# UNIVERSITY OF SOUTHAMPTON

FACULTY OF ENGINEERING AND THE ENVIRONMENT

Centre for Environmental Sciences

&

Institute for Complex Systems Simulation

Volume 1 of 1

# Spatial methods for modelling species distributions

by

**Nicholas William Synes**

Thesis for the degree of Doctor of Philosophy

October 2015

UNIVERSITY OF SOUTHAMPTON

# ABSTRACT

FACULTY OF ENGINEERING AND THE ENVIRONMENT

Ecological Modelling

Thesis for the degree of Doctor of Philosophy

# SPATIAL METHODS FOR MODELLING SPECIES DISTRIBUTIONS

Nicholas William Synes

Species distribution modelling methods are used for a variety of applications including: to assess current patterns of biodiversity, to make predictions about the impacts of environmental and climate change, and to assist in conservation planning. However, important factors are often neglected both in the pre-processing of data (e.g. ignoring sampling bias), and in the construction of models (e.g. ignoring ecological processes). In terms of the pre-processing of data, recent improvements in distance sampling methods are used to convert count data to abundance estimates, utilising both distance and habitat data from a previously conducted bird count survey. Biotic interactions are studied using MaxEnt and pairs of virtual species; a novel iterative method is demonstrated, using each species prediction as a subsequent variable for the partner species. Population dynamics and dispersal are studied using RangeShifter, a recently developed individual-based model. A number of climate change adaptation actions are applied to a section of UK landscape data, and the range shifting ability of a set of focal species is measured. Many previous studies have predicted climate change impacts on species; some have started to incorporate simple measures of dispersal ability. This work demonstrates the importance of considering both dispersal and population dynamics when predicting the future distributions of species and assessing their ability to track climate change. Finally, dynamic feedbacks between species and their environment are studied by coupling RangeShifter with CRAFTY, a recently developed agent-based model of land-use dynamics. Socio-ecological system dynamics are crucial in determining species distributions, but have rarely been studied as a truly coupled system. The coupled model presented here is the first of its kind, modelling both animals and land-use agents at an individual level. A case study is presented, demonstrating the feedback mechanisms that exist between pollinators and farms that rely on them, and the potential risk posed by agricultural intensification.

# Table of Contents

# List of Tables

# List of Figures

# DECLARATION OF AUTHORSHIP

I, Nicholas William Synes, declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

*"Spatial methods for modelling species distributions"*

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:

Moreira, F., Leitão, P.J., **Synes, N.W.**, Alcazar, R., Catry, I., Carrapato, C., Delgado, A., Estanque, B., Ferreira, R., Geraldes, P., Gomes, M., Guilherme, J., Henriques, I., Lecoq, M., Leitão, D., Marques, A.T., Morgado, R., Pedroso, R., Prego, I., Reino, L., Pedro, R., Tomé, R., Zina, H., Osborne, P.E., 2012. Population trends in the steppe birds of Castro Verde in the period 2006-2011: consequences of a drought event and land use changes? Airo 22, 79–89.

**Synes, N.W.**, Watts, K., Palmer, S.C.F., Bocedi, G., Bartoń, K.A., Osborne, P.E., Travis, J.M.J., 2015. A multi-species modelling approach to examine the impact of alternative climate change adaptation strategies on range shifting ability in a fragmented landscape. Ecological Informatics 30, 222–229. doi:10.1016/j.ecoinf.2015.06.004

Signed: ..........................................................................................................................

Date: ..........................................................................................................................

# Acknowledgements

Thank you to my supervisor Dr. Patrick Osborne for his support throughout my PhD. It was through the research project on my MSc that Dr. Osborne inspired my interest in the research topics covered in this thesis.

Thank you to Dr. Kevin Watts. His support since a chance encounter with Dr. Osborne has been crucial to the development of my thesis, and has led to a number of collaborations and opportunities..

Thank you to Prof. Justin Travis, Dr. Stephen Palmer, Dr. Greta Bocedi, and Dr. Kamil Bartoń for so readily welcoming me into their group. Thank you also to Dr. Calum Brown for his help and support.

Thank you to my family for the support they have always given me, and their encouragement to pursue whatever makes me happy. Finally thank you to my wife-to-be, Kelly-Anne Smith, for always supporting me, and particularly for looking after me during the most challenging times.

# Definitions and Abbreviations

| | |
|---|---|
| ABM | agent-based model/modelling |
| AIC | Akaike information criterion |
| AUC | area under the receiver operating characteristic curve |
| CDS | conventional distance sampling |
| GARP | genetic algorithm for rule-set production |
| GIS | geographic information system |
| ha | hectare |
| IBM | individual-based model/modelling |
| MCDS | multiple covariate distance sampling |
| NLM | neutral landscape model/modelling |
| SDM | species distribution model/modelling |

# Chapter 1: Introduction

Species distribution models (SDMs) are a commonly used set of techniques for predicting the geographic distribution of species from species sample data and suitable predictor variables (Anderson *et al.*, 2006). Most SDMs model the species' fundamental niche, using abiotic predictor variables only (Guisan and Thuiller, 2005), i.e. the environmental space within which the species can exist. However, the actual distribution of a species is determined by many other factors including biotic interactions, dispersal, population dynamics, and land-cover.

Many previous studies and literature reviews have identified and discussed the current limitations of SDMs (Pearson and Dawson, 2003; Araújo and Guisan, 2006; Ibáñez *et al.*, 2006; Dormann, 2007; Thuiller *et al.*, 2008; Franklin, 2010; Iverson *et al.*, 2011). Criticisms have included the limitations of using historical inventory species data (Hortal *et al.*, 2008) which are often incomplete and spatially biased (Araújo and Guisan, 2006), the assumptions of constancy of limiting factors (Lo *et al.*, 2010), the lack of biotic interactions (Elith and Leathwick, 2009), the use of simplistic global dispersal, and no evolutionary adaptation (Dormann, 2007), the lack of population dynamics/viability testing (Keith *et al.*, 2008), the static nature of SDMs (Pearson and Dawson, 2003; Ibáñez *et al.*, 2006; Franklin, 2010), and interactions between the effects of climate and land-use rarely being considered (Thuiller *et al.*, 2008). Other issues also need careful consideration when applying SDMs, for example different modelling algorithms can give different predictions (Araújo *et al.*, 2005; Anderson *et al.*, 2006; Pearson *et al.*, 2006); the selection of environmental predictor variables can greatly impact results (Synes and Osborne, 2011); and collinearity is a common issue when dealing with multiple environmental predictor variables (Dormann *et al.*, 2013).

One of the first steps when applying an SDM approach is to obtain spatially referenced observations of the study species. Historical inventories of species location data are frequently used (e.g. Ponder *et al.*, 2001; Reutter *et al.*, 2003; Stockman *et al.*, 2006; Liu *et al.*, 2013). Such data has often been collected ad-hoc, under different conditions and biases which are rarely identified in the meta-data; this can result in geographic and taxonomic biases (Graham *et al.*, 2004; Anderson, 2012). Such data is often collated from multiple sources, resulting in regional variations in sampling efforts. This can lead to incomplete descriptions of the environmental responses of species (Hortal *et al.*, 2008; Beck *et al.*, 2014). Historical inventory data can also be prone to spatial errors due to differences in, or lack of, georeferencing (Wieczorek *et al.*, 2004; Graham *et al.*, 2008). It is therefore preferable (though admittedly often not feasible) to collect species data specifically for the study, meaning that sampling methods can be standardised, reducing geographic bias and errors. With careful field design and data processing, positional errors and bias can be minimised (Hirzel and Guisan, 2002; Osborne and Leitão, 2009).

Historical inventory data is generally based only on species presences (Elith and Leathwick, 2007), but it is generally preferable to use data that includes known species absences (Brotons *et al.*, 2004; Václavík and Meentemeyer, 2009). However, true absence is difficult to confirm as the species may simply have gone undetected. Where feasible, i.e. for smaller study areas and species with high detectability, it is generally preferable to collect abundance data rather than presence-absence data (Joseph *et al.*, 2006), as this allows for the core of a species' range to be identified (Iverson *et al.*, 2011). By contrast, the use of presence-absence data can lead to the inclusion of uncertain distribution edges. A number of alternative SDMs are available that can take advantage of the extra information that abundance data provides, for example: generalised additive models (Hastie and Tibshirani, 1990; Guisan *et al.*, 2002) and boosted regression trees (Elith *et al.*, 2008). However, abundance data is difficult to calculate because raw count data is only a relative measure of abundance (Buckland *et al.*, 2008; Kéry and Royle, 2010). Field survey counts will always be constrained by imperfect detection: mobile species are more difficult to detect (Granholm, 1983), and their detectability may vary by habitat (Gu and Swihart, 2004), season (Selmi and Boulinier, 2003), observer (Diefenbach *et al.*, 2003), and distance from observer (Buckland *et al.*, 2001). Field and study design methods can be utilised to reduce the detectability bias in count data, but bias cannot be removed, and statistical methods should be used to account for it (Elphick, 2008).

The main factor that reduces the detectability of a species is its distance from the observer (Buckland *et al.*, 2001). When habitat is also expected to influence the detectability of a species, point rather than line transect surveys are generally favoured since they allow habitat associations to be more readily incorporated (Buckland *et al.*, 2008). Chapter 2 makes use of existing detailed point transect field survey data for bird species in the Castro Verde region of Portugal to test how the use of distance sampling (Thomas *et al.*, 2010), and in particular the inclusion of habitat and species covariates, can be used to improve abundance estimates. The incorporation of these methods (to improve abundance estimates) into SDMs is left for future work. Such work will require a hierarchical modelling framework to incorporate the combined effects of habitat on detectability, abundance and spatial distribution (Royle *et al.*, 2007; Sillett *et al.*, 2012).

A crucial factor often missing from SDM studies is the influence of biotic interactions on the observed distributions of species. The majority of SDM studies have focused on the use of abiotic predictor variables (Guisan and Thuiller, 2005) since environmental conditions are key determinants of a species' distribution, and biotic interactions are difficult to quantify. However, biotic interactions can affect species response differently along environmental gradients (Callaway *et al.*, 2002; Brooker, 2006; Sutherst *et al.*, 2007; Kissling *et al.*, 2010; Van der Putten *et al.*, 2010), and may be particularly important when projecting distributions under climate change (Davis *et al.*, 1998; Dormann, 2007). Whilst biotic interactions are rarely considered, the species occurrence data used to generate predictions will always inadvertently include the effects of biotic interactions, leading to potential misrepresentations of the species' responses to the chosen abiotic predictor variables. Some studies have shown that the inclusion of predictor variables representing the distributions of interacting competitors (Leathwick and Austin, 2001; Anderson *et al.*, 2002) and mutualists (Gutiérrez *et al.*, 2005; Araújo and Luoto, 2007) can increase the predictive power of SDMs. However, biotic interactions are generally difficult to incorporate because they are dynamic, with species both influencing and being influenced by those interactions (Soberón, 2007).

Using a novel iterative approach, Chapter 3 studies the inclusion of the distributions of interacting species as SDM predictor variables. This work utilises "virtual" or "artificial" species (Hirzel *et al.*, 2001) to investigate the potential improvements that can be made to SDM predictions by including interacting species. The benefit of this approach is that the underlying relationship is known, and so predictions can be directly compared to a known "truth". Whilst the iterative approach does not result in an increase in predictive power, potential issues of collinear predictor variables are identified. There is scope for future work to expand on this methodology, studying different types and strengths of species interactions to identify which interactions provide the most predictive power. Furthermore, future work should investigate the influence of spatial resolution on model results, since this is a potentially important difference between the influence of biotic and abiotic factors over a species' distribution (Pearson and Dawson, 2003; Soberón, 2007; Wisz *et al.*, 2013). Such an approach may require hierarchical integration of predictor variables at different scales, as previously demonstrated by Pearson *et al.* (2004) with climate and land-cover data.

When studying the impacts of environmental change, one of the most important considerations is to what extent species will be able to reach and fill their future fundamental niche (i.e. predicting their realised niche). The ability to track climate change varies greatly both between and within taxonomic groups (Hickling *et al.*, 2006), with dispersal ability a crucial factor in a species' ability to track climate change (Best *et al.*, 200; Schloss *et al.*, 2012; Travis *et al.*, 2013). The representation of dispersal in SDMs has often been limited, particularly with the early use of simple universal or no dispersal rules (e.g. Araújo *et al.*, 2004; Thomas *et al.*, 2004; Thuiller, 2004; Araújo *et al.*, 2006; Thuiller *et al.*, 2006). More detail has been brought to dispersal in SDMs through use of dispersal kernels, in particular to study the spread of invasive species (e.g. Williams *et al.*, 2008; Václavík and Meentemeyer, 2009), and methods that account for species-specific dispersal ability have been shown to reduce uncertainty in projections of species distributions under climate change (Engler and Guisan, 2009). Modelling of dispersal is particularly important in fragmented landscapes, as limited habitat availability constrains the ability of species to shift their ranges (Wilson *et al.*, 2009). Furthermore, in fragmented landscapes the intervening matrix between habitat patches can influence dispersal success and population viability (Ricketts, 2001; Vandermeer and Carvajal, 2001; Prevedello and Vieira, 2010; Villard and Metzger, 2014). It is increasingly recognised that process-based models of dispersal, that capture the interaction between species-specific dispersal abilities and landscape structure, are required to improve our understanding of the distribution of species populations in fragmented landscapes (Palmer *et al.*, 2011; Pe'er *et al.*, 2011; Baguette *et al.*, 2013).

Population dynamics are also crucial to our understanding of species distributions in changing environmental conditions (Franklin, 2010), with a number of studies incorporating meta-population models or population viability models into SDM approaches (e.g. Keith *et al.*, 2008; Wilson *et al.*, 2009; Carroll *et al.*, 2010; Lawson *et al.*, 2010). Chapter 5 uses RangeShifter (Bocedi *et al.*, 2014a), a platform for individual-based modelling of population dynamics and dispersal, to examine the impacts of different climate change adaptation strategies on species range shifting ability. A broad range of species life-history and dispersal characteristics are used, including stage structuring, density dependent dispersal and inter-specific variation in movement behaviour. This allows for differences in range shifting ability to be discussed in the context of species ecology. The climate change adaptation strategies follow a set of different spatial rules (see Chapter 4, which describes the GIS toolbox developed to generate these landscapes), allowing opposing theories about connectivity to be tested (see Hodgson *et al.*, 2009; Doerr *et al.*, 2011; Hodgson *et* *al.*, 2011a). Chapter 5 highlights the utility of individual-based models such as RangeShifter for studying habitat connectivity. Evidence is given for the usefulness of different connectivity measures, and the details that conservation practitioners should consider before choosing landscape management strategies.

The study in Chapter 5 does not consider climate effects on the species; a purely process-based approach is used. A number of studies have suggested and some have developed “hybrid” models which incorporate process-based ecological processes such as population dynamics and dispersal into SDMs (Keith *et al.*, 2008; Drielsma and Ferrier, 2009; Engler and Guisan, 2009; Kearney and Porter, 2009; Franklin, 2010; Midgley *et al.*, 2010; Schurr *et al.*, 2012; Conlisk *et al.*, 2013). RangeShifter can facilitate such approaches, since habitat suitability landscapes can be loaded. However, there are many difficulties in using such “hybrid” methods, particularly in realistic parameterisation (Franklin, 2010; Schurr *et al.*, 2012). Greater knowledge is required on the interactions between ecological processes and environmental conditions before truly integrated SDM population models can be developed and effectively utilised. For example, rising temperatures can result in changes in growth rates, fecundity levels and mortality risk (Dullinger *et al.*, 2004). Incorporating such effects into future hybrid models is an important next step.

Whilst many studies on the future distributions of species focus on the impacts of climate conditions, habitat and land-cover condition and configuration are also important factors in the distributions of species (Chamberlain *et al.*, 1999; Benton *et al.*, 2003; Luoto *et al.*, 2007). Furthermore, as Chapter 5 demonstrates, habitat availability and configuration play an important role in species-specific range shifting ability. A number of studies have included land-cover data alongside climate data as predictor variables in SDMs (e.g. Pearson *et al.*, 2004; Pompe *et al.*, 2008; Hof *et al.*, 2011; Barbet-Massin *et al.*, 2012b). Such studies have shown improved SDM performance when land-cover is considered, although its influence is generally at finer spatial scales than the influence of climate conditions (Pearson *et al.*, 2004; Luoto *et al.*, 2007; Barbet-Massin *et al.*, 2012b). At large scales, land-cover is broadly correlated with climate (Thuiller *et al.*, 2004), but at finer scales agriculture and anthropogenic influences become greater. Climate change, land-cover change and habitat destruction are expected to have interacting impacts on species distributions (Travis, 2003; McRae *et al.*, 2008; Nathan *et al.*, 2011). At finer scales, future land-use is likely to be dynamically related to species distributions, with the potential for the presence of pest species to result in habitat degradation and land-cover change (Pimentel *et al.*, 2005; Aukema *et al.*, 2006), and the presence of endangered species to result in habitat protection (Noss *et al.*, 1997; Rissman *et al.*, 2007; Beatley, 2014).

The modelling of interactions between human decision-making and ecology, commonly termed “socio-ecological system modelling”, is becoming increasingly popular due to its potential for identifying unexpected behaviours, non-linear dynamics and feedback loops (Liu *et al.*, 2007). Socio-ecological systems are ubiquitous, and an improved understanding of their dynamics is crucial for tackling the challenges of global sustainability (Liu *et al.*, 2015). The development of models to represent such systems can be a technical challenge due to the difficulty in integrating work from two separate fields of study, a task which may require multi-disciplinary collaborative work (Luus *et al.*, 2013; Malawska *et al.*, 2014). Nevertheless, a number of socio-ecological system models have been developed, for example to study the impacts of farmer decision-making on local biodiversity or pest species (Rebaudo *et al.*, 2011; Carrasco *et al.*, 2012; Polhill *et al.*, 2013), or of homeowner decision-making on habitat quality (Linderman *et al.*, 2005; Monticino *et al.*, 2007). However, the representation of ecology in such systems remains limited. Whilst human decision-making is often represented at the individual-level, the ecological system is often simplistic and aggregated. Chapter 6 presents the integration of an agent-based model of land-use dynamics (CRAFTY: Murray-Rust *et al.*, 2014), with an individual-based model of animal population dynamics and dispersal (RangeShifter: Bocedi *et al.*, 2014a). The coupled model allows land-use agents and animals to interact with each other through land capitals which represent ecosystem service potential. This work demonstrates the potential of such model integrations to identify important interactions between species distributions and land-use decision-making.

