
The importance of space and time in conservation biology

Understanding how animals respond to environmental change



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Abstract

In an ever-changing world with an increasing human population, improving the efficiency of conservation management strategies is vital to mitigate against continued losses to global biodiversity. Empirical studies highlighting how species respond to environmental change can provide evidence to enable the development of such strategies. There are two strands of research explored in the current work that aim to address these issues. The first is an analysis of changes in species distributions over time with respect to environmental changes. The second is a critical comparison of behaviour, resource use and population performance across ecological gradients within a species' range. In chapter two, local population changes (10 km² spatial resolution) in 64 species of British passerine were examined from 1970 and 1990. These were analysed using a spatially explicit linear mixed effects model selection framework, which predicted these changes in occupancy with respect to biological traits and environmental changes, namely changes in human land use and climate. In chapter three, a more targeted approach was used to investigate the variation in social network structure across ten independent sub-populations of Cape mountain zebra, *Equus zebra zebra*, with respect to variation in habitat availability, demography and population performance. In British passerines, rare species with fragmented ranges were found to be the most likely to undergo local extinctions. Furthermore, human land use was highlighted as a more reliable predictor of local occupancy than climate change at this spatial and temporal resolution. Our findings emphasize the need to increase and maintain diverse, interconnected networks of appropriate habitat. For Cape mountain zebra, individual connectivity, group size, the proportion of bachelors, and the ties of each adult male were all influenced by the availability of palatable grass and water. In optimal habitat, there were more connected individuals, larger groups and a smaller proportion of bachelors. Along with other recent studies of the habitat preferences of Cape mountain zebra, our research suggests that mesic habitats with a high availability of palatable grass are vital to maintain productive populations with a higher proportion of heterogeneous family groups. Understanding how species respond to environmental changes can only increase in importance as human populations rise.

For Dennis Hulls

'We should preserve every scrap of biodiversity as a priceless treasure

While we learn to use it and come to understand what it means to humanity'

E.O.Wilson

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Declaration

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Chapter 1

Thesis Introduction

Preventing biodiversity loss in an ever-changing world

1.1 The state of global biodiversity

Global biodiversity is under direct and serious threat from anthropogenic activity. Evidence now suggests that we have entered a sixth, anthropogenically induced mass extinction (Barnosky et al. 2011; Ceballos et al. 2015). The World Wildlife Fund (WWF) estimates that there may have been total global population declines of as much as 52% in vertebrates since the 1970s (WWF, 2014). Although the estimate for vertebrates may not be wholly representative of other taxa, indices monitoring global biodiversity all suggest severe declines (Jones et al. 2011). Furthermore, projections derived from both population and distribution responses suggest that ongoing climate change may result in ~25% of terrestrial species being committed to extinction by 2050 (Thomas et al. 2004). This biodiversity crisis has resulted in the establishment of global targets to prevent further losses (Tittensor et al. 2014). However, a review of these targets has revealed that not enough is being done to meet biodiversity targets amid continued human population increase (Tittensor et al. 2014).

1.2 Anthropogenic impacts on biodiversity

The 'evil quartet of the biological apocalypse' proposed by Jared Diamond highlights overexploitation, habitat destruction, invasive species and chains of extinction as the key threats facing biodiversity (Diamond, 1989). E.O. Wilson includes pollution and human population increase in these threats (Wilson, 1989). More recently, the threat of anthropogenically induced climate change has been identified as a key driver of biodiversity decline (Thomas et al. 2004). Most, if not all of these threats can be attributed directly or indirectly to anthropogenic activity, and evidence now suggests that these extinction drivers act in synergy (Brook et al. 2008). Although it is clear that anthropogenic activity is affecting biodiversity, how these threats relate more specifically to population changes, particularly at a local scale, remains unclear for many species.

Arguably the greatest threat to terrestrial vertebrates is the loss of habitat (Brook et al. 2008; Purvis et al. 2000b; Jetz et al. 2007), although climate change is also predicted to greatly impact upon species in the near future (Alagador et al. 2014; Thomas et al. 2004). Studies have attributed climate change (Bradshaw et al. 2014) and habitat loss (Owens and Bennett, 2000) in isolation as the dominant drivers of population change, but a relative comparison of the importance of the two has not been elucidated. Unfortunately, in a changing world where human development takes priority, damage limitation strategies that target the most important environmental drivers are crucially important (Redford et al. 2011).

Aside from environmental changes, not all species are equally likely to go extinct. Within vertebrates, the probability of population decline has been associated with a variety of biological traits. Large body size, slow life history, long distance migration, habitat specialisation and high trophic status have been identified as traits in mammals and birds that render them more vulnerable to environmental stochasticity and population decline (Purvis et al. 2000a; Cardillo et al. 2005; Salido et al. 2012; Shultz et al. 2005). Small, fragmented populations have also been associated with increased local extinction and range changes (Bradshaw et al. 2014). Despite these insights, there is a large variation in population changes amongst vertebrates (Cowlshaw et al. 2009). Ultimately, no one driver of population decline acts individually, and so understanding the combined effect of species traits and environmental change is important to prevent further declines.

1.3 The flaws of conservation strategies

To counteract biodiversity loss, conservation ultimately aims to target the causes of extinction, however, a more targeted approach towards species or ecosystems that are vulnerable is often needed to prevent extinction. Conservation biology seeks to understand the causes for species decline

and the consequences this has on vulnerable species, with the intention of informing management strategies (Caughley, 1994). Previous emphasis on anecdotal and experience-based information has resulted in inefficient conservation management (Kerley et al. 2012). This is epitomised by the introduction of the concept of refugee species; species that are confined to sub-optimal habitat as a result of persecution/degradation in/of optimal areas (Kerley et al. 2012). This concept was initially applied to the European bison, but several studies have now highlighted confinement to sub-optimal areas (González, 2015; Imong et al. 2014; Augé et al. 2011). Many species have suffered population declines as a result of anthropogenic activity, and it was previously assumed that range contraction would be towards core, optimal habitat (Channel and Limolino, 2000). Management strategies therefore targeted species where remnant populations occurred, but evidence suggests that in fact a greater number of species contracted to the periphery of their ranges (Channel and Limolino, 2000). Kerley et al. (2012) also propose that there may be many more refugee species than currently recognised. Aside from species that are wholly confined to sub-optimal habitat, a lack of understanding of the habitat preference of target species may lead to inefficient management.

1.4 Thesis aims - The importance of space and time in conservation

Empirical evidence documenting the variation in population performance, behaviour and resource use in different habitats within a species range over time can greatly improve the efficiency of management strategies (Caughley, 1994). Conservation strategies are increasingly using evidence about the variation of performance across species distributions (Aldridge and Boyce, 2007; Furrer and Pasinelli, 2015). Furthermore, modelling population responses to future and past changes in climate may highlight current priority areas that may become redundant and vice versa (Bradshaw et al. 2014; Alagador et al. 2014). Biodiversity continues to decline, and we must now increase strategies that fully consider species responses to environmental changes (Rands et al. 2010; Caughley, 1994; Kerley et al. 2012; Legge, 2015). Understanding what/where environmental changes are having the biggest impact

and optimising how/where to conserve vulnerable species will only become more important as human populations increase. There are two areas of research that I believe will aid in the development of such strategies. The first is through the documentation of changes in species' distribution, which can be analysed with respect to changing environmental variables to highlight vulnerable species and disruptive environmental changes. The second is to analyse population performance, behaviour and resource use within a species range, to highlight optimal source areas which may be targeted in future management strategies.

The aim of this thesis is to highlight the importance of understanding how species respond to environmental change, using two case studies; British species of passerine and the Cape mountain zebra. In chapter two, a spatially explicit modelling approach is used to predict local occupancy changes in 64 species of British passerine from 1970 to 1990. Linking occupancy changes to environmental change data at the same spatio-temporal resolution and biological traits, this research aims to understand the biological traits and environmental changes that are associated with the largest changes in local occupancy. Doing so also assesses the relative importance of climate change versus land use in predicting population change. Such data can be used to inform landscape scale management strategies of passerines. In chapter three, a more targeted approach is used to test how variation in the availability of suitable habitat across the meta-population of the Cape mountain zebra influences social network structure. Comparing social networks from populations of zebra in different habitats, I am able to highlight how population structure breaks down in marginal habitat and verify the habitat preferences of this species.

1.5 Alternative format

The thesis is being presented in the alternative format in accordance with the rules and regulations of the University of Manchester. The two results chapters presented herein are in manuscript form in the style suitable for their intended journal of submission. However, elements have been reformatted to ensure these form a cohesive body of work. Below are the details of each manuscript, its intended journal and contribution of each author to the work presented.

Chapter 2: Range connectivity, rarity and human land-use predict local colonisation and extirpation in British passerines better than climate change

Authors: John Jackson, Bethan Purse, Lara Salido, Chris Knight, Rob Marrs, Adam Butler, David Noble and Susanne Shultz.

Intended Journal: Proceedings of the Royal Society of London B: Biological Sciences.

Author Contributions: JJ carried out analyses, drafted and revised the manuscript. SS, BVP, LS designed the study and contributed to analyses. RM, CK, AB contributed to the analyses and provided critical feedback on manuscript drafts. DN contributed data and contributed to manuscript revisions.

Chapter 3: The breakdown of social structure in marginal habitat: A case study of the Cape mountain zebra, *Equus zebra zebra*

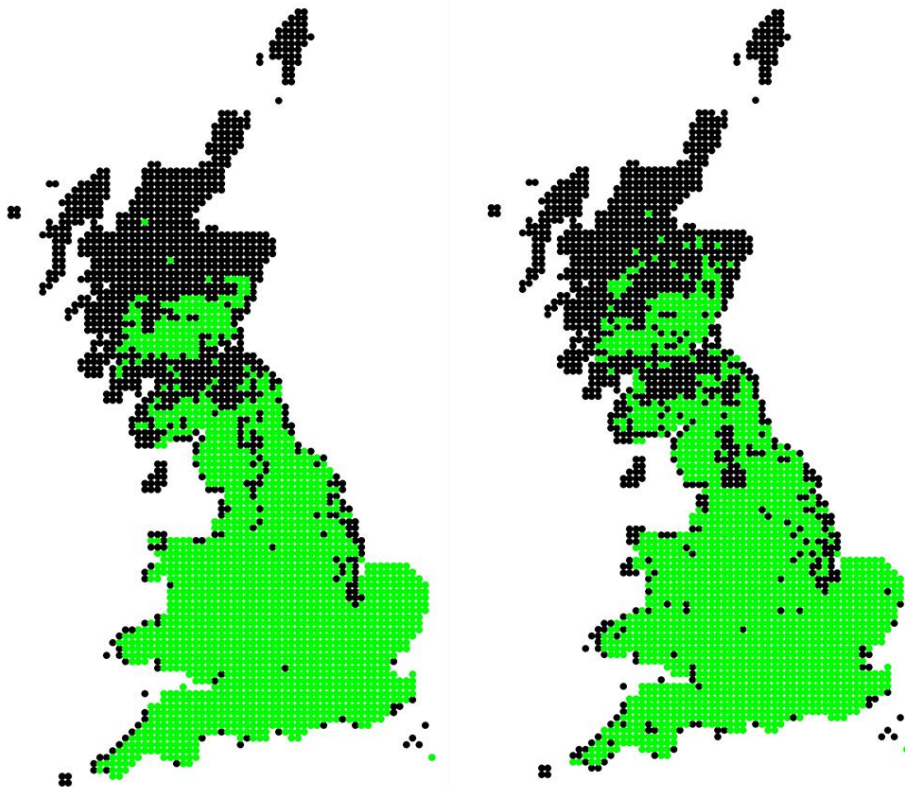
Authors: John Jackson, Nienke Alberts, Jess Lea, Shelby Matevich and Susanne Shultz

Intended Journal: Ecology Letters

Author Contributions: Data were collected and processed by: JL, NA, SM, SS and JJ. JJ and NA analysed results. JJ wrote the manuscript. SS designed the study.

Chapter 2

Range connectivity, rarity and human land-use predict local colonisation and extirpation in British passerines better than climate change



2.1 Abstract

Human activities have widespread consequences for the natural environment, including population and range changes, phenology shifts and disease emergence. To understand broad scale range and population changes, it is important to evaluate how species traits, environmental change and their interactions impact on local and regional extinction and colonisation processes. Here we consider these processes in 64 British passerines over two decades (1970-1990). In accordance with previous studies, species traits including large inter-connected ranges, habitat and dietary generalism were associated with increased colonisation and decreased extinction at the regional scale. However, at a local scale, species traits and environment together predict extirpation and colonisation processes. In particular, local occupancy changes were more likely in species with small, fragmented ranges. Of environmental factors, land use was consistently more important than climate in predicting occupancy changes. Extirpation was more likely in areas where species were locally isolated and the landscape dominated by arable, open or urban cover. Local colonisation was more likely, and extirpation less likely, in areas that had undergone land use change. Together, this suggests that unchanging monotypic landscapes, such as dense urban or intense arable areas struggle to maintain species diversity. These models underscore the importance of local landscape characteristics in species responses to environmental change and highlight the relative importance of local land use over climate change for local, short-term, occupancy changes. Furthermore, while climate change is undoubtedly important in driving species abundance patterns over long-time scales and at global levels, local and regional land-use is crucial for proactively managing biodiversity.

2.2 Introduction

Human activities are directly responsible for the current sixth extinction wave (Barnosky et al. 2011; Ceballos et al. 2015). As both climate and land-use changes potentially impact on species population persistence (Wilcove et al. 1998), understanding how and where species respond to these threats is a major conservation challenge. It is irrefutable that climate change impacts biodiversity on a global scale. Responses to climate change include changes in phenology (Crick and Sparks, 1999; Crick, 2004; Visser, 2008; Moussus et al. 2011), and shifts in species distributions (Barbet-Massin et al. 2012), community structure and trophic interactions (Walther et al. 2002; Tylianakis et al. 2008; Davey et al. 2013). Although there is no doubt that anthropogenic climate change has serious consequences for biodiversity, habitat modification is the single biggest risk factor for terrestrial species (Jetz et al. 2007; Hoffmann et al. 2010). Moreover, synergies are apparent between such extinction drivers that compound the pressures experienced by species, this necessitates conservation policies that deal with multiple threats simultaneously (Brook et al., 2008).

Not all animal taxa are equally prone to extinction; high-trophic level, small-range, large body-size and low population density are all associated with high extinction risk in mammals at the global level (Cardillo et al. 2005). Similarly, large-bodied species, habitat specialists and long distant migrants have undergone the largest population declines in European birds (Gregory et al. 2005; Salido et al. 2012; Julliard et al. 2004). Slow and idiosyncratic life history, resource specialisation and migration also render bird species more vulnerable to increasing environmental stochasticity, habitat fragmentation and geographical shifts in suitable habitats (Vanschaik and Dunbar, 1990; Shultz et al. 2005; Both and Visser, 2001). Small population size, especially across fragmented habitats, is associated with high probability of local extinction events whereas widespread species are less vulnerable (Wilson et al. 2004; Bradshaw et al., 2014). In contrast, flexibility in resource use and phenology (Salido et al. 2012) and large relative brain size (Shultz et al. 2005) have been associated with resilience to population decline in birds. The consistent variability seen between species in demographic responses is matched,

if not exceeded, by variability between sites subject to different degrees of environmental change (Cowlshaw et al. 2009). Thus, the interaction between intrinsic traits and extrinsic environmental factors are likely to be important in determining the fate of a species (Blackburn and Duncan, 2001).

Species Distribution Models (SDMs), commonly used for predicting species responses to environmental change (Barbet-Massin et al. 2012; Jetz et al. 2007), can identify the environmental conditions associated with species presence and use these criteria to forecast geographic changes in suitable conditions and hence distribution changes. These climate envelope models are largely inference-based as they do not measure actual distributional changes. An alternative approach to understanding how environmental factors influence distribution change is to model actual changes in species occupancy. Occupancy changes may be difficult to predict based solely on species traits (Fréville et al. 2007), or on habitat characteristics (Comont et al. 2014), such that it is essential to concurrently evaluate both traits and environmental conditions to predict distributional shifts. Changes in area of occupancy for British birds were recently related to changes in climate, life history and range traits, and suggested that warmer winters differentially impact on cold-adapted, northerly species (Bradshaw et al. 2014). Higher resolution passerine distribution data can be used to model local extinction and colonisation rates in relation to environmental change and can provide a more detailed understanding of the causes of distribution shifts.

Here we evaluate colonisation and extinction processes in British passerines by employing a spatial mixed model framework that identifies the relative impact of both species traits and environmental drivers, and the interactions between the two, on the probability of both local and regional colonisation and extinction events. Passerines are an ideal model taxon for evaluating these impacts for several reasons. First, as a highly mobile group with good dispersal ability, they are expected to show responses in local distribution patterns over short-time scales (Barbet-Massin et al. 2012). Second, as a well-recorded group there are detailed presence/absence data across Great Britain, facilitating the use of occurrence data in distribution models. Impacts of land use as well as climate

are considered alongside range connectivity and biological traits. We predict that species that are specialised in habitat use or diet, have inflexible phenology, large-body size (reflective of “slower” life histories) or migrate long distances will be more extinction prone and less likely to colonise. Widely distributed species with highly-connected populations are expected to be able to take advantage of local changes in climate and land use, whereas more isolated populations are expected to be extinction-prone (Schnell et al. 2013). Warm and warming winters are expected to increase both extinction and colonisation rates. Highly modified and monotypic landscapes, such as intensely farmed arable and urban areas are predicted to be associated with poor colonisation and species loss. Moreover, intensification of use across these landscapes is expected to hamper colonisation and increase extinction, particularly in habitat and diet specialists.

