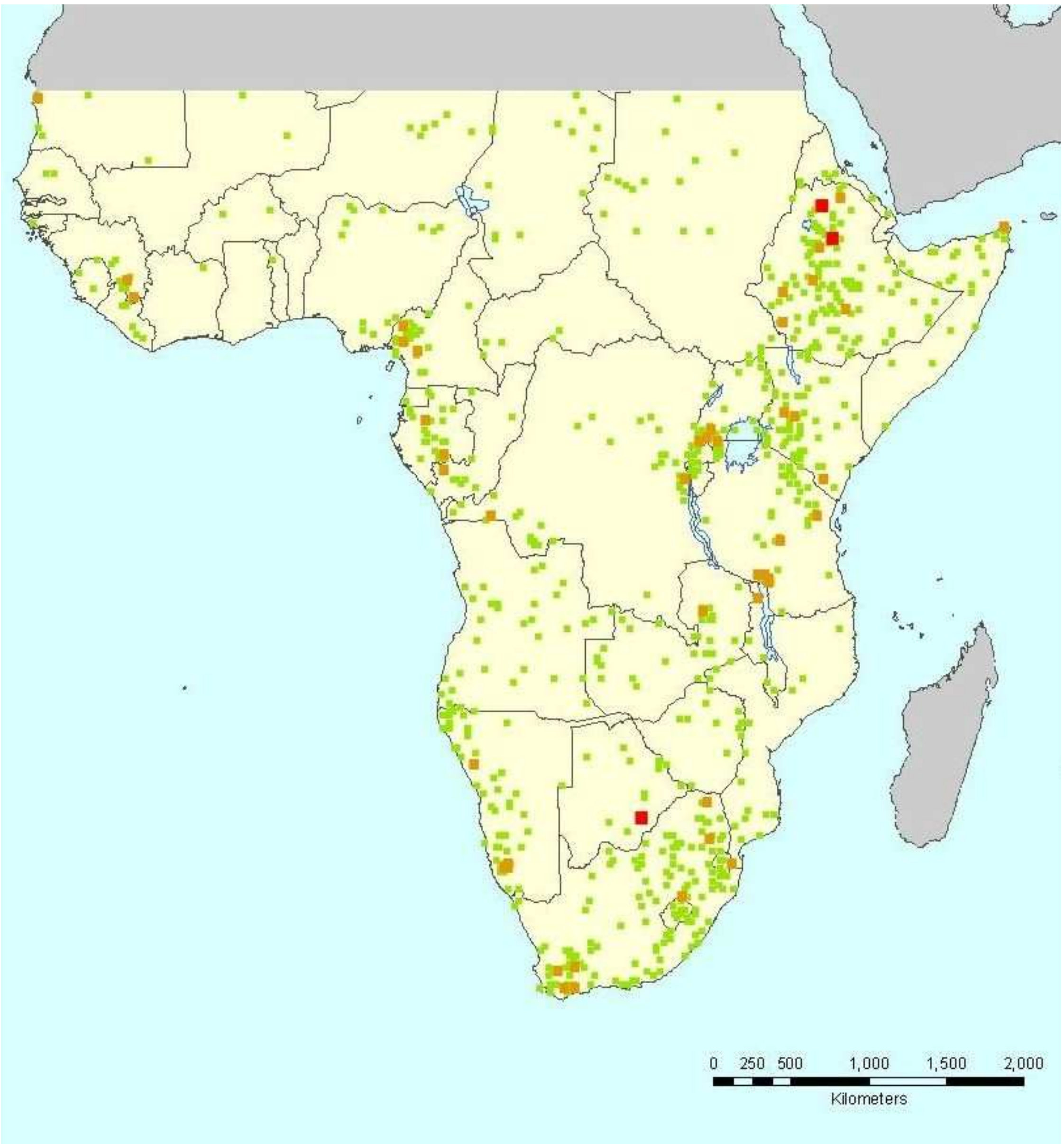

Figure 1.2 *(D)* ***From Chapter 2, p51.*** *Map of quarter-degree cells selected by Marxan to protect sub-Saharan African bird species for projected 2085 species distributions coloured depending on the how many future scenarios (ECHAM4 / OPYC, GFDL-R30, HadCM3) they are selected in. Red = 3 times, Orange = 2 times, Green = 1 time.*

D

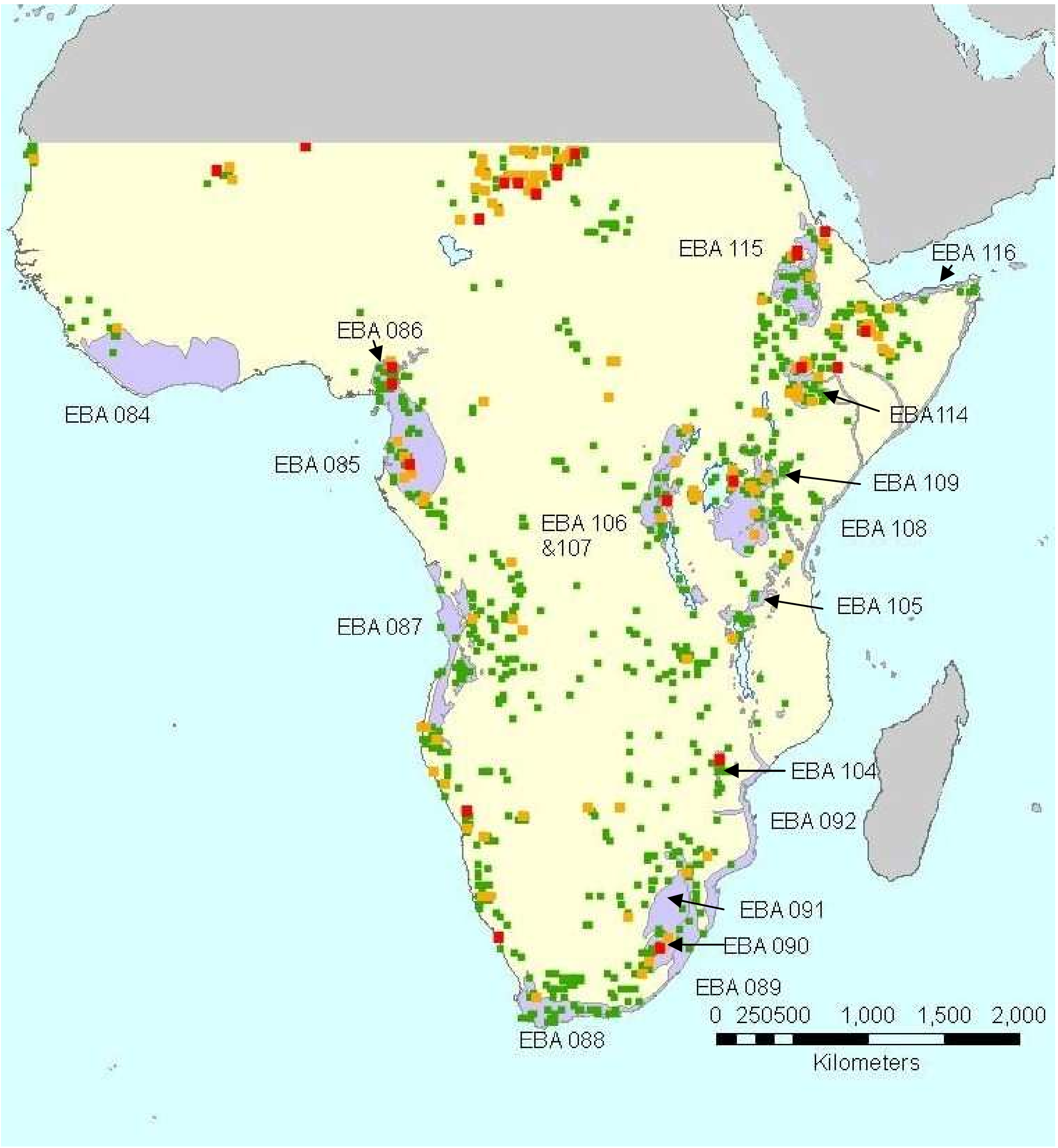

Figure 3.3 *(D) Optimum networks of quarter-degree cells created by Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for projected species distributions in 2085. Quarter-degree cells selected in one or more climate scenario are represented by different colours; one – green, two – orange, three – red. The cells are not shown to scale. EBAs are shaded in grey and labelled.*