## 1.1 Publication overview

Several parts of this work have been presented in International Conferences and Workshops:

- **Nicholas W. Synes**, Kevin Watts, Stephen C.F. Palmer, Greta Bocedi, Kamil A. Bartoń, Justin M.J. Travis, Patrick E. Osborne. *Landscape-scale conservation: the role of space and time in the realisation of biodiversity benefits. Spatial Ecology & Conservation 2 – Ecological Research and Training. Held in Birmingham, UK, from 17th to 20th June 2014 – Oral* presentation.
- **Nicholas W. Synes**, Kevin Watts, Stephen C.F. Palmer, Greta Bocedi, Kamil A. Bartoń, Justin M.J. Travis, Patrick E. Osborne. *Landscape-scale conservation: the role of space and*

*time in the realisation of biodiversity benefits.* Student Conference on Complexity Science 2014. Held in Brighton, UK, from 19th to 22nd August 2014 – Oral presentation.

- **Nicholas W. Synes**, Kevin Watts, Stephen C.F. Palmer, Greta Bocedi, Kamil A. Bartoń, Justin M.J. Travis, Patrick E. Osborne. *Individual-based modelling to study habitat connectivity under future landscape management scenarios.* German Ecological Society (GfÖ) Annual Meeting. Held in Hildesheim, Germany, from 8th to 12th September – Oral presentation.

- **Nicholas W. Synes**, Kevin Watts, Stephen C.F. Palmer, Justin M.J. Travis, Patrick E. Osborne. *Coupled socio-ecological systems: linking local ecology to land-use decision making*. Agent-based modelling of land-use workshop, University of Edinburgh. Held in Edinburgh, UK, from 4th to 5th May 2015 – Oral presentation.

- **Nicholas W. Synes**, Kevin Watts, Calum Brown, Stephen C.F. Palmer, Greta Bocedi, Justin M.J. Travis, Patrick E. Osborne. *Coupled socio-ecological system modelling: linking local ecology to land-use decision making*. International Association for Landscape Ecology World Congress 2015. Held in Portland, USA, from 6th to 10th July 2015 – Oral presentation.

- **Nicholas W. Synes**, Kevin Watts, Stephen C.F. Palmer, Greta Bocedi, Kamil A. Bartoń, Justin M.J. Travis, Patrick E. Osborne. *Climate change adaptation to assist range shifting: the key considerations for achieving long term conservation goals at a landscape-scale*. International Association for Landscape Ecology World Congress 2015. Held in Portland, USA, from 6th to 10th July 2015 – Oral presentation.

The results from Chapter 2 formed the basis of a paper published in the Portuguese Society for the Study of Birds' peer-reviewed journal Airo (Moreira *et al.*, 2012). This paper focuses on the conservation implications of the analysis in Chapter 2. I am third author on the paper and contributed the majority of the analysis, sections of the methodology write up and provided comments and corrections on the manuscript. This chapter utilises existing data, the collection of which was led by Pedro J. Leitão, second author on the Airo paper.

- Moreira, F., Leitão, P.J., **Synes, N.W.**, Alcazar, R., Catry, I., Carrapato, C., Delgado, A., Estanque, B., Ferreira, R., Geraldes, P., Gomes, M., Guilherme, J., Henriques, I., Lecoq, M., Leitão, D., Marques, A.T., Morgado, R., Pedroso, R., Prego, I., Reino, L., Pedro, R., Tomé, R., Zina, H., Osborne, P.E., 2012. Population trends in the steppe birds of Castro Verde in the period 2006-2011: consequences of a drought event and land use changes? Airo 22, 79–89.

Chapter 5 is published in the international peer-reviewed journal Ecological Informatics (Synes *et al.*, 2015). I am first author on this paper, and wrote the first draft of the manuscript, with all authors providing comments, corrections and changes. All authors helped devise the questions addressed and methods used in this paper, I conducted all modelling work and analyses.

- **Synes, N.W.**, Watts, K., Palmer, S.C.F., Bocedi, G., Bartoń, K.A., Osborne, P.E., Travis, J.M.J., 2015. A multi-species modelling approach to examine the impact of alternative climate change adaptation strategies on range shifting ability in a fragmented landscape. Ecological Informatics 30, 222–229. doi:10.1016/j.ecoinf.2015.06.004

Chapter 4 is in preparation for submission to Ecography as a Software Note (short format) article (authors: **Nicholas W. Synes**, Kevin Watts, Justin M.J. Travis, Patrick E. Osborne). Chapter 6 is in preparation for submission to the Proceedings of the National Academy of Sciences (authors: **Nicholas W. Synes**, Kevin Watts, Calum Brown, Stephen C.F. Palmer, Greta Bocedi, Justin M.J. Travis, Patrick E. Osborne). The work in Chapter 5 presents only a small number of the computer simulations that were undertaken. Another manuscript is planned from this work, as well as a number of extensions of the methodology.

# Chapter 2: Use of species and habitat covariates to improve distance sampling estimates of abundance

## 2.1 Abstract

Bird population surveys collect count data that is heavily biased by the fact that not all birds at any survey location can be detected. The main factor that affects whether or not a bird will be detected is its distance from the observer. Distance sampling is a commonly used method for dealing with the issue of imperfect detection that all animal population studies face. Recent advancements in the method mean that multiple covariates known to impact upon detectability can now be included. This study uses bird count data from the Castro Verde special protection area in Portugal to test the use of multiple covariate distance sampling methods. The Castro Verde data covers two separate years, one of which followed a severe drought event in the region. Detailed habitat information for the region (in the form of the percentage coverage of five different habitat types) allowed for the analysis of how different habitats affect species detectability.

Results showed that the use of a species covariate can improve abundance estimates. This is especially true for rare or under-surveyed species for which sample size is an issue. The use of habitat covariates was also found to improve the models, although they had little effect on final abundance estimates. Bird detectability was found to vary between different habitats, with the number of detections in woodland areas falling far quicker with distance than in open habitats. Of the eight species studied, two have undergone large population increases in the five years between the two surveys, one has had a 50% reduction in population size, and the rest have remained relatively stable. These population trends are discussed in the context of the known habitat preferences of the species.

## 2.2 Introduction

### 2.2.1 Estimating species abundance

Accurate estimation of species populations and population trends is crucial for the effective protection of wildlife and threatened species. Estimates of species abundance can be used to identify threats to species populations and guidelines for restricting urban development (Dallimer *et al.*, 2009), to identify core areas of habitat for the protection of species (Chávez-León and Velázquez, 2004) to study population trends using time-series data (Fewster *et al.*, 2000; Pagel *et al.*, 2014), to assess extinction risk (Araújo *et al.*, 2005; Wilson *et al.*, 2011) or to assess the threat or impact of invasive species (Cerasale and Guglielmo, 2010; Parker *et al.*, 2013). However, due to the nature of ecological data, it is still a great challenge to generate accurate population estimates. Populations can never be fully counted, so instead field sampling methods must be used. Sampling methods invariably introduce bias and reduce precision. The use of sampled data to estimate populations necessitates the use of statistical methods to try to account for the biases of data collection, and to quantify and reduce the uncertainty in the data. Research into methods for estimating species populations generally looks to either improve data collection methods to reduce the bias or to develop statistical methods to account for the bias (Elphick, 2008).

Raw count data is often used to estimate bird population densities (Bächler and Liechti, 2007) but this method is overly simplistic, and likely to be inaccurate (Farnsworth *et al.*, 2002; Rosenstock *et al.*, 2002). The number of birds counted during a survey is in fact only a relative measure of abundance rather than an absolute measure (Buckland *et al.*, 2008). The problem with using raw count data is that the data is always constrained by imperfect detection. Whilst suitable survey techniques can allow stationary objects such as plants to be detected with certainty, highly mobile species such as birds are far less likely to be detected (Granholm, 1983). The main factor that reduces the detectability of a species is its distance from the observer (Buckland *et al.*, 2001). Use of abundance estimates adjusted for detectability at distance gives more robust estimates of population trends than use of raw density estimates (Norvell *et al.*, 2003).

Distance based sampling methods are frequently used for a wide variety of species; one particularly popular area of use is for studying bird species abundance (e.g. Marsden, 1999; Chávez-León and Velázquez, 2004; Freeman *et al.*, 2007; Cimprich, 2009; Gottschalk and Huettmann, 2011; Amundson *et al.*, 2014; Peele *et al.*, 2015). Distance sampling has been used for studies over a wide range of geographical scales, from national (Freeman *et al.*, 2007) to small scale (<50,000 hectares) studies of protected areas (Marsden *et al.*, 2005). Distance sampling methods have also been tested with simulated data; the advantage of this is that it allows the characteristics of the study species to be controlled, and is thus a useful way to test the method and its ability to deal with bias (Elphick, 2008). Ekblom (2010) used a simulation study with two hypothetical bird species; it was found that distance sampling methods can give estimates similar to the true abundance (true abundance values were always within the 95% confidence intervals).

The two most common survey techniques for estimating bird abundance are point transect surveys and line transect surveys. Point transect surveys are where an observer remains stationary at one point for a predetermined period of time during which they record all bird detections (visual or audible). Line transect surveys are where the observer moves along a predetermined line through the environment at a consistent speed recording all bird detections. Methods can vary between studies in terms of the duration of counts (or the length of the line), the number of survey points/lines, the survey effort at each point/line (the number of times it is visited), and the amount of extra information that is recorded for each location or observation.

Whilst use of line transects is generally considered favourable compared with point transects (due to the higher proportion of detections close to the observer), point transects should be used if the quality of line transects is likely to be compromised (Buckland *et al.*, 2008). This can happen, for example, when traversing a straight line placed randomly in the environment is made difficult by dense and uneven habitat. Use of point transects can also be advantageous when surveying multiple species; from point transects, observers have more time to identify species and make recordings since they do not need to think about navigation. Another benefit of using point transect surveys is that they are more practical for incorporating habitat associations into the study (Buckland *et al.*, 2008). Since observers are motionless throughout the survey, habitat associations are the same for all detections at any one point; this issue is far more complicated for line transects.

Both good survey design and strict adherence to the predetermined field methods are crucial for reliable use of the distance sampling methodology (Cassey and McArdle, 1999). For a detailed guide to bird survey design and field techniques for distance sampling, see Bibby *et al.* (1998) and Buckland *et al.* (2015). Observers must be experienced in species identification, and trained in specific field methods such as distance estimation and the correct recording of data (Buckland *et al.*, 2001). Without sufficient distance estimation training, distance errors can lead to bias in density estimates (Marques, 2004). Furthermore, the process of an observer getting to a point transect before the survey begins can influence the behaviour and locations of the birds (Lee and Marsden, 2008). If the observer disturbs birds whilst approaching the point, it is possible that the birds will become louder as a warning to others (Haselmayer and Quinn, 2000), or that they will move towards or away from the observer (Rosenstock *et al.*, 2002). Such varied reactions are difficult to measure and can result in either under or over-estimation bias. It is therefore crucial for observers to minimise the disturbance they cause prior to and during surveys.

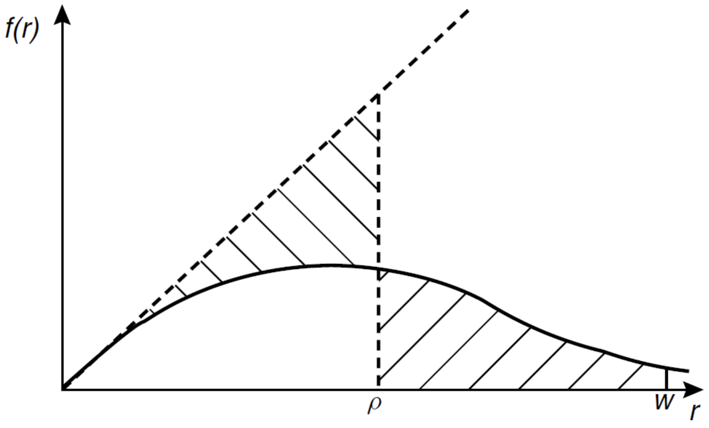
### 2.2.2 Distance sampling theory

If it were possible to count all birds within a set of plots, then the density of the animals in a wider region could be estimated by:

$$\hat{N} = A\frac{n}{a},$$

where $\hat{N}$ is the estimated density of the species in the region, $A$ is the area of the region, $n$ is the total number of birds in the plots, and $a$ is the total area of the plots. This estimate is reliant on the fact that the sampled plots were chosen randomly from the wider region (Marques, 2009). Since complete detection of mobile species is not possible, the above estimate is too simplistic. Use of distance sampling methods acknowledges the fact that not all birds within a point transect survey region can be detected. For point transect sampling, the observer records every detected bird at each survey point during a pre-determined period of time, and the radial distance to the location at which the animal was detected. The number of detections at increasing distance from the observer is then used to create a detection function.

*Figure 2.1: [From Buckland et al. (2005)] An example probability density function of distances, $f(r)$. Since it is a probability density function, the area under the curve is equal to 1. Furthermore, since ρ is the point at which as many birds are detected beyond ρ as are missed within ρ, the two shaded areas are equal in size.*



If the survey consists of $k$ points, and any birds detected within a radial distance $w$ of the point are recorded, then the total surveyed area is

$$a = k\pi w^2.$$

If $n$ birds are detected, and the estimated probability that a bird is detected within the surveyed area is $\widehat{P}_a$, then bird density can be estimated by

$$\widehat{D} = \frac{n}{a \times \widehat{P}_a}$$

Buckland *et al.* (2001) define an effective radius $\rho$, which is the radius < $w$ at which as many birds are detected beyond $\rho$ as are missed within $\rho$ (Figure 2.1). Then we have

$$\widehat{P}_a = \frac{\pi\hat{\rho}^2}{\pi w^2}.$$

The equation for the density estimate then becomes

$$\hat{D} = \frac{n}{k\pi w^2 \times \hat{\rho}^2/w^2} = \frac{n}{k\pi\hat{\rho}^2}\,.$$

The area under the probability density function (equivalent to the area of the triangle in Figure 2.1) gives:

$$\rho^2 \times f'(0)/2 = 1\,.$$

It therefore follows that

$$\hat{D} = \frac{n\hat{f}'(0)}{2k\pi}\,.$$

This is the equation that the Distance software (Thomas *et al.*, 2010) uses to estimate the density of the study species; it does this by modelling the probability density function of detection distances, and calculating the slope of the fitted function at radial distance $r = 0$. This equation highlights the importance of detections at zero distance from the point transect, since it is the slope at this point that controls the density estimate.

Three assumptions are crucial for the distance sampling methodology to provide reliable estimates of density (Buckland *et al.*, 2005):
1) Objects at the point are always detected, g(0) = 1.
2) Objects are detected at their initial location, prior to any movement in response to the observer.
3) Distances are measured accurately, or are correctly allocated into distance intervals.

*1) Objects at the point are always detected,* g*(0) = 1.* Perfect detection close to the observer is crucial because this gives the scale by which counts at greater distances are adjusted. Bächler and

Liechti (2007) found that few papers that use distance sampling methods discuss the importance of the g(0)=1 assumption. They suggest that the assumption of perfect detection close to the observer is violated in many published studies. One example of the violation of this assumption was given by Applegate *et al.* (2011) in a case study on a single species of bird.

*2) Objects are detected at their initial location, prior to any movement in response to the observer.* The detection of animals at their initial location is important because movement consistently towards or away from the observer will result in systematic bias, and abundance will be under or over-estimated (Ekblom, 2010). It has been suggested that "settling down" periods should be used, whereby the observer arrives at a point then waits a few minutes before beginning the survey to allow animals to settle after the disturbance of the observer's movement (Bibby *et al.*, 1998). However, Lee and Marsden (2008) found that movement away from the observer was more common than attraction to the observer, resulting in underestimates of abundance when "settling down" periods are used.

The assumption that all animals will be detected at their initial location also makes it important for the length of surveys to be carefully chosen. Granholm (1983) found that the movements of birds into a point transect area during a survey could lead to biased density estimates due to cumulative rather than instantaneous counts. This bias is best reduced by minimising the count period. However, there is a delicate balance: if counts are too short then animals near the observer may be missed (violation of assumption 1), if they are too long then animals are more likely to move both within, and into and out of the study area (violation of assumption 2). Fuller and Langslow (1984) compared results from point transect surveys of 5, 10, 15 and 20 minutes in length. They concluded that surveys of between 5 and 10 minutes in length are best. In their study, 5 minute counts were able to record 50% or more of the species that were recorded in 20 minute counts. They suggest that the potential for multiple counts of individuals, and for the movement of birds into the study area reduces the benefits of longer counts. It has also been suggested that count duration should be chosen dependent on the study species (Lee and Marsden, 2008), however for multiple species studies such an approach would be impractical.

*3) Distances are measured accurately, or are correctly allocated into distance intervals.* The assumption that distances are measured accurately is particularly important for point transect surveys since errors increase geometrically with distance (Bibby *et al.*, 1998). In fact, Buckland *et* *al.* (2008) give an example where bias in estimates due to measurement error from point transect surveys are more than double the bias in estimates from line transect surveys. If the accurate measurement of distance is expected to be a problem, then the grouping of distance data into intervals can help. Distance sampling methods have been shown to be robust to the use of grouped distance data (Ekblom, 2010), although it is important that measurement accuracy is enough for the distances to be assigned to the correct groups. Alldredge *et al.* (2007a) identified two sources of error in the collection of distance data from auditory cues: locating the cue, and estimating the distance. They found that giving observers training in distance estimation reduced errors by approximately 15%. So long as observers are given training in distance estimation, and recorded distances are grouped into intervals appropriate to their accuracy, then this assumption should not be violated.