2.3 Methods

2.3.1 Species data

Species distribution data were extracted from the two British breeding bird atlases for the periods 1968-72 (Sharrock, 2010) and 1988-91 (Gibbons, 1993). Of all the 10 × 10-km Ordnance Survey grid squares in Great Britain, the study area was restricted to 2022 squares that were sampled in both periods and for which environmental data were available (Figure A1; Figure A2). For each square in each atlas period, the presence or absence (i.e. whether a breeding pair occurred within the grid square at any point during the atlas period) of 64 breeding passerines, for which detailed trait information was available, was recorded. We differentiate species traits into three groups that have been associated with responsiveness to environmental change (Julliard et al. 2004; Gregory et al. 2005; Cardillo et al. 2005): life-history (body weight and productivity), phenology (laying date, clutch laying period and migration strategy) and resource-use (habitat dependency and diet group) (Table 2.1). A measure of the range size of each species was also included to capture species prevalence

across Great Britain. Further details of the methodology by which species traits were retrieved from the literature are given in Salido et al.(2012).

For each species in each grid square, we use the predictor term ‘population connectivity’ to describe the degree of clustering of occupied squares, such that the population connectivity term for a given species in a given grid square, x_i , is given by:

$$x_i = \sum_{j=1}^k e^{-\lambda d_{ij}}$$

where for k occupied grid squares, d_{ij} is the Euclidean distance in km between the centre of grid square i and the j th occupied grid square within a neighbourhood of radius 60km, which exceeds median dispersal distances for UK passerines (Sutherland et al. 2000), and λ is the decay function with distance between these squares. High values indicate that grid squares were surrounded by other grid squares occupied by the focal species and zero values when no occupied grid-squares occurred within this neighbourhood. Extinction and colonisation models were fitted using a range of λ values (0.1, 0.15, 0.2, 0.3, which are equivalent to spatial ranges of decay of 40km, 30km, 20km and 10km respectively based on simulation of parameter values). The best-fitted λ for both colonisation and extinction models was 0.15, meaning that the probability of extinction/colonisation in a given square was most strongly predicted by the occupancy of squares within 30km.

Table 2.1. Extrinsic and intrinsic variables used in spatial and species-level extinction and colonisation models of passerines in Great Britain. All ‘change’ variables are differences between the variable in the two atlas periods.

Factor	Description	Species or grid square level variable	Source
<i>Extrinsic: Climatic</i>	February minimum temperature (Temperature 1990) Change in February minimum temperature	Grid Square	United Kingdom Climate Impacts Programme (http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/index.html)
<i>Extrinsic: Land cover</i>	Urban Cover Change in Urban Cover Arable Cover Change in Arable Cover Open Cover Change in Open Cover Woodland Cover Change in Woodland Cover	Grid Square	Hazeu et al. (2008) HISLU60 and PLCM1990 ECOCHANGE Project maps.
<i>Intrinsic: Phenology-related</i>	Median date of the 1 st egg laying (Julian day) Latest recorded date- earliest recorded laying date (no. days) Migration strategy (Migrant, partial migrant and resident)	Species	Robinson (2005) (http://blxl.bto.org/birdfacts). Robinson (2005) (http://blxl.bto.org/birdfacts). Dudley et al. (2006)
<i>Intrinsic: Resource use</i>	Diet (Generalist, seed eaters, insectivorous) Habitat (Farmland species, woodland species, generalists, specialist other)	Species	Snow and Perrins (1998) BWP Newson et al. (2006) Siriwardena et al (1998), Gregory et al (2007), Snow & Perrins (1998). BWP
<i>Intrinsic: Life history</i>	Average body weight for the species (g) Average number of clutches per year	Species	Snow & Perrins (1998). BWP Snow & Perrins (1998). BWP
<i>Intrinsic: Range characteristics</i>	Range size Population connectivity	Species and grid square	
<i>Trait environment interactions</i> x	February minimum temperature: phenology Change in February minimum temperature: phenology Habitat cover: habitat specialisation Habitat change: habitat specialisation Habitat/land cover: range size Habitat change: range size (Climate) Temperature change: Range size	Species and grid square	

2.3.2 Environmental predictors

The key environmental pressures that were included for this study were those of land cover and climate (A1). Monthly climate data were taken from the Met Office's UK Climate Projections (UKCP09) dataset (downloadable from <http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/>) and were extracted at a 5km² resolution for two decadal periods, broadly coincident with the atlas periods i.e. 1961-70 for the first atlas period and 1981-1990 for the second atlas period. Following resampling to the 10km grid, values of February minimum temperature were averaged across the years in the two decades. Climatic changes will be particularly disruptive if they occur during the most vulnerable periods of the species life cycle, namely overwintering and/or breeding for passerines. February minimum temperature is taken to reflect the pre-breeding season conditions (Salido, 2013). Furthermore, February minimum temperature was consistently a better predictor of community composition in British passerines at a 10 km² resolution than average minimum and maximum temperatures or precipitation in other seasonal periods (late breeding, early breeding, total breeding, nestling and post breeding periods) (Salido, 2013). Therefore, only the average February minimum temperature in the second decadal period and the change in average February minimum temperature between the two decadal periods were used as climatic predictors. Land cover variables of urban, arable, forest and open (pasture or open grass land) were extracted from the HISLU60 and PLCM1990 ECOCHANGE datasets at a spatial resolution of 1km² (Hazeu et al. 2008). Proportions over each 10 km grid square were then calculated for each of the land cover variables.

2.3.3 Modelling approach

Extinction and colonisation events were identified as disappearance or appearance of species in sampled grid squares. In each grid square, species were classified as extinct (present in 1968-71, absent in 1988-91), persisting (present in both atlas periods), colonised (absent in 1968-71, present in 1988-91) or failed to colonise (absent in both atlases).

First, to understand the overall contribution of extinction and colonisation events in driving range changes at the species level, we examined descriptive characteristics of range change patterns. Species level extinction rate was the number of extinction events expressed as a proportion of the number of squares occupied in the first period, whilst species-level colonisation rate was the number of colonisation events expressed as a proportion of the number of squares unoccupied in the first period.

Second, we evaluated the relationship between colonisation or extinction events and species traits at the species level. We used a phylogenetic general linear mixed model with a binomial response (colonisation/failure or extinction/persistence) using the *HLCor* function in the *spaMM* R package (Rousset and Ferdy, 2014). The full set of possible trait models were evaluated sequentially using a factorial design. The best-fit species level model with the lowest Bayesian Information Criterion (BIC, (Schwarz, 1978)) was selected. We use BIC for all model selection because it is more conservative and imposes a greater penalty for additional parameters than the Akaike Information Criterion (AIC), which is often used for this purpose. For both sets of models, we assessed over-dispersion by evaluating the ratio of model residual deviance to degrees of freedom and by a likelihood ratio test between a binomial and a beta-binomial model.

Third, for each species in each square, extinction/persistence and colonisation/failure was used to create binary dependent variables for separate analyses of extinction and colonisation. Occupancy changes could then be analysed in relation to traits and environmental conditions using generalised linear mixed models (GLMMs) with logit-links and Bernoulli error structures (i.e. a special case of binomial where the number of trials is 1). Models were fitted using the *glmer* function, with bobyqa optimisation, in the *lme4* R package (Bates et al. 2012). All models included a random effect of species and grid squares.

Due to the large number of predictors, an all subsets approach for this final analysis was not feasible computationally or practically. Therefore, the following stepwise approach was used, and best-fit

models selected (refer to A2). In step 1, models with all possible combinations of *trait* variables were fitted and the best-fit model was carried forward. In step 2, models were fitted starting with the best *traits* model and adding all possible combinations of environmental variables and the best *trait and environment model* was carried forward. We also reversed the steps to add all traits to the best *environment* model, ensuring that the selection order did not alter the best *trait and environment model*. To evaluate the best-fit models, we compared them with global models for extinction and colonisation incorporating seven trait variables and ten environmental variables on extinction and colonisation events.

In step 3, we then explored potential interactions between traits and environmental variables in the best *trait and environment model*. It was considered *a priori* that life history and phenological traits should interact with climate factors and climate changes whilst resource use traits would interact with habitat and climate factors and changes. Similarly, species with larger ranges are expected to be able to take advantage of local shifts towards more favourable climate and habitat more frequently. Thus, three types of interactions were considered. These were (i) between range size (number of occupied squares) and all environmental variables, (ii) between resource use traits and habitat change variables, and (iii) between phenological variables and temperature variables (see Table 2.1). Models were fitted with all possible combinations of *a priori* identified interaction terms for which both main effects were already in the best *trait and environment model*, and the final *trait, environment and trait-environment interactions model* was again selected. This selection approach should identify the most important variables predicting local changes in distribution. Our confidence in the latter is enhanced if the same combination of key explanatory variables results from the two different model selection orders.

We did not incorporate explicit phylogenetic or spatial covariance error structures during the model selection process due to the computational intensity of optimisation for such a large dataset. We expected that the population connectivity term should account for a substantial fraction of any spatial

autocorrelation. However, we did incorporate species nested within family as a random factor in the model selection procedure and evaluated both the spatial and phylogenetic autocorrelation of the model residuals using a one-tailed Moran's I test, *Morans.I* function in the ape package (Paradis et al. 2004) and a phylogenetic variance covariance matrix derived from Thomas (2008). We also ran the final model using glmmPQL in the in the R MASS package, incorporating an exponential correlation structure and compared the model coefficients between the final model with and without a spatial correlation structure (reported in Appendices). To evaluate overall model fit, we report the accuracy statistics between the fitted and observed values of colonisation and extinction for each species within each square.

2.4 Results

More species showed an overall range contraction than range expansion (45 versus 19 of 64 species); the mean proportional range change across Britain was -0.06 ± 0.17 S.E. In absolute terms, mean change in range size between 1970 and 1990 was -61.27 ± 115.57 (range: -542 - 140) grid squares. Of the total 129408 occupancy records across all species, there were 5133 colonisation (unoccupied -> occupied) and 9054 extinction (occupied -> unoccupied) events. Amongst species, the proportion of unoccupied squares that were subsequently colonised was 0.22 ± 0.18 (range 0.07-0.99) and the proportion of occupied squares that were subsequently extirpated was 0.15 ± 0.17 (range 0.005-0.926). Sites with a large degree of urban cover at the first time point were more likely to undergo further urbanisation (urban, urban change $r = 0.86$, $P < 0.001$), open areas were likely to become more open ($r = 0.49$, $p < 0.001$), and arable to become more arable ($r = 0.47$, $p < 0.001$) (Figure A3). The vast majority of grid squares used in this study had a low proportion of urban cover, and cells with high urban cover were unlikely to change so that the majority of urban cover change occurred within grid squares with low cover but near those with high urban cover (Figure A3).

2.4.1 Characteristics of colonising species

Widely distributed species were both more likely to colonise and less likely to be extirpated (Table 2.2a). Large body size, and long clutch period were both associated with a reduced probability of colonisation. Herbivores were the least likely, and insectivores the most likely to colonise (Table 2.2a). Woodland species were more likely, and farmland and specialist species less likely to be extirpated than generalists (Table 2.2b). Average number of clutches, migration strategy and median first laying date were dropped from all models.

Table 2.2. Species level colonisation (a) and extinction (b) models. Colonisation events were summed over all squares for each species evaluated as a binomial glm. As a measure of variable importance, Δ BIC values are the increases in BIC when each term in turn is dropped from the final model.

a.	Factor	Estimate \pm s.d.	t-value	p	Δ BIC
	(Intercept)	-0.20 \pm 0.58	-0.35	0.73	
	Range size	0.67 \pm 0.05	13.99	<0.001	99.03
Diet	Insectivore/Herbivore v. Omnivore	-0.46 \pm 0.31	-1.48	0.15	14.79
	Insectivore v. Omnivore	0.21 \pm 0.33	0.63	0.53	
	Body Weight	-0.67 \pm 0.18	-3.75	<0.001	13.24
	1st Clutch Period	-0.01 \pm 0.001	-3.26	0.002	9.95
<hr/>					
b.					
	(Intercept)	-1.59 \pm 0.44	-3.63	<0.001	
	Range size	- 0.86 \pm 0.06	-14.86	<0.001	94.29
Habitat	Woodland v. Generalist	0.20 \pm 0.34	0.58	0.56	8.81
	Farmland v. Generalist	-0.48 \pm 0.26	-1.86	0.07	
	Specialist Other v. Generalist	-0.26 \pm 0.30	-0.87	0.4	

2.4.2 Features associated with colonisation

Across species, areas that were adjacent to occupied squares were much more likely to be colonised (Table 2.3a). Colonisation rates were greater in species with small ranges. Although squares that were

dominated by urban cover were less likely to be colonised, increases in open and urban cover were associated with higher colonisation rates across all species. There were, in addition, effects of open cover, open cover change and arable cover on colonisation probability, but the direction of these effects depended on the range size of the species in question: species with small ranges were more likely to colonise areas with more open cover and increasing arable cover (Figure 2.1). In contrast, areas with more forest cover were more likely to be colonised. Population connectivity was by far the most dominant predictor of colonisation across species in each square. Accuracy statistics indicated a significant correspondence between observed and predicted values (AUC= 0.916, Nagelkerke's r^2 = 0.507) (Figures 2.2A and 2.2C). There was significant but low magnitude phylogenetic (I = 0.11 \pm 0.02, p < 0.001) and spatial (I = 0.11, expected I = -4.95×10^{-4} , p < 0.001) autocorrelation in the residuals of the final model. Incorporating an explicit spatial correlation term using glmmPQL did not impact substantially on the model parameters or standard errors, but did marginally reduce spatial autocorrelation (Table A7a).

2.4.3 Features associated with Extinction

Extinction rates were greater in species with small range size and in areas isolated from other occupied squares (Figure 2.3) such that more isolated sites were more likely to undergo extinction events (Table 3b). Areas dominated by open cover were associated with high extinction rates, whereas areas with increasing urban or arable cover were associated with low extinction rates. Range size interacted with land cover, such that species with small ranges were particularly prone to extinction where arable and urban cover was high, whereas they were less prone to extinction where open cover decreased. Poor population connectivity was by far the dominant predictor of extinction across species in each square. Just as for colonisation, accuracy statistics indicated a significant correspondence between observed and predicted values (AUC= 0.931, Nagelkerke's r^2 = 0.511) (Figures 2.2B and 2.2D). Again there was significant but low magnitude phylogenetic (I = 0.04 \pm 0.03, p = 0.024) and spatial autocorrelation (I = 0.14, expected I = -4.95×10^{-4} , p < 0.001) in the final model residuals. As with the colonisation models,

incorporating an explicit spatial correlation term using glmmPQL did not impact substantially on the model parameters or standard errors, but did marginally reduce spatial autocorrelation (Table A7b).

Table 2.3. Table of coefficients from binomial model of impacts of trait, environment predictors and their interactions on spatial patterns in a) colonisation and b) extinction events of passerines between 1968-72 and 1988-91 in Great Britain. As a measure of variable importance, Δ BIC values are the increases in BIC when each term in turn is dropped from the final model. Where main effects are also involved in interaction terms, the Δ BIC is calculated by dropping both the main effect and all interaction terms[†]. By comparing this overall value with the Δ BIC for individual interaction terms, one can crudely assess the relative importance of main effect and interaction terms.

a.	Coefficient	Z	p-value	Δ BIC
(Intercept)	-29.8 \pm 4.24	-5.33	<0.001	
Population Connectivity	2.33 \pm 0.04	56.33	<0.001	3871
Range size [†]	-4.47 \pm 0.68	-6.62	<0.001	74
Open cover 1990 [†]	-1.10 \pm 0.30	-3.63	<0.001	47
Range size: Open cover 1990	-1.44 \pm 0.19	-7.49	<0.001	42
Forest cover 1990	0.25 \pm 0.04	7.07	<0.001	37
Open change	1.72 \pm 0.28	6.05	<0.001	25
Urban change	4.26 \pm 0.71	5.95	<0.001	23
Urban cover 1990	-6.31 \pm 1.31	-4.81	<0.001	11
Arable change [†]	0.99 \pm 0.30	3.35	<0.001	7
Range Size: Arable change	-0.45 \pm 0.11	-4.13	<0.001	5
Temperature 1990	-0.07 \pm 0.02	-3.17	0.001	-1
Random effects:				
Groups	Name	Variance	Std.Dev.	
Family	(Intercept)	0.17	0.42	
Species w/in Family	(Intercept)	0.42	0.65	
Grid square	(Intercept)	0.85	0.92	

b.	Coefficient	Z	p-value	Δ BIC
(Intercept)	82.7 \pm 3.40	24.26	<0.001	
Population Connectivity	-2.89 \pm 0.04	-70.93	<0.001	6168
Arable cover 1990 [†]	5.50 \pm 0.37	14.71	<0.001	288
Range size [†]	-20.79 \pm 1.33	-15.61	<0.001	279
Open cover 1990	6.76 \pm 0.37	18.37	<0.001	226
Range size: Arable cover 1990	-2.21 \pm 0.15	-14.40	<0.001	188
Urban cover 1990 [†]	10.17 \pm 0.85	12.02	<0.001	132
Range size: Urban cover 1990	-3.38 \pm 0.32	-10.50	<0.001	100
Open change [†]	-1.66 \pm 0.28	-6.01	<0.001	59
Range size: Open change	-0.42 \pm 0.07	-6.39	<0.001	27
Urban change	-3.36 \pm 0.58	-5.82	<0.001	10
Arable change	-1.20 \pm 0.30	-4.07	<0.001	5
Random effects:				
Groups	Name	Variance	Std.Dev.	
Family	(Intercept)	0.07	0.26	
Species w/in Family	(Intercept)	0.58	0.76	
Grid square	(Intercept)	1.45	1.20	