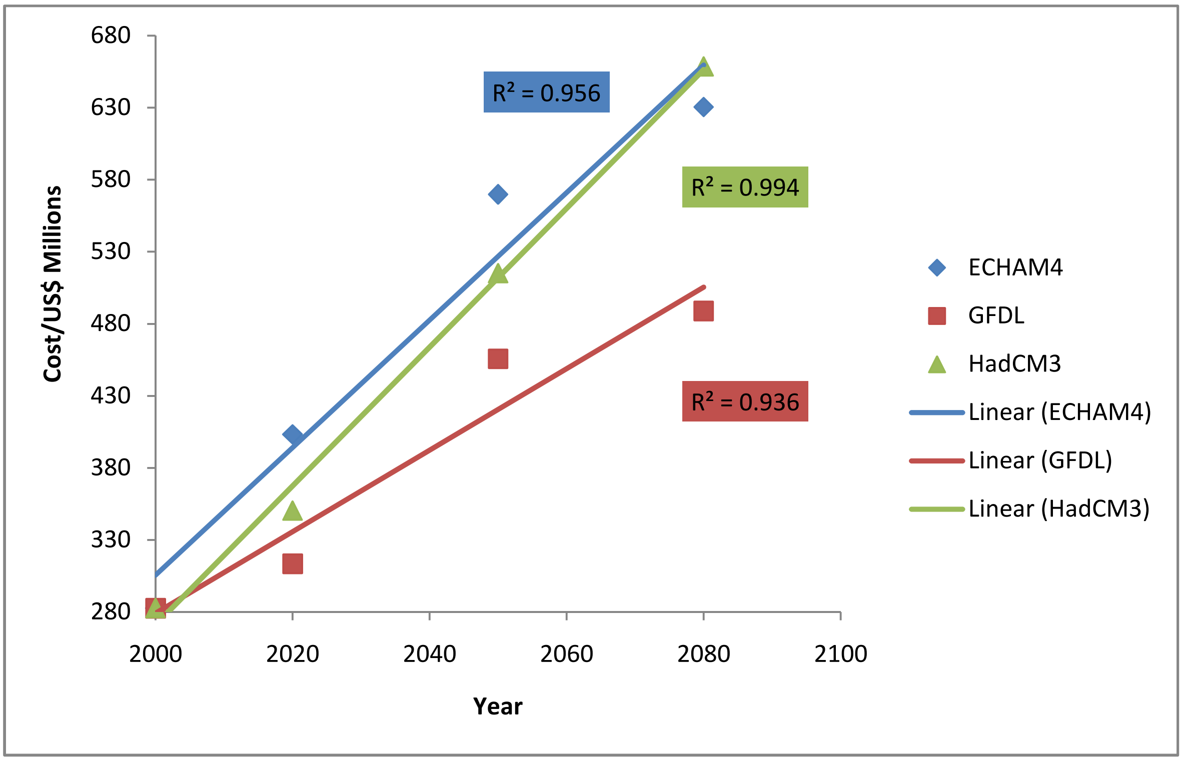

Figure 3.4 *The total opportunity costs of each optimum quarter-degree cell network created by Marxan. Separate linear regression lines indicate the trend of cost under the three future climate change scenarios.*

Networks combining IBA and quarter-degree cells and accounting for opportunity costs

Data on the species which caused the selection of individual cells is presented in the supplementary material (S3.3.1 & S3.3.2).

(1) All IBAs fixed into the network, regardless of current protection status

For the present-day species distributions, only 76 additional quarter-degree cells were required alongside the existing IBA network in order to achieve total representation of all species (Table 3.2). The main group of these additional quarter-degree cells is found in a cluster on the Chad-Niger border, with some smaller groupings in Mali, Guinea, Somalia and Eritrea as well as along the west coast of southern Africa (Fig. 3.5a).

The 2025 network includes an average of 95 additional quarter-degree cells included in the network. Groups of selected cells similar to those selected for the present are found on the Chad-Niger border as well as in Mali, Somalia and Eritrea (Fig. 3.5b). In addition to these groups of cells, there are additional cells selected across Cameroon, Equitorial Guinea, The du Chaillu Mountains of Gabon and Congo; the Namib-Karoo region in Western Namibia and North-West South Africa; and increased selection of additional cells between 12° and 20° South.

The 2055 networks have an average of 112 additional cells, and have similar patterns of selection to the 2025 networks. However, there is greater selection of cells in areas of Southern Africa which include the Drakensberg Mountains, the Highveld and CFR, and in the Ethiopian Highlands (Fig. 3.5c). These same trends continue into 2085, where networks include, a similar number of additional quarter-degree cells to 2055 (115 on average) with major concentrations of additional cells in the Chad-Niger border, the Ethiopian Highlands, the du Chaillu Mountains, in the West of the Republic of Congo, the Drakensberg Mountains and Highveld of South Africa, the CFR and throughout the Namib-Karoo biome, both in South Africa and western Namibia (Fig. 3.5d). Relatively few cells were selected in all three future GCM scenarios as necessary additions to the network, (shaded red in Figures 3.5b-d) in any time period, though the localities of these cells were similar throughout the Century.

There is an overall increase in price of the networks over time (Fig. 3.6) although the trends are not as convincing as Fig. 3.4. This increase in price is likely to be because of both an increase in the number of cells selected and an increase in the selection of cells in areas of high opportunity costs.

A

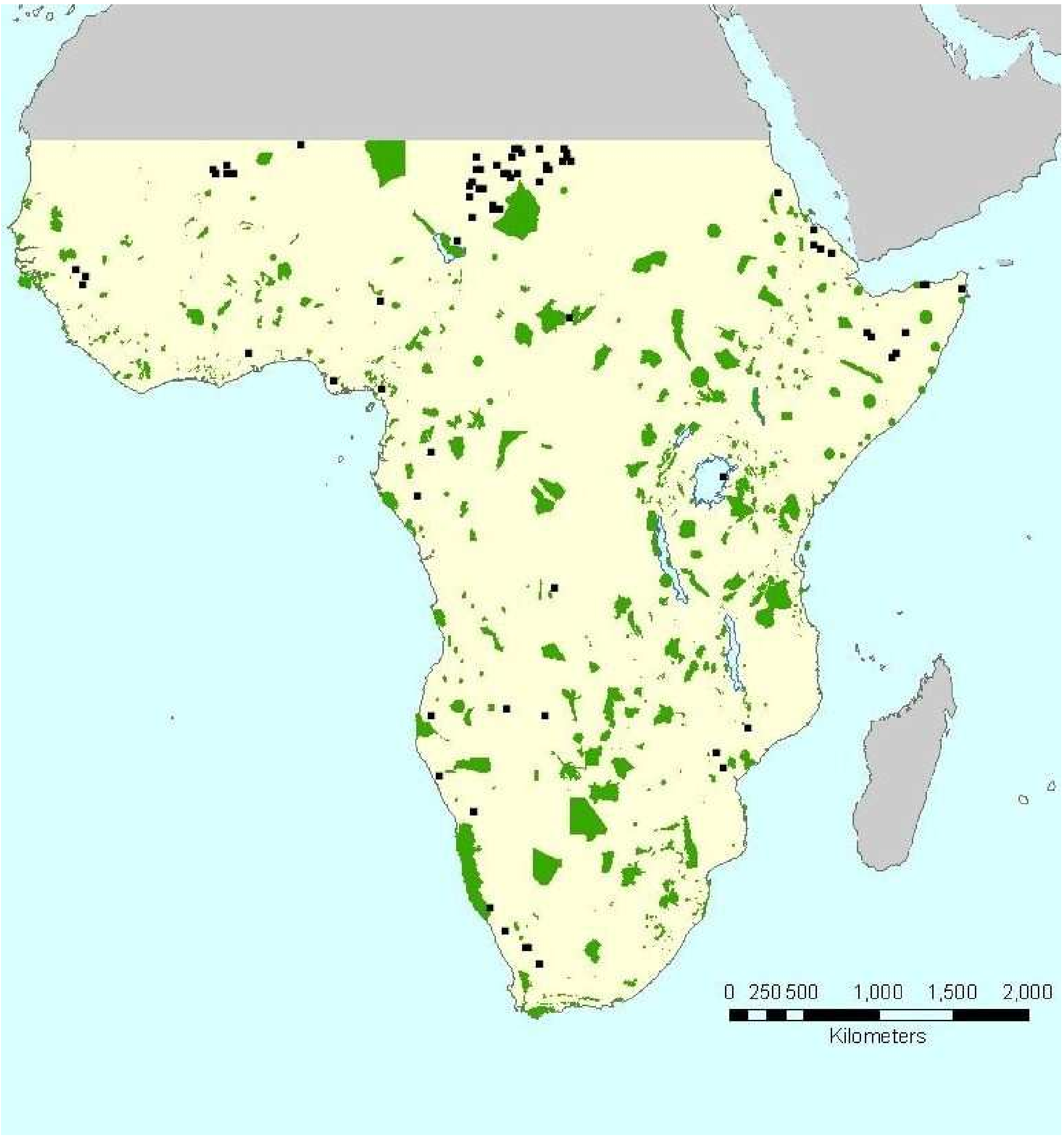

Figure 3.5 *(A) Optimal networks of all IBAs and additional quarter-degree cells created by Marxan to protect sub-Saharan African bird species using opportunity cost as a selection factor for current species distributions. The quarter-degree cells are shaded black and are not shown to scale. IBAs are shaded green.*