### 2.2.3 Other factors that affect detectability

The detectability of a bird does not depend solely on its distance from observer; there are many other factors that may be important, for example species characteristics, habitat, season and observer skill (Ramsey *et al.*, 1987; Diefenbach *et al.*, 2003; Selmi and Boulinier, 2003; Gu and Swihart, 2004; Johnston *et al.*, 2014). The distance sampling methodology makes distance the main factor that affects detectability; other factors can be introduced as covariates to the model. The methodology allows for the fitting of both a key function and adjustment terms to the detectability of species. Covariates can then be used to adjust the scale of both the key function and the adjustment terms. This means that covariates can be set to either adjust only the scale, or both the scale and the shape of the overall detection function. Both possibilities have been shown to be plausible (see Otto and Pollock, 1990; Marques *et al.*, 2007).

#### 2.2.3.1 Species

Different species have different levels of detectability due to size, colour, song and behaviour. There are three possible approaches to modelling the detectability of multiple species. Firstly, if sample sizes are large enough for each species then individual models can be built. If sample sizes are not large enough for all species, another option is to build one detection function based on data from all species, and then to stratify the results by the individual species samples (Rosenstock *et al.*, 2002). The final option is to use a species covariate, which means that a global detection function is built for all species, but then a species covariate is used to adjust the scale (and potentially the shape) of the detection function according to each species' sample data (Alldredge *et al.*, 2007a; Marques *et al.*, 2007). The advantage of this method is that the pooling of data from multiple species increases the sample size from which the detection function is modelled, whilst still allowing for between species variability to be included. Use of covariates for multiple species analyses has been demonstrated to provide more parsimonious models and more precise estimates than individual models which can often be over parameterised (Alldredge *et al.*, 2007a). If survey data is to be pooled together for multiple species, then it is important that the species have similar characteristics and are expected to exhibit similar levels of detectability (Johnston *et al.*, 2014). One example of a characteristic that can be used to group species is their maximum detection distance (Alldredge *et al.*, 2007a).

#### 2.2.3.2 Habitat

In densely vegetated habitats, detections are usually based on auditory cues (Alldredge *et al.*, 2007b), and the availability of the bird depends both on it being present and on the probability that it sings/calls during the count (Farnsworth *et al.*, 2002). This means that detection functions are likely to be different between densely and sparsely vegetated habitats (Brewster and Simons, 2009). However, few studies have included habitat as a factor affecting detectability. Cerasale and Guglielmo (2010) used habitat-specific detection functions, but did not find that this approach improved their estimates. Sillett *et al.* (2012) found that detectability was a function of the percent cover of forest habitat, however they did not compare abundance estimates with estimates from models without habitat-specific detectability. For species that are rarely detected by auditory cues, the habitat they are present in is likely to have an even larger impact on detectability. This highlights the importance of considering the effects of both species and habitat on detectability.

#### 2.2.3.3 Observer

Even when trained and experienced observers are used, they are often found to be a large source of variation in detectability (Norvell *et al.*, 2003; Buchanan *et al.*, 2006; Diefenbach *et al.*, 2003). Variability of detection functions between observers is difficult to rectify; although training in distance estimation has been shown to improve observer accuracy by approximately 15% (Alldredge *et al.*, 2007b). The problem with observer variability is that it is very hard to separate from other factors. If observers work in regions that favour certain species, or are dominated by certain habitats then any variability between observer detection functions could be attributed to real effects. However, it is very difficult to assign observers to point transects that are fully stratified by habitat and species because (i) if the study region is large it may be logistically impossible to have every observer travel to points throughout the region, and (ii) stratifying the locations that each observer will visit by species relies on knowledge which is probably not yet ascertained.

#### 2.2.3.4 Summary of factors that affect detectability

The detectability of animals is dependent on many factors which include distance, species, habitat, season and observer. Whilst previous distance sampling studies have included covariates for species and habitat, few have investigated the effects of including covariates for both. Only one previous study has been identified which uses habitat percentage coverage information, but in that study only one species is considered (Sillett *et al.*, 2012). More commonly, where the effect of habitat on detectability is considered, the predominant habitat type at each survey point is typically used (e.g. Marques *et al.*, 2001). It is also possible that the detectability of habitats will vary between regions and over time, so it may be important to consider this effect when studying population trends. For example, woodland habitat may grow denser over time, gradually reducing detectability; alternatively, drought may reduce the density of some habitats, increasing detectability. If the aim is to make comparisons over time, then it should not necessarily be assumed that detectability will remain constant (Buckland *et al.*, 2008).

This study uses point count data for multiple bird species which was collected in two different years for the same region. Prior to the first survey period, the region was affected by a significant drought event. This study uses distance sampling methods, and habitat percentage cover data to derive corrected abundance estimates for the two years, identifying changes in population sizes over this period.

## 2.3 Methods

### 2.3.1 Study area

Castro Verde special protection area (SPA) is an area of about 80,000 ha. It has a Mediterranean climate with temperatures averaging 30 - 35°C in July, and 5 - 8°C in January, with annual rainfall approximately 500 to 600 mm. The area has a mixture of cereal, fallow, woodland and shrub habitats. The agricultural system generally cultivates cereal land for two years followed by two to three years (but potentially up to seven years) as fallow land, before being returned to cereal cultivation. Therefore, fallow land generally occupies 50% or more of Castro Verde SPA (Moreira, 1999). The habitat of the region is threatened by changes in farming practices and agricultural abandonment (Moreira, 1999).

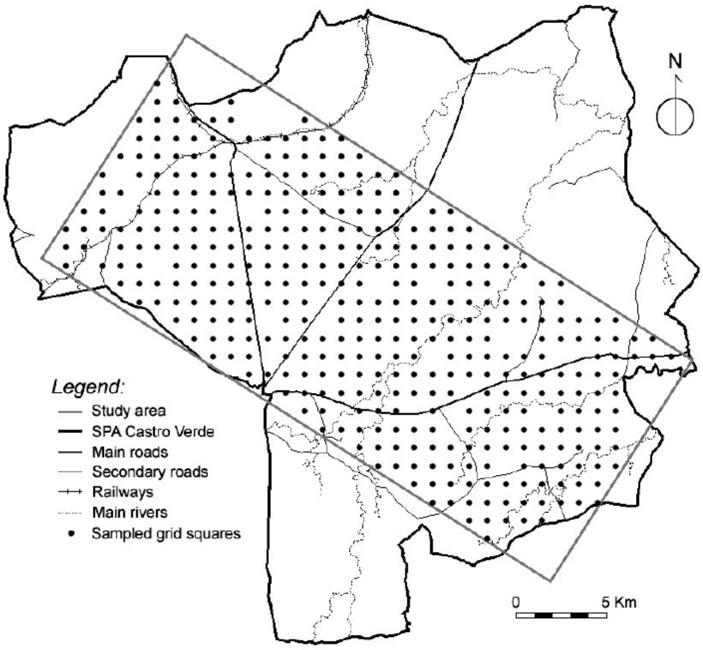
Castro Verde SPA has international importance for several steppe bird species with unfavourable conservation status (Moreira *et al.*, 2007). It holds high densities of breeding Little Bustards (*Tetrax Tetrax*) and Calandra Lark (*Melanocorypha calandra*). Moreira *et al.* (2007) provided the first assessment of the distributions and populations of a number of important bird species in the region. In 2005, the Castro Verde region was hit by the worst drought in Portugal for 60 years, resulting in a poor agricultural year, especially for cereal fields (Moreira *et al.*, 2007). This drought may have had negative impacts on resident bird populations (Moreira *et al.*, 2007). This study uses the same data used by Moreira *et al.* (2007), with the addition of new data collected in 2011.

### 2.3.2 Sample design

The sampling area was a rectangular area across the centre of the SPA, corresponding to an area of 44,860 hectares (Figure 2.2). The rectangle corresponded to an area where pseudo-steppe habitat prevailed (Moreira *et al.* 2007). Total steppe area in the region is 55,490 hectares, and so bird abundance estimates were extrapolated to this entire region. A grid of 391 sample points were placed systematically throughout the study area, with one sample point for each GAUSS 1x1 km grid square (Hayford Gauss projection, International Ellipsoid, Datum Lisboa IGeoE). To keep the points accessible for observers, the sample points were placed on dirt tracks. They were placed as close to the centre of each square as possible. For the Distance estimate method, points are assumed to be randomly located, so this was not followed for this study. However, a systematic survey design was used, as recommended (Thomas *et al.*, 2010), resulting in a set of sampled points representative of the habitat available in the area.

A 125 m circular buffer around each point was checked to ensure that it lay completely within pseudo-steppe habitat, and within a single grid square. If these conditions were not met, then the grid square was not surveyed.

*Figure 2.2: [From Moreira et al. (2007)] The Castro Verde special protection area (SPA study area - rectangle, the sampling area, and the sample points).*



### 2.3.3 Sampling methods

In 2006, the majority of bird counts were carried out between the 29th of April and the 8th of May, with the remainder of counts being carried out by two observers over a larger period of time (between the 20th March and the 12th May). In 2011, all bird counts were carried out between the 18th April and the 11th May. Each count lasted for 5 minutes. This count duration was chosen since it has been suggested as a suitable duration to ensure complete detection of species at the point whilst also minimising chances of birds not being detected at their initial locations (Fuller and Langslow, 1984). A distance limit of 125 m was set since detections beyond this distance would be hard to identify and measure accurately. All observations within 125 m of the observer were registered, along with the radial distance. All counts were carried out in the first 4 hours after sunrise or in the last two hours before sunset. All observers were experienced in bird identification; they also all attended a joint training session to improve their accuracy in estimating distances (Moreira *et al.*, 2007).

### 2.3.4 Habitat data

Habitat data was available in the form of the percentage coverage of five different habitat types: bare soil, cereal, fallow, woodland/shrub, and water. The variable for the percentage coverage of water was discarded due to its very low occurrence in the point transects. These habitat variables came from previously conducted support vector analysis of a temporal series of Landsat images. Each variable was log transformed to remove the issue of the habitat variables summing to a constant value.

### 2.3.5 Bird data

In total, 2,177 detections were made in 2006 and 2,705 were made in 2011; this accounted for a total of 62 different bird species. For this study, only the eight species with the greatest frequency of occurrence were selected for further analysis (Table 2.1), although data for the other species were retained in some analyses to improve pooled measures of detectability. Five of the bird species in this study are Passeriformes (small perching birds). The three other species in the study are either Galliformes or a Gruiform; these are larger species which are known to be more detectable by auditory cues than Passeriformes. Owing to these known differences in detectability between species, a new variable was created to classify two broad groups of species in this study, a method previously used by Alldredge *et al.* (2007a). One group contained *Aleruf*, *Cotcot* and *Tettet* (two Galliformes and a Gruiform) which are likely to have greater detectability at distance (see Table 2.1 for full species names). The other group contained the remaining five Passeriform species, which are expected to have a sharper drop in detectability at distance, especially in dense habitats where most detections are by auditory cues (Alldredge *et al.*, 2007b).

### 2.3.6 Distance methods

The program Distance (Thomas *et al.*, 2010) was used to analyse the count and distance data, and associated covariates. Whilst distance data were collected to the nearest 5 metres with a maximum distance of 125 metres, for analysis these values were transformed into intervals with cut points at 0, 20, 40, 60, 80, 100, 120 metres. It was important to place the distance data into intervals because of the variability in the way that different observers recorded distance; some rounded to the nearest 5 m, others rounded to the nearest 10 m. This difference in accuracy created data spikes which would not be appropriate for the fitting of a detection function (Figure 2.3a). Use of 20 metre intervals was found to provide a smoother graph of the frequency of distance measurements (Figure 2.3b).

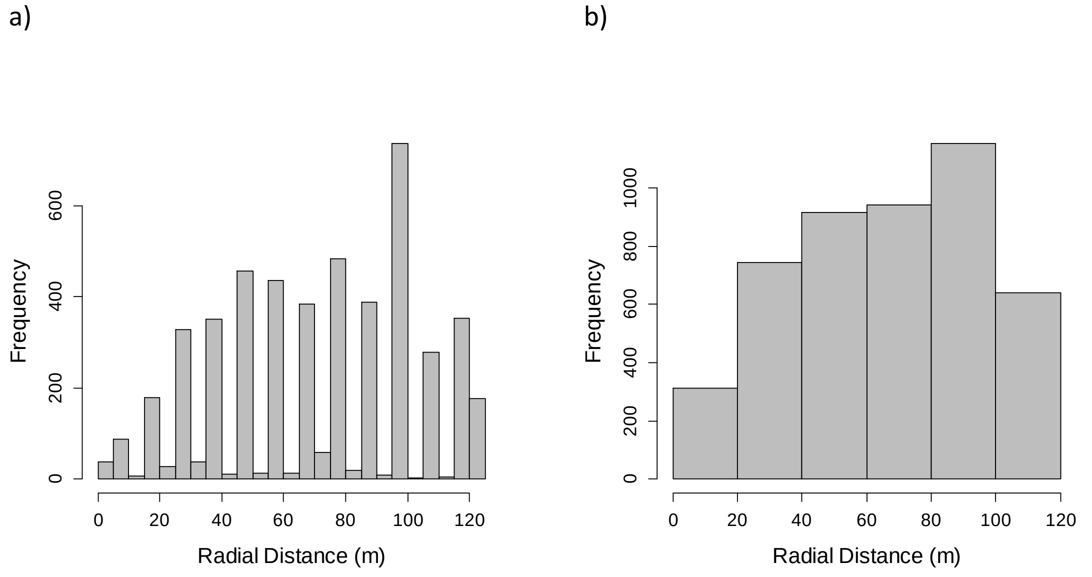
*Table 2.1: The eight species with the greatest frequency of occurrence selected for analysis in this study. Species Group is a variable created to classify broadly between species based on their maximum detectability distance.*

| ***Abbreviation*** | ***Scientific name*** | ***Common name*** | ***Order*** | ***Species Group*** |
|---|---|---|---|---|
| *Aleruf* | *Alectoris rufa* | Red-legged Partridge | Galliform | B |
| *Calbra* | *Calandrella brachydactyla* | Short-toed Lark | Passeriform | A |
| *Cisjun* | *Cisticola juncidis* | Zitting Cisticola | Passeriform | A |
| *Cotcot* | *Coturnix coturnix* | Quail | Galliform | B |
| *Melcal* | *Melancorypha calandra* | Calandra Lark | Passeriform | A |
| *Milcal* | *Miliaria calandra* | Corn bunting | Passeriform | A |
| *Saxtor* | *Saxicola torquatus* | Stonechat | Passeriform | A |
| *Tettet* | *Tetrax tetrax* | Little Bustard | Gruiform | B |

Distances were truncated at 120 metres, meaning that any observations at distances of 120 metres or greater were removed from the analysis; this is in accordance with the guidance of Buckland *et al.* (2001) that the 10% of detections associated with the largest distances should be discarded. Distance software then uses the midpoint of these intervals for analysis. Selection of truncation distance is a balance between the fact that larger truncation distances will result in small tail probabilities that increase bias, and the fact that smaller truncation distances mean more data is discarded, reducing precision. Distance sampling methodology has been shown to be robust to right truncation (Ekblom, 2010). Truncation of distances also has the advantage that it reduces the complexity of the detection function, generally allowing for a better fit to the remaining data (Dallimer and King, 2008).

Observers have previously been shown to be a source of detection function variability (Norvell *et al.*, 2003; Buchanan *et al.*, 2006; Diefenbach *et al.*, 2003). Initial investigation of the dataset suggested that some observers had significantly different detection functions (Figure 2.4). However, the difficulty in dealing with the effects of inter-observer variability is that the variability caused by the observer and the variability caused by the environment, species and time of observations can rarely be disentangled. For example, some observers only participated in surveys in 2006 and some only in 2011; the abundance of some species is likely to have changed significantly between these two survey periods, so this may cause observers from only 2006 to have very different detection functions from observers in 2011. Another issue is that observers were assigned to regions of the Castro Verde SPA (for the logistical reason that it maximised the number of point transects they could visit); this means that some observers may have justifiably different detection functions. It is therefore unwise to remove observers from the analysis unless there are known issues with their skills; in fact, it is not possible to remove observers from this study without introducing bias (i.e. removing data for a region creates bias in the survey design; removing data for a year creates bias in sample size between years).

*Figure 2.3: a) Histogram of the original distance data (note the far smaller frequency of distances at multiples of 5 m compared to multiples of 10 m – this is due to rounding differences between observers). b) Histogram of the distance data as it was used in this study, with distances grouped into 20 m intervals, and truncated at 120 m.*



### 2.3.7 Conventional distance sampling models

Firstly, conventional distance sampling (CDS) models were run for each species individually. CDS models do not include any covariates. This method has the disadvantage that there may be too few observations to fit an accurate detection function (particularly for rare or poorly surveyed species). For each species, half-normal and hazard-rate functions were used to fit the detection function, with the best model chosen by AIC. No adjustment terms were used since this was simply to identify the best general function for each species, and to test the improvements that can be made over these basic models. Use of adjustment terms can also lead to over-fitting to the data, especially when sample size is small. Observations from both years were used to generate the detection function, but estimations of abundance were stratified by year.

A CDS model was also run on all the species data combined; this included the eight species chosen for this study (Table 2.1) and an extra group which contained all observations made of other species during the surveys. This method creates one detection function for all species combined. This method has the advantage of sharing information from all species, thus helping to build realistic detection functions for rare or under surveyed species (Rosenstock *et al.*, 2002). This helps to increase precision since it effectively increases the sample size for the creation of the detection function. However, the disadvantage is that it can bias estimates when observations of multiple species are pooled to create the detection function. If the species are known to have similar detectability, then it can be useful to share this information; Alldredge *et al.* (2007a) grouped species for analysis according to their maximum detection distance. However, if species are pooled when significant differences exist, this can lead to under or over estimating bias.