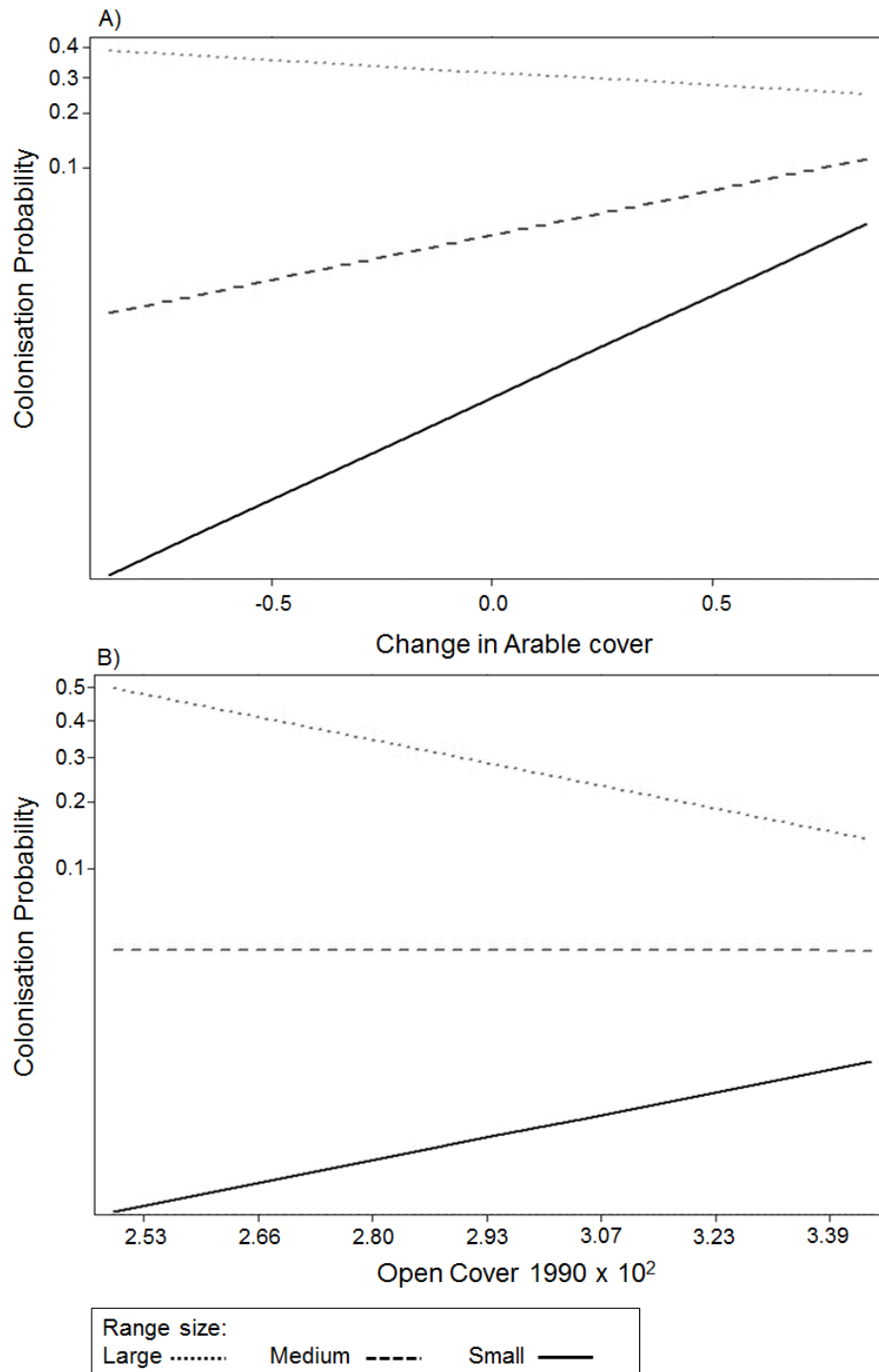


Figure 2.1 Key trait-environment interactions affecting the likelihood of colonisation events in models of passerine colonisation between 1968-72 and 1988-91 in Great Britain. A) Key Interaction between species range size and the change in arable cover. B) Key interaction between species range size and open cover in 1990.

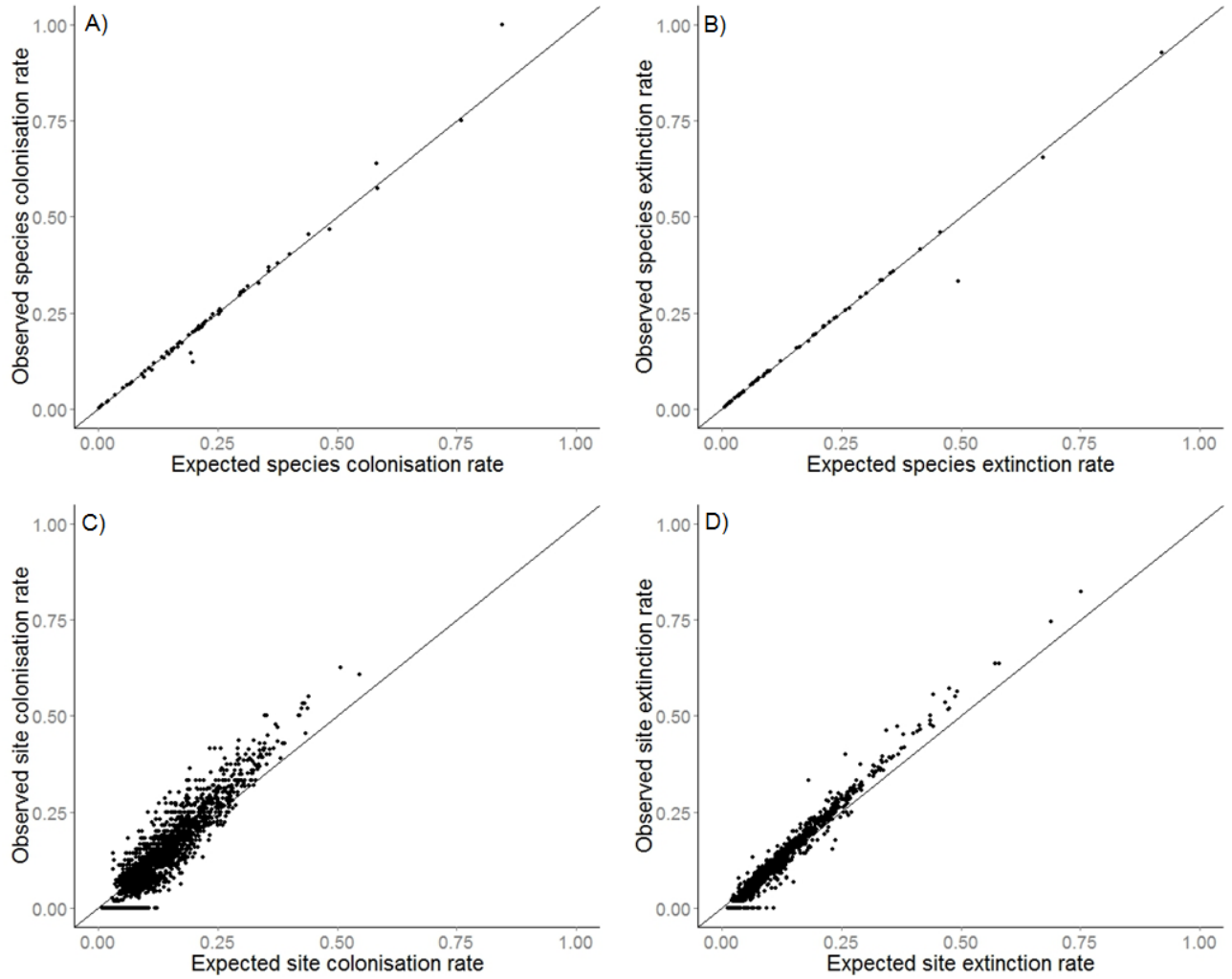
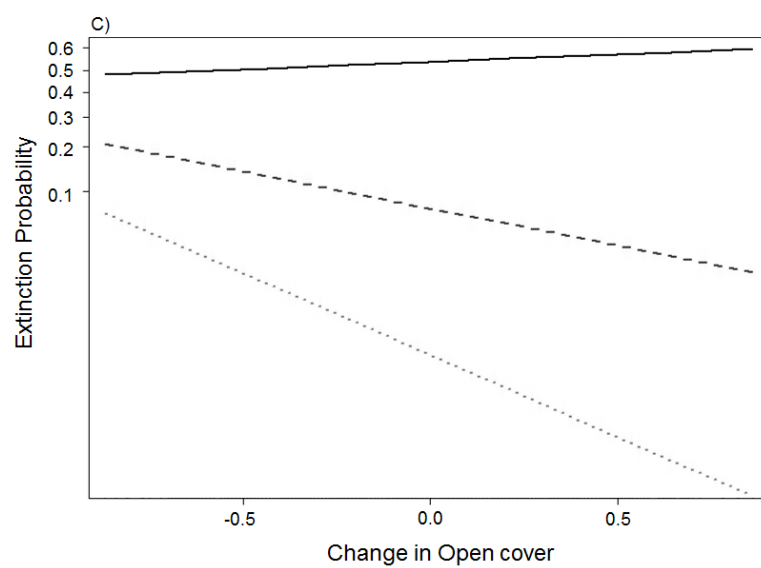
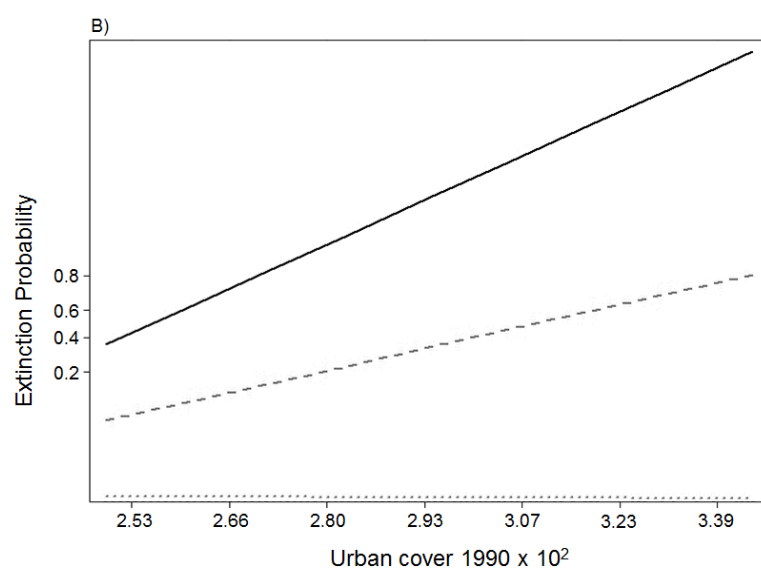
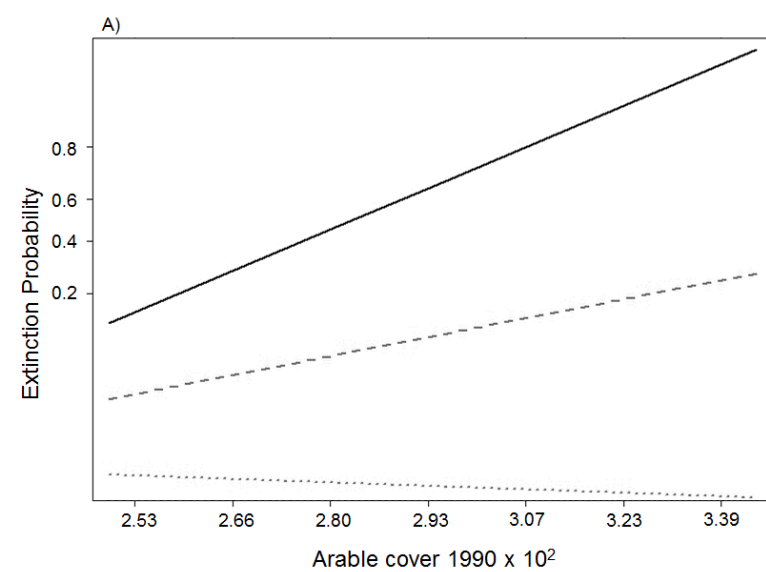


Figure 2.2 Goodness-of-fit plot for the models of spatial patterns in extinction and colonisation events of passerines between 1968-72 and 1988-91 in Great Britain. (A & C) colonisation, (B & D) extinction. Expected rates for individual species (A & B) and grid squares (C & D) were calculated from the means of the model-fitted probabilities (Cox and Snell, 1989). Solid lines indicate 1:1 relationship. The fitted values from all models were highly correlated with the observed values (species colonisation $r^2 = 0.98$, extinction $r^2 = 0.98$; grid squares colonisation $r^2 = 0.86$, extinction $r^2 = 0.97$).



Range size:
 Large Medium ---- Small —

Figure 2.3 Key trait-environment interactions affecting the likelihood of extinction events in models of passerine colonisation between 1968-72 and 1988-91 in Great Britain. A) Key interaction between species range size and arable cover in 1990. B) Key interaction between species range size and urban cover in 1990. C) Key interaction between species range size and the change in open cover.

2.5 Discussion

Changes in British passerines distributions are best predicted by the connectivity of occupied grid squares: isolated squares were much more likely to see extinction events if occupied and less likely to be colonised if unoccupied. Though occupancy at a 10km grid square level is a relatively coarse measure of avian population networks, the strong effect of connectivity in our results for both colonisation and extinction suggests that those species that are distributed in a network of small local populations are much more vulnerable than those that occur in large and continuous populations. The occupancy dynamics of the frontier populations in our species will behave as a metapopulation, where both patch size and connectivity are expected to impact on persistence of local populations (Pellet et al. 2007). Previous studies have also demonstrated that extinction is more likely and colonisation less likely where populations are more isolated from networks of other populations (Brashares, 2003). At the 10 km grid square level, population connectivity has been shown to predict range changes in butterflies and plants (Wilson et al. 2004) as well as in ladybirds (Comont et al. 2012). Newson et al. (2014) also found that population connectivity reduced local population declines in woodland bird species. Overall, a sufficiently inter-connected population is necessary for successful invasion or colonisation of new habitat, as well as the maintenance of genetic diversity (Lewis and Kareiva, 1993).

Another key predictor of local colonisation and extinction was range size, such that more widely distributed species were both less likely to colonise and less likely to go extinct (Table 2.3), suggesting that their ranges are relatively stable. In contrast, species with small ranges were more likely to undergo extirpation, but were also more likely to colonise new areas. However, at the species level, large range size was associated with low extinction but high colonisation rates suggesting that they may be more likely to show overall range increases (Table 2.2). Interestingly, the effect of range size

was stronger for extirpation than for colonisation. Species that are more abundant are less likely to undergo local extinctions as well as overall declines (McCarthy and Thompson, 2001), and so widely distributed species are also expected to be resistant to local population declines. It can be hypothesised that widespread species occupy a greater proportion of the total area available and thus are slower to colonise further but are far less likely to undergo extirpation. Moreover, range size in birds (Bock and Ricklefs, 1983) and other groups (Bell, 2001) is positively correlated with abundance, which may provide resilience to declines resulting in local extinction.

Of the remaining variables, land cover and change in land cover predicted local occupancy changes much better than our climate indicator. Although lower temperatures in the second time period were associated with high colonisation, the effect on the model was negligible compared to other variables. In fact, when interaction terms were also taken into account, the predictive power of the best-fit model was marginally increased when temperature was dropped. Generally, monotypic landscapes dominated by a high coverage of open, arable or urban land cover showed fewer local colonisations and a greater number of extinctions. Land cover change was associated with high colonisation and low extinction, suggesting that heterotypic landscapes with a wide range of appropriate habitats are important for maintaining populations locally. Interestingly, positive urban change was also associated with local colonisation and reduced extinction. This suggests that the impact of global climate change may be mediated by local land use at the spatial and temporal scale considered here. Our results that patterns of spatial autocorrelation and connectivity are more informative than climate mirrors criticisms about the utility of climate variables in species distribution models more generally. Beale et al. (2008) show that when autocorrelation and connectivity are included, climate provides no added value in distribution models for the majority of European birds they investigated.

Several of the biological traits were important for predicting range changes across Britain as a whole, but not for local extinction and colonisation events. For example, large body size correlated with poor overall expansion ability. Body-size has previously been associated with extinction and occupancy

changes in species at local and regional scales in some studies (Gaston and Blackburn, 2002; Owens and Bennett, 2000; Bradshaw et al. 2014) but not others (Foufopoulos and Mayer, 2007; Angert et al. 2011; Brashares, 2003). Our results support the latter group of studies, in that body size did not predict probability of either extinction or of colonisation at the 10 km grid-square level. One reason for the lack of repeatability in body size as a predictor is that body mass is correlated with a suite of other life-history traits, including productivity, population density and dispersal capability, all of which can affect species establishment and persistence in a variety of direct and indirect ways (Blueweiss et al. 1978; Juanes, 1986; Paradis et al. 1998). Thus, when body size does predict extinction, it is probably as a proxy for other underlying traits that are sensitive to environmental processes.

Our results differ substantially from those obtained in a previous study by Bradshaw et al. (Bradshaw et al. 2014), which assessed predictors of overall range change in passerines using the same occupancy datasets. They predicted species level range changes using climate data (temperature and precipitation) averaged across an entire range along with body size, natal dispersal distance and overall population 'clumpiness' or geographic fragmentation. Climate was found to be the key driver in range change, but the effect of climate depended on the distribution of the species in question. Large bodied species with greater natal dispersal capability were less likely to undergo range changes and geographical fragmentation was associated with range expansion. Moreover, they report differences in occupancy changes between species at higher and lower latitudes. Our results, which measure local climate effects suggest that land use may be more important in driving range change locally. There are differences between the two studies that may account for the differences in their findings. First, we explicitly consider the local environment for each 10 km grid-square rather than averaging over an entire species range. Second, in addition to climate we explore the impact of land use on occupancy change. Third, we use a measure of local population connectivity, whereas Bradshaw et al. (2014) use an overall measure of geographical fragmentation. The interconnectivity of grid cells is a crucial driving force of occupancy changes, and so only by accounting for this connectivity are the relative effects of land-use and climate uncovered. Fourth, we incorporate

additional biological traits that characterise ecological niche and find that resource use traits predict range change processes better than life history ones. While we too find that body weight was associated with lower overall colonisation probability, we do not find the converse relationship for extinction. These discrepancies are largely attributable to the inclusion of a wider range of species traits in the current study.