B

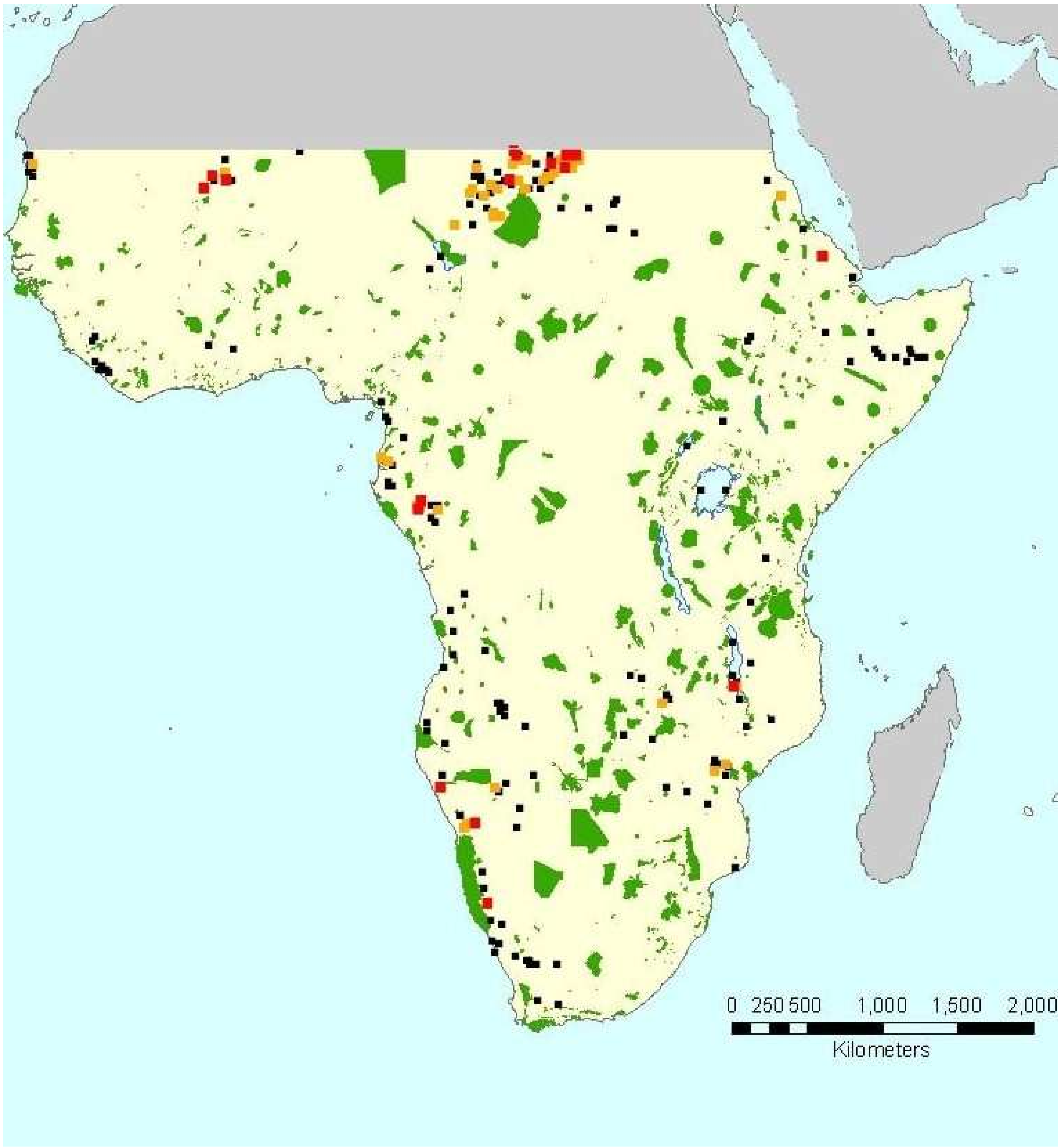

Figure 3.5 *(B) Optimal networks of all IBAs and additional quarter-degree cells created by Marxan to protect sub-Saharan African bird species using opportunity cost as a selection factor for projected species distributions in 2025.Cells selected in one or more climate scenario are represented by different colours; one – black, two – orange, three – red. The cells are not shown to scale. IBAs are shaded green.*

C

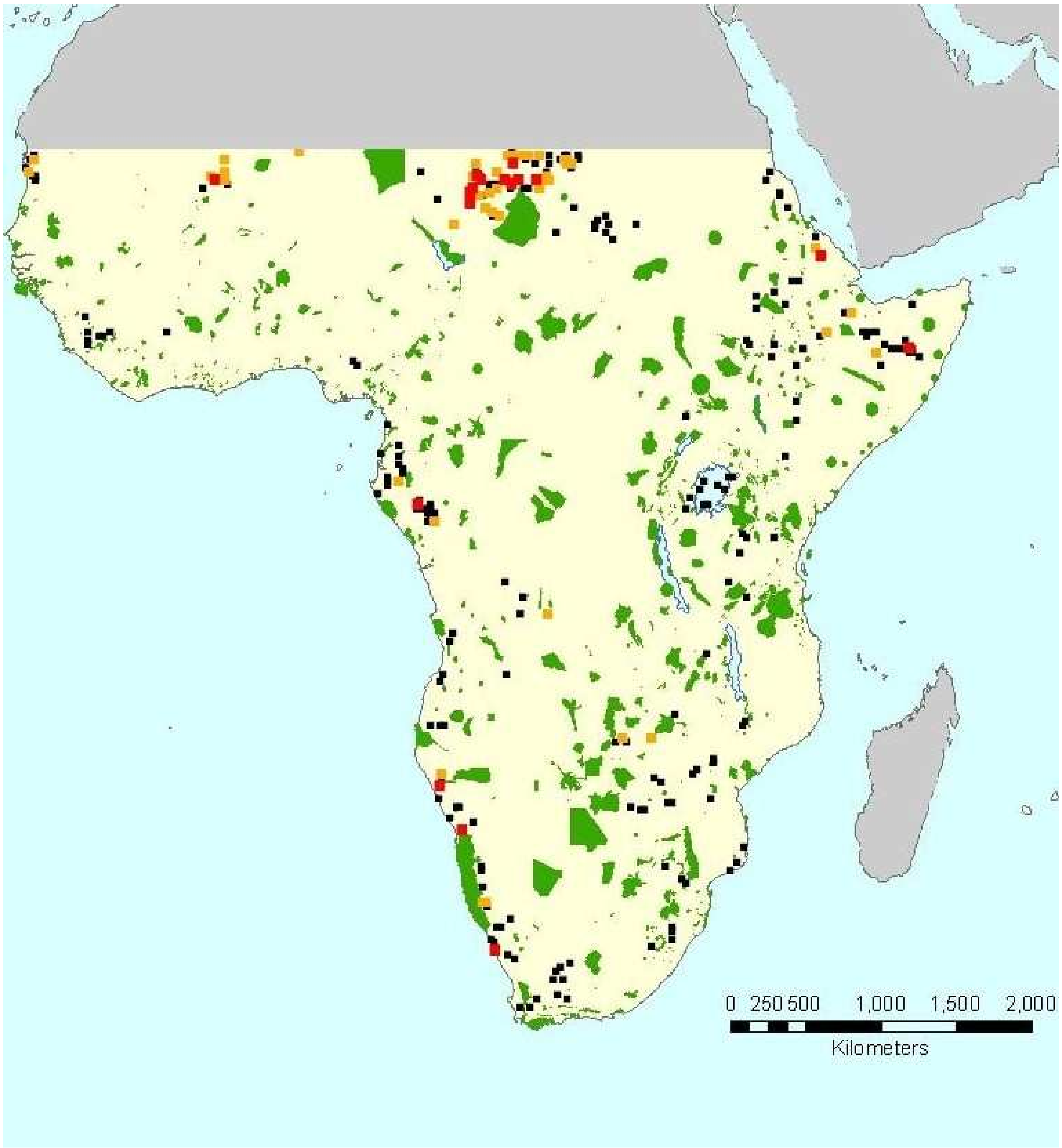

Figure 3.5 *(C) Optimal networks of all IBAs and additional quarter-degree cells created by Marxan to protect sub-Saharan African bird species using opportunity cost as a selection factor for projected species distributions in 2055.Cells selected in one or more climate scenario are represented by different colours; one – black, two – orange, three – red. The cells are not shown to scale. IBAs are shaded green.*