*Figure 2.4: Box plot for each observer showing median and inter-quartile range of radial distance for their observations. This shows the significant variability between some observers, with some having no observations within 10 m of themselves.*

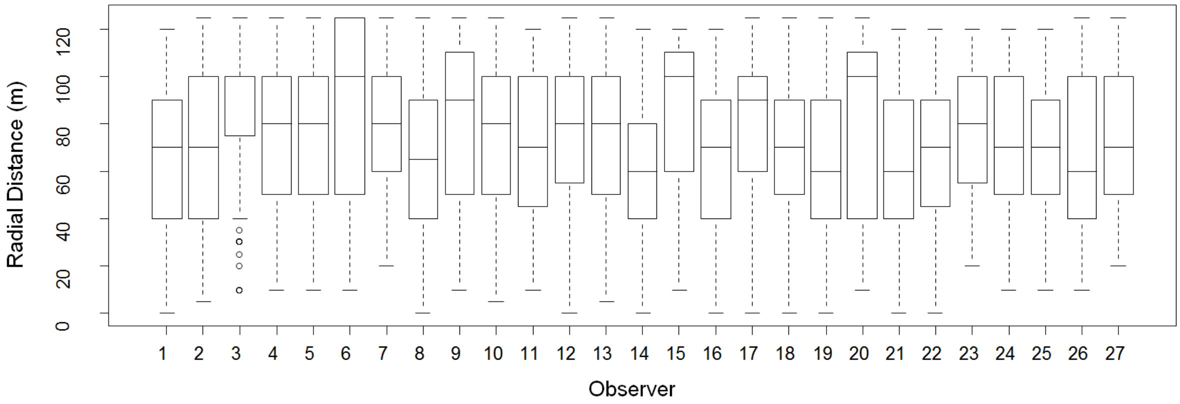


*Table 2.2: Covariates used in the multiple covariate distance sampling (MCDS) models.*

| **Covariate name** | **Description** |
|---|---|
| *Species* | Each species is classified separately. |
| *SpGroup* | Two species groups: Passeriformes, and Galliformes/Gruiformes. |
| *DomHab* | The habitat type with the greatest percentage coverage within the point transect buffer. |
| *Ba* | Percentage coverage of bare soil within the point transect buffer. |
| *BaFa* | Percentage coverage of bare soil and fallow within the point transect buffer. |
| *Ce* | Percentage coverage of cereal within the point transect buffer. |
| *Fa* | Percentage coverage of fallow within the point transect buffer. |
| *Wo* | Percentage coverage of woodland/shrub within the point transect buffer. |

### 2.3.8 Multiple covariate distance sampling models

A series of multiple covariate distance sampling (MCDS) models were run to allow for the incorporation of covariate effects on the detectability of birds. The covariates used in this study are listed in Table 2.2 and relate to either species or habitat properties. All MCDS models were run with the option of using either the half-normal or the hazard-rate key function; the best model was selected using minimum AIC.

Adjustment terms were initially experimented with, but these generally lead to over-fitting to the data. Adjustment terms allow the detection function to fit to specific characteristics of the data. However, unless there are known ecological reasons for humps or troughs in detectability at certain distances from the observer, it seems erroneous to over-fit to such trends in the data. A better method is to introduce covariates to explain changes in detectability. Using covariates to group and distinguish between stratum allows for the development of more parsimonious models of detectability (Alldredge *et al.*, 2007a).

A MCDS model was created with only *Species* as a covariate. This allowed for the creation of graphs to interpret how the effect of species changed the scale of the detection function. Another MCDS model was created with the four habitat variables (*Ba*, *Ce*, *Fa* and *Wo* – see Table 2.2).

Further analyses were also made to investigate the expectation that species in Bare Soil and Fallow habitats would have similar detectability.

### 2.3.9 Model selection

A total of nine covariates, based on either species or habitat data, were available for the MCDS models (Table 2.2). This part of the study aimed to develop the best possible detection function model based on combinations of the available covariates. A forward stepwise selection procedure was used; one covariate was added to the model at a time, with the most explanatory covariate (based on AIC) added to the model before each variable was again tested in turn. This procedure was stopped when the addition of new covariates no longer reduced AIC.

## 2.4 Results

The CDS individual species model results confirm the different shapes of the detection functions of *Cotcot* (Galliform) and *Tettet (Gruiform)*; the data for both of species was best modelled by a hazard-rate key function, compared with all modelled Passeriform species for which detectability was best modelled by the half-normal key function. Although note that the detectability for *Aleruf* (Galliform) was best modelled by a half-normal key function (Table 2.3).

*Table 2.3: The functions chosen according to minimum AIC for the conventional distance sampling individual species models, stratified by year (n is the sample size). AIC is not given here since it is meaningless for use across different datasets.*

| Species | Key function | n |
|---|---|---|
| *Aleruf* | Half-normal | 110 |
| *Calbra* | Half-normal | 88 |
| *Cisjun* | Half-normal | 369 |
| *Cotcot* | Hazard-rate | 140 |
| *Melcal* | Half-normal | 493 |
| *Milcal* | Half-normal | 1518 |
| *Saxtor* | Half-normal | 132 |
| *Tettet* | Hazard-rate | 311 |

*Table 2.4: Abundance estimates ($\widehat{N}$), stratified by year, from the individual species models, and from the combined species model (95% confidence intervals in parentheses).* CV *is the coefficient of variation which is the ratio of the standard deviation to the mean. These were conventional distance sampling models which do not use covariates.*

| Species | Year | Individual species models |  | Combined species model |  | % difference in $\widehat{N}$ |
|---|---|---|---|---|---|---|
|  |  | $\widehat{N}$ | *CV* | $\widehat{N}$ | *CV* |  |
| *Aleruf* | 2006 | 2,190<br>(1,396-3,437) | 0.23 | 3,417<br>(2,440-4,784) | 0.17 | 64.1% |
|  | 2011 | 3,546<br>(2,375-5,295) | 0.21 | 5,532<br>(4,428-7,202) | 0.14 |  |
| *Calbra* | 2006 | 7,792<br>(4,990-12,166) | 0.23 | 4,799<br>(3,313-6,953) | 0.19 | 162.4% |
|  | 2011 | 3,830<br>(2,365-6,203) | 0.25 | 2,359<br>(1,558-3,571) | 0.21 |  |
| *Cisjun* | 2006 | 4,654<br>(3,371-6,431) | 0.17 | 3,742<br>(2,769-5,056) | 0.15 | 124.4% |
|  | 2011 | 32,692<br>(27,302-39,147) | 0.09 | 26,275<br>(22,937-30,099) | 0.07 |  |
| *Cotcot* | 2006 | 1,144<br>(735-1,779) | 0.23 | 2,440<br>(1,610-3,699) | 0.21 | 46.9% |
|  | 2011 | 4,193<br>(3,254-5,404) | 0.13 | 8,948<br>(7,303-10,964) | 0.10 |  |
| *Melcal* | 2006 | 19,369<br>(15,099-24,846) | 0.13 | 19,442<br>(15,608-24,217) | 0.11 | 99.6% |
|  | 2011 | 20,584<br>(16,530-25,633) | 0.11 | 20,662<br>(17,170-24,864) | 0.09 |  |
| *Milcal* | 2006 | 64,588<br>(56,542-73,778) | 0.07 | 62,474<br>(55,298-70,580) | 0.06 | 103.4% |
|  | 2011 | 63,074<br>(55,594-71,560) | 0.06 | 61,009<br>(54,407-68,413) | 0.06 |  |
| *Saxtor* | 2006 | 5,222<br>(3,638-7,496) | 0.19 | 5,125<br>(3,912-6,714) | 0.14 | 101.9% |
|  | 2011 | 5,720<br>(3,942-8,299) | 0.19 | 5,613<br>(4,222-7,462) | 0.15 |  |
| *Tettet* | 2006 | 5,609<br>(4,426-7,108) | 0.12 | 12,121<br>(9,834-14,939) | 0.11 | 46.3% |
|  | 2011 | 6,098<br>(4,874-7,630) | 0.11 | 13,178<br>(10,848-16,008) | 0.10 |  |

The CDS combined species model created one detection function based on the pooled observations of all species. This means the abundance estimates are more precise (narrower confidence intervals), but that the results will be biased if the species have different detectability. Table 2.4 shows the abundance estimates from the CDS individual species models, and from the CDS combined species model. Using the combined species model reduces the coefficient of variation, and generally narrows the 95% confidence interval in comparison to individual models for each species. It also shows that whilst either similar or larger abundance estimates for the Passeriform species are given by the individual models, for the non-Passeriforms (*Aleruf*, *Cotcot* and *Tettet)*, much smaller abundance estimates are given by the individual species models compared with the combined species model.

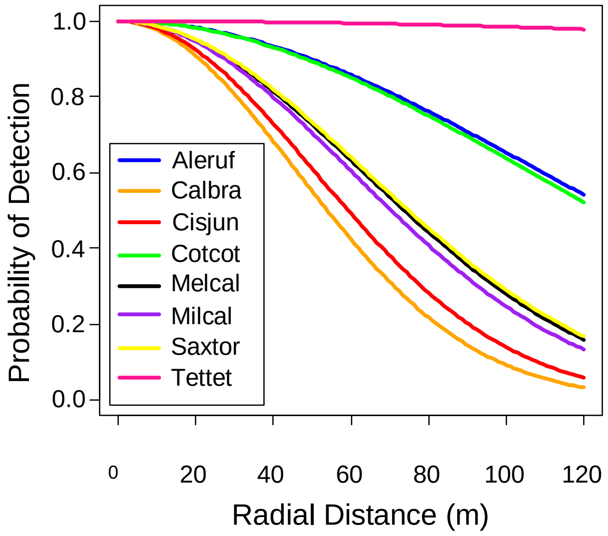
The detection function for the MCDS model with only *Species* as a covariate (Figure 2.5) demonstrates the expected separation between the Passeriform species and the Galliform and Gruiform species. *Aleruf*, *Cotcot* and *Tettet* are all modelled to have notably higher detectability at distance from the observer. In contrast, the detectability of all the Passerines deteriorates sharply as distance is increased.

The best MCDS model (based on AIC) used the half-normal key function and the covariates: *Species*, *DomHab*, *Fa*, and *Wo.*

Table 2.5 shows the covariates used and the corresponding ΔAIC values for the different MCDS models tested during the forward stepwise selection procedure to identify the best model.

Table 2.6 shows the final abundance estimates from the species covariate MCDS model and the best MCDS model; it also gives a direct comparison of the results of this paper with the results of Moreira *et al.* (2007), a previous study on the Castro Verde SPA which used only the raw bird count data to estimate abundance.

*Figure 2.5: The detection functions created by a multiple covariate distance sampling (MCDS) model with Species as the only covariate in the model.*



Detectability was found to vary in different habitat types (Figure 2.6), although this had minimal effect on the final abundance estimates (Table 2.6). The graphs were created from a MCDS model with only the percentage coverage of each habitat type as covariates. Detectability was found to deteriorate most rapidly in Woodland/Shrub habitat. Species were most detectable at distance in the Bare Soil habitat type, with very similar detectability in Fallow habitat.

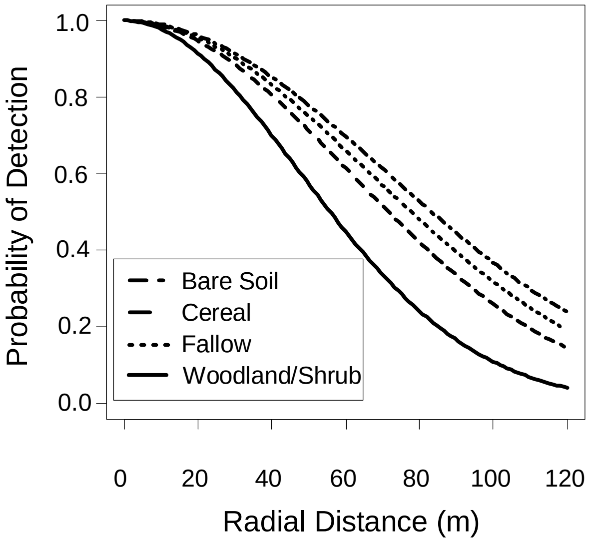
*Table 2.5: The full list of models tested during the forward stepwise selection process to find the best combination of covariates (shaded cells indicate which covariates were included in each model). ΔAIC values give the difference in AIC between the current model and the best model (i.e. the best model has ΔAIC = 0).*

| **Covariates** | | | | | | | **ΔAIC** |
|---|---|---|---|---|---|---|---|
| **Species** | **SpGroup** | **DomHab** | **BaFa** | **Ce** | **Fa** | **Wo** | |
| ■ | | | | | | | 8.84 |
| | ■ | | | | | | 45.3 |
| | | ■ | | | | | 146.35 |
| | | | ■ | | | | 139.47 |
| | | | | ■ | | | 143.39 |
| | | | | | ■ | | 140.35 |
| | | | | | | ■ | 135.82 |
| ■ | ■ | | | | | | 10.84 |
| ■ | | ■ | | | | | 14.05 |
| ■ | | | ■ | | | | 7.07 |
| ■ | | | | ■ | | | 10.58 |
| ■ | | | | | ■ | | 7.07 |
| ■ | | | | | | ■ | 1.79 |
| ■ | ■ | | | | | ■ | 3.79 |
| ■ | | ■ | | | | ■ | 0.63 |
| ■ | | | ■ | | | ■ | 2.57 |
| ■ | | | | ■ | | ■ | 2.97 |
| ■ | | | | | ■ | ■ | 2.57 |
| ■ | ■ | ■ | | | | ■ | 2.58 |
| ■ | | ■ | ■ | | | ■ | 0.21 |
| ■ | | ■ | | ■ | | ■ | 1.79 |
| ■ | | ■ | | | ■ | ■ | 0 |
| ■ | ■ | ■ | | | ■ | ■ | 1.99 |
| ■ | | ■ | ■ | | ■ | ■ | 2 |
| ■ | | ■ | | ■ | ■ | ■ | 0.17 |

*Table 2.6: Abundance estimates ($\widehat{N}$) from the species covariate model, and the final chosen model (95% confidence intervals in parentheses). Covariates used in the final model were:* Species, Wo, DomHab, and Fa. CV *is the coefficient of variation which is the ratio of the standard deviation to the mean. The data from Moreira et al. (2007) are the previous abundance estimates for each species in the Castro Verde SPA in 2006; these estimates were not adjusted for detectability.*

| **Species** | **Year** | **Moriera *et al.* (2007)** | **MCDS with species covariate** | | **Final MCDS model** | | **Δ(%) 2006-2011** |
|---|---|---|---|---|---|---|---|
| | | | **$\widehat{N}$** | ***CV*** | **$\widehat{N}$** | ***CV*** | |
| *Aleruf* | 2006 | 1,511 | 3,504<br>(2,506-4,898) | 0.17 | 3,518<br>(2,516-4,918) | 0.17 | |
| | 2011 | - | 5,673<br>(4,366-7,371) | 0.13 | 5,696<br>(4,383-7,401) | 0.13 | +61.9 |
| *Calbra* | 2006 | 2,906 | 4,922<br>(3,402-7,120) | 0.19 | 4,942<br>(3,416-7,149) | 0.19 | |
| | 2011 | - | 2,419<br>(1,600-3,658) | 0.21 | 2,429<br>(1,607-3,673) | 0.21 | -50.9 |
| *Cisjun* | 2006 | 2,616 | 3,838<br>(2,845-5,176) | 0.15 | 3,853<br>(2,856-5,197) | 0.15 | |
| | 2011 | - | 26,946<br>(23,618-30,743) | 0.07 | 27,055<br>(23,712-30,868) | 0.07 | +602.2 |
| *Cotcot* | 2006 | 930 | 2,503<br>(1,653-3,789) | 0.21 | 2,513<br>(1,660-3,804) | 0.21 | |
| | 2011 | - | 9,177<br>(7,509-11,214) | 0.10 | 9,214<br>(7,539-11,260) | 0.10 | +266.7 |
| *Melcal* | 2006 | 12,320 | 19,938<br>(16,046-24,775) | 0.11 | 20,019<br>(16,110-24,876) | 0.11 | |
| | 2011 | - | 21,190<br>(17,660-25,425) | 0.09 | 21,275<br>(17,731-25,528) | 0.09 | +6.3 |
| *Milcal* | 2006 | 32,370 | 64,070<br>(56,969-72,056) | 0.06 | 64,328<br>(57,196-72,350) | 0.06 | |
| | 2011 | - | 62,568<br>(56,068-69,822) | 0.06 | 62,821<br>(56,291-70,107) | 0.06 | -2.3 |
| *Saxtor* | 2006 | 3,080 | 5,256<br>(4,019-6,872) | 0.14 | 5,277<br>(4,036-6,900) | 0.14 | |
| | 2011 | - | 5,756<br>(4,338-7,639) | 0.14 | 5,779<br>(4,355-7,670) | 0.14 | +9.5 |
| *Tettet* | 2006 | 8,426 | 12,430<br>(10,111-15,281) | 0.11 | 12,480<br>(10,152-15,343) | 0.11 | |
| | 2011 | - | 13,515<br>(11,156-16,372) | 0.10 | 13,569<br>(11,201-16,438) | 0.10 | +8.7 |

*Figure 2.6: The effect of habitat on detectability. Lines represent modelled detectability in 100% coverage of each habitat type, with data pooled for both years.*



## 2.5 Discussion

The fact that the detectability of *Cotcot* and *Tettet* were both best modelled by a hazard-rate function suggests that these two species have fundamentally different detectability to the other species in this study. The hazard rate function allows for fitting to data that has a shoulder (i.e. for species that do not have instantly deteriorating detection rates as distance from the observer). The fact that *Aleruf* was best modelled by a half-normal function is perhaps surprising since it was expected to have similar detection characteristics to *Cotcot* and *Tettet*. This expectation was based on the fact that *Calbra*, *Cisjun*, *Melcal*, *Milcal* and *Saxtor* are Passerines. In comparison, *Aleruf* and *Cotcot* are of the same order, Galliform, whilst *Tettet* is of the order Gruiform. All three of these species are markedly larger and have louder auditory cues than the Passerine species. Figure 2.5 illustrates the similarities in the detection functions of *Aleruf*, *Cotcot* and *Tettet* when they are included in a MCDS model using a half-normal key function. These three species stand out as having significantly higher detection rates at distances greater than 40 m from the observer. Whilst the hazard-rate function provided the best fit individually to these species, their increased detectability at distance can still be modelled within a pooled species half-normal framework.