The focus on local occupancy change that we have adopted in the current study is analytically challenging. The data are binary, and consist of a species-by-site matrix of values. Models, therefore, ideally need to account simultaneously for the binary nature of the response variable (through the use of a binomial distribution), the relatively complex residual correlation structure (which contains structure relating to both spatial correlation and phylogenetic correlation), random effect and the main effects of explanatory variables (and their interactions). Existing software packages each deal with some of these issues, but none appears to deal satisfactorily with all of them simultaneously. In order to compare model fit, handle binary response data and incorporate random effects, we used the *glmer* approach in the initial model selection together with an estimate of patch connectivity, which indirectly deals with spatial autocorrelation. Following this, we explicitly incorporated a spatial correlation structure in the final model. Even so, implementation is problematic as model fitting with such a large dataset is computationally intensive and the sparseness of binary data limits convergence. We addressed these issues by employing a step-wise model selection process (refer to A2), increasing model iterations and changing the optimization algorithm. Thus, we had to make some compromises to handle the data. Although these changes improved model performance, it was reassuring that the results (i.e. factors retained and coefficients) were robust to each of these changes.

As well as analytical challenges, there were practical limitations in the current study that were considered in the analyses. Firstly, owing to the complexity of ecological interactions, there are a very large number of potential environmental predictors in this cohort of species. A smaller subset of environmental variables that encompass a range of habitats was selected in order to minimize the

computational intensity of the model selection process whilst uncovering the overarching patterns that drive local occupancy in passerines. Secondly, the response variable used in the final analyses was binary, however, in the raw atlas data for each species captured the number of breeding pairs in each season of the study period. A binary response variable therefore does not necessarily distinguish between abundant species that were recorded in a grid square in every season and rarer species that may only have been recorded once. This was addressed by incorporating a range size predictor variable that characterised the overall prevalence of a particular species.

Passerines in Britain already represent a disturbed community, and none of the species recorded in this study are listed as endangered on the IUCN red list. However, multiple species have seen regional declines in occupancy across Great Britain in this study period e.g. *Emberiza cirius* (the Cirl Bunting). Extirpation is a pre-requisite for overall population declines, and thus understanding the biological traits and environmental changes that are associated with these local declines is also vital (Collen et al. 2011) as is understanding how local environment is associated with species occupancy changes. There is a presumption that local extinction processes scale up to global extinction risk, and vice versa, however, there is little evidence to link the two. Extirpation is particularly critical for ecosystem functioning, but few previous studies have documented their causes (Ceballos et al. 2015). Moreover, Colles et al. (2009) argued that extinction processes that are important at short temporal scales do not always translate into long-term macroevolutionary turnover events. Our finding of the importance of biological traits at the regional, but not at the local scale further highlights gaps in our understanding of this scaling process.

The overwhelming importance of range connectivity and isolation together with local land use has direct relevance for conservation planning. Habitat management decisions need to be informed by the connectivity patterns of suitable habitats (Newson et al. 2014; Carroll et al. 2010). Landscape-scale attributes such as patch isolation and habitat availability have been shown to be important in buffering against weather mediated population declines in some woodland bird species (Newson et al. 2014).

Furthermore, the maintenance of heterogeneous landscapes with a wide diversity of potential habitat may also reduce local population declines. For example, Carroll et al. (2010) show that, while fixed wildlife reserve networks may become ineffective as species change distribution under climate change, reserve design can be optimised by considering habitat breadth for focal and lesser known taxa. There is also evidence that reclaiming suitable habitat will prevent local population losses by allowing species to spread into favourable areas (Hodgson et al. 2011). An ideal scenario would see a larger, interconnected network that incorporates local land use or habitat management schemes. For British birds, we suggest that afforestation and changes to upland management may also impact on local population dynamics more quickly and intensely than gradual temperature change. In terms of mitigating against population loss, these results are actually heartening. Whilst it may be intractable to influence global environmental change, it is eminently feasible to engage with local land use management strategies.

As well as offering enhanced insight into the mechanisms causing vulnerability, the trait-environment modelling approach taken in this study provides substantial additional information compared to species-traits-only approaches on how best to focus conservation effort since accurate predictions of locations of colonisation and extinction events in particular kinds of species are produced. The approach is widely applicable to any taxa for which past changes in occupancy and detailed ecological trait data are documented. Climate change undoubtedly drives global abundance patterns over long-time scales, but local intervention and the mitigation of land use change are crucial for proactively managing biodiversity.

Chapter 3

*The breakdown of social structure in marginal habitat:
A case study of the Cape mountain zebra, *Equus zebra zebra**



3.1 Abstract

Confinement to marginal habitat as a result of anthropogenic disturbance influences the ability of a population to grow and is often assumed to affect behaviour and social structure in vulnerable species. However, the impact of marginality on social and population structure is poorly understood. Social networks provide a novel tool to compare populations of the same animal species and can reveal nuanced differences in social and population structure. Here we investigate the variation in social network structure across ten independent sub-populations of the Cape mountain zebra (CMZ), *Equus zebra zebra*, in relation to habitat suitability. Individual connectivity, the distribution of ties in adult males, group size and the proportion of bachelor males within a population were all influenced by the availability of palatable grass species and water. In optimal habitats, there were larger groups, a smaller proportion of bachelors and an increase in individual connectivity and heterophily in the ties of adult males. Differences in social network structure were not dependent on either network or group size. The availability of palatable grass and water is thus vital to maintain productive, heterogeneous and interconnected family harems of CMZ and future management strategies should prioritise these habitats. Comparing social networks in populations with varying ecological pressures can highlight population responses to marginality, and can ultimately provide evidence to improve the efficiency of management strategies.

3.2 Introduction

Anthropogenic activities have resulted in widespread population declines and forced many species into sub-optimal, marginal habitat. Mitigating against these declines and identifying ecological and anthropogenic pressures, especially in small fragmented populations, is a primary goal of conservation efforts. Population growth rates are key indicators for long-term population viability, however, accurate assessment of population performance can be problematic. Demographic stochasticity in small populations may result in snap-shots of growth or fecundity being unreliable indicators of long-term performance and stability, especially in reintroduced or heavily managed species (Lea et al. *in prep*). Moreover, obtaining accurate estimates of population sizes, especially where population density is low can be difficult even with intensive monitoring. Thus, neither demography nor population growth estimates necessarily capture population viability when used in isolation.

Behavioural indicators provide an alternative and efficient way of evaluating population viability and identifying (Berger-Tal et al. 2011). For example, quantifying the *structure* rather than the *size* of populations, by evaluating how animals associate, group, and use their space, can reveal whether and how pressures such as resource limitation, demographic imbalance or predation affect the population. The socio-ecological model provides a framework for evaluating social responses to the environment as it assumes that animal grouping patterns are a direct response to ecological challenges (Linklater, 2000; Dammhahn and Kappeler, 2009; Jarman, 1974; Emlen and Oring, 1977). Although there has long been a call for conservation action to be informed by animal behaviour (Geist and Walther 1974; Harcourt 1999; Lindell, 2008), the two disciplines are often still not integrated (Angeloni et al. 2008). Moreover, we should not just conserve the number of animals, we should also conserve their behaviours. Often, human impact on the environment is so great that the normal behaviour of animals is completely disrupted (Rubenstein, 2010). Whilst species with greater behavioural flexibility will be better able to cope with anthropogenic pressures in the short-term, altered behaviours could lead to further problems in the long-term (Manor and Saltz, 2003; Berger-Tal et al. 2011), which could affect

the wider ecosystem (Wright et al. 2010). We should therefore try to conserve behaviours, such as sociality, within an animal's normal range of behaviours.

Behavioural differences have been documented between marginal and optimal habitats, and such differences are assumed to have knock on effects for overall social structure and population performance (Augé et al. 2011; Blondel et al. 2006). However, relating differences in population structure to underlying ecological pressures is not straightforward. Group typology often varies little between closely related species, let alone between populations of the same species (Linklater, 2000, Shultz et al. 2011). It is therefore crucial to use a method that can reveal subtle differences between populations.

Social network analysis allows for fine-grained comparisons between population structures, and uses individual level data to analyse patterns at the group or the population (Krause et al. 2009; Whitehead, 2008; Lusseau and Newman, 2004; Croft et al. 2008). In a social network, nodes represent individuals and ties are the relationships between individuals (e.g. based on repeated associations, grooming, aggression). As such, a social network can help to characterise and quantify the underlying structure of a population (Croft et al. 2008; Hinde 1976). Through comparisons of social networks, differences in sociality between populations can be quantified and explained in terms of ecology. For example, in Grevy's zebra (*Equus grevyi*), variation in association preferences, the fidelity of tie choices, and the degree of sub-structuring of association networks were shown to be the result of different ecological pressures (Rubenstein, 1994; Sundaresan et al. 2007a).

Only a handful of studies have assessed how differences in ecology relate to social network structure within the same species. Henzi et al. (2009) demonstrated that social engagement in female chacma baboons, *Papio hamadryas ursinus*, cycles seasonally based on the availability of resources. Long term association data from Pacific orca, *Orcinus orca*, revealed that the abundance of Chinook salmon, *Oncorhynchus tshawytscha*, is significantly correlated with overall network connectivity; increased clustering coefficients, degree centrality and mean half weight indices are associated with higher

salmon abundance (Foster et al. 2012). Fewer studies still have critically compared how network structure varies across populations in response to ecological variation. One example is a study in which the association network of two populations of Atlantic orca were compared; the orca that mainly fed on seals had a lower association index than the population whose primary food source was fish (Beck et al. 2012). Such an approach can be extended to a wider range of populations to evaluate how associations and sub-structuring vary across populations experiencing different threats or challenges.

Comparing network structure of independent populations is not trivial, as the surface structures of a network, such as its size, can have a considerable influence on network metrics (Anderson et al. 1999), making scale-free comparisons across populations of different sizes difficult (but see Faust and Skvoretz 2002; Faust, 2006; Croft et al. 2008). Sub-setting networks is a potential solution, however sub-setting non-human animal networks without losing any underlying structure (e.g. discrete family groups) is not easy. One solution to these issues is the NetSimile approach, in which network metrics are calculated for the complete network of each node or ego (focal nodes with specific characteristics) and the means and moments (variation, skew etc.) of these metrics across the network are captured (Berlingerio et al. 2012). Because NetSimile captures the variation as well as the central tendency for each of the metrics, the resulting features describing the network are not dependent on the total number of nodes. For example, Berlingerio et al. (2012) have used NetSimile successfully to compare networks that varied in size by an order of 1×10^2 . Furthermore, capturing information about the variation in the features of nodes or egos can account for nuanced differences between individual association patterns across two networks. Crucially for animal social networks, the NetSimile approach allows network comparisons that incorporate discrete social characteristics that are part of the network.

3.2.1 The Cape mountain zebra: a model for testing variation in population structure

The Cape mountain zebra (CMZ), *Equus zebra zebra*, occurs in the Cape Floristic Region of South Africa (Novellie, 2008). CMZ were critically endangered in the 1970s, when they were reduced to a global population size of 80 animals, but subsequent conservation management has resulted in a large population increase (Millar, 1970; Hrabar and Kerley, 2015; Novellie et al. 2002; Novellie, 2008). However, CMZ are now spread over more than 75 sub-populations, including many privately owned reserves with very few individuals. These sub-populations range in size from less than ten individuals at Bontebok National Park to over 1000 individuals at Mountain Zebra National Park (Hrabar and Kerley, 2015). Furthermore, two of the three relic populations (Gamkaberg Nature Reserve and Kamannassie Nature Reserve) represent less than 3% of the total population (Hrabar and Kerley, 2015).

Most commonly, Cape mountain zebra exist in discrete, independent social groups; either in stable harem family groups in which one male monopolises breeding, or in bachelor groups that are mainly comprised of adult/sub-adult males (Figure 3.1, Novellie, 2008). Bachelor groups are not reproductively active and their prevalence may play a pivotal role in the performance of CMZ populations.

CMZ show a preference for habitats with a high number of palatable grass species, including protein rich grasses such as *Themeda triandra* (Watson and Chadwick, 2007; Grobler 1983; Weel et al. 2015; Lea et al. *in prep*). The Cape Floristic Region is characterised by fynbos shrubland vegetation, which has a high diversity of plant species but a low grass abundance (Campbell and Van der Meulen, 1980). In addition to diet analysis of CMZ, palaeontological evidence from ungulate assemblages in the Pleistocene-Holocene transition indicates that a loss in open grassland habitat severely reduced the populations of *Equus zebra* (Faith, 2012). Further land conversion to agriculture and intensive grazing has also had a large impact on the availability of grassland habitat (Faith, 2012). Many studies have emphasised the importance of grass availability in the maintenance of stable CMZ populations

(Watson et al. 2005; Watson and Chadwick, 2007; Smith et al. 2011, Weel et al. 2015). The availability of water has also been implied as a key driver of performance and social structure in equids, particularly in species that occur within arid environments (Rubenstein, 1994; Moehlman, 1998). CMZ have been introduced into several arid habitats with limited grass, and these populations have shown limited growth (Hrabar and Kerley, 2015; Lea et al. *in prep*).

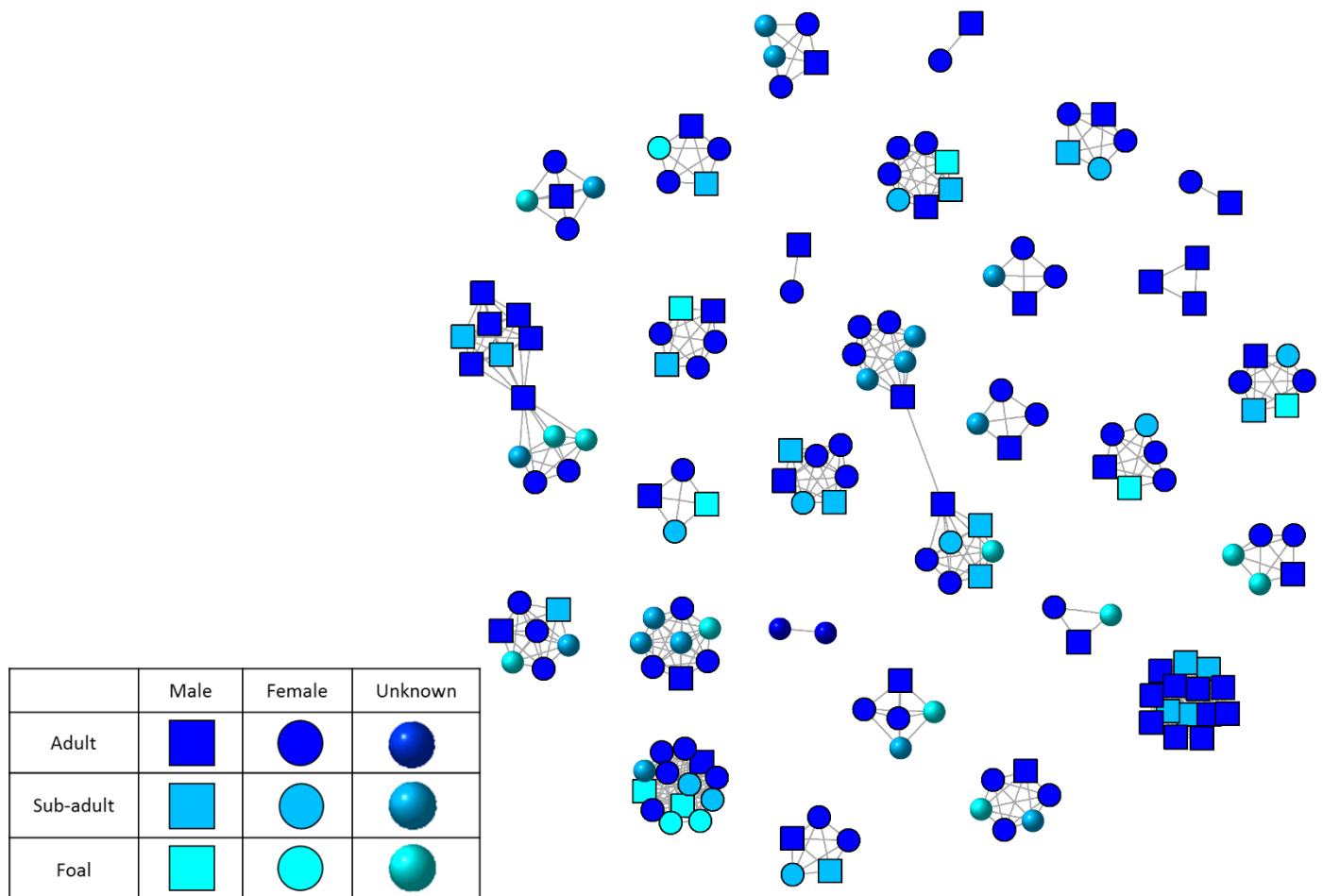


Figure 3.1 An example of the social network structure of Cape mountain zebra (CMZ) from Mountain Zebra National Park, December 2012. The colour and shape of each node denotes the age-sex classification of each individual within the network. Unknown individuals were primarily foals and young sub-adults.

Here, we assess how habitat suitability affects population structure, by comparing the social network structure of ten independent CMZ populations across habitats with a range of grass abundance and water availability. We also examine the relationship between habitat suitability and the proportion of bachelors, the size of family groups, and overall group size within each network. Finally, we measure the effect of social network structure on population performance, because population growth, density and foal:mare of CMZ sub-populations are significantly lower in areas with a decreased abundance of palatable grass (Lea et al. *in prep*).

While resource availability has been shown to affect sociality in animals (Foster et al. 2012; Beck et al. 2012; Henzi et al. 2009), to our knowledge this is the first study to compare social network structure in such a large number of independent populations of the same species. We predict that in optimal habitats, there will be cohesive, heterogeneous family groups. In marginal habitats, we predict that social groups will be less structured as a result of a greater proportion of bachelors that disturb family harems.