D

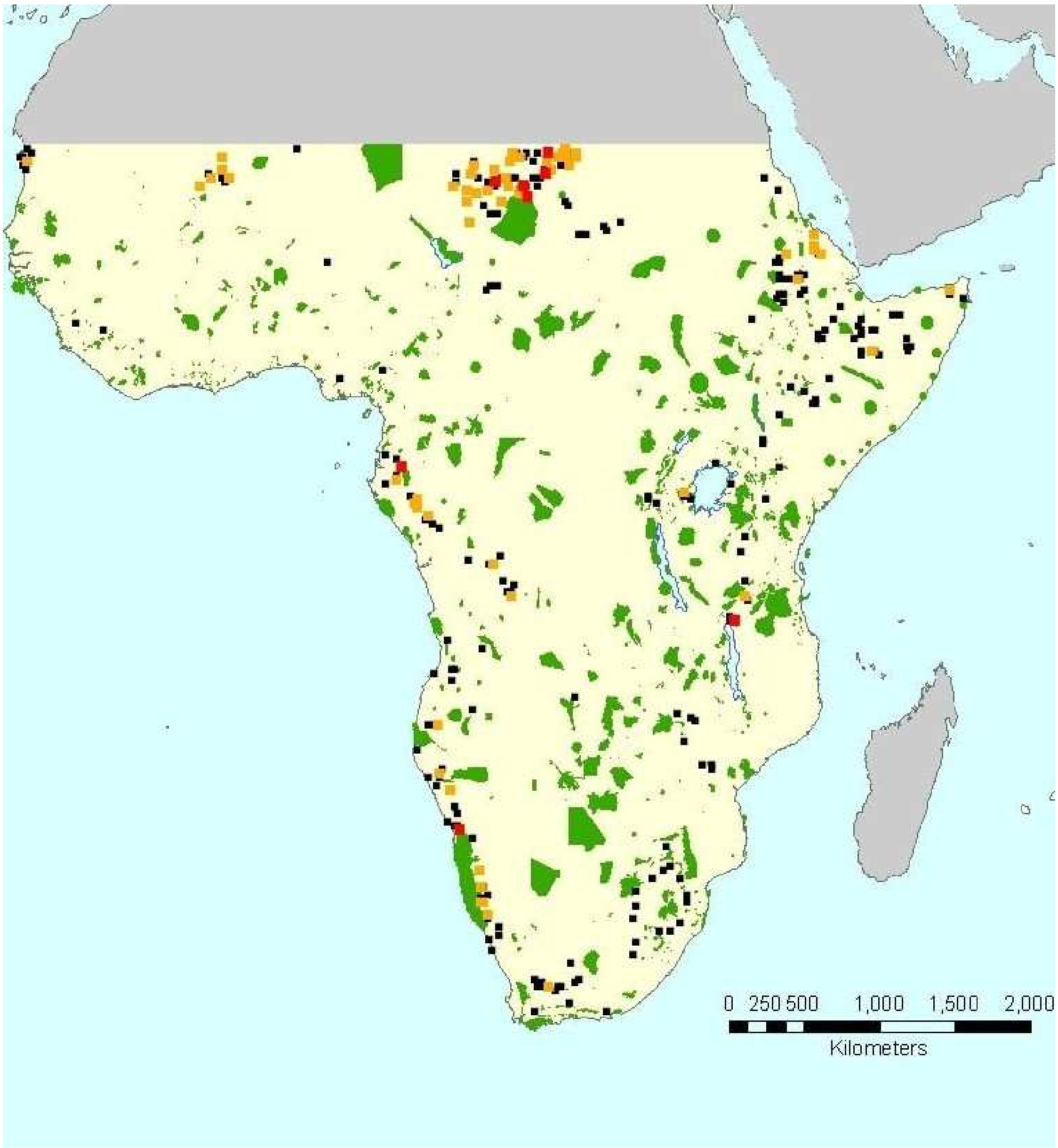

Figure 3.5 *(D) Optimal networks of all IBAs and additional quarter-degree cells created by Marxan to protect sub-Saharan African bird species using opportunity cost as a selection factor for projected species distributions in 2085.Cells selected in one or more climate scenario are represented by different colours; one – black, two – orange, three – red. The cells are not shown to scale. IBAs are shaded green.*

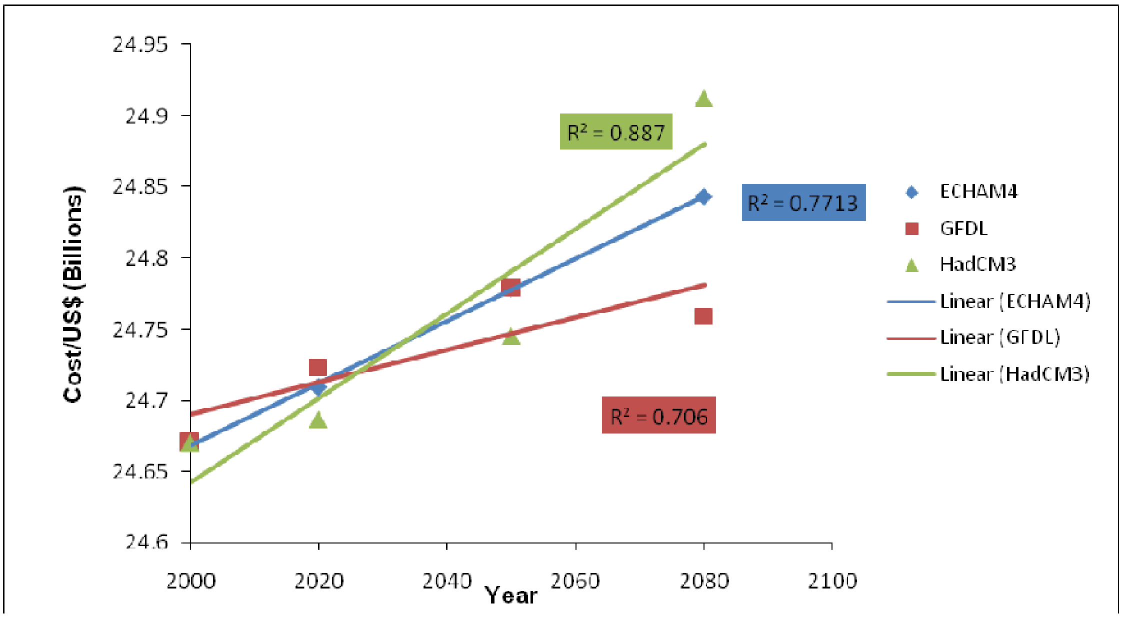

Figure 3.6 *Opportunity costs for IBA network and additional quarter-degree selected by Marxan to reach species targets for the three different climate scenarios and four time periods. Separate linear regression lines indicate the trend of cost over the Century.*

(2) Protected IBAs Fixed into the network

The distributions of additional cells for the present (Fig. 3.7a) are very similar to those for Figure 3.5a, although there is a larger number of cells selected in Eritrea and Somalia as well as in the Cameroon Highlands. A greater number of additional cells were selected than for the IBA and quarter-degree network with all IBAs fixed in (Table 3.2). The same patterns of selection are seen for all time periods in both Fig.s 3.5 and 3.7 although there are more additional cells selected in all time periods for Fig. 3.7.

In terms of cost, the total cost of the networks for each of the climate scenarios increase over time (Fig. 3.8). The total costs of the reserve networks are less expensive than those for the networks with all IBAs fixed in because of the unprotected IBAs that are not included within the network.