The pooling of species observations to develop a global detection function can increase precision because of the increased sample size (Table 2.4). However, estimates will be biased if species have fundamentally different detection functions (Buckland *et al.*, 2008), as demonstrated in this study. For this reason, it is important to include covariates to explain these differences. The fact that *SpGroup* was not a useful covariate (Table 2.5) suggests that within group differences between species were too large for the grouping of Passeriformes and Galliformes/ Gruiformes to be beneficial to the model. Whilst it is clear that *Aleruf*, *Cotcot* and *Tettet* have markedly different detection functions to the other species, there is enough variation between each individual species for the *SpGroup* covariate to be redundant in comparison to the *Species* covariate (Figure 2.5).

The order with which the covariates were added to the model in the forward selection procedure (Table 2.5) gives an indication of the importance of each variable to the model. The first covariate added to the model was *Species*; this is logical because of the differences between species discussed above. The next most important variable was *Wo* (percentage coverage of woodland/shrub); since this covariate represents the habitat with the greatest impact on detectability it is not surprising that it holds the most useful habitat-based information on detectability. A similar result has been demonstrated by Sillett *et al.* (2012), who found the percentage of forest cover to be an important determinant of the detectability of their study species. In a 100% woodland habitat, detectability is most severely reduced by distance; if there is 0% woodland habitat, then the habitat must be bare soil, cereal or fallow (or any mixture of the three), which all allow for greater detection rates than woodland habitat. The next most important variable was *DomHab*, although these additional covariates now create only small reductions in AIC (Table 2.5). *DomHab* is perhaps useful because it holds information on what habitat is dominant when the percentage of woodland is low, allowing detectability to be adjusted when bare soil, cereal or fallow habitats dominate. The next covariate added to the MCDS model by forward selection was *Fa*; whilst this covariate does improve the model, its effect is minimal. The usefulness of *Fa* to the model perhaps derives from the fact that fallow habitat generally covers more than 50% of the Castro Verde region (Moreira, 1999). Therefore the percentage of fallow habitat simply holds more information than the other remaining covariates.

It is important to note that the covariates used in this study are highly correlated and so the importance of the variables should always be interpreted with caution. The habitat variables are highly correlated due to the fact that they are based on percentage coverage, i.e. a high percentage for one habitat type necessitates that the other habitat types will be of a low percentage. The *Species* and *SpGroup* covariates are also clearly highly correlated. When one of these covariates is added to the model, the new information that the other covariate can provide is drastically reduced. Similarly for the habitat covariates, due to the forward stepwise selection procedure, once a habitat covariate has been added, additional habitat covariates will contain less new information. In this situation, a principal components analysis could be used to convert the correlated habitat variables into a set of uncorrelated variables. However, this method was not used in this study as it also removes the ecological context of the habitat covariates, i.e. differences in detectability between different principal components could no longer be attributed to habitat types.

### 2.5.1 Population trends

Substantial population increases (more than 250%) were identified between 2006 and 2011 for Zitting Cisticola (*Cisjun*) and Quail (*Cotcot*), species with known associations with taller and denser vegetation such as cereal fields (Delgado and Moreira, 2000; Moreira *et al.*, 2007). In the 2005 drought year, cereal crops had low vegetation development, resulting in farmers introducing livestock grazing in the failed cereal fields (Moreira *et al.*, 2007). This reduction in cereal habitat in 2005 is likely to have had a negative impact on the local population of cereal associated bird species, through a combination of mortality and dispersion to more suitable areas. Whilst pre-drought population numbers are not known, these results suggest that populations of Zitting Cisticola (*Cisjun*) and Quail (*Cotcot*) are recovering from the impacts of the drought. Whilst most species either made gains or had relatively stable populations between 2006 and 2011, Short-toed Lark (*Calbra*) had a noticeable decline in numbers. The 95% confidence intervals for the two years only have a small overlap, suggesting a real reduction in abundance. This species is associated with sparse vegetation and bare ground (Delgado and Moreira, 2000; Moreira *et al.*, 2007), so the availability of suitable habitat may have increased for this species during the 2005 drought, perhaps explaining the decrease in population from 2006 to 2011. However, the species is a trans-Saharan migrant, so population trends may also be influenced by climatic and habitat conditions in their wintering grounds.

## 2.6 Conclusion

The results of this study suggest that the use of a species covariate can improve estimates when individual species have low sample sizes. Previous studies (Alldredge *et al.*, 2007a; Marques *et al.*, 2007) have come to similar conclusions. The addition of habitat covariates made only very small changes to abundance estimates, and made no clear difference to the size of confidence intervals. However, the inclusion of habitat variables did improve the models in terms of AIC. This suggests that whilst habitat variables did not change abundance estimates, in agreement with Sillett *et al.* (2012), they allow the model to explain more of the variation in detectability. This chapter has demonstrated that sharing distance sampling data for multiple species can improve the estimation of detectability. Whilst the focus thus far has been on data collection and pre-processing, the following chapter moves on to the modelling phase but continues to utilise co-occurring species data. Chapter 3 tests a novel iterative species distribution modelling method, with the distributions of interacting species used to predict the co-occurring species.

# Chapter 3: Incorporating biological interactions into species distribution models: the use of virtual species to test hypotheses

## 3.1 Abstract

Use of biotic information is commonly suggested as a way to improve the predictive performance of species distribution models (SDMs). However, use of such data is rare; there appear to be two main reasons for this: (1) knowledge of how species interactions affect distributions is still limited, (2) modelling methods require spatially explicit predictor variables covering the full extent of the study area. For this study, pairs of artificial species were created based on plausible climatic responses. These species pairs were given interaction terms through resource competition, leading to the generation of species with distributions constrained by both abiotic and biotic factors. MaxEnt was then used to predict the distribution of one of the pair of species based on climatic predictor variables. MaxEnt was subsequently run iteratively using the partner species' distribution and the climatic variables as predictors. Models were run until 500 predictions were created for each species. AUC (area under the receiver operating characteristic curve) and map comparison techniques were used to assess the accuracy of predictions. Predictive maps were found to repeatedly expand and contract, with no clear improvement with repeated iterations. The percentage contribution of the species based predictor variables was found to increase with repeated iterations; although this did not correspond to improved predictions. Since artificial species were used, the "true" distributions were known; this allowed for the evaluation of AUC as a method for measuring predictive accuracy against direct map comparisons. AUC was found to be insensitive to variations in predictions.

## 3.2 Introduction

The vast majority of species distribution modelling (SDM) studies have focused on the use of abiotic predictor variables (Guisan and Thuiller, 2005) since environmental conditions are key determinants of a species' distribution. The region of environmental space within which a species can exist is often referred to as its fundamental niche, and it is the fundamental niche which most SDM research tends to predict. However, the environment is only one of many constraints on a species' distribution. The realised niche is the actual distribution of a species (the locations where the species will actually be found), and is determined by environmental factors, biotic interactions, dispersal, colonisation history and migration. These ideas of fundamental and realised niches (Hutchinson, 1978) can be applied to both the Grinnellian and Eltonian niche concepts (Soberón, 2007). A species' Grinnellian niche is the habitat within which it exists, and is defined by those variables that have a direct impact on the species due to physiological responses (Soberón, 2010). These direct variables (Austin and Smith, 1990) are independent of the species, i.e. a species has no impact on them. A species' Eltonian niche is defined by the community within which it exists, and its location in the food web (Soberón, 2010). Whilst the climate data required for investigating a species' Grinnellian niche are now readily available and frequently used, data for the Eltonian niche is far harder to collect. Unlike the Grinnellian niche, for the Eltonian niche the species has a direct impact on those variables that define its niche; this makes the domain of the Eltonian niche dynamic and complex (Soberón, 2007). To be able to understand and map species' realised distributions, modelling of both Grinnellian and Eltonian niches is required.

Some studies have attempted to include biotic interactions in SDMs, but this is rare. Leathwick and Austin (2001) investigated competition between tree species in New Zealand; firstly modelling abundance from environmental predictors, and then including statistical terms describing the abundance of other species. They found that inclusion of abundance data of competitors helped to explain the target species' abundance, and led to changes in species' responses to temperature variables. This study shows the potential importance of biotic interactions in understanding a species' distribution, and the complexity involved in introducing such terms. Whilst Leathwick and Austin (2001) and Gutiérrez *et al.* (2005) demonstrated that the use of biotic interactions can improve predictive power at local extents, more recent studies have shown that biotic interactions can also improve predictions at regional (Araújo and Luoto, 2007) and continental extents (Heikkinen *et al.*, 2007; Sutherst *et al.*, 2007). An issue to contend with when attempting to model species interactions is that the strength and impact of these interactions can vary along environmental gradients (Sutherst *et al.*, 2007). In fact, in some cases the nature of interactions can even change in different environmental conditions (Brooker, 2006).

One of the main problems with using SDMs is the difficulty in evaluating their performance when the "truth" is unknown (Austin *et al.*, 2006). The use of artificial species data is an important step in studying the predictive power of SDMs, and their sensitivity to inconsistencies in data. With artificial data, a species' distribution can be fully defined so that its "true" distribution is exactly known, and the quality of predictions can be accurately measured. There are numerous examples in the literature of artificial data being developed for use in SDMs. The basic concept is to take an environmental variable and then create a viable ecological response curve to that variable. Minchin (1987) developed software called COMPAS which can be used to generate artificial species data, and has since been used to evaluate different SDM methods (Austin *et al.*, 2006). One limitation of COMPAS is that it generates artificial species based on entirely fictitious environmental data. However, other studies have created virtual species from real environmental data (e.g. Hirzel *et al.*, 2001; Moisen and Frescino, 2002). Hirzel *et al.* (2001) created 11 predictor variables with either Gaussian, linear or truncated linear response curves for each species. Meynard and Quinn (2007) generated 18 artificial species with random, linear, Gaussian, threshold or mixed response curves. Legendre *et al.*, (2002) used only linear responses to environmental variables. The variety of response curves used in different studies indicates the lack of knowledge about how species respond to environmental gradients. There is also debate on the subject of whether species responses are unimodal or multimodal. Oksanen and Minchin (2002) suggest that most species responses are unimodal, and that it is interactions between different environmental responses and biotic interactions which can sometimes cause multimodal responses in field data.

The overall response of a species to environmental variables is a combination of each relevant individual environmental response; how the interaction between responses is modelled varies between studies. Species can be given additive responses (Hirzel *et al.*, 2001), multiplicative responses (Barbet-Massin *et al.*, 2012a), or mixed responses (Wintle and Bardos, 2006). Whilst complex variations in the interactions between responses to environmental variables are likely to exist in reality, implementing varied or more complex interactions would require guesswork on the theories behind them; this is beyond current ecological knowledge.

By generating artificial pairs of interacting species, this study aims to assess how predictions of each species distribution can help improve the predictions for the other species. If a species distribution changes, then this change will impact upon those species that it interacts with. Species distributions are not stable, but constantly changing (at the very least at small scales) due to the multitude of biotic interactions that all species are influenced by, and the dynamical system that this creates (Davis *et al.*, 1998). This study applies this idea to species distribution modelling, repeatedly predicting a species' distribution based on a partner species' distribution which is also repeatedly predicted in a feedback loop. The desired outcome from this methodology would be to observe predictions tending towards a greater precision, with perhaps some fluctuation in precision due to uncertainty from the SDM approach. The use of artificial species in this study also allows for the analysis of AUC as a measure of SDM predictive accuracy. Recent studies have brought doubt on the usefulness of the AUC measure (Lobo *et al.*, 2010), and have demonstrated its inability to differentiate between substantially different predictions (Synes and Osborne, 2011). Since the species' "true" distributions are known, map comparison techniques can be used to precisely quantify the accuracy of predictions, and therefore assess the performance of the AUC measure.

## 3.3 Methods

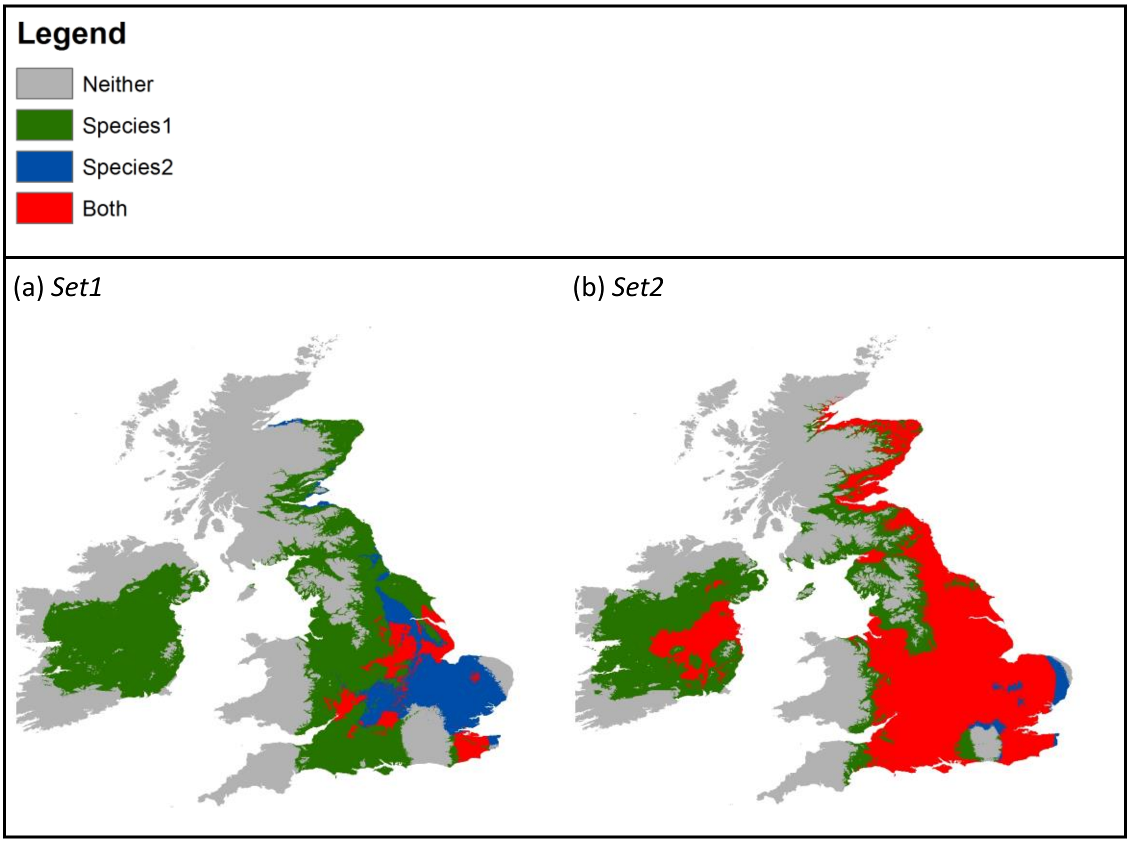
### 3.3.1 Climate data

Climate data were obtained from the WorldClim dataset (version 1.4; Hijmans *et al.* (2005), http://www.worldclim.org/) at 30 arcsec resolution. These climate data were cropped to cover the United Kingdom and Ireland. This extent was chosen as a balance between covering a large enough area to realistically represent a full species distribution, whilst also minimising computer processing time. The WorldClim dataset includes 19 different bioclimatic variables; for this study five were selected for their expected importance in limiting species distributions: (1) mean diurnal range, (2) maximum temperature of the warmest month, (3) minimum temperature of the coldest month, (4) annual precipitation, (5) precipitation of the driest quarter.

### 3.3.2 Species data

Two different pairs of species were generated by assigning Gaussian responses to each climate variable. For the first pair of species (*Set1*), both were given identical responses to temperature, with the only differentiation between species being in precipitation threshold. *Set1 Species1* was given a far greater tolerance of wetter conditions, and a requirement for more rain in the driest months. *Set1 Species2* on the other hand has a far narrower tolerance of precipitation, generally preferring drier conditions. For the second pair of species (*Set2*), again both were given identical responses to temperature, with the only differentiation between species being in precipitation threshold. *Set2 Species1* has a greater tolerance of wetter conditions than *Set2 Species2*, but they have been created so that they are physiologically far more similar than the species in *Set1* (Figure 3.1). Each individual response variable was scaled to values between 0 and 1 so that each had equal weighting in the overall species response.

*Figure 3.1: The "true" distributions of the artificial species.*



For each species, the responses to the five different climatic variables were multiplied together to give an overall physiological response. Previous studies with virtual species have defined additive (Hirzel *et al.*, 2001), multiplicative (Barbet-Massin *et al.*, 2012a) and mixed (Wintle and Bardos, 2006) responses to climatic variables. Additive responses suggest that climatic variables are independent, and that unsuitability of one variable can be compensated for by another. This may be true for some variables, but in general one unsuitable climate factor will cause a location to be unsuitable, regardless of any other climate factors. Real species most likely have a mixed response to climatic variables, with some variables able to compensate for others whilst others will be truly crucial. For this study multiplicative responses were chosen due to the assumptions (and guesswork) that would be required to design a realistic mixed response physiology, it simply makes more sense to acknowledge that ecological knowledge is currently insufficient to be that precise.

Finally, a presence/absence threshold of 0.5 was set for the species' overall environmental response (i.e. for each pixel, if the species' response is above 0.5 then it is recorded as present, otherwise it is recorded as absent).

### 3.3.3 Species interaction

Interaction between the species pairs was created through resource competition. Godsoe and Harmon (2012) created a model of competition based on consumer resource dynamics; a consumer resource model creates interactions between species by assigning each species an ability to deplete a given resource. Whilst Godsoe and Harmon (2012) created a dynamic consumer resource model, for this study the concept was simplified to allow for the basic concept of resource competition to be implemented on a spatial grid.

Firstly, a new variable was created to represent the resource for which the species would compete. The new variable was growing degree days (GDD), created as specified by Synes and Osborne (2011). Growing degree days is a good proxy for a resource variable because it is known to be an important limiting factor on plant growth (Prentice *et al.*, 1992); it is therefore a variable likely to be highly important in dictating the vegetative biomass of an area. The rule for resource competition was as follows: for each pixel, if annual GDD was greater than or equal to 1,750 for Set1, or 1,700 for Set2, then the species could co-exist. Below this value only one species could exist; the species was chosen according to which one had the higher multiplicative environmental response for that pixel.