3.3 Materials and Methods

3.3.1 Data collection and group recognition

Data was collected between December 2012 and May 2015 throughout daylight hours (i.e. 06:00 – 18:00). A total of 81 days of sampling were undertaken. Ten focal populations were used for the purpose of this study; Camdeboo National Park, Mount Camdeboo Private Reserve, Karoo National Park, Mountain Zebra National Park, Gamkaberg Nature Reserve, De Hoop Nature Reserve, Swartberg Private Game Reserve, Welgevonden Game Farm, Samara Private Game Reserve and Bakkrans Nature Reserve (Figure 3.2). For each zebra encountered, the GPS location and the age-sex classification was recorded and a photo was taken. Photographs were then used to identify individual animals using HotSpotter™ pattern species instance recognition software (Crall et al. 2013). We used the individual

identification and age-sex data to compile a snapshot of the population demography for the sampling period. Following the assumptions of the ‘gambit of the group’, individuals were considered to be associated if they were observed in a group during an encounter (Croft et al. 2008; Franks et al. 2010). Individuals were assumed to be members of a group when they were within ~50m of other zebra *and* individuals moved together as a cohesive unit. Individuals, especially stallions, from separate groups occasionally interacted (including both aggressive and passive encounters); where individuals separated from their social group and interacted we recorded an additional association between the interacting dyad/s only.

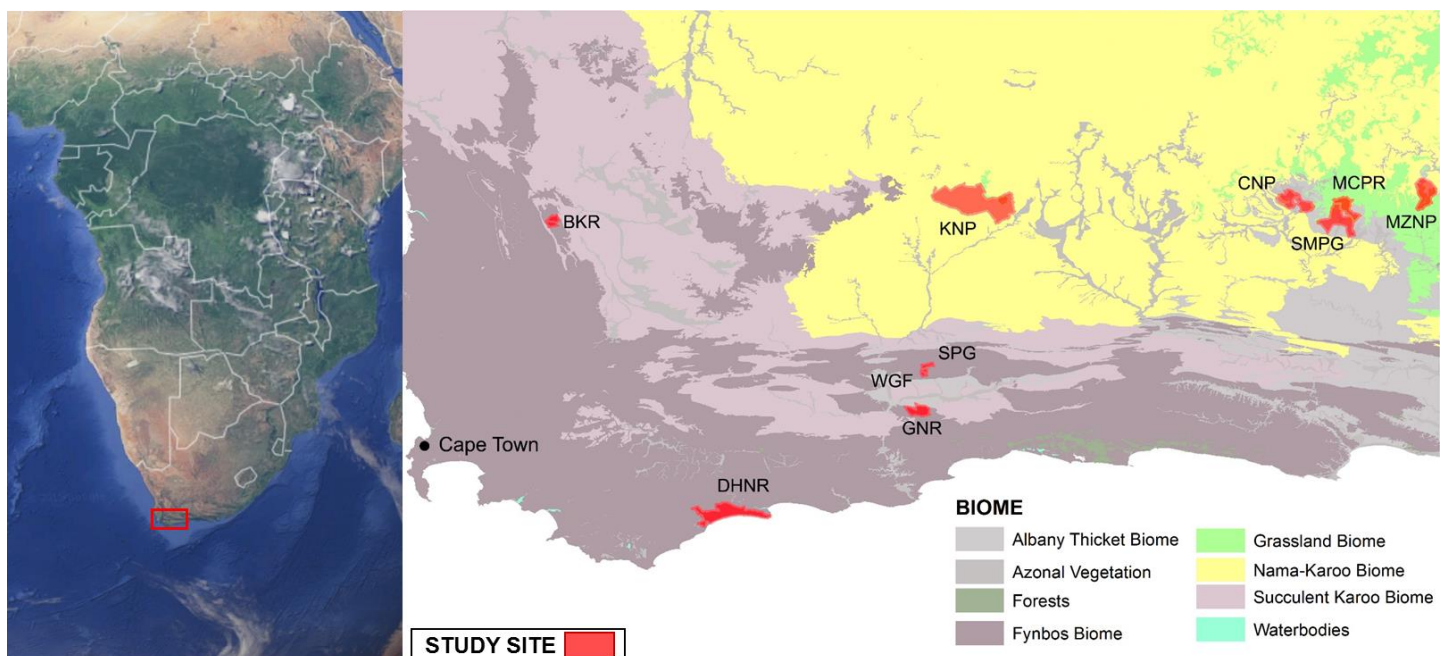


Figure 3.2 Focal Cape mountain zebra sub-populations in the Eastern and Western Cape regions of South Africa and the underlying biome in each focal population. Vegetation data gathered from Mucina and Rutherford (2006). Reserves abbreviated as follows: Bakkrens Nature Reserve (BKR), Camdeboo National Park (CNP), De Hoop Nature Reserve (DHNR), Gamkaberg Nature Reserve (GNR), Karoo National Park (KNP), Mount Camdeboo Private Reserve (MCPR), Mountain Zebra National Park (MZNP), Samara Private Game Reserve (SMPG), Swartberg Primate Game Reserve (SPG) and Welgevonden Game Farm (WGF).

3.3.2 Ecological variable extraction

Data on the abundance of palatable grass species within reserves was taken from Lea et al (*in prep*), where the percentage cover of distinct vegetation types within each reserve was calculated by overlaying reserve boundaries on the National Vegetation Map of South Africa, Lesotho and Swaziland, compiled by Mucina and Rutherford (2006). Each vegetation type/community has an associated list of common and dominant species. A standardised palatable 'grassiness' index (or vegetation index, VI) for each reserve was estimated by totalling the number of palatable Graminoid species within each vegetation community, with dominant species weighted by a factor of two. For each reserve, the richness values were multiplied by the percentage area cover of that community and summed. These scores were then standardised between zero and one across all reserves (where a zero represents no palatable grass and a one represents a high coverage of grass rich vegetation communities). The overall availability of water for each reserve was scored binomially using mean annual rainfall data from Mucina and Rutherford (2006) in conjunction with visual observations of water supplementation during field data collection, to identify reserves with limited drinking water (*i.e.* with few locations with water available year-round).

3.3.3 Social network construction

The association data from individuals within and between groups were used to construct association matrices, from which binary social networks were derived. Nodes within each of these networks are individual zebra, and ties are associations between those individuals. Data from multiple sampling events were grouped by sampling period (each approx. 1-2 weeks), which were used to construct an annual association network. Networks were only retained in subsequent analyses if they met the following criteria: A) there were at least three sampling events (range 3-9) within each sampling period for a particular population, and B) there were at least 15 individuals identified in each sample. Three networks were constructed for Mountain Zebra National Park (2012, 2013, 2014) two for Gamkaberg

Nature Reserve (2013, 2015), Mount Camdeboo Private Reserve (2013, 2015) and Samara Private Game Reserve (2010, 2011), and one for each of the remaining populations. Egonet networks were then generated from the annual networks for a subset of adult males, such that each harem male and one random male from each bachelor group was a focal individual within each egonet.

3.3.4 Social network analysis

Comparisons between association networks were made using an adapted version of the NetSimile approach (Berlingiero et al. 2012). The algorithm was modified by using ego metrics in accordance with Crossley et al. (2015) and Borgatti et al. (2013) to capture the structure and variation in the ties of adult males. Six undirected network metrics were calculated for each node and each ego network (Table 3.1) using the *igraph* package for R (Csardi and Nepusz, 2006; R Core Team, 2014). Summary statistics were then calculated for all metrics (Table 3.1). Metrics were dropped if they were highly correlated (>95%) or showed lack of variation across populations. The means and moments of each feature were collated as a signature vector for each network, which could be compared to the other networks (Berlingiero et al. 2012). Where multiple networks were available for a reserve, an average signature vector was calculated for subsequent analyses.

The metrics within each signature vector were not independent, and so the dimensions of each signature vector were reduced using a principal component analysis (PCA) with an oblimin rotation, allowing factors not to be orthogonal, using the *psych* package of R (Revelle, 2011; R Core Team, 2014; Croft et al. 2008). The component(s) retained in the ecological analysis were those with eigenvalues greater than one (Jackson, 1993). The Kaiser-Meyer-Olkin (KMO) measure of sampling adequacy was used to test the reliability of variables included within the components (Kaiser, 1970).

Initially, to verify the scalability of the signature vectors used in this analysis, the Pearson's product moment correlation coefficient of principal component scores and network size was calculated.

Table 3.1 Network metrics and summary statistics used to compare 10 independent sub-populations of Cape mountain zebra. Metrics were calculated for each network at the level of each node (all individuals) or each focal ego (a subset of adult males).

Level	Network metric	Description	Summary Statistics	Source
Node	Degree	The number of ties for node i	\bar{x} , median, σ_x , skewness, kurtosis	Berlingiero et al. (2012)
	Clustering coefficient	The local, undirected transitivity for node i	\bar{x} , median, σ_x	Berlingiero et al. (2012)
	Average clustering coefficient of each nodes ties	The average local, undirected transitivity for all ties of node i	\bar{x} , median, σ_x	Berlingiero et al. (2012)
Ego	Degree	The number of ties for ego i	\bar{x} , median, σ_x , skewness, kurtosis	Berlingiero et al. (2012)
	Index of Qualitative Variation (IQV)	The tie dispersion for ego i . The proportion of ties in each attribute category, such that if IQV = 0, all ties are in one categories and if IQV = 1, all ties are in different categories.	\bar{x} , median, σ_x , skewness, kurtosis	Crossley et al. (2015); Borgatti et al. (2013)
	Yules Q Homophily Index	A measure of the similarity of ego i to its respective ties, such that if Yules Q = -1, all ties are in different attribute categories to i and if Yules Q = 1, all ties are in the same attribute category to i .	\bar{x} , median, σ_x , skewness, kurtosis	Crossley et al. (2015); Borgatti et al. (2013)

We examined the effect of the habitat on the population structure in three ways. First, to test for the effect of habitat suitability on social network structure, we analysed the principal component scores against both water and grass availability using univariate linear models. As we calculated one signature vector for each of the ten study sites, univariate models were most appropriate, because the sample size was not sufficient to include multiple predictors or to evaluate an interaction between the habitat suitability measures. Instead, we evaluated the relationship between grass and water availability to identify a potential interaction between them. Second, we tested whether the availability of palatable grass and water affected overall network size and the proportion of adult males that were bachelors using univariate linear models. Third, we tested if grass and water availability affected the size of groups within networks using generalised linear mixed effects models (GLMMs) with Poisson distributions and a random effect of reserve in the *lme4* package of R (Bates et al. 2012). The model fit of each GLMM was estimated using marginal R^2 (Nakagawa and Schielzeth, 2013).

Lastly, to explore the effect of social network structure on population performance, we regressed the percentage increase in population size per year since the establishment of each park, the estimated population density and Foal:Mare (Lea et al. *in prep*) against the principal component scores.

3.4 Results

A total of 1012 zebra were present in all networks between 2010 and 2015 and the size of networks ranged from 17 to 269 individuals. The initial principal component analysis yielded a five-component solution, which explained 84% of the variation in the signature vectors. However, the proportion of variation explained by the third, fourth and fifth components (33% cumulative variation explained) was far less than components one and two (51 % cumulative variation explained; Table A8; Figure A4) and only five variables were contained within these three components. As a result, variables included in the third, fourth and fifth components of the initial PCA were dropped alongside variables that did not load strongly on to any component (standardised loading <0.7), or were very highly correlated. A second PCA with nine variables, yielded a two-component solution that explained 86% of the variation in the subset (Table A9; Figure A5), with a KMO score of 0.51 (Table A10), indicating adequate sampling. These two components were used in all subsequent analyse of population structure and ecology.

In principal component one, the mean clustering coefficient of each node, Yules Q Homophily index skewness and Yules Q Homophily index kurtosis loaded positively (Table A9), and the standard deviation of each nodes clustering coefficient loaded negatively (Table A9). In subsequent analyses principal component one is titled 'network *sub-structuring*', such that networks with a higher principal component one score have a higher node-wise clustering coefficient with less variation and a positively skewed, leptokurtic distribution of Yules Q homophily. In principal component two, the mean node-wise degree, the standard deviation of node wise degree, the skewness of ego degree and the kurtosis of IQV loaded positively (Table A9), and the skewness of IQV loaded negatively (Table A9).

In subsequent analysis principal component two is titled '*group variation*', such that networks with a high principal component two score will have higher and more variable node-wise degrees, positive skew in ego-wise degrees and negatively skewed, leptokurtic IQV.

3.4.1 Measures of population structure

The NetSimile approach successfully removed scaling effects as there was no significant correlation between either network *sub-structuring* or *group variation* and network size ($R = 0.06$, d.f. = 9, $p = 0.870$ and $R = 0.16$, d.f. = 9, $p = 0.654$, respectively; Figure A6).

Network sub-structuring was not correlated with the size of groups within networks ($n = 233$, $\beta = 0.13 \pm 0.07$, $z = 1.88$, $p = 0.060$, marginal $R^2 = 0.023$) or *group variation* ($R = 0.39$, d.f. = 9, $p = 0.254$). However, *Network sub-structuring* was negatively correlated with the proportion of bachelors ($R = 0.65$, d.f. = 9, $p = 0.042$). Whilst *group variation* was not associated significantly with the proportion of bachelors ($R = 0.04$, d.f. = 9, $p = 0.901$), there was a positive correlation between *group variation* and the size of groups within networks ($n = 233$, $\beta = 0.14 \pm 0.05$, $z = 2.95$, $p < 0.01$, marginal $R^2 = 0.036$). Thus, *network sub-structuring*/ bachelor proportion and group size/*group variation* measure different aspects of population structure.

3.4.2 Effect of habitat suitability on population structure

Network sub-structuring was positively correlated with grass abundance ($F = 5.70$, d.f. = 9, $p = 0.044$; Figure 3.3a) and was significantly higher in habitats in which water was freely available, compared to water-restricted habitats ($t = 2.49$, d.f. = 9, $p = 0.025$; Figure 3.3b). Furthermore, the proportion of bachelors was negatively correlated with grassiness and significantly higher in water-restricted habitats ($F = 21.54$, d.f. = 9, $p < 0.01$ and $t = -2.94$, d.f. = 9, $p = 0.02$, Figures 3.3c and 3.3d). Together, these results suggest that in reserves with a high availability of palatable grass and water, individuals

were more connected (with less variation in clustering coefficients), adult males showed greater heterophily with respect to homophily, and following this there were a smaller number of bachelors as a proportion of the total adult males. Grass availability was lower in water-limited habitats ($t = 4.58$, $d.f. = 9$, $p < 0.01$; Figure A7), and so it is likely that there is a significant interaction between the habitat suitability measures affecting *network sub-structuring* and the proportion of bachelors. There was no correlation between *group variation* and grass abundance ($F = 0.20$, $d.f. = 9$, $p = 0.664$), and no significant difference in *group variation* between water-restricted and water-rich reserves ($t = 0.72$, $d.f. = 9$, $p = 0.492$).

Overall network size was not associated with grass abundance ($F = 3.66$, $d.f. = 9$, $p = 0.092$). Groups within networks, however, were significantly larger where more palatable grass ($n = 233$, $\beta = 0.40 \pm 0.13$, $z = 2.98$, $p < 0.01$, marginal $r^2 = 0.047$) and water ($n = 233$, $\beta = 0.31 \pm 0.12$, $z = 2.64$, $p < 0.01$) were available.

3.4.3 Effect of social network structure on population performance.

Neither *Network sub-structuring* nor *Group variation* were not correlated with population density ($F = 0.04$, $d.f. = 9$, $p = 0.85$ and $F = 1.71$, $d.f. = 9$, $p = 0.227$, respectively), Population growth rate ($F = 1.99$, $d.f. = 9$, $p = 0.195$ and $F = 0.47$, $d.f. = 9$, $p = 0.513$, respectively), or Foal:Mare ($F = 4.26$, $d.f. = 9$, $p = 0.073$ and $F = 4.21$, $d.f. = 9$, $p = 0.074$, respectively).