A

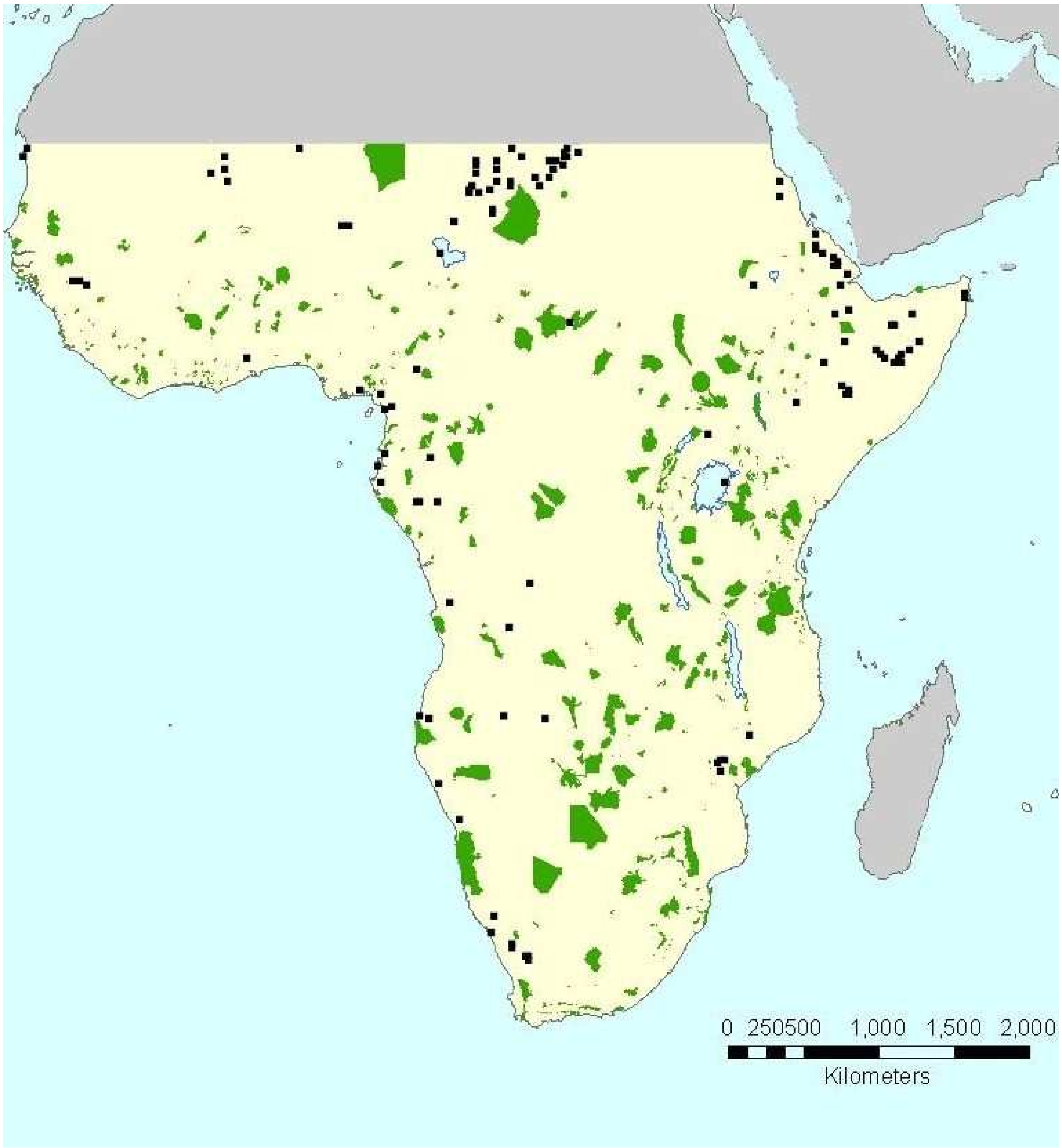

Figure 3.7 *(A) Optimal network of currently protected IBAs and additionally selected quarter-degree cells created using Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for current species distributions. The quarter-degree cells are shaded black and are not shown to scale. Currently protected IBAs are coloured green.*

B

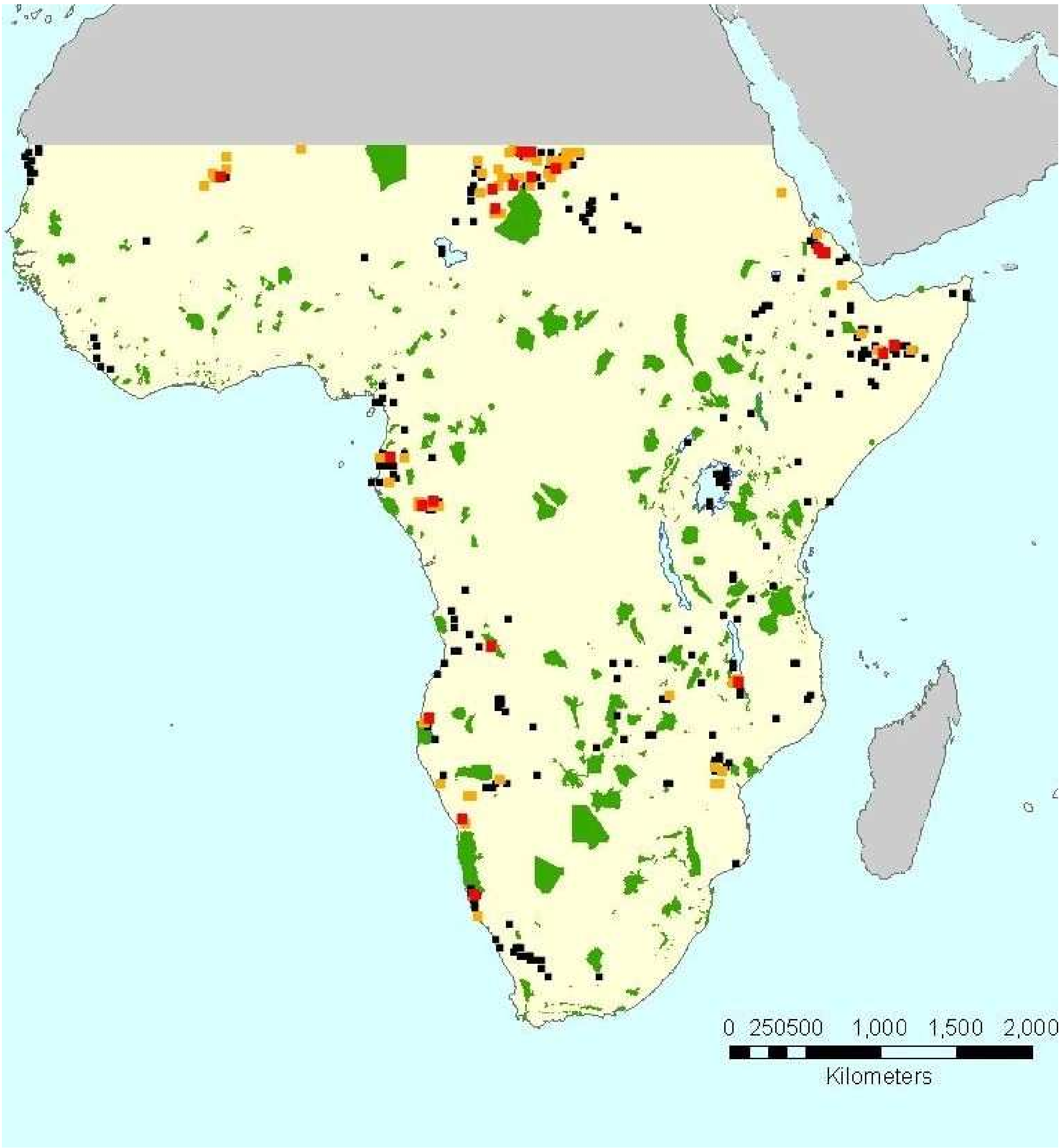

Figure 3.7 *(B) Optimal network of currently protected IBAs and additionally selected quarter-degree cells created using Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for projected species distributions in 2025. Additional quarter-degree cells are coloured black, orange and red depending on how many climate scenarios they were selected in; 1, 2 and 3 respectively. The quarter-degree cells are not shown to scale. Currently protected IBAs are coloured green.*