### 3.3.4 Sampling

The "true" distribution of the artificial species was sampled to match the method of data collection for real species. Sampling methods are known to commonly be biased (Williams *et al.*, 2002), for example with samples being taken in easily accessible areas or near to human infrastructure. It has been recommended that the best sampling method is random stratification across an environmental gradient with major control over the species' distribution (Hirzel and Guisan, 2002), rather than the more common random geographic stratification. For this study, samples were randomly stratified across the gradient for "maximum temperature of the warmest month". A total of 300 samples were collected for each species. All samples were of presence data; no absence data were collected.

### 3.3.5 Modelling procedures

The SDM algorithm MaxEnt (Phillips *et al.*, 2006) was used to make predictions from the sample data; it has been found to perform well with presence-only data (Anderson *et al.*, 2006). MaxEnt was chosen for its ease of use, and for the deterministic nature of its algorithm. Some SDMs rely on algorithmic stochasticity to generate predictions (e.g. GARP – Stockwell, 1999), and therefore repeated predictions based on a single dataset can exhibit variability. For this study, it is important that any variability in predictions can be attributed solely to the predictor variables and so a deterministic algorithm is required. MaxEnt's default parameter values were used since they were found to produce good results in a broad range of situations (Phillips and Dudík, 2008). The only change from default values was to set aside 25% of the sample points to allow for the calculation of AUC (area under the receiver operating characteristic curve), as is the common method for estimating model accuracy in SDM studies (Vaughan and Ormerod, 2005). The 25% of sample points set aside for testing were kept the same across each model run so that AUC values could be compared.

For *Species1* in *Set1* and *Species1* in *Set2*, MaxEnt was first run once with the five original climatic variables as predictors; this gave an initial prediction for each species. After this, MaxEnt was run iteratively with the 5 climatic variables and the previous prediction of the partner species (the other species in its set) as predictors. This process was conducted for both the species in Set1 and the species in Set2, with the predictors for one species always containing all five climatic predictors as well as the most recent prediction of the partner species. This process was repeated until 500 prediction maps were created for each species.

The default output from MaxEnt is a logistic format, which is a value between 0 and 1 for each pixel; this can be considered as a probability of presence (Phillips and Dudík, 2008). To allow for the comparison of MaxEnt output maps with the "true" species distributions, the MaxEnt outputs were converted to presence-absence maps with the "maximum training sensitivity and specificity" threshold. Jiménez-Valverde and Lobo (2007) found this to be a good threshold in studies where prevalence of the species was not low (all species in this study have relatively high prevalence, see Table 3.1).

*Table 3.1: Species prevalence.*

| **Set** | **Species** | **Percentage of pixels in which species is present** |
|---|---|---|
| *Set1* | *Species1* | 42% |
| *Set1* | *Species2* | 13% |
| *Set2* | *Species1* | 59% |
| *Set2* | *Species2* | 37% |

### 3.3.6 Output and map comparisons

MaxEnt calculates AUC values for each map prediction, based on the data set aside for testing (25% in this study). MaxEnt also calculates the percentage contribution that each predictor variable makes towards the model; these are calculated by adding the increase in regularised gain to the contribution of the corresponding variable for each iteration of the training algorithm (Phillips *et al.*, 2006). These data were all recorded for each model run.

Each predicted map was compared to the “true” species distribution using direct pixel comparisons to give the total number of correct pixels, the total number of false positives (over predictions) and the total number of false negatives (under predictions). Map comparisons were also made using the fuzzy numerical statistic from the Map Comparison Kit (Visser and De Nijs, 2006). This statistic compares two numerical maps (in this case: 0 - absence, 1 - presence), but also includes fuzziness of location; this means that for each pixel-to-pixel comparison, a radius is used to check the similarity of pixels in the local neighbourhood. For this analysis, a radius of five pixels was used so that localised fuzziness in predictions could be accounted for. The fuzzy numerical statistic can take values between 0 (fully distinct) and 1 (fully identical).

## 3.4 Results

Species distribution predictions all attained high AUC scores, with the lowest score across all models being 0.7543. Fuzzy numerical values were also high, with the lowest being 0.7297 (Table

3.2). The maximum values achieved for AUC and fuzzy numerical indicate that the best predictions for the species in *Set1* were more accurate than the best predictions for the species in *Set2*. A one-way analysis of variance showed a highly significant effect of which set the species came from on the AUC scores ($F_{1,1998} = 35.9$, $p < 10^{-9}$). Similarly, a one-way ANOVA showed a highly significant effect of which set the species came from on fuzzy numerical values ($F_{1,1998} = 2721.6$, $p < 10^{-16}$). For both AUC and fuzzy numerical, predictions from *Set1* were more likely to attain higher scores than predictions from *Set2*.

*Table 3.2: Minimum, maximum, mean and standard deviation for AUC and fuzzy numerical values for each species across the model runs for* Set1 *and* Set2*.*

| **Model Set** | **Species** | **Measure** | **Min** | **Max** | **Mean** | **SD** |
|---|---|---|---|---|---|---|
| *Set1* | *Species1* | AUC | 0.7597 | 0.8005 | 0.7815 | 0.0074 |
| *Set1* | *Species1* | Fuzzy Numerical | 0.7308 | 0.8981 | 0.817 | 0.0287 |
| *Set1* | *Species2* | AUC | 0.9451 | 0.954 | 0.9495 | 0.0009 |
| *Set1* | *Species2* | Fuzzy Numerical | 0.9476 | 0.9683 | 0.959 | 0.003 |
| *Set2* | *Species1* | AUC | 0.7543 | 0.792 | 0.7768 | 0.0078 |
| *Set2* | *Species1* | Fuzzy Numerical | 0.5431 | 0.7309 | 0.6291 | 0.0292 |
| *Set2* | *Species2* | AUC | 0.9066 | 0.9167 | 0.9131 | 0.0015 |
| *Set2* | *Species2* | Fuzzy Numerical | 0.7297 | 0.8349 | 0.7842 | 0.0188 |

*Table 3.3: Mean and standard deviation for the number of predicted presence pixels across all model runs for each species.*

| **Model Set** | **Species** | **Mean** | **SD** |
|---|---|---|---|
| *Set1* | *Species1* | 153,601.2 | 22,164.85 |
| *Set1* | *Species2* | 82,214.32 | 6,842.117 |
| *Set2* | *Species1* | 140,663.8 | 20,504.92 |
| *Set2* | *Species2* | 92,726.73 | 11,356.16 |

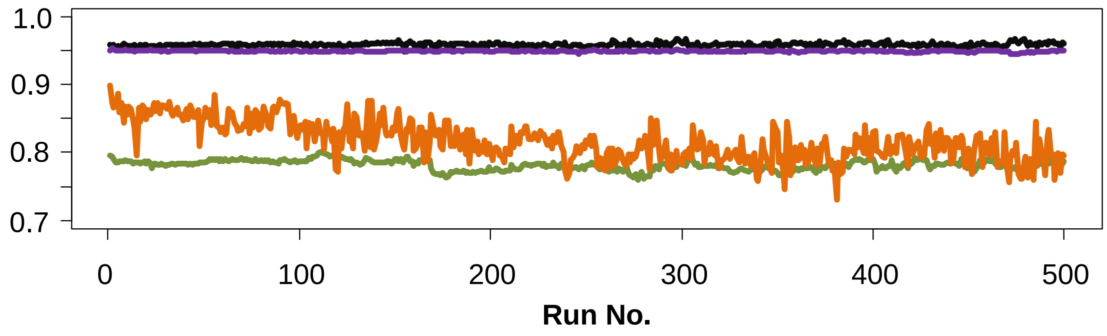
Linear regressions of AUC against fuzzy numerical for each species in each set gave varied results. Whilst two gave no significant result, the other two gave significant results but with very low R-squared values and visually unimpressive correlations (Figure 3.3). These results suggest there was minimal, if any, correlation between AUC and fuzzy numerical values.

AUC and fuzzy numerical values for *Set1* (Figure 3.2a) and *Set2* (Figure 3.2b) varied throughout the model run, with no discernible pattern. In *Set1*, for *Species1* the maximum AUC and fuzzy numerical values (Table 3.2) were attained at run 111 and 1 respectively; for *Species2* the maximum AUC and fuzzy numerical values were attained at run 2 and 479 respectively. In *Set2*, for *Species1* the maximum AUC and fuzzy numerical values (Table 3.2) were attained at run 377 and 1 respectively; for *Species2* the maximum AUC and fuzzy numerical values were attained at run 464 and 245 respectively.

*Figure 3.2: AUC and fuzzy numerical values plotted against model run number for each species in (a) Set1 and (b) Set2.*

**Legend**
- Species1 AUC
- Species2 AUC
- Species1 Fuzzy
- Species2 Fuzzy

(a) *Set1*



(b) *Set2*

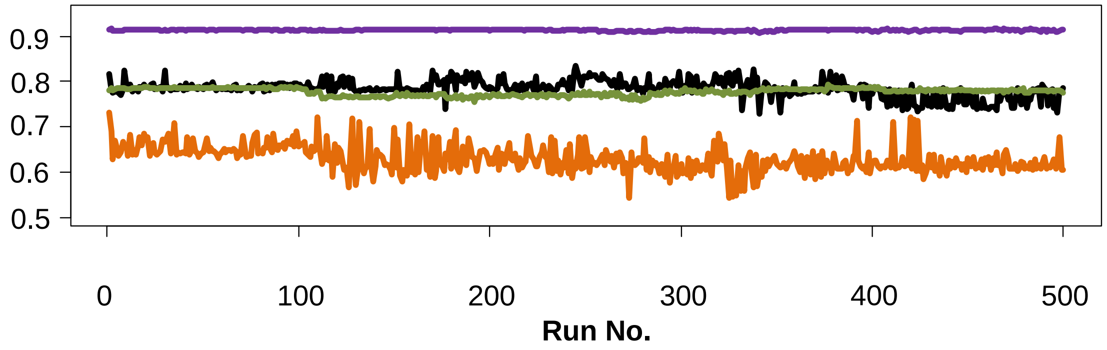
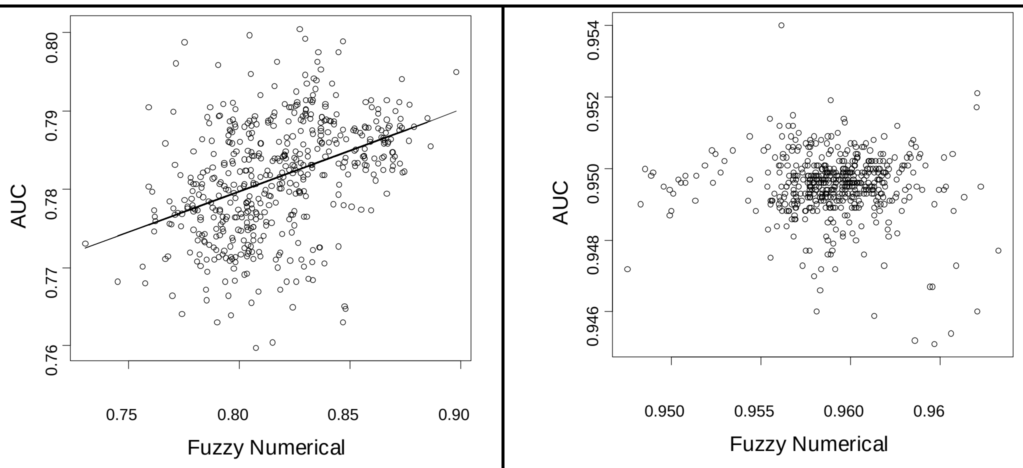
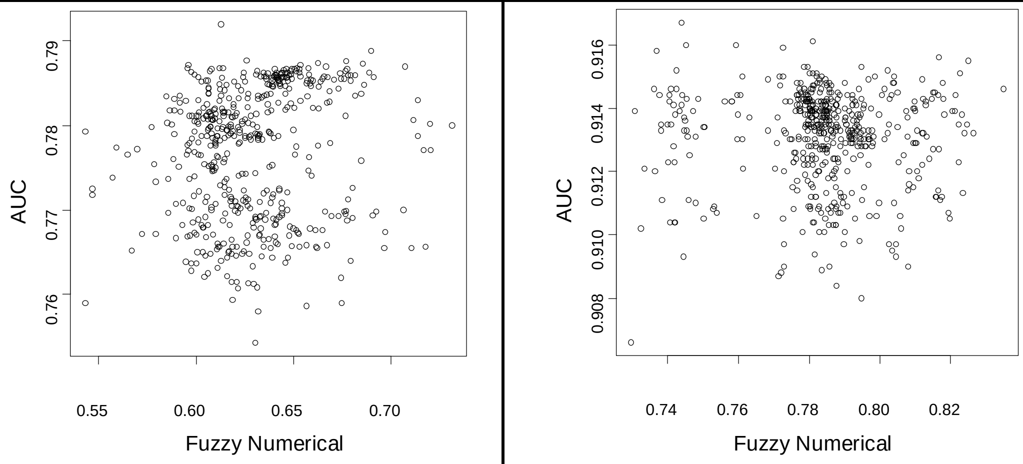


*Figure 3.3: Scatter plots of AUC values against fuzzy numerical values for each species. Where a significant result was found, the regression line is plotted (although it should be noted that the R-squared value is very poor).*



*Set1*, *Species1*: $F_{1,498}$ = 100.7, $p < 10^{-16}$, R-squared value: 16.8%

*Set1*, *Species2*: No significant result (p = 0.15)



*Set2*, *Species1*: $F_{1,498}$ = 8.96, $p<0.005$, R-squared value: 1.7%

*Set2*, *Species2*: No significant result (p = 0.83)

Analysis of predictor variable contributions show that the importance of the partner species as a predictor variable increases as the model run number increases. A linear regression model to predict the contribution of *Set1 Species2* as a predictor for *Set1 Species1* in terms of the run number gave a highly significant result ($F_{1,498}$ = 2057, $p < 10^{-16}$), with an R-squared value of 80.5% showing that the run number (i.e. the number of iterations of MaxEnt) explains most of the variation in the contribution of the predictor variable. Significant results were also found for the contribution of *Set1 Species1* as a predictor for *Set1 Species2* ($F_{1,498}$ = 135.4, $p < 10^{-16}$, R-squared value: 21.4%), the contribution of *Set2 Species2* as a predictor for *Set2 Species1* ($F_{1,498}$ = 547.2, $p < 10^{-16}$, R-squared value: 52.4%), and the contribution of *Set2 Species1* as a predictor for *Set2 Species2* ($F_{1,498}$ = 613.7, $p < 10^{-16}$, R-squared value: 55.3%), although these results show less explanation of the variance.

Linear regression was also used to predict the fuzzy numerical value in terms of the contribution of the species predictor variable. Results were mixed; whilst all results were significant, three of the four had R-squared values less than 16% showing minimal explanation of variance. The other result was for the contribution of *Set1 Species2* as a predictor for *Set1 Species1*; the linear regression was highly significant ($F_{1,498} = 455.8$, $p < 10^{-16}$), with an R-squared value of 47.8%. This result had a negative gradient meaning that as the percentage contribution of *Species2* as a predictor for *Set1 Species1* increased, the fuzzy numerical value decreased.

## 3.5 Discussion

The high AUC values obtained across model predictions indicate that all predictions were fair to excellent. However, the maximum fuzzy numerical values indicate that even the best predictions were still quite distinct from the “true” species distributions. The standard deviation for AUC scores was generally lower than the standard deviation for fuzzy numerical values. This indicates that the AUC measure is relatively insensitive to changes in predictive accuracy when compared with the fuzzy numerical measure. Linear regression of fuzzy numerical values against AUC indicates that the relationship between the two measures is limited. Whilst the scales of the axis indicate broadly similar values, the limited correlations show that AUC does not have the same sensitivity to predictive accuracy as the fuzzy numerical measure. Unfortunately, the fuzzy numerical method cannot generally be used in SDM studies because it relies on the species’ “true” distribution being known. However, this study does give further evidence of the problems with using AUC, and its insensitivity to variability in predictions (Lobo *et al.*, 2010).

The significant result that predictions in *Set1* were more likely to attain higher AUC and fuzzy numerical values than predictions in *Set2* indicates that there must be something in the underlying species distributions that affects MaxEnt’s predictive ability. The species in *Set1* have only a small distributional overlap; perhaps MaxEnt benefited from this since the presence of one species generally explains the absence of the other. The resource competition as set up for *Set1* resulted in competitive exclusion being the dominant outcome; the distributions of species that competitively exclude each other have been found to be good predictors of each other’s distributions (Anderson *et al.*, 2002). On the other hand, the species in *Set2* coexist for the majority of their distributions. Whilst the distributions of mutualist species can be used to improve the predicted distributions of their associates (Gutiérrez *et al.*, 2005), the coexistence of the species in *Set2* is due to a low resource threshold allowing the two species to coexist, rather than an underlying mutualist behaviour. It appears that such an interaction is difficult for MaxEnt to identify. Furthermore, there are still large areas (particularly for *Species1*) where the species exist in isolation; this may explain why *Species1* from *Set2* was the worst predicted species.

These issues may have been compounded by the fact that MaxEnt does not use true species absence data. Instead, MaxEnt uses pseudo-absences (also referred to as background data) which are taken from across the study extent during the modelling procedure. Pseudo-absences can therefore be taken from locations where the species is in fact present; this may have reduced MaxEnt's ability to identify the bordering regions along which the species in both *Set1* and *Set2* exclude each other. For future studies of species with competitive interactions, it may be better to use a "true" presence-absence SDM technique such as Generalised Additive Models (GAMs). GAMs can take confirmed absences as input data, and perhaps this will allow the model to better identify those bordering regions in which species exclude each other.

The positive correlation between species distribution predictor variable importance and model run number suggests that the species distribution predictor variable gains information (increasing its predictive capacity) with successive iterations of MaxEnt. However, it was also found that the increasing importance of the species distribution predictor variable corresponded to a worsening of predictions for *Set1 Species1*, and broadly unchanged predictive accuracy for the other species. This implies that the increased importance of the species distribution predictor variable is not due to new information, but is in fact due to it absorbing information held by the climatic predictor variables. This is an issue of correlated variables; once the species distribution predictor variable has absorbed important information from the climatic variables, MaxEnt ranks it as the most important variable in the model. This however leads to other important information in the climatic variables being neglected. This may explain the variability in the number of pixels predicted as presences throughout the iterations of MaxEnt. Since MaxEnt is a deterministic algorithm (Phillips *et al.*, 2006), these fluctuating predictions can only be accounted for by the species distribution predictor variable.