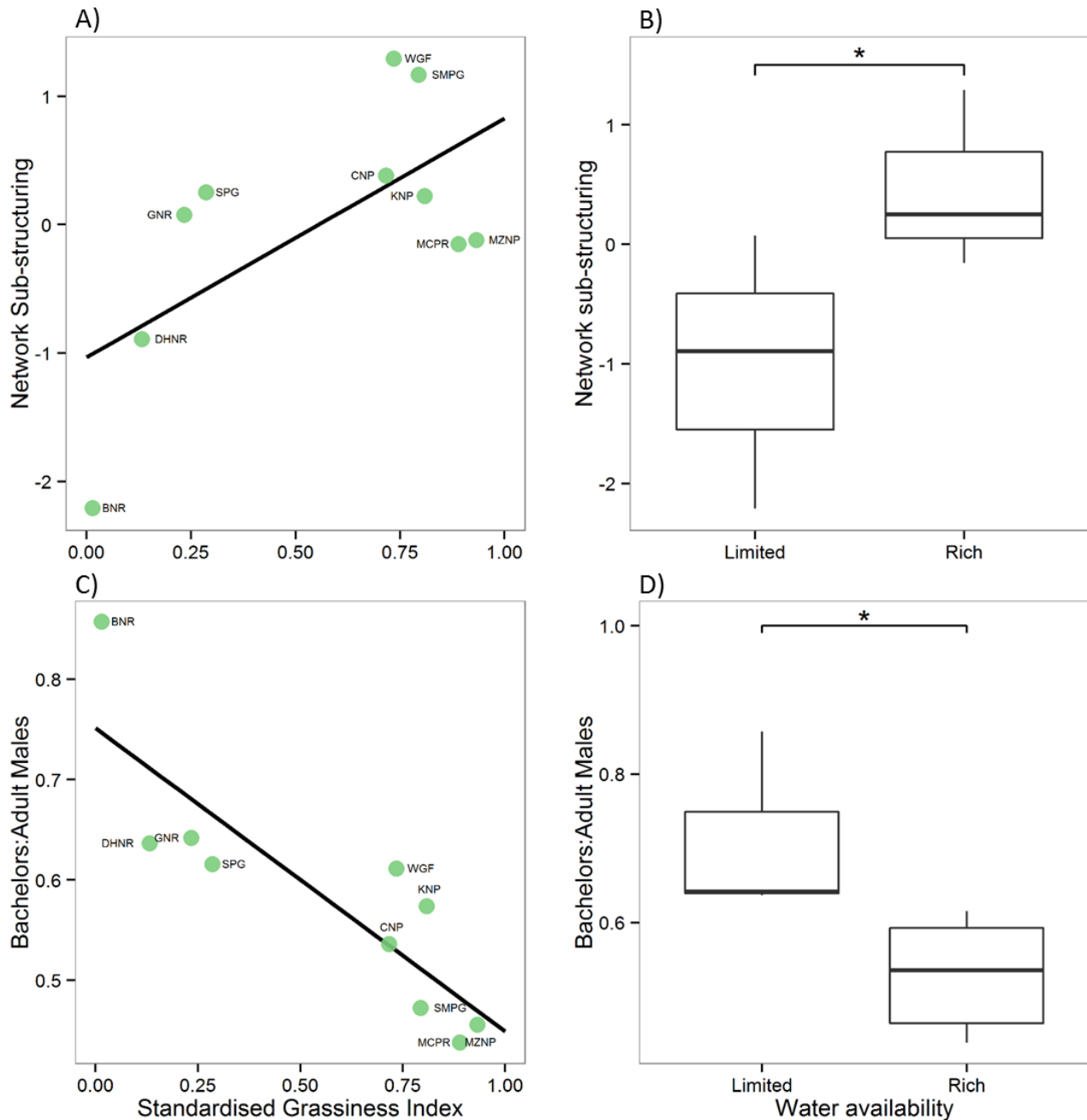


Figure 3.3 The change in population structure associated with variation in the availability of suitable habitat. A) The correlation between the availability of palatable grass and *Network sub-structuring*. B) Differences in *Network sub-structuring* between water-rich and water-limited habitats. C) The correlation between the availability of palatable grass and the proportion of adult males that were bachelors. D) Differences in the proportion of adult males that were bachelors between water-rich and water-limited habitats. Reserves are abbreviated as follows: Bakkrans Nature Reserve (BKR), Camdeboo National Park (CNP), De Hoop Nature Reserve (DHNR), Gamkaberg Nature Reserve (GNR), Karoo National Park (KNP), Mount Camdeboo Private Reserve (MCPR), Mountain Zebra National Park (MZNP), Samara Private Game Reserve (SMPG), Swartberg Primate Game Reserve (SPG) and Welgevonden Game Farm (WGF).

3.5 Discussion

Our results demonstrate that Cape mountain zebra population network structure is responsive to both ecology and demography. In reserves with a decreased availability of palatable grass and water, there were smaller groups, lower, more variable, clustering of social networks, increased homophily in adult males and a greater proportion of bachelors with respect to adult males. Moreover, these relationships were not simply an effect of network size. While network structure has been shown to vary with ecology (Foster et al. 2012; Beck et al. 2012; Henzi et al. 2009), to our knowledge no other study has compared social network structure in independent populations of the same species.

Low and variable clustering coefficients in marginal habitat is most likely the result of an increase in associations between individuals in different groups. Between-group associations can occur when population density is high or when males harass a family group. It is likely that a greater proportion of CMZ bachelors in marginal habitats increases the disturbance to other groups, reducing group cohesiveness and therefore individual connectivity. The cause of biases in the proportion of bachelors is unknown: it could result from biased birth sex ratios or from higher mare mortality in marginal habitats. There is strong incentive for bachelors to establish new, or take over existing, family groups (Novellie, 2008). Male harassment has been identified as a key driver of female associations in Grevy's zebra and bachelor disturbance and aggression is well documented in equids and can lead to reproductive failure (Sundaresan et al. 2007b; Rubenstein, 1994). Thus, a high proportion of bachelor males in the population can destabilise network structure by breaking down cohesive family groups.

Critically for conservation management, we have demonstrated that social networks may be able to elucidate how marginality impacts on population structure and performance. Furthermore, a breakdown in population structure may be an important mechanism by which Allee effects cause low-density populations to enter an extinction vortex. In the zebra populations, the impact of habitat on sub-structuring was most obvious in the two reserves with the lowest abundance of grass (Bakkrans Nature Reserve and De Hoop Nature Reserve). One could speculate that social structure is relatively

robust apart from in populations in extremely marginal habitats. Cape mountain zebra have recently been introduced into a number of habitats with low grass availability (Hrabar and Kerley, 2015). Although these populations are within the Cape mountain zebra's historic distribution, they have shown poor population growth, have male-biased sex ratios and less structured social networks (Lea et al. *in prep*).

Ecology has been identified as a key driver of group sizes of many species, including equids (Jarman, 1974; Janson and Goldsmith, 1995; Rubenstein, 1994). This is generally accepted to be because a greater abundance of resources can sustain larger groups with reduced competition (Krause and Ruxton, 2002). Highly social mammals such as primates and cetaceans may experience changes to connectivity as a result of travelling further distances to forage, reducing the time available to associate with other individuals (Janson and Goldsmith, 1995; Foster et al. 2012). Similar break down in structure associated with resource limitation has been found in several other species, including orca (Foster et al. 2012), onagers (Sundarasan et al. 2007a), and baboons (Henzi et al 2009).

The subtle changes in social network structure associated with the variation in habitat availability in the current work will ultimately have knock-on effects for population performance. However, in this relatively small subset of ten CMZ sub-populations, we found no effect of social network structure on population performance. As with all results in this study, caution is needed when drawing statistical inference from data with a small sample size. The practical limitations of obtaining social network data prevented sampling in further sub-populations, which would further elucidate on the breakdown of social structure in marginal areas. Our confidence is improved as the reserves with the poorest population performance were also those in marginal habitat (Lea et al. *in prep*), and decreased connectivity and a greater proportion of non-breeding bachelors in these areas are most likely to reduce performance. The results in the current study underscore the importance of understanding both population structure and performance and how this relates to pressures facing the populations when developing conservation strategies.

There are several further implications for conservation and population management that can be taken from this work. First, there is natural variation in social structure within species that is important to understand when assessing species characteristics. Second, social network structure can be used as a tool in conjunction with demographics to help elucidate the long-term stability and future performance of a population. Third, the potential impact of different harvesting, off-takes and translocations strategies should be considered in light of the impact on the source population demographics. Leaving, or creating, biased sex-ratios may undermine population health and slow recovery rates.

Chapter 4

Thesis Discussion

4.1 How do animals respond to environmental change?

The results presented in this body of work have demonstrated that environmental variation impacts upon both local population dynamics temporally and spatially in passerines, and on social structure spatially in CMZ. In chapter two, the biological traits and environmental changes associated with local colonisation and extirpation in British passerines was investigated. Between 1970 and 1990, rare species with highly fragmented ranges were the most likely to undergo local population declines. Furthermore, unchanging landscapes dominated by one land use type struggled to maintain passerine diversity. Land use was more predictive of local colonisation and extirpation process than climate change at a 10km² spatial resolution. Predicting how a large group of species with a variety of biological traits respond to changes in habitat and climate has provided results that have direct relevance for the conservation management of passerines at the landscape scale. Specifically, future management strategies should aim to increase and maintain diverse interconnected habitat networks allowing a variety of species to access a variety of habitat types. The connectivity of a diverse range of habitats will allow previously unconnected sub-populations to form stable population networks that are resistant to environmental change (Carroll et al. 2010; Newson et al. 2014).

In chapter three, association data from ten independent sub-populations of CMZ was used to test how spatial variation in the availability of suitable habitat influences social network structure. In mesic reserves with a greater abundance of palatable grass species there were larger groups, a smaller proportion of bachelors, more connected individuals and a greater proportion of heterophily with respect to homophily in adult males. Social network comparisons have revealed the subtle differences in social network structure that are associated with confinement to marginal habitat. Again, this has provided further empirical evidence that has direct relevance for the management of CMZ. In concurrence with all recent studies documenting the habitat preferences of CMZ, priority needs to shift from mountainous regions of the CFR dominated by fynbos vegetation to mesic areas with a

greater abundance of palatable grass (Weel et al. 2015; Lea et al. *in prep*; Faith, 2012). A number of sub-populations of CMZ, particularly those in the Eastern Cape such as Mountain Zebra National Park, are thriving and have fully recovered from the population crash that saw CMZ near extinction in the 1970s (Lea et al. *in prep*). The problem remains that although there has been a large conservation management effort for CMZ, many of the areas that have had reintroductions have struggled to maintain self-sufficient populations (Hrabar and Kerley, 2015). Expensive transport of zebra to new reserves and the supplementation of struggling populations could be alleviated if grassland habitats were reclaimed and prioritised. A potential solution would be to reclaim disused agricultural land in lowland areas of the CFR, however overgrazing in such areas has affected the availability of natural grassland habitat, and potential sites would need to be assessed for their habitat suitability (Faith, 2012). Another strategy that is being adopted is the systematic burning of fynbos vegetation to promote the growth of Graminoid species, however this also transforms the landscape and may prevent locally adapted species from thriving (Lea et al. *in prep*).

Unfortunately, anthropogenic interests are often in direct conflict with ecosystems. Areas with high primary productivity and a rich species diversity are also of interest for agricultural development, and anthropogenic interests will often overshadow the needs of biodiversity (Balmford et al. 2001). Economic and commercial interests may limit the efficiency of conservation management strategies, but the accumulation of empirical evidence documenting species responses to environmental change will ultimately allow better management decisions to be made in the future. There are good examples of where habitat preference and the variation in population performance across a species distribution have been used to inform management (Redford et al. 2011). Aldridge and Boyce (2007) used a detailed spatial modelling approach to inform the conservation of the threatened greater sage-grouse in Alberta, Canada. Spatially explicit data documenting brood and nest sites were combined with a suite of ecological predictors such as anthropogenic activity and habitat availability to highlight priority

areas to be targeted with management (Aldridge and Boyce, 2007). An alternative approach has been to collate expert information to identify priority areas (Thorbjarnarson et al. 2006; Leblond et al. 2014). While this approach can provide valuable, relatively inexpensive information to be used for conservation management, there is a need to move to methods looking beyond anecdotal and experienced based information (Legge, 2015). Indeed, this is the key issue for refugee species such as the European bison; human perception of habitat preference has misinformed management (Kerley et al. 2012). The development of more sophisticated spatially explicit modelling frameworks, such as those used in the current work, now means that thorough, systematic studies highlighting habitat preference separately from anthropogenic biases can be used to inform management. The current work has used empirical analysis to highlight landscapes or habitats that are most suitable for species persistence without the use of experience based information. This is a key step that needs to be taken in management strategies of the future.

4.2 Future directions

Both studies presented in this thesis have the potential to be expanded for future research. For the study of British passerines, a key advancement that could be made that could be used to inform how environmental variation influences local population dynamics is through the use of more recent Passerine occupancy data at a spatial resolution of 2km² (Balmer et al. 2013). The incorporation of this data could provide two new avenues for research to provide more detail about how passerines respond to environmental change. The first would be to extrapolate occupancy data for a similar subset of species at a resolution of 10 km² to understand in more depth how occupancy varies over a longer time scale. Comparing occupancy and environmental data from 1960 to 2011, it can be predicted that climate changes would have a greater impact on population dynamics, as this is hypothesised to be the key predictor of range changes over a longer time scale (Alagador et al. 2014). The second avenue of research would be to analyse more recent occupancy data with respect to

environmental variation at the finer spatial resolution achieved in this atlas. Doing so would reveal more detail in how land use varies at a finer spatial scale. It can be predicted that this would reveal much finer scale habitat mosaics that influence occupancy even with a 10km grid square.

The study of British passerines was limited in both the ecological breadth of predictors, and the use of binary occupancy data to summarise occupancy dynamics across the study periods. The first issue could be addressed by performing analyses on a smaller subset of closely related passerine species with similar traits. The occupancy of this smaller subset of species could be modelled with respect to a wider variety of habitat and climatic predictors at the landscape scale, to identify how subtle variation in the local environment influences occupancy. The second issue could be addressed in two main ways. Indirectly, the incorporation of population record data for this group of passerines would distinguish between rare and common species more efficiently. Directly, this issue could be addressed by developing a modelling framework that incorporated a continuous response term with the average number of breeding pairs seen per year in a grid square over the study period.

More broadly, the use of a spatially and temporally explicit modelling approach can be applied to any group of species in which occupancy and distribution has been recorded alongside environmental changes. Range changes have been analysed with respect to environmental change in invertebrates such as ladybirds and butterflies and in plants (Wilson et al. 2004; Comont et al. 2012). However, local population processes in vertebrates can also be analysed in this way, providing that occupancy has been recorded at a high enough spatial resolution. Another key area that needs to be addressed regarding occupancy change is the relationship between local population processes and overall population changes. While local population declines are a prerequisite for overall decline, how local population changes influence overall decline remains unclear (Collen et al. 2011). Indeed, biological traits were far more predictive at the regional level than locally in the current work. Future research may analyse local occupancy change with respect to overall population changes rather than just

occupancy, to pull apart the key features of local occupancy changes that drive widespread population declines.

The results from CMZ provide evidence that population structure varies depending on the availability of suitable habitat, and this will apply to many species that exhibit variation in population performance across their meta-population. The variation in social structure will ultimately have knock-on effects for population performance, which also depends on ecological variation (Lea et al. *in prep*). However, demographic stochasticity, translocations and newly established populations all mean that the relationship between population performance and social structure could not be elucidated in such a small number of sub-populations of CMZ. Future work would examine how social structure and population performance interact in more detail, by collecting social network data for a greater number of sub-populations.

A key feature of CMZ social network structure in sub-optimal habitat was the degradation of individual connectivity. Individuals were less connected on average in marginal habitat. This raises questions about the individual connectivity of CMZ and the stability of social groups. Future research projects may analyse a single sub-population in more detail over a much longer period of time. From here the affinity of individuals to harem and bachelor groups could be elucidated, which influences the formation of novel family groups. Two sub-populations that occur in optimal and marginal habitats, respectively could be compared to group cohesion and stability.

4.3 Conclusions

Ultimately, without significant socio-economic changes in human society, widespread recovery of the world's ecosystems is unlikely. However, understanding how animals respond to environmental change can provide valuable information that can be used in the formation of efficient, effective conservation strategies. This thesis has demonstrated the value of using biological understanding to

inform conservation. The development of efficient, effective management strategies will only increase in importance as human populations rise.

Appendices

Supplementary information for chapter 2.

A1. Environmental predictors used in square-level extinction and colonisation models of passerine colonization and extinction between 1968-72 and 1988-91 in Great Britain

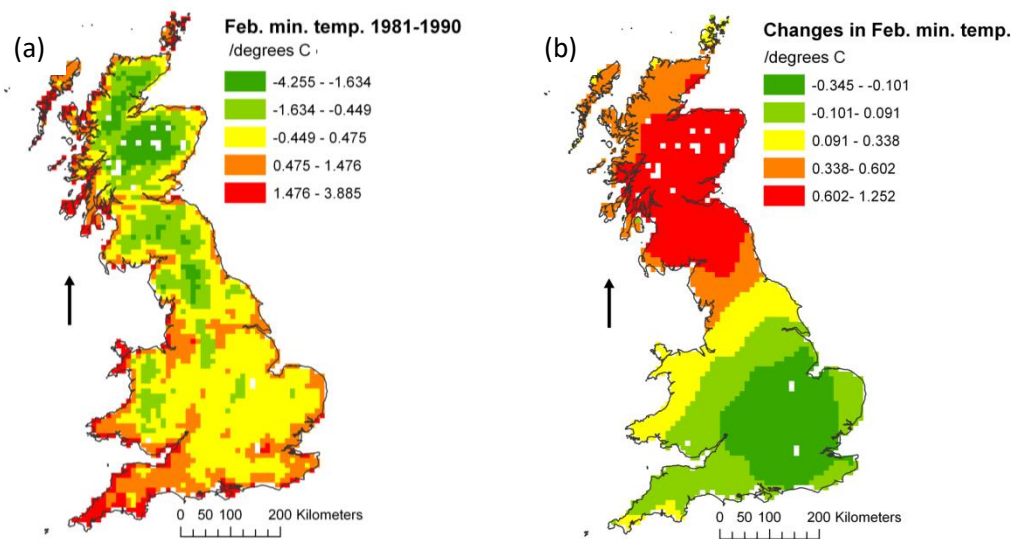


Fig. A1. Geographic distribution of (a) average February minimum temperatures 1981-1990 (b) changes in average February minimum temperatures (between the 1961-1970 and 1971-1980 periods) across the study region. In both panels white grid squares are those missing environmental or bird data in one or both periods.

Average February minimum temperatures were highest in 1981-1990 in south England and Wales and in coastal areas up and down Great Britain (Figure A1a). The lowest February minimum temperatures in 1981-1990 were found in Scotland and in upland areas of England and Wales. By contrast the largest increases in February minimum temperature were found in Scotland and north England whilst some areas of the south east of England decreased in February minimum temperature between the study periods (Figure A1b).

Urban cover was highest in 1990 in England in the central and south-east around London and Birmingham, in north England around Manchester and Liverpool and in the central belt of Scotland between Glasgow and Edinburgh. In these centres, urban cover continued to increase between the study periods but decreased in most other regions of England and remained stable in Scotland (top panel, Figure A2).

Woodland cover was highest in 1990 in pockets of south-east England and central and north Wales and across many areas of Scotland. Increases in woodland cover were concentrated in these same geographic areas (middle panel, Figure A2).

Farmland cover (including arable but excluding livestock farming types) was relatively high in 1990 in north and north east Scotland (particularly along the coast), in east England and in central and south east England. Increases in farmland cover were concentrated in these same geographic areas (bottom panel, Figure A2).