C

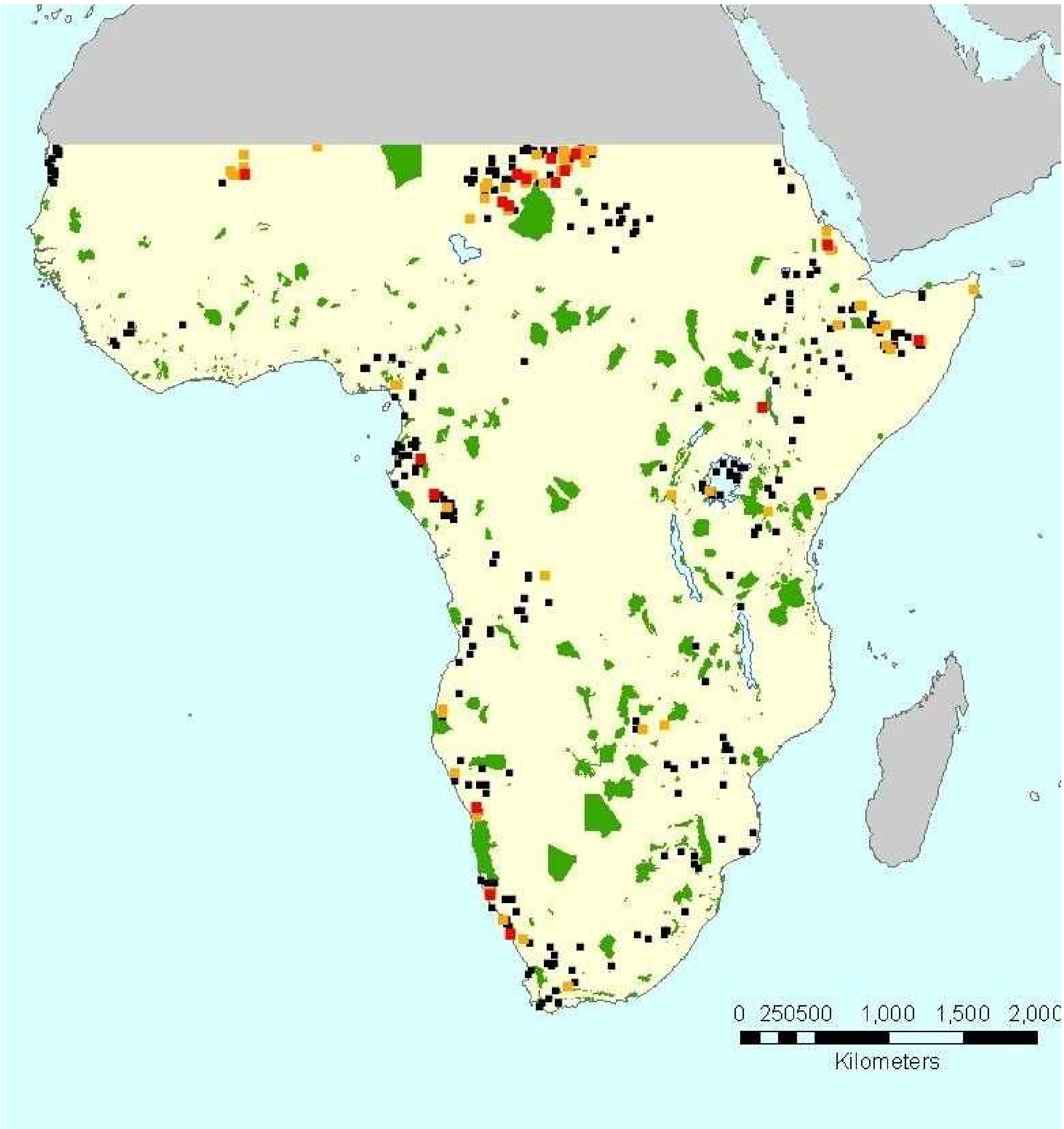

Figure 3.7 *(C) Optimal network of currently protected IBAs and additionally selected quarter-degree cells created using Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for projected species distributions in 2055. Additional quarter-degree cells are coloured black, orange and red depending on how many climate scenarios they were selected in; 1, 2 and 3 respectively. The quarter-degree cells are not shown to scale. Currently protected IBAs are coloured green.*

D

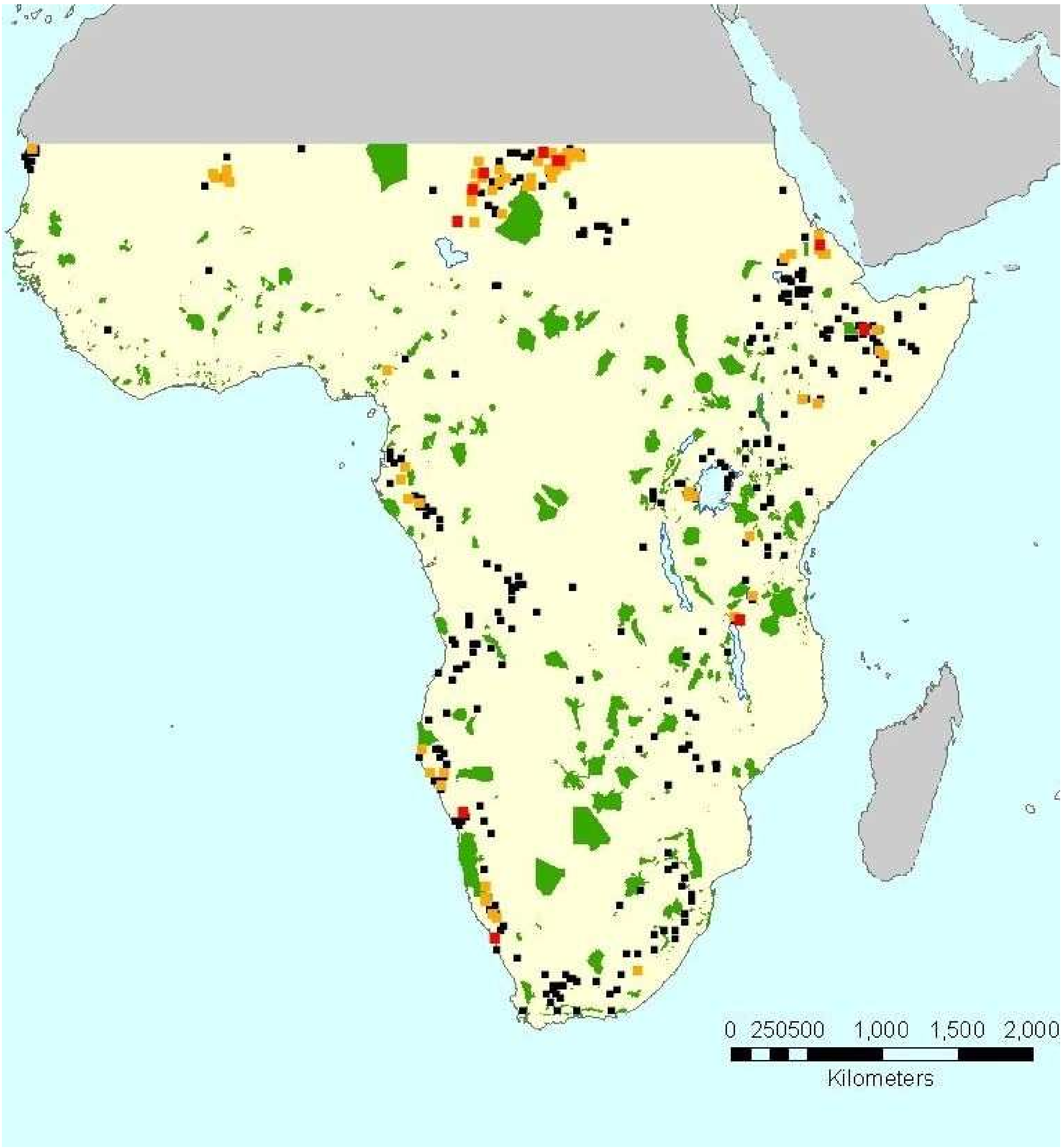

Figure 3.7 *(D) Optimal network of currently protected IBAs and additionally selected quarter-degree cells created using Marxan to protect sub-Saharan African bird species with opportunity costs included as a selection factor for projected species distributions in 2085. Additional quarter-degree cells are coloured black, orange and red depending on how many climate scenarios they were selected in; 1, 2 and 3 respectively. The quarter-degree cells are not shown to scale. Currently protected IBAs are coloured green.*

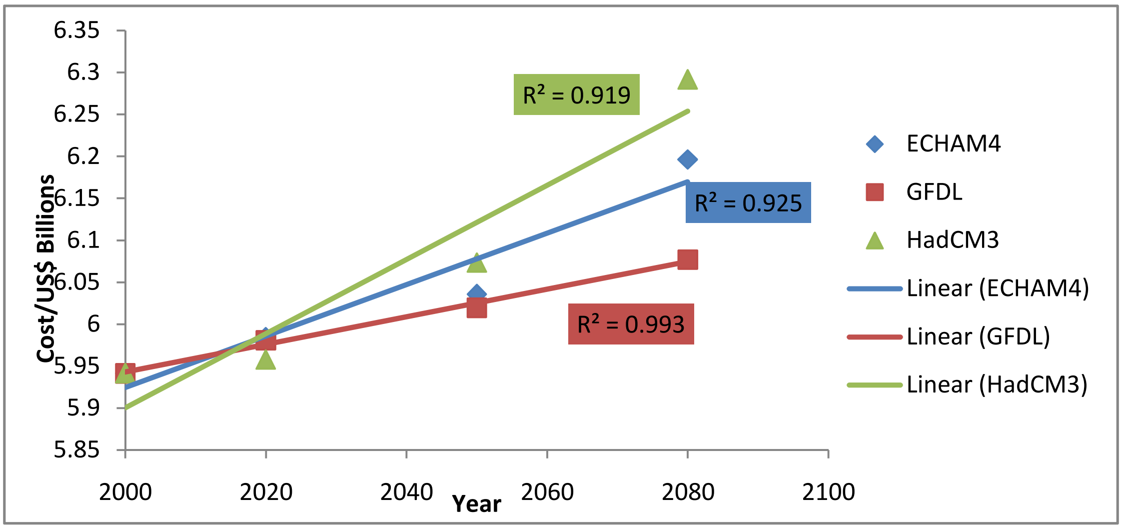

Figure 3.8 *Opportunity costs for currently protected IBAs and additional quarter-degree cells networks selected by Marxan. Separate linear regression lines indicate the trend of cost over the Century. Created for three different climate scenarios and four time periods.*

Table 3.1 *Data from the reserve selection simulations for IBAs and quarter-degree (Qdeg) cells for each time period and climate scenario. Includes data of the cost of equivalent networks selected without the use of opportunity costs.*