Correlated variables are an important issue in species distribution modelling (Graham, 2003; Dormann *et al.*, 2013). For this study, predictor variables were chosen due to their perceived ecological importance. Perhaps future studies on this topic should use principal component analysis (PCA) to generate uncorrelated predictors. This technique was not used here because it removes the ecological meaning of the predictor variables. However, when studies are conducted using simulated data, perhaps use of ecologically justifiable variables is less important. Use of uncorrelated variables should lead to increased predictive accuracy.

Whilst this work did not identify improvements in predictions through the iterative method, only two sets of interacting species were studied. Future work could expand on this methodology to test different types and strengths of biotic interactions. Such work would be beneficial if it could identify which types of interactions result in species distributions that can be useful predictors of their interacting species. Another factor likely to have influenced these results is the spatial resolution of the predictor variables. The influence of biotic and abiotic factors may vary at different scales (Pearson and Dawson, 2003; Soberón, 2007; Wisz *et al.*, 2013), so future work should test the influence of scale on the predictive power of the distributions of interacting species. Such an approach may require hierarchical integration of predictor variables at different scales, as previously demonstrated by Pearson *et al.* (2004) with climate and land-cover data.

# Chapter 4: Spatio-Temporal Land Management Action Generator (STeLMAG): A Python-based GIS toolbox for automated replication of landscape management scenarios in real landscapes

## 4.1 Abstract

A new GIS toolbox, STeLMAG, is presented for the implementation of land management actions on raster-based landscapes. The toolbox allows users to control rules which determine the habitats to be managed, the size distribution of new habitat patches, maximum and minimum distances between new and existing habitat patches, the quality of new habitat and the spatially dependent transition of habitat quality through time. Within this rule set, actions are applied stochastically allowing for actions to be replicated based on the same rule set but with variations in the spatial allocation of new habitat. A brief example of STeLMAG's application to a highly anthropogenic landscape is presented, demonstrating how the toolbox can help inform decisions on how and where to increase habitat area in order to improve connectivity. Outputs from STeLMAG can easily be exported for analysis in the growing number of connectivity tools and models for simulating animal movement.

## 4.2 Background

Habitat fragmentation is causing biodiversity loss throughout the world (Fahrig, 2003; Ewers and Didham, 2006; Lindenmayer and Fischer, 2013); in interaction with climate change it poses an even greater threat (Travis, 2003; Opdam and Wascher, 2004). These threats have led to research on optimising reserve network design for the protection of species and their habitats (Rodrigues and Gaston, 2002). In recent years, the focus has shifted towards long-term population persistence and habitat connectivity (Nicholson *et al.*, 2006; Pressey *et al.*, 2007), rather than the creation of large nature reserves and the representation of in-situ species (Cabeza and Moilanen, 2003). This shift in focus has been led by a greater understanding of the effects of population isolation on genetic diversity (Templeton *et al.*, 1990; Debinski and Holt, 2000) and the need to facilitate natural adaptive responses to climate change (Dawson *et al.*, 2011; Hoffmann and Sgro, 2011). Thus habitat connectivity has seen a great deal of research in recent years and many questions remain on how best to manage landscapes to maintain connectivity for a wide range of taxa (Crooks and Sanjayan, 2006).

Studying the effects of fragmentation on habitat connectivity in field-based studies is rarely feasible due to the costs and time-scales involved in replication, and the difficultly in collecting sufficient species movement and population data (but see: Haddad and Baum, 1999; Haddad *et al.*, 2003; Haddad and Tewksbury, 2005). Instead, simulation studies are increasingly used to model ecological processes in artificial landscapes. The creation of artificial landscapes can be categorised into two main approaches: (1) a pattern-based approach which is neutral to the underlying processes that shape the landscape patterns, i.e. “neutral landscapes” (Gardner *et al.*, 1987); (2) a process-based approach which creates spatial patterns based on underlying processes (Pe’er *et al.*, 2013). Neutral landscape models (NLMs) are useful because they allow for the study of specific landscape features, where landscape effects can be separated from the intrinsic properties of ecological processes. NLMs also allow for replication of landscapes with similar spatial characteristics over a wide variety of configurations, meaning that robust statistical analysis of spatial structure is possible (Chipperfield *et al.*, 2011).

Many NLMs have been developed over the last few decades, from simple binary maps (Gardner *et al.*, 1987), to more recent attempts to represent mosaics of agricultural and forested landscapes with polygonal landscapes (Gaucherel, 2008), a wide array of different models now exist (see references in: Ricotta *et al.*, 2002; Wang and Malanson, 2008). Neutral landscapes have been used in many studies of animal movement, for example to study: the threshold at which fragmentation impacts on movement behaviour (With *et al.*, 1999); the impacts of habitat loss and fragmentation on population density (Hiebeler, 2000); the importance of spatial pattern and dispersal behaviour for dispersal success (King and With, 2002); methods for controlling invasive species in heterogeneous landscapes (Andersen *et al.*, 2005); the effects of habitat configuration and stochasticity in survival and reproduction on population dynamics (Fraterrigo *et al.*, 2009); the impact of landscape structure on dispersal distance (Bonte *et al.*, 2010); the importance of cell-size when modelling dispersal in fragmented landscapes (Bocedi *et al.*, 2012); the impact of landscape spatial pattern on the speed of range shifting (Hodgson *et al.*, 2012). Most studies on animal movement in neutral landscapes do not consider dynamics transitions of the landscape since the majority of NLMs generate only static representations of the landscape, but see Cambui *et al.*, (2015) for an NLM that creates landscapes to represent progressive loss of habitat. NLMs have also been incorporated within individual-based modelling platforms (e.g. Bocedi *et al.*, 2014a), and multiple NLMs have also recently been collated in a Python package, for direct integration with geographic information systems (Etherington *et al.*, 2015).

Although an increasing set of methods are used in NLMs, they still have difficulty capturing some key spatial characteristics of real landscapes (Li *et al.*, 2004). Whilst the similarity of neutral landscapes to real landscapes can be improved by adding extra rules, for example to represent rivers and wetlands, these may no longer be classified as “neutral” models, instead becoming process-based landscape models. Whilst pattern-based models (i.e. NLMs) are generally useful for theoretical studies, process-based models may be more useful to study landscape specific questions. Process-based landscape models have been developed with varying levels of complexity: from simple models of roads transecting a landscape (Pe’er *et al.*, 2013), to models of urban growth (Wu *et al.*, 2009), to the broad array of land-use change models developed for different scales and regions (e.g. Le *et al.*, 2008; Verburg and Overmars, 2009; Meiyappan *et al.*, 2014; Murray-Rust *et al.*, 2014). The landscapes generated by such process-based models have been used to study the impacts of land-use change on species distributions, the connectivity of ecological networks and biodiversity in more general terms (Martínez *et al.*, 2009; Brady *et al.*, 2012; Piquer-Rodríguez *et al.*, 2012; Akber and Shrestha, 2015). Other studies have investigated how real landscapes can be managed to improve habitat connectivity, using bespoke (un-replicated) GIS methods to create land management strategies (e.g. Mokany *et al.*, 2013; Gimona *et al.*, 2015). Such studies typically assume instantaneous implementation of land management strategies (i.e. a static landscape), even though temporal habitat succession and disturbance are important drivers of meta-population dynamics (Wilcox *et al.*, 2006). No software packages or tools have been found for the creation and replication of conservation-focused land management actions. Habitat management strategies are rarely transferable between different species, landscapes and habitats (Cabeza and van Teeffelen 2009), so a tool is required that can apply conservation and land management actions across any set of landscapes and habitat types.

A new GIS toolbox, STeLMAG (Spatio Temporal Land Management Action Generator), is presented for the creation of rule-based land management action replicates on real landscape data. With habitat connectivity still a much debated topic (e.g. Hodgson *et al.*, 2011a; Doerr *et al.*, 2011), it is believed that STeLMAG is a unique set of tools that can aid researchers and land managers in the selection of site and species specific habitat management strategies. NLMs have become widely used due to the ease of creating replicate landscapes, a frequent difficulty in landscape ecology field studies (Ricotta *et al.*, 2002). STeLMAG allows for the creation of replicates since the land management actions are rule-based, but the procedures are stochastic. STeLMAG can also generate transitional landscapes allowing for temporal habitat quality transitions to be studied. Since STeLMAG is a GIS toolbox, landscapes can easily be exported to a wide range of connectivity tools and individual-based models to evaluate the consequences of different land management actions. STeLMAG has already been used to generate a selection of climate change adaptation strategies for a real UK landscape, allowing the use of an individual-based model of animal population dynamics and dispersal to test impacts of different strategies on range shifting ability (see Synes *et al.*, 2015).

### 4.2.1 Software requirements

STeLMAG requires ArcGIS 10.2 or above, and the spatial analyst extension (ESRI, 2013). It also requires the Python packages: NumPy and SciPy.

## 4.3 Methods and features

### 4.3.1 Tools

The STeLMAG toolbox is divided into three tools: ExistingPatches, CustomPatches_Adjacent and CustomPatches_ExSitu. An example landscape (Figure 4.1) is used to illustrate the use of these tools. For a full list of parameter options, see Appendix A.

#### 4.3.1.1 ExistingPatches

This tool applies land management actions to entire contiguous patches of a given habitat type, changing the habitat quality of the randomly selected set of patches.

#### 4.3.1.2 CustomPatches_Adjacent

Existing habitat patches are expanded by the creation of new adjacent habitat patches. The sizes of new adjacent patches are defined by a beta distribution, the limits of which are defined by the user. For examples, see Table 4.1 - *CustomPatches_Adjacent*.

### 4.3.1.3 CustomPatches_ExSitu

New habitat patches are created with no requirement for adjacency to existing habitat. The sizes of new patches are defined by a beta distribution, the limits of which are defined by the user (see Table 4.1 - *CustomPatches_ExSitu,* Positional rule: Random). The locations of new patches can optionally be controlled by setting minimum and/or maximum distances from existing patches (Table 4.1 - *CustomPatches_ExSitu*, Positional rule: 300 – 600 m buffer).

*Figure 4.1: The study landscape prior to any land management actions, as used by Watts et al. (2010). The red outline indicates the single habitat patch from which the hypothetical study species population was initiated. Movement costs determine the associated cost of movement through each habitat type for the study species.*

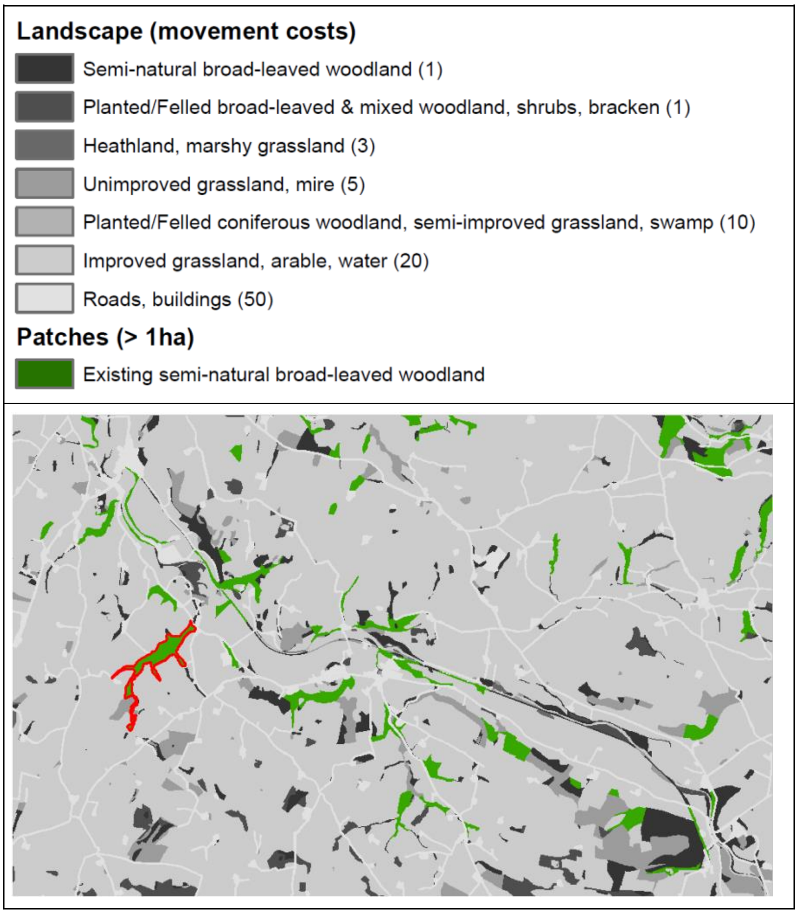
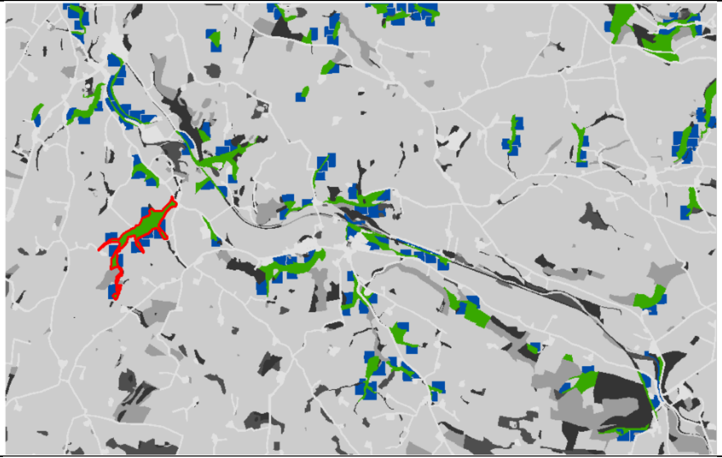
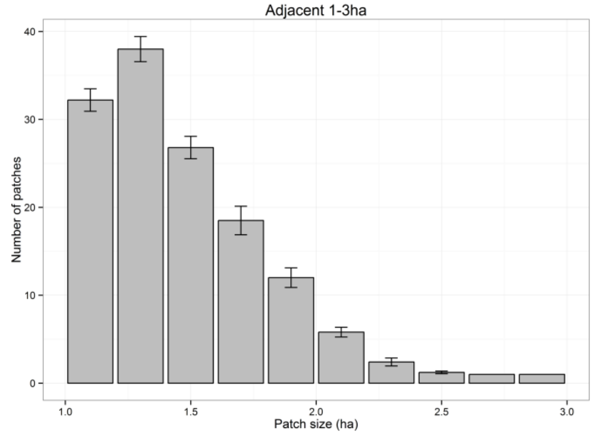
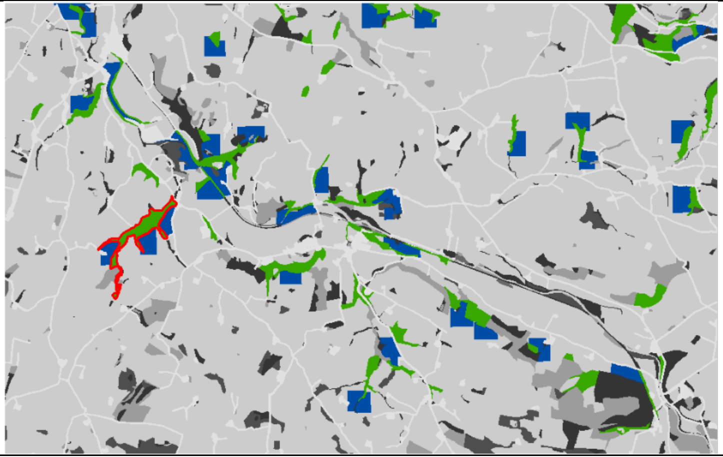
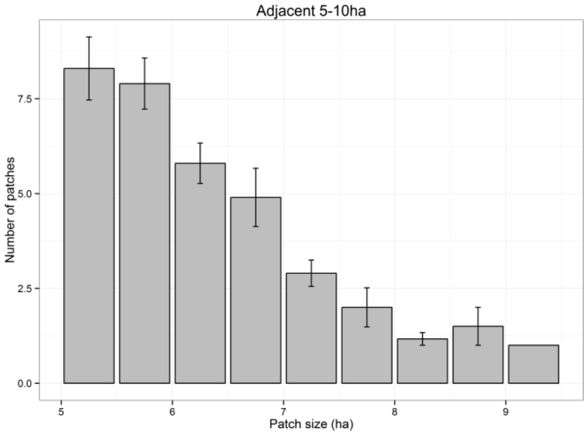
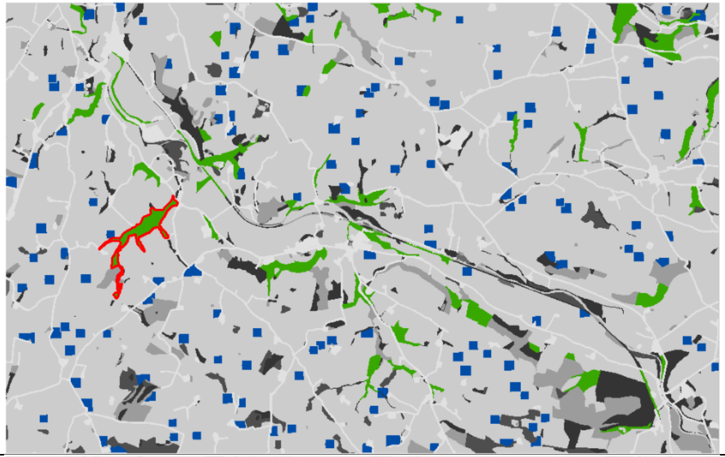
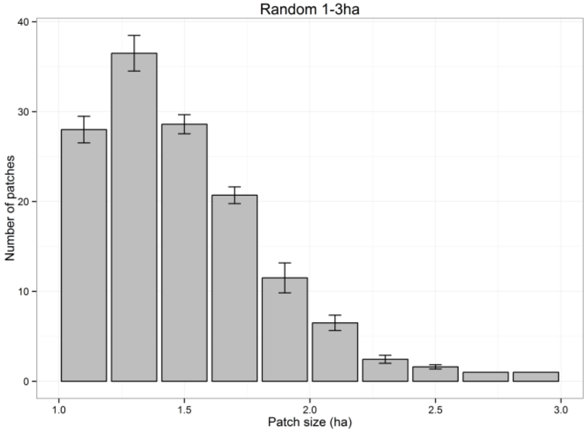
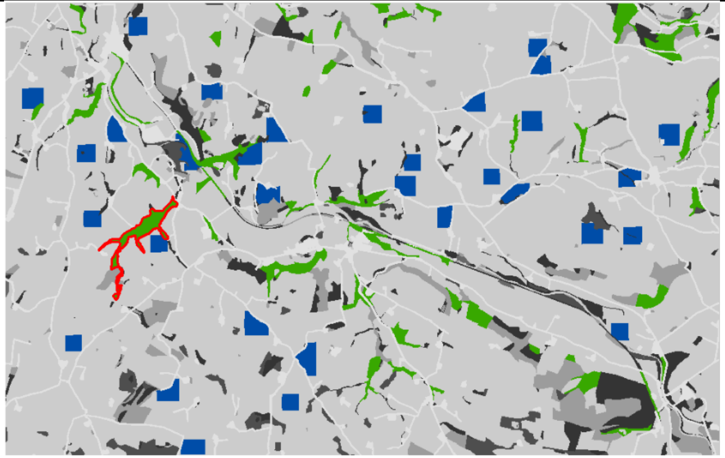
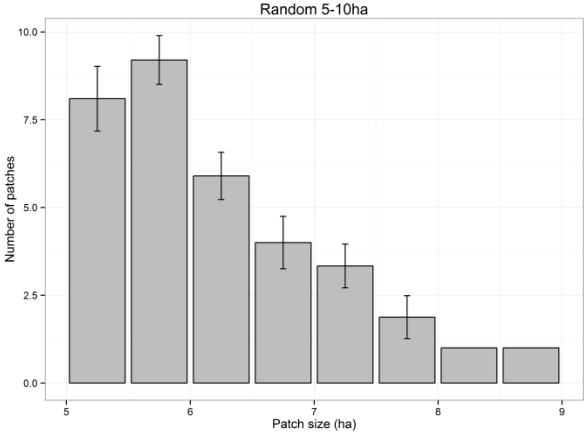
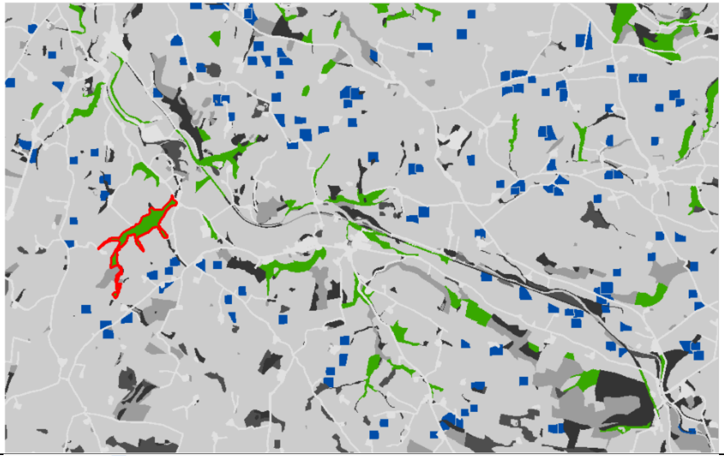
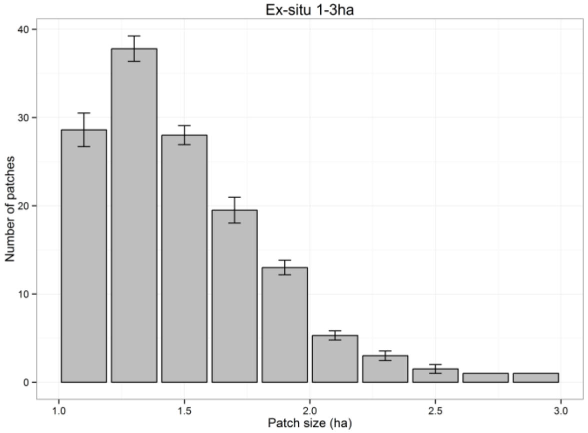
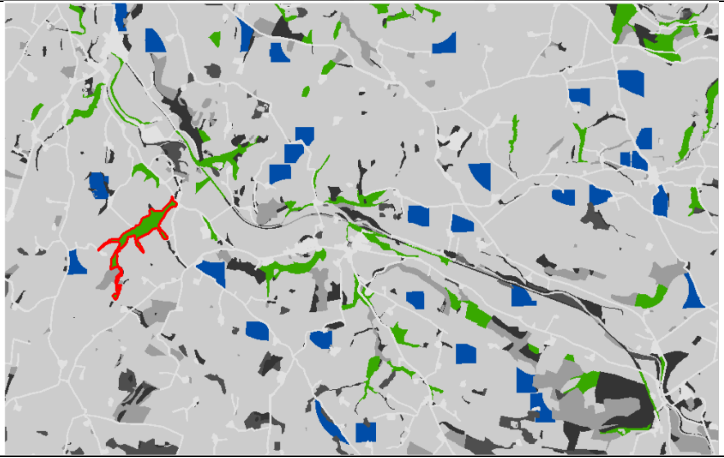
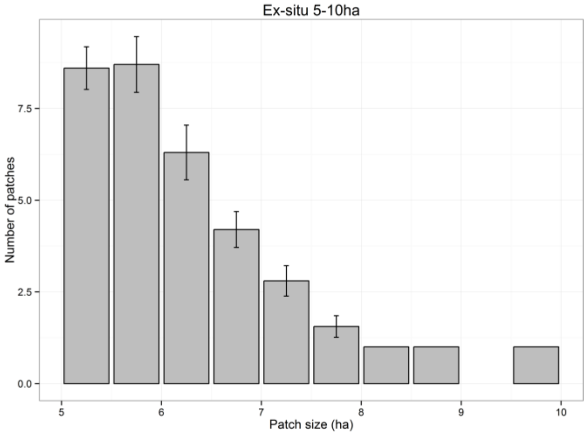