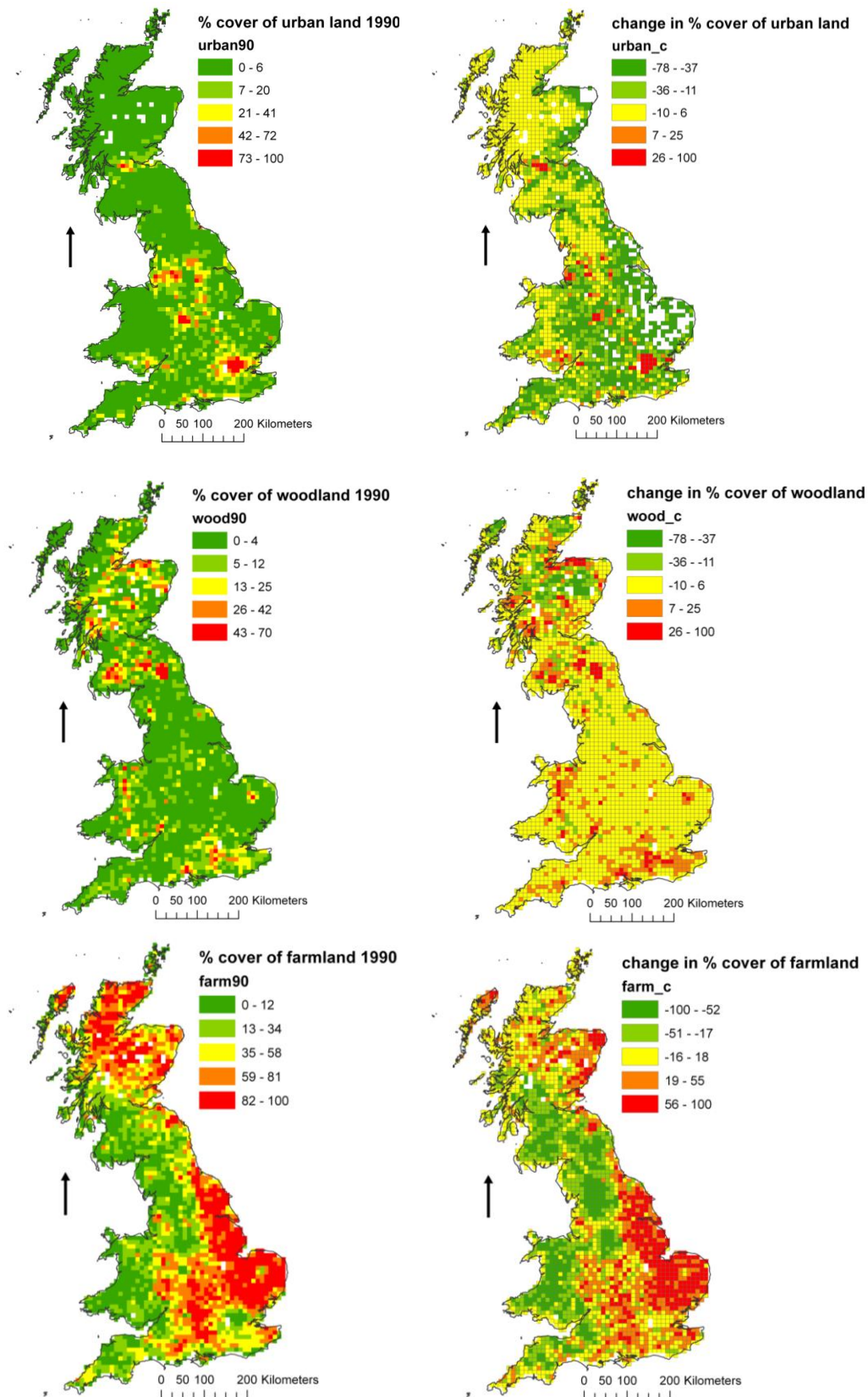


Figure A2. Geographic distribution of urban, woodland and farmland cover and land cover changes per hectad across the study region. The right hand panels show the values of land cover predictors in the second time period, between 1981 and 1990 and the left hand panels depict the difference in these predictors between the first (1961-1970, represented by 1960 Ecochange Land Cover map) and second (1971-1980, represented by the

1990 CEH Land Cover Map) periods. In all panels, white grid squares are those missing environmental or bird data in one or both periods.

A2. Step-wise model selection for key environmental and trait predictors for local **passerine extinction and colonisation between 1968-72 and 1988-91 in **Great Britain****

In each step of the selection process, the model with the lowest BIC score was carried forward. Each of these models is highlighted in bold. All models include a term for population connectivity to account for spatial autocorrelation. An additional term of model weight was included to estimate the relative importance of each of the model combinations with respect to the others based on BIC differences (Burnham et al. 1995). The relative weight of evidence for each candidate model was calculated using:

$$wi = \frac{\exp(-\frac{1}{2}\Delta iBIC)}{\sum \exp(-\frac{1}{2}\Delta iBIC)}$$

For *environment* models predicting passerine colonisation, there was little difference in model weighting between the top five models (Table A1b & Table A2a). Based on the change in BIC when each of the variables in the best-fit model were dropped, we believe that the closeness in model weighting and BIC scores can be explained by the marginal effect of temperature 1990 within the best model (Table 2.3a). The model BIC is penalised heavily for the inclusion of the additional temperature variable, but the explanatory power of the best model is not significantly better than that without temperature, thus the weight of the best model is not higher.

Colonisation model selection

We first selected the best-fit trait-only model, which included population connectivity and range size (Table A1a). When this model was taken forward to include environment and trait variables; the best ‘main effect model’ retained open, forest and urban cover; changes in urban, open and arable cover; and temperature (Table A1b). We then incorporated biologically relevant trait-environment interactions into the model (Table A3). The same model was selected regardless of whether traits or environmental factors were evaluated first (Table A2). The retained interactions were between range size and open cover and range size and arable change (Table A3; Table 2.3a).

Extinction model selection

As with the colonisation models, the trait-only model for extinction included population connectivity and range size (Table A4a). The environmental variables added were: open, arable and urban cover, and open, urban and arable change (Table A4b). Again, the same trait and environmental variables were selected regardless of order (Table A5). The final model added interactions between range size and both arable and urban cover (Table A6; Table 2.3b).

Table A1. Predictors, log-likelihoods and information criterion for five top models **of passerine colonization between 1968-72 and 1988-91 in Great Britain** from steps 1 and 2 of order 1. Key to predictor abbreviations is given in table 1. Models in bold are those taken forward to the next stage (or the final model). All models include Population Connectivity as one of the model terms.

(a) Step 1, order 1, trait only models

nvar	LL	AIC	BIC	ΔBIC	Model weight	predictors in model			
2	-10341.5	20693.0	20735.8	0.0	0.966	Population Connectivity	+	Range size	
3	-10340.5	20693.0	20744.3	8.5	0.014	Population Connectivity	+	Log10(Average body weight)	+ Range size
3	-10341.0	20694.0	20745.4	9.6	0.008	Population Connectivity	+	Average first clutch period	+ Range size
3	-10341.1	20694.1	20745.5	9.7	0.008	Population Connectivity	+	Average laying date	+ Range size
3	-10341.5	20695.0	20746.4	10.6	0.005	Population Connectivity	+	Average weight at birth	+ Range size

(b) Step 2, order 1, trait + environment models

nvar	LL	AIC	BIC	ΔBIC	Model weight	predictors in model ~ Range size +				
8	-10288.2	20600.5	20703.2	0.0	0.297	Population Connectivity	+	Urban change	+	Urban cover 90
						Temperature 90	+	Open cover 90	+	Arable change
						Population Connectivity	+	Urban change	+	Urban cover 90
7	-10293.7	20609.5	20703.6	0.4	0.242	Open change	+	Open cover 90	+	Arable change
7	-10293.9	20609.7	20703.9	0.7	0.209	Population Connectivity	+	Urban change	+	Urban cover 90
						Temperature 90	+	Open cover 90	+	Open change
						Population Connectivity	+	Urban change	+	Urban cover 90
6	-10299.3	20618.6	20704.2	1.0	0.178	Open change	+	Open cover 90	+	Forest cover 90
						Population Connectivity	+	Urban change	+	Urban cover 90
						Population Connectivity	+	Urban change	+	Urban cover 90
8	-10289.6	20603.2	20706.0	2.8	0.075	Forest change	+	Temperature 90	+	Open cover 90

Table A2. Predictors, log-likelihoods and information criterion for five top models **of passerine colonization between 1968-72 and 1988-91 in Great Britain** from steps 1 and 2 of order 2. Key to predictor abbreviations is given in table 1. Models in bold are those taken forward to the next stage (or the final model). All models include Population Connectivity as one of the model terms.

<i>(a) Step 1, order 2, environment only models</i>											
nvar	LL	AIC	BIC	ΔBIC	Model weight	predictors in model					
8	-10313.1	20648.2	20742.4	0.0	0.251	Population Connectivity	+	Urban change	+	Urban cover 90	+
						Temperature 90	+	Open cover 90	+	Arable change	+
7	-10318.4	20656.8	20742.4	0.04	0.246	Population Connectivity	+	Urban change	+	Urban cover 90	+
						Open cover 90	+	Arable change	+	Open change	
6	-10323.8	20665.6	20742.6	0.2	0.222	Population Connectivity	+	Urban change	+	Urban cover 90	+
						Open cover 90	+	Open change			
7	-10318.5	20657.0	20742.6	0.3	0.218	Population Connectivity	+	Urban change	+	Urban cover 90	+
						Temperature 90	+	Open cover 90	+	Open change	
4	-10335.6	20685.2	20745.1	2.8	0.063	Population Connectivity	+	Forest cover 90		Open cover 90	+
										Open change	
<i>(b) Step 2, order 2, environment + trait models</i>											
nvar	LL	AIC	BIC	ΔBIC	Model weight	predictors in model ~ Urban change + Urban cover 90 + Forest cover 90 + Temperature 90 + Open cover 90 + Arable change 90 + Open change +					
2	-10288.2	20600.5	20703.2	0.0	0.969	Population Connectivity	+	Range size			
3	-10287.2	20600.5	20711.8	8.6	0.013	Population Connectivity	+	Log10(Average body weight)	+	Range size	
3	-10287.9	20601.9	20713.2	10.0	0.007	Population Connectivity	+	Average first clutch period	+	Range size	
3	-10288.0	20602.0	20713.3	10.1	0.006	Population Connectivity	+	Average laying date	+	Range size	
3	-10288.2	20602.5	20713.8	10.6	0.005	Population Connectivity	+	Average weight at birth	+	Range size	

Table A3. Predictors, log-likelihoods and information criterion for five top interaction models **of passerine colonization between 1968-72 and 1988-91 in Great Britain**, from step 3. Key to predictor abbreviations is given in table 1. Models in bold are those taken forward to the next stage (or the final model). All models include Population Connectivity as one of the model terms.

(c) Step 3, trait + environment + trait:environment interaction models

nvar	LL	AIC	BIC	ΔBIC	Model weight	predictors in model ~ Population Connectivity + Range size + Urban change + Urban cover 90 + Forest cover 90 + Temperature 90 + Open cover 90 + Arable change 90 + Open change +			
2	-10260.3	20548.7	20668.5	0.0	0.833	Range size:Open cover 90	+	Range size: Arable change	
2	-10262.7	20553.3	20673.2	4.7	0.080	Range size:Open cover 90	+	Range size:Open change	
1	-10268.3	20562.7	20674.0	5.4	0.055	Range size:Open cover 90			
3	-10259.0	20548.0	20676.4	7.9	0.016	Range size:Forest cover 90	+	Range size:Open cover 90	+ Range size: Arable change
3	-10259.0	20548.0	20676.4	7.9	0.016	Range size:Forest cover 90	+	Range size:Open cover 90	+ Range size:Open change

Table A4. Predictors, log-likelihoods and information criterion for five top models **of passerine extinction between 1968-72 and 1988-91 in Great Britain** from steps 1 and 2 of order 1. Key to predictor abbreviations is given in table 1. Models in bold are those taken forward to the next stage (or the final model). All models include Population Connectivity as one of the model terms.

(a) Step 1, order 1, <i>trait only models</i>													
nvar	LL	AIC	BIC	ΔBIC	Model weight	predictors in model							
2	-19383.0	38776.1	38823.2	0.0	0.911	Population Connectivity	+	Range Size					
3	-19379.9	38771.9	38828.4	5.2	0.067	Population Connectivity	+	Log10(Average body weight)	+	Range Size			
3	-19381.5	38774.9	38831.4	8.3	0.015	Population Connectivity	+	Average laying date	+	Range Size			
3	-19382.6	38777.2	38833.7	10.5	0.005	Population Connectivity	+	Average weight at birth	+	Range Size			
3	-19383.0	38778.1	38834.6	11.4	0.003	Population Connectivity	+	Average first clutch period	+	Range Size			
(b) Step 2, order 1, <i>trait + environment models</i>													
nvar	LL	AIC	BIC	ΔBIC	Model weight	predictors in model ~ Range Size +							
7	-19250.7	38523.3	38626.9	0.0	0.704	Population Connectivity	+	Urban change	+	Urban cover 90	+	Arable cover 90	+
						Open cover 90	+	Arable change	+	Open change			
8	-19246.5	38517.0	38630.0	3.11	0.149	Population Connectivity	+	Urban change	+	Urban cover 90	+	Arable cover 90	+
						Arable change	+	Open cover 90	+	Open change	+	Forest change	
6	-19258.8	38537.6	38631.8	4.9	0.061	Population Connectivity	+	Forest change	+	Urban cover 90	+	Arable cover 90	+
						Open cover 90	+	Open change					
6	-19258.9	38537.7	38631.9	5.0	0.058	Population Connectivity	+	Forest change	+	Urban cover 90	+	Arable cover 90	+
						Open cover 90	+	Arable change					
5	-19265.3	38548.7	38633.4	6.5	0.027	Population Connectivity	+	Urban cover 90	+	Arable cover 90	+	Open cover 90	+
						Open change							

Table A5. Predictors, log-likelihoods and information criterion for five top models **of passerine extinction between 1968-72 and 1988-91 in Great Britain** from steps 1 and 2 of order 2. Key to predictor abbreviations is given in table 1. Models in bold are those taken forward to the next stage (or the final model). All models include Population Connectivity as one of the model terms.

(a) Step 1, order 2, environment only models										
nvar	LL	AIC	BIC	ΔBIC	Model weight	predictors in model				
7	-19273.0	38566.0	38660.2	0.0	0.696	Population Connectivity	+	Urban change	+	Urban cover 90
						Open cover 90	+	Arable change	+	Open change
8	-19268.8	38559.6	38663.1	2.9	0.160	Population Connectivity	+	Urban change	+	Urban cover 90
						Arable change	+	Open cover 90	+	Open change
6	-19281.2	38580.3	38665.1	4.9	0.061	Population Connectivity	+	Forest change	+	Urban cover 90
						Open cover 90	+	Open change	+	Arable cover 90
6	-19281.2	38580.5	38665.2	5.0	0.056	Population Connectivity	+	Forest change	+	Urban cover 90
						Open cover 90	+	Arable change	+	Arable cover 90
5	-19287.7	38591.4	38666.7	6.5	0.027	Population Connectivity	+	Urban cover 90	+	Arable cover 90
						Open change	+	Open cover 90	+	Open cover 90
(b) Step 2, order 2, environment + trait models										
nvar	LL	AIC	BIC	ΔBIC	Model weight	predictors in model ~ Urban change + Urban cover 90 + Arable cover 90 + Open cover 90 + Arable change + Open change +				
2	-19250.7	38523.3	38626.9	0.0	0.915	Population Connectivity	+	Range Size		
3	-19247.7	38519.3	38632.3	5.4	0.062	Population Connectivity	+	Log10(Average body weight)	+	Range Size
3	-19249.0	38522.1	38635.1	8.2	0.015	Population Connectivity	+	Average laying date	+	Range Size
3	-19250.1	38524.3	38637.3	10.4	0.005	Population Connectivity	+	Average weight at birth	+	Range Size
3	-19250.6	38525.3	38638.3	11.4	0.003	Population Connectivity	+	Average first clutch period	+	Range Size

Table A6. Predictors, log-likelihoods and information criterion for five top interaction models **of passerine extinction between 1968-72 and 1988-91 in Great Britain**, from step 3. Key to predictor abbreviations is given in table 1. Models in bold are those taken forward to the next stage (or the final model). All models include Population Connectivity as one of the model terms.

<i>(c) Step 3, order 1, trait + environment + trait:environment interaction models</i>										
nvar	LL	AIC	BIC	ΔBIC	Model weight	predictors in model ~ Population Connectivity + Range Size + Urban change + Urban cover 90 + Arable cover 90 + Temperature 90 + Open cover 90 + Arable change + Open change +				
3	-19110.6	38249.3	38381.1	0.0	0.663	Range Size:Urban cover 90	+	Range Size:Arable cover 90	+	Range Size:Open change
3	-19112.1	38252.2	38384.0	2.9	0.155	Range Size:Urban cover 90	+	Range Size:Arable cover 90	+	Range Size:Arable change
4	-19106.6	38243.2	38384.4	3.3	0.128	Range Size:Urban cover 90	+	Range Size:Arable cover 90	+	Range Size:Open cover 90 + Range Size:Open change
4	-19107.9	38245.9	38387.1	6.0	0.033	Range Size:Arable cover 90	+	Range Size:Open cover 90	+	Range Size:Open change + Range Size:Urban change
4	-19108.4	38246.7	38388.0	6.9	0.021	Range Size:Urban cover 90	+	Range Size:Arable cover 90	+	Range Size:Open cover 90 + Range Size:Arable change

A3. Linear relationships between land cover proportions in each of the grid squares in 1990 and the respective cover change in that grid square.