	Time period	no. IBAs	Cost/ million US$	Cost of networks without cost as a selection factor / million US$	Shortfall-unrepresented	Shortfall-underrepresented
IBA network	Present	253	1685	6325	0	21
	E25	227	5013	6690	1	27
	H25	244	1177	6951	1	24
	G25	232	7865	12672	3	23
	E55	236	1464	9025	5	33
	H55	240	5667	8513	2	37
	G55	230	4500	6382	2	38
	E85	230	1706	2322	8	35
	H85	223	1489	7492	8	35
	G85	223	5423	6111	7	34
	Time period	no. Qdeg cell	Cost/ million US$	Cost of networks without cost as a selection factor / million US$	Shortfall-unrepresented	Shortfall-underrepresented
quarter-degree network	Present	344	283	1200	0	0
	E25	324	403	1290	0	1
	H25	326	350	1233	0	0
	G25	338	313	1369	0	0
	E55	332	570	1419	0	0
	H55	346	515	1450	0	0
	G55	339	456	1414	0	0
	E85	321	630	1391	0	14
	H85	317	659	1414	0	9
	G85	333	489	1079	1	6

	time period	IBAs	Qdeg cells	cost/ million US$	*Spp.* shortfall-unrepresented	*Spp.* shortfall-underrepresented
All IBAs fixed	Present	803	76	24,670	0	0
	E25	803	95	24,709	0	1
	H25	803	98	24,687	0	0
	G25	803	92	24,723	0	0
	E55	803	117	24,779	1	0
	H55	803	103	24,745	0	2
	G55	803	115	24,779	0	2
	E85	803	119	24,844	2	2
	H85	803	116	24,912	2	4
	G85	803	109	24,759	2	2
Protected IBAs fixed	Present	494	117	5,940,	0	0
	E25	494	134	5,984	0	0
	H25	494	135	5,958	0	0
	G25	494	160	5,980	0	0
	E55	494	133	6,035	0	1
	H55	494	166	6,072	0	1
	G55	494	142	6,019	0	0
	E85	494	150	6,196	2	2
	H85	494	141	6,291	1	5
	G85	494	151	6,077	2	2

Table 3.2 *Data from the reserve selection simulations of the combined IBA and quarter-degree (Qdeg) networks including* number of additional cells selected, cost of the networks and the species shortfall of the networks.

Discussion

This study is one of the first to show that the opportunity costs of conservation could increase over time as a result of species range shifts caused by climate change. This outcome could be a result of climatic changes shifting species' distributions into areas of high primary productivity. These areas coincide with areas of high agricultural productivity and therefore have high opportunity costs as a result of increased crop yields (Naidoo & Iwamura 2007). This relationship was only observed when quarter-degree cells were used as planning units. The IBA networks, instead, showed erratic patterns of opportunity cost which could arise because the non-uniform sizes, and therefore costs, of IBAs could have a disproportionate effect on the overall cost of the network when added or removed. The networks where quarter-degree cells were used as planning units provide a better indication of how conservation in the future will incur greater opportunity costs, as cell size is constant for all sites.

The quarter-degree networks were substantially cheaper than the IBA networks. This is because the area of land that was protected in the quarter-degree cell networks was much smaller than that of the IBA networks due to the size of the quarter-degree cells. However, although these networks appear to provide more adequate protection for species than do the IBA networks, and for a cheaper price, realistically, being rather small, they may not support sufficient habitat types for all species for which a cell is simulated to be suitable. Furthermore, they might not be able to support viable populations, for some species, to ensure population survival in the long-term. IBAs, by contrast, have been designed with the persistence of populations in mind and therefore are likely to provide adequate protection for the species they are designed to protect (Fishpool & Evans 2001).

The results indicate that the ability of the IBA network to provide protection for bird species in sub-Saharan Africa in the future could be greatly improved by the addition of a small number of quarter-degree cells to the existing network. When only the officially protected IBAs were fixed into the network, there was only a small increase in the number of additional cells required to incorporate the majority of species within the network in the future, when compared to the network that fixed all IBAs. This brings into question the importance to conservation of the remaining 309 unprotected IBAs in sub-Saharan Africa, especially given the variable persistence of species in the future. However such results should be treated with some caution as the systematic conservation techniques used here are insensitive to the ecological processes that must be considered to conserve species (Moilanen 2008). It is also important to consider that the conservation targets used here are not shared by the IBA program and therefore inefficiencies identified within the network by the results of this study could be inconsequential to the effectiveness of the network.

The increase in the cost of networks over the Century is caused by changes in species distribution due to climate change. Fuller *et al*. (2007) showed that in 2000, 90% more land would need to be protected to provide adequate protection for mammal species in Mexico than would have been in 1970 due to the fragmentation and degradation of habitat. With a projected increase in the rate of global habitat degradation, including sub-Saharan Africa (Tilman *et al*. 2001), combined with the predicted increases in opportunity costs of land necessary for conserving African avifauna, the cost of waiting to adapt PA networks, such as the IBA network, to climate change could be substantial. Hannah *et al*. (2007) came to similar conclusions when performing reserve selection simulations for future climate scenarios for plants in West Europe and the Cape Floristic Region in South Africa and for mammals and birds in Mexico. Their results indicated that acting now to adapt PA networks to climate change will save money in the future because increasing the area of protected land to cope with current and future threats simultaneously is more efficient than doing so sequentially. The results of this study, combined with the inefficiency of adapting to conservation when changes from climate change become apparent (Fuller *et al*. 2007; Hannah *et al*. 2007) suggests that action should be taken to adapt networks to climate change now in order to avoid unnecessary costs in the future. Drechsler and Wätzold (2007) suggest that the optimum use of conservation funds is to spend evenly over time, with some precautionary savings initially to take uncertainty into account. However, they did not factor climate change into their calculations which, although affected by uncertainty, can be modelled with some accuracy and therefore represents another aspect in optimising the allocation of funds. More research is needed to assess the risks of both the 'cost of waiting' and investment in an uncertain future.

The use of opportunity cost as a selection factor in reserve selection created PA networks that were cheaper than if cost had not been used. The inclusion of cost in reserve selection could therefore be an important way of minimising the costs of adapting PA networks to climate change.

When producing networks comprised of only quarter-degree cells, it was apparent that many cells coincided with the Endemic Bird Areas (EBAs) for the present as well as the future time periods, highlighting the continuing importance of EBAs to conservation in the future. Many EBAs are currently under threat from anthropogenic processes, such as agriculture, these processes being positively correlated with the level of threat to range-restricted bird species found within an EBA (Scharlemann *et al*. 2005). Balmford *et al*. (2001) identified several EBAs in sub-Saharan Africa which are under threat and in need of additional conservation initiatives. These areas (Cameroon Highlands, Ethiopian Highlands, Albertine Rift, Eastern Arc Mountains and Drakensberg Mountains) were identified in this study as crucial for the current and projected conservation of avian biodiveristy. Immediate investment in well established conservation measures, such as improving connectivity within the landscape, should ensure species persistence in these areas over the Century (Noss 2001).

The differences in the costs of optimum networks among the GCM scenarios suggest that a wetter climate scenario (such as GFDL-R30) would incur lower opportunity costs than a drier scenario (ECHAM4), especially in the latter half of the 21st Century. This highlights the importance of obtaining accurate climate predictions to conservation, because differences in the nature of climate change will alter the adaptation strategy itself and also its cost. Identifying areas which are likely to maintain stable climates over the 21st Century despite future climate change projections are likely to be especially important as refugia for species that become isolated by changing climatic conditions (Killeen & Solorzano 2008; Klein *et al*. 2009; Noss 2001). These refugia may be associated with areas of endemism from historical climatic events and may therefore be of current importance to conservation as well (Medail & Diadema 2009; Ohlemuller *et al*. 2008).

This study does not aim to create accurate predictions of the costs of future reserve networks, but seeks to highlight the effects that opportunity costs can have on the location of PAs in the future. Providing accurate predictions is limited by several factors which affect the accuracy of the opportunity cost data. Firstly, the opportunity costs have been derived from agricultural productivity and therefore ignore other factors which influence the price of land. In particular, Naidoo and Iwamura (2007) draw attention to the insensitivity of the data to the logging industry in the Congo basin which will have an impact on both the cost of land and the extent of habitat degradation in the region. A second avenue of inaccuracy in the opportunity cost data is that the effects of climate change on the productivity of agriculture is not taken into account. The changes in climate which are predicted to cause changes in the distribution of bird species may also alter patterns of agricultural activity, changes in cropping types and perhaps switches from agriculture to pastoral farming or vice versa across sub-Saharan Africa. Finally, increases in human population over the coming century will create an increased demand for food throughout the continent which will in turn increase the need for agricultural land (Zhang *et al.* 2006), therefore increasing opportunity costs to conservation across the continent. This in turn will alter the opportunity costs of conservation. Future work studying the impacts of climate change on the opportunity costs of conservation will help to create more accurate predictions of the cost of adapting PA networks.

Conclusions

The results from this study provide further evidence of the negative impacts that climate change is predicted to have on species, but also shows that climate change could also have negative impacts on the economic costs of conservation. Areas which were identified as of particular importance to conservation over the coming Century were also areas which are of importance to conservation in the present. Several studies have identified that the ‘cost of waiting’ to conserve species against future threats is inefficient and can incur substantial additional costs to conservation in the long-term. Therefore, increasing the efficacy of PA networks in areas which are essential to conservation in both the present and the future is a high priority. However, for conservation organisations and governments to make commitments for the future, there must be a degree of certainty that such investments are wise and therefore the increasing accuracy of BEMs which predict future areas of conservation priority must be pursued. In the meantime, the inclusion of cost in reserve selection can help conservation to introduce increased economy into adaptation methods.

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Chapter 5: Synopsis

This study explored ways in which the sub-Saharan Africa Important Bird Areas (IBAs) network could potentially be adapted to cope with projected future climatic change, which is likely to be a major threat to its ongoing role in the protection of bird species. As this study covered a vast area, suggestions for adaptation in the network were only made at a large-scale, in terms of suggesting sites/regions to protect; small-scale management strategies were beyond the scope of this study. Several key points were identified (and are discussed below) which, alongside further research, can be used to provide advice on the adaptation of the IBA network to remain robust to projected future climate change.

Areas of increasing and decreasing importance in reserve selection

Simulations of optimal networks, based on a reserve selection algorithm approach, demonstrated that, across the 21st Century, the importance of some regions, defined by complementarity, are altered and hence priority regions for protection may shift. A general pattern, based on climate simulations for the current Century, was the decrease over time in the inclusion of sites in West Africa in an optimal network and an increase in selection of sites in Eastern and Southern Africa. Although this is a simplification of the results, it highlights both the large-scale changes that are projected in species' regional persistence over the Century and the need for new conservation strategies for those areas threatened by diverse risks from climate change.

Additional sites to complement the current IBA network

Identifying those species that will be under-represented in the current network in the future permits additional sites to be selected which will continue to protect such species. This approach not only identifies those areas where the network will fall short in the future, but also highlights regions which are predicted to increase in species diversity in the future, and which may provide the most efficient means of conserving species. There were several areas which were highlighted by multiple additional sites throughout the Century; the Horn of Africa, Namib-Karroo region, the Cameroon and Gabon lowlands (EBA 085) and Western Angola (EBA 087). In the latter half of the Century, there was increased selection in Northern Ethiopia (EBA 115), North-East Tanzania, the Eastern Arc Mountains and the Highveld (EBA 091) as well as an increase in the average number of additional cells required to reach conservation targets. The increase in the number of cells required to reach species representation targets indicates how climatic change is likely to decrease the IBA network's ability to reach conservation targets. The majority of areas identified for additional sites in the future are areas of high biodiversity and endemism currently, therefore increasing conservation measures in these areas represents investment into both present and future conservation strategies.

Key Stable Sites (KSSs)

PAs which act as a continual refuge for species are defined as 'Key Stable Sites' (KSSs). KSSs will be of great importance to conservation efforts in the coming Century by acting as climate refugia for species across the continent. Protection of these sites, with management focused on species predicted to have long-term protection within the PA, will be essential for the local persistence of species. Selected KSSs were widely dispersed across sub-Saharan Africa with a large proportion of which being selected in all three GCM scenarios. The selection of these sites in different climate scenarios indicates their climatic stability which can be linked to their altitudinal ranges. The protection and management of these sites is essential for species persistence over the coming Century, however, the KSS network designed had a significant shortfall of species which had no defined KSSs. The identification of KSSs for these species could provide invaluable additional sites to the IBA network.

Increasing opportunity costs

Shifting bird populations necessitating additions to the current PA network could cause increased opportunity costs to conservation. This has significant implications to the funding of climate change adaptation over the Century. Identifying methods to continue to protect biodiversity, whilst minimising opportunity costs, permits conservation organisations to most effectively use their available budgets. The opportunity cost data used in this study has several caveats which are highlighted in Chapter 4, including an insensitivity of the opportunity cost data to climate change impacts and the omission of logging as an additional source of opportunity costs. One potential way to include opportunity cost for areas that have the potential to be logged, such as the Congo Basin, is to use data from the Open Source Impacts of REDD Incentives Spreadsheet (Osiris v2.6 (http://www.conservation.org/osiris/ 2009)). This is a static one-year global partial equilibrium market for agricultural land cleared from tropical forest which provides data on the amount of money a country would have to be paid to stop deforestation (Conservation International 2009) and therefore represents an opportunity cost for deforestation. REDD (Reduce Emissions from Deforestation and forest Degradation) is a United Nations Framework Convention on Climate Change (UNFCCC) scheme to reduce carbon dioxide emissions from deforestation in developing countries through financial incentives (Miles and Kapos 2008). Combining the Osiris v2.6 data with that utilised in this study would allow more accurate estimation of the impacts of opportunity costs on conservation, particularly in forested regions in areas of Central and West Africa.

In a recent paper, Mawdsley *et al*. (2009) reviewed climate change adaptation strategies for wildlife management. Several of the strategies reviewed are consistent with the results from this study as well as other strategies which would undoubtedly improve the efficacy of the IBA network. They recommend: 1) increasing the extent of existing PAs, which is synonymous with the additional quarter-degree cells identified in this study; 2) protecting refugia, which I have undertaken by identifying KSSs; and 3) focusing management on species likely to go extinct, which I identify as under-represented species in the KSS network analyses. Two further points identified by Mawdsley *et al*. (2009) are not explicitly addressed in this study, but could be incorporated into follow-up studies that build on these preliminary findings. The first, is the development of dynamic landscape conservation plans to cope with the spatial and temporal heterogeneity of climate change impacts. In this study I highlight such spatial and temporal heterogeneity of climate change impacts across sub-Saharan Africa and suggest such dynamic plans at a course scale. However, here I make no recommendations with regards to planning at the level of the individual site, though Hole *et al.* (in Press) do categorise the IBAs of Africa into groups likely to require different management strategies in the future. The second adaptation strategy suggested is to improve the matrix to increase landscape permeability to species movement, which is essential to facilitate species migration into the areas predicted to increase in species diversity. By combining simulated shifts in ranges, along with the identification of key PAs required for a future-proof network, follow on work could identify key regions through which habitat specific species will need to move but where suitable habitat does not currently exist. The Pathway Analysis Through Habitat (PATH) tool (Hargrove *et al.* (2005); discussed in chapter 1) could be used to map individual species' movements through a landscape as it tracks climatic change. Other habitat connectivity software is available which could be used to create habitat corridors which facilitate the migration of species due to climate change. However, it is unclear whether it is possible to correctly orientate habitat corridors to cope with climate change (Willis *et al.* In Press) or whether corridors can be effective for more than one species.

This study has often highlighted the fact that many of the areas which are predicted to be of importance to conservation in the future are areas which are already key for conservation in the present. Furthermore, strategies suggested to adapt PA networks to future climatic change are currently regarded as good practice for conservation (Noss 2001) making it rational to implement such measures now. In addition to the importance of starting immediately to adapt conservation strategies to cope with climate change, from a perspective of facilitating early range alterations, there is also a 'cost of waiting' to invest in conservation (Hannah *et al.* 2007). An important goal of conservation science should be to produce reliable projections of species' range shifts and to suggest the most effective means of facilitating such shifts, so that thinly stretched resources can be used with the greatest efficiency.

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Supplementary Material

Results from this thesis which were too large to put into the text are supplied electronically as supplementary material.

Data can be found in the supplementary material as excel 2007 files. They are presented in the following order:

Supplementary Material (Folder)
- **S1** (Folder)
  - - Selected Quarter-degree Cells. Selected by Marxan for present and projected future species distributions
  - - Unrepresented species in the quarter-degree networks
- **S2** (Folder)
  - **S2.1**
    - - IBA shortfall species_Chapter 3
    - - Selected IBAs_Chapter 3. IBAs selected by Marxan for present and projected future species distributions
  - **S2.2**
    - - Selected additional quarter-degree cells. Cells selected by Marxan to complement the IBA network and reach species representation targets
    - - Unrepresented Species IBA and Qdeg network
    - **S2.2.1** (Folder)
      - - Lists of key species for additional cell selection. Species which caused selection of additional cells
  - **S2.3**
    - - Selected KSSs. KSSs selected by Marxan
- **S3** (Folder)
  - **S3.1**
    - - Selected IBAs with cost. IBAs selected by Marxan with opportunity costs as a selection factor
  - **S3.2**
    - - Under-represented species in quarter-degree network with cost
  - **S3.3**
    - **S3.3.1** (Folder)
      - - Lists of species key for additional cell selection (All IBAs). Species which caused the selection by Marxan of cells which complement the IBA network and help reach species representation targets.
    - **S3.3.2** (Folder)
      - - Lists of species key for additional cell selection (protected IBAs). Species which caused the selection by Marxan of cells which complement only the protected IBAs network and help reach species representation targets.

Species IDs used in Supplementary Material (File) – Use as species key