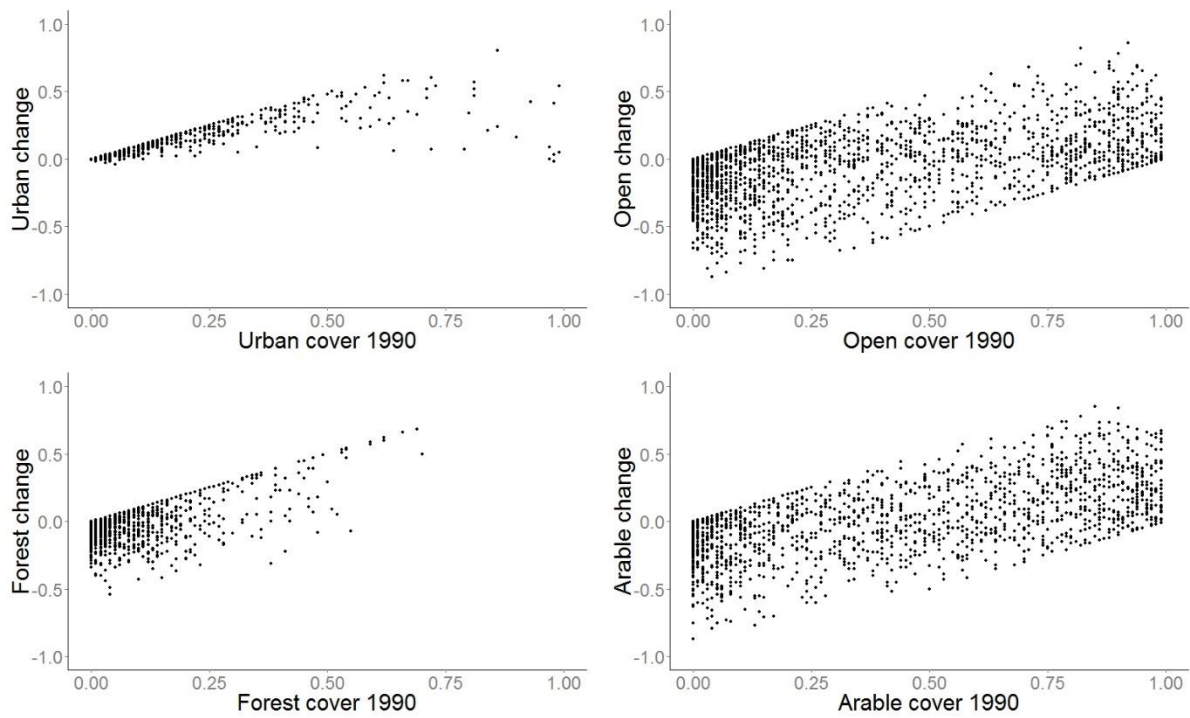


Figure A3. Linear relationships between the proportions of each of the land cover variables in each grid square with their respective cover change in the same grid square.

Table A7. Table of coefficients from glmmPQL binomial model of impacts of trait, environment predictors and their interactions with spatial Matern correlation term and family as a random effect on *spatial patterns in a) colonisation and b) extinction events* of passerines between 1968-72 and 1988-91 in Great Britain.

a.	Coefficient	Z	p-value
(Intercept)	-29.8 +/- 4.24	-7.03	<0.001
Population Connectivity	2.33 +/- 0.04	56.40	<0.001
Range size†	-4.47 +/- 0.68	-6.61	<0.001
Open cover 1990†	-1.11 +/- 0.30	-3.71	<0.001
Range size: Open cover 1990	-1.45 +/- 0.19	-7.51	<0.001
Forest cover 1990	0.25 +/- 0.04	7.07	<0.001
Open change	1.72 +/- 0.28	6.06	<0.001
Urban change	4.26 +/- 0.66	6.49	<0.001
Urban cover 1990	-6.31 +/- 1.11	-5.66	<0.001
Arable change†	0.99 +/- 0.30	3.36	<0.001
Range Size: Arable change	-0.45 +/- 0.11	-4.12	<0.001
Temperature 1990	-0.07 +/- 0.02	-3.17	0.002
Random effects:			
Groups	Name	Variance	Std.Dev.
Species	(Intercept)	0.557	0.747
Grid square	(Intercept)	0.846	0.920

b.	Coefficient	T	p-value
(Intercept)	49.29 +/- 2.74	17.97	<0.001
Population Connectivity	-1.85 +/- 0.03	-58.05	<0.001
Arable cover 1990†	2.79 +/- 0.21	13.48	<0.001
Range size†	-17.51 +/- 1.25	-13.94	<0.001
Open cover 1990	3.75 +/- 0.19	20.02	<0.001
Range size: Arable cover 1990	-2.04 +/- 0.15	-13.83	<0.001
Urban cover 1990†	6.87 +/- 0.56	12.22	<0.001
Range size: Urban cover 1990	-2.67 +/- 0.29	-8.95	<0.001
Open change†	-0.85 +/- 0.11	-7.64	<0.001
Range size: Open change	-0.38 +/- 0.05	-7.30	<0.001
Urban change	-2.50 +/- 0.29	-8.68	<0.001
Arable change	-0.56 +/- 0.12	-4.86	<0.001
Random effects (Std.Dev):			
Groups	Name	Intercept	Residual
Family	Std.Dev.	0.28	
Species w/in			
Family		0.62	0.90

Supplementary information for chapter 3

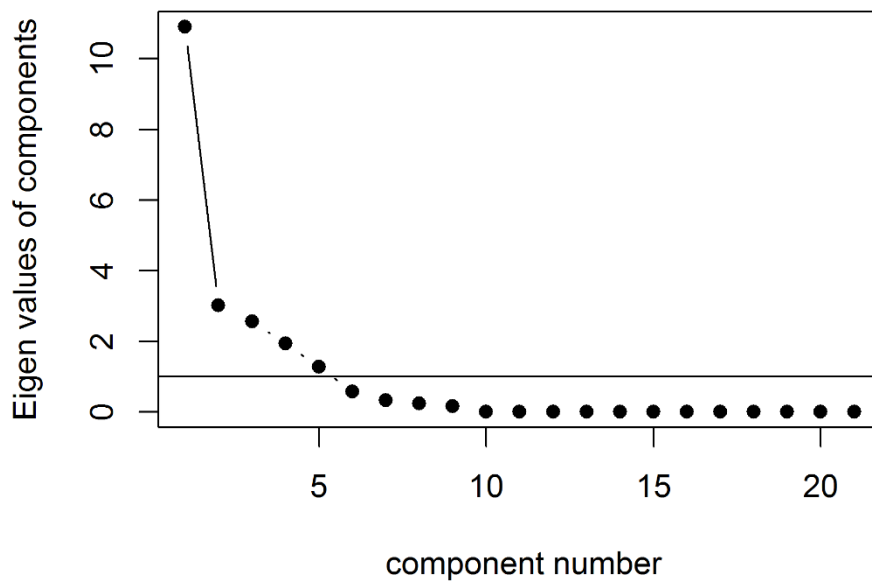


Figure A4. Scree plot of the change in Eigen values against the increase in the number of components for a principal component analysis of 25 network feature statistics characterising Cape mountain zebra populations.

Signature feature abbreviations

Network metric

- D** node-wise degree
- T** node-wise clustering coefficient
- aT** average clustering coefficient of each nodes ties
- ED** ego degree
- IQV** ego tie dispersion – Index of Qualitative variation (IQV)
- YQ** ego:alter similarity – Yules Q Homophily index

Summary statistic

- mn** mean
- md** median
- sd** standard deviation
- sk** skewness
- k** kurtosis

Table A8. Standardised loadings from a principal component analysis of 25 signature vector features from ten Cape mountain zebra populations. Factors and loadings highlighted in red are those excluded from subsequent analyses, which includes any factor with a loading < 0.7 in any component, any factor that was highly correlated with other factors ($R > 0.95$), and any factor in components three, four and five.

Factor	Standardised loading				
	PC1	PC2	PC3	PC4	PC5
Dmn	0.24	0.86	-0.03	0.00	0.18
Dmd	-0.02	0.55	0.04	0.44	0.42
Dsd	0.06	0.97	0.04	-0.05	-0.04
Dsk	0.37	0.14	0.13	0.66	0.26
Dk	-0.28	-0.26	0.02	0.91	0.00
Tmn	0.88	-0.03	0.17	0.11	0.15
Tsd	-0.98	-0.14	0.17	-0.02	0.10
aTmn	0.86	-0.05	0.22	0.09	0.15
aTmd	0.58	-0.23	0.63	0.04	0.16
aTsd	-0.98	-0.15	0.21	-0.02	0.12
EDmn	0.31	0.42	-0.01	0.15	0.64
EDmd	-0.25	-0.21	-0.11	0.18	0.88
EDsd	-0.15	1.02	0.03	-0.12	-0.02
EDsk	0.32	0.77	-0.10	0.13	0.18
EDk	0.28	0.61	0.01	0.64	-0.04
IQVmn	-0.26	0.43	0.80	0.10	0.10
IQVmd	0.13	0.26	0.68	0.36	0.05
IQVsd	-0.10	-0.35	-0.07	0.47	-0.74
IQVsk	-0.19	-0.71	-0.41	-0.06	0.09
IQVk	-0.10	0.84	0.30	-0.10	-0.01
YQmn	-0.62	0.10	-0.61	0.12	-0.09
YQmd	-0.58	0.23	-0.63	-0.04	-0.16
YQsd	-0.01	-0.36	-0.78	0.08	0.37
YQsk	0.81	-0.04	0.32	-0.14	0.10
YQk	0.82	0.23	-0.06	-0.27	-0.09
Eigen value	6.60	6.21	3.43	2.47	2.33
Proportion of variation	0.26	0.25	0.14	0.10	0.09

Table A9. Standardised loadings from a principal component analysis of a subset of nine signature vector features from ten Cape mountain zebra populations.

Factor	Standardised loading	
	PC1	PC2
Dmn	0.89	0.15
Dsd	1.02	-0.08
Tmn	-0.02	0.97
Tsd	-0.02	-0.91
EDsk	0.82	0.17
IQVsk	-0.83	-0.18
IQVk	1.00	-0.17
YQsk	-0.02	0.96
YQk	0.11	0.84
Eigen value	4.21	3.51
Proportion of variation	0.47	0.39

Table A10. Kaiser-Meyer-Olkin (KMO) measures of sampling adequacy (MSA) for a subset of nine signature vector features from ten Cape mountain zebra populations. Overall KMO highlighted in bold.

Overall KMO 0.51								
MSA for each factor								
Dmn	Dsd	Tmn	Tsd	EDsk	IQVsk	IQVk	YQsk	YQk
0.53	0.62	0.44	0.42	0.65	0.62	0.46	0.43	0.46

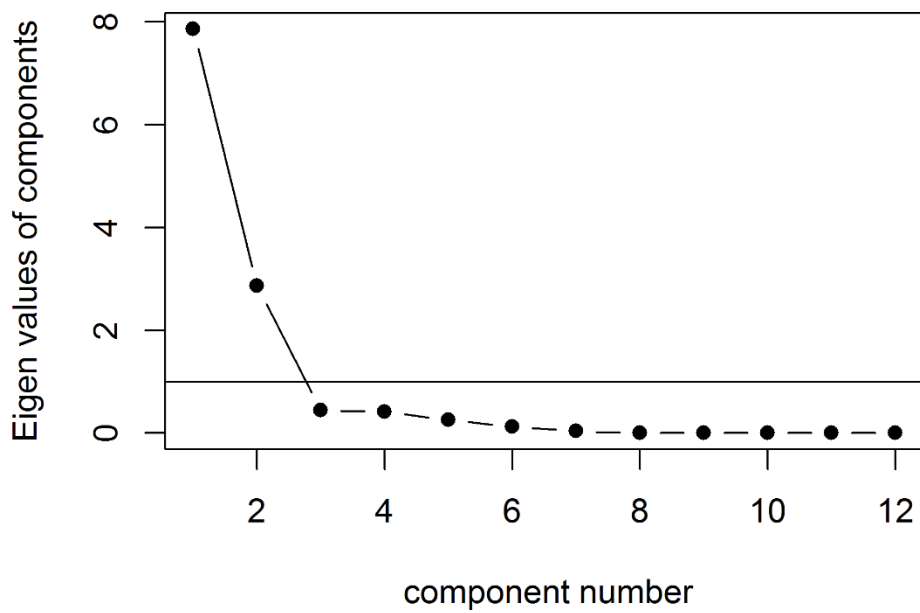


Figure A5. Scree plot of the change in Eigen values against the increase in the number of components for a principal component analysis of 12 network feature statistics characterising ten Cape mountain zebra populations.

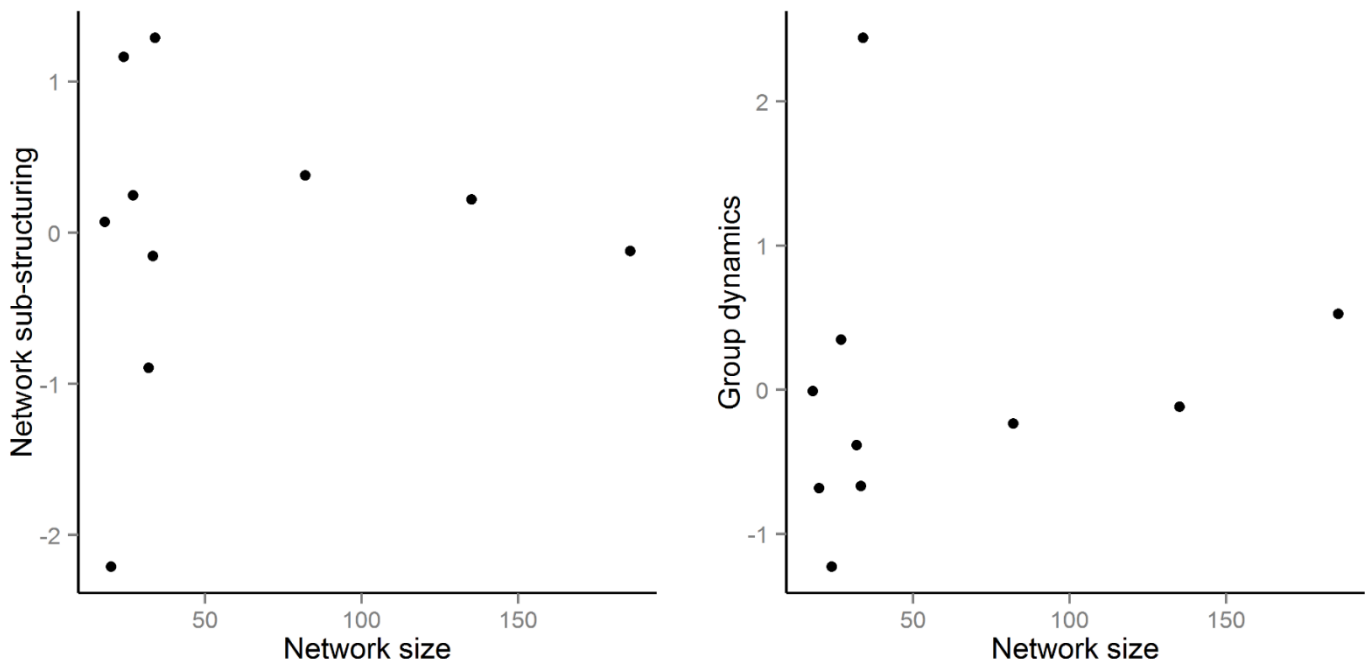


Figure A6. The effect of network size on two principal component scores characterising ten Cape mountain zebra populations. A) The correlation between network size and network sub-structuring (including node-wise clustering coefficient and the distribution of homophily in adult males). B) The correlation between network size and group dynamics (including the mean and standard deviation of node-wise and ego-wise degree as well as ego Index of Qualitative Variation).

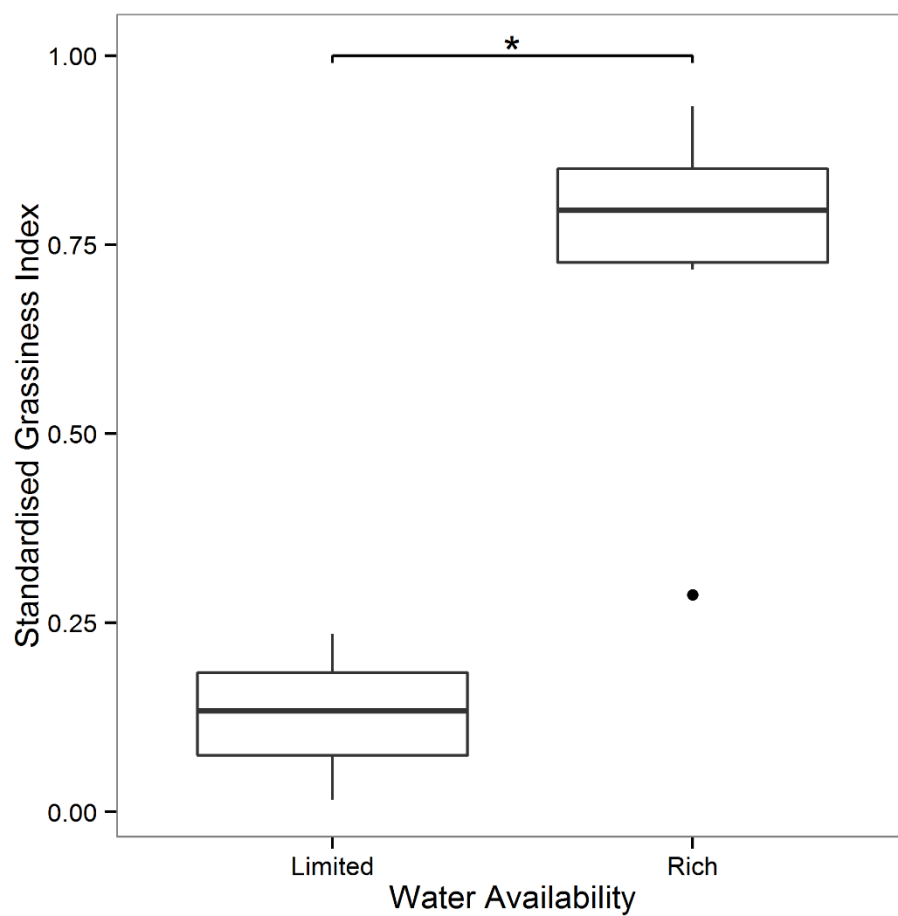


Figure A7. Differences in the availability of palatable grass species between water-rich and water-limited reserves.

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