*Table 4.1: Example land management actions generated by the STeLMAG toolbox.*

| **Tool** | **Positional rule** | **Patch size (ha)** | **Example landscape**<br>**Patches (> 1ha)**<br>🟩 Existing semi-natural broad-leaved woodland<br>🟦 New semi-natural broad-leaved woodland | **New patch size distribution** |
|---|---|---|---|---|
| **CustomPatches_Adjacent** | **Adjacent** | **1 - 3** |  |  |
| **CustomPatches_Adjacent** | **Adjacent** | **5 - 10** |  |  |

| | | | | |
|---|---|---|---|---|
| **CustomPatches_ExSitu** | **Random** | **1 - 3** |  |  |
| **CustomPatches_ExSitu** | **Random** | **5 - 10** |  |  |

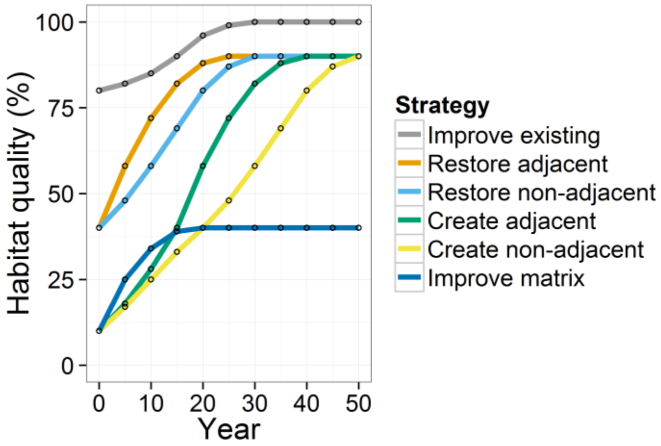
| | | | | |
|---|---|---|---|---|
| **CustomPatches_ExSitu** | **300 - 600 metre buffer** | **1 - 3** |  |  |
| **CustomPatches_ExSitu** | **300 - 600 metre buffer** | **5 - 10** |  |  |

### 4.3.2 Tool outputs

Each tool returns raster-based maps in the following categories:

- a set of "change" rasters: binary maps indicating the areas in which the land management actions have been applied;
- a "patch" raster prior to those changes: the contiguous areas of study habitat prior to land management actions, with each region/patch given a unique number;
- a set of "patch" rasters after those changes: the contiguous areas of the study habitat after land management actions, with each region/patch given a unique number;
- an optional set of "transition" rasters: indicating the temporal transition of habitat quality, as defined by the user (Figure 4.2).

*Figure 4.2: Illustrative example of temporal habitat quality transitions. These examples are to demonstrate possible uses of the STeLMAG toolbox, not actual habitat quality transitions. If temporal habitat quality transitions are provided, the STeLMAG toolbox generates a set of rasters to represent these transitions.*



## 4.4 Example

The STeLMAG toolbox was applied to a small section (measuring 9.79 x 6.19 km; ~6,060 ha at 10 m resolution) of highly anthropogenic landscape (Figure 4.1) as used previously by Watts *et al.* (2010).

For each strategy, a total of 200 ha of land management actions were applied to the landscape in either of two different patch size distribution scenarios: patches were 1 to 3 ha in size, or patches were 5 to 10 ha in size. The strategies tested were:

- to expand existing woodland patches (using the *CustomPatches_Adjacent* tool – see Table 4.1);
- to create new woodland patches in spatially randomised locations in the landscape (using the *CustomPatches_ExSitu* tool – see Table 4.1);
- to create new woodland patches in spatially randomised locations in the landscape, but restricted to a zone of between 300 and 600 m from existing woodland patches (using the *CustomPatches_ExSitu* tool – see Table 4.1).

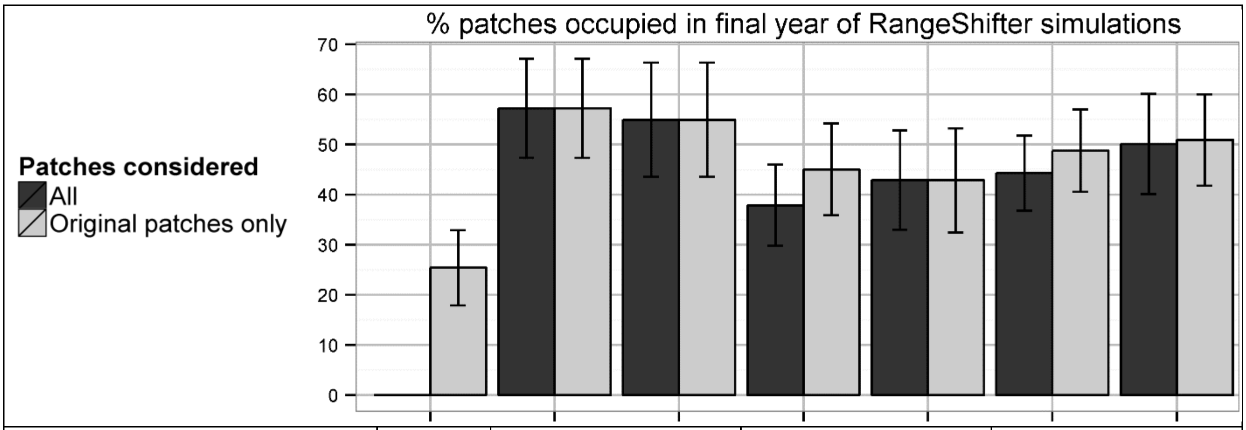
(Note: the *ExistingPatches* tool was not used, but see the *Improve-In-situ* strategy from Synes *et al.* (2015) for an example.) Ten replicate landscapes were created for each patch size distribution (two) within each strategy (three), resulting in 60 new landscape configurations.

A hypothetical species inhabiting a woodland network was modelled using RangeShifter (Bocedi *et al.*, 2014a), an individual-based model of population dynamics and dispersal, and parameterised based on the species defined in example 2 from that paper. The same parameterisation was used as the female-only model, but habitat specific probabilities of mortality were also included, matching the final section of their example. For each simulation, the species was initialised in the same single patch (see Figure 4.1).

Twenty replicate simulations were run in RangeShifter for each of the 61 landscapes (the original landscape plus 60 new landscape configurations), with each simulation lasting for 100 years. Patch occupancy in the final simulation year was calculated (1) based on all habitat patches, and (2) based only on those patches present in the original landscape. Temporal habitat quality transitions were not defined, as the use of dynamic landscapes is not currently available in RangeShifter. However, it is anticipated that this will be a key future usage of STeLMAG, since habitat succession is an important driver of meta-population dynamics (Wilcox *et al.*, 2006) but has rarely been considered in ecological models.

All tested habitat management strategies resulted in greater occupancy of the original habitat patches (Figure 4.3). This is not surprising given that 200 ha of additional habitat was created in each strategy. However, the gain in occupancy varied between strategies, demonstrating the importance of the different spatial rules used. The *Adjacent* strategy resulted in the largest gain in occupancy whilst the *Random* strategy resulted in the smallest gain. Since the *Random* strategy has no spatial restrictions, there is a greater probability of new habitat patches being created in locations where they will not improve connectivity. The *Ex-situ* strategy demonstrates the improvements that can be made to habitat connectivity when habitat creation is restricted to specific distances around existing habitat patches, improving the chance of new habitat being used as "stepping stone" features. The simulation results also indicate that the size distribution of new patches can influence their benefit for habitat connectivity (e.g. *Adjacent* and *Ex-situ* strategies, Figure 4.3), but a more detailed analysis would be needed to make any further conclusions about these differences.

*Figure 4.3: Landscape metrics and RangeShifter simulation results for the original landscape, and the ten replicate landscapes for each patch size distribution (1-3 ha and 5-10 ha) within each land management strategy (Adjacent, Random and Ex-situ 300-600 m).*



| **Landscape metrics** | **Original** | ***Adjacent*** | | ***Random*** | | ***Ex-situ* 300-600 m** | |
|---|---|---|---|---|---|---|---|
| | | **1-3 ha** | **5-10 ha** | **1-3 ha** | **5-10 ha** | **1-3 ha** | **5-10 ha** |
| *No. replicate landscapes* | 1 | 10 | 10 | 10 | 10 | 10 | 10 |
| *Woodland area (patches > 1 ha)* | 202.67 | 402.67 | 402.67 | 402.67 | 402.67 | 402.67 | 402.67 |
| *No. woodland patches (> 1 ha) ± SD* | 50 | 46.2 ± 1.14 | 44.5 ± 1.08 | 171.8 ± 3.52 | 75.6 ± 2.63 | 186.2 ± 1.40 | 82.7 ± 0.95 |
| *Mean woodland size (patches > 1 ha) ± SD* | 4.05 ± 3.66 | 8.72 ± 7.28 | 9.05 ± 9.43 | 2.34 ± 2.56 | 5.33 ± 4.0 | 2.16 ± 2.22 | 4.87 ± 3.04 |

## 4.5 Conclusion

The development of STeLMAG was motivated by the work in Chapter 5, and the lack of existing tools with the functionality of this toolbox. Chapter 5 moves on to use an agent-based model of population dynamics and dispersal to investigate the potential for different climate change adaptation strategies to assist species range shifting. Population dynamics and dispersal have rarely been considered in previous SDM research. Whilst Chapter 5 is a purely process-based model, it is expected that future studies will integrate this methodology with correlative SDM approaches. In order to systematically generate a set of climate change adaptation strategies for this work, a toolbox was required capable of replication based on a set of spatial and area-based rules. The STeLMAG toolbox was used to replicate a set of climate change adaptation strategies across six different landscapes. Chapter 5 presents the work for one of these landscapes.

## 4.6 Software availability

The STeLMAG GIS toolbox is open-source and freely available here:
http://www.arcgis.com/home/item.html?id=ad369e24395f4eed9e919b05795df1cd

# Chapter 5: A multi-species modelling approach to examine the impact of alternative climate change adaptation strategies on range shifting ability in a fragmented landscape

## 5.1 Abstract

An individual-based model of animal dispersal and population dynamics was used to test the effects of different climate change adaptation strategies on species range shifting ability, namely the improvement of existing habitat, restoration of low quality habitat and creation of new habitat. These strategies were implemented on a landscape typical of fragmentation in the United Kingdom using spatial rules to differentiate between the allocation of strategies adjacent to or away from existing habitat patches. The total area being managed in the landscape was set at realistic levels based on recent habitat management trends. Eight species were parameterised to broadly represent different stage structure, population densities and modes of dispersal. Simulations were initialised with the species occupying 20% of the landscape and run for 100 years. As would be expected for a range of real taxa, range shifting abilities were dramatically different. This translated into large differences in their responses to the adaptation strategies. With conservative (0.5%) estimates of the area prescribed for climate change adaptation, few species display noticeable improvements in their range shifting, demonstrating the need for greater investment in future adaptation. With a larger (1%) prescribed area, greater range shifting improvements were found, although results were still species-specific. It was found that increasing the size of small existing habitat patches was the best way to promote range shifting, and that the creation of new stepping stone features, whilst beneficial to some species, did not have such broad effect across different species.

## 5.2 Introduction

Climate change is expected to have increasingly detrimental effects for biodiversity, reducing available habitat (Huntley *et al.*, 2008) and increasing extinction risk for many species (Thomas *et al.*, 2004). Species distribution modelling studies have shown that the environmental niches of species will shift polewards under climate change (Parmesan *et al.*, 1999; Walther *et al.*, 2002;

Hickling *et al.*, 2006; Chen *et al.*, 2011), meaning that existing conservation areas are likely to become less suitable for many of the species that currently occupy them (Carroll *et al.*, 2010; Araújo *et al.*, 2011). Furthermore, there is growing concern that habitat fragmentation, which is already a key factor in global biodiversity declines (Wilcox and Murphy, 1985), may further reduce species' abilities to shift their ranges (Fahrig, 2003; Hansen and Hoffman, 2011). These impacts from climate change and habitat fragmentation need to be considered in unison to fully understand the impacts on biodiversity (Opdam and Wascher, 2004; Barbet-Massin *et al.*, 2012a).

The selection of conservation areas generally focuses on balancing the number and size of habitat patches (Hodgson *et al.*, 2009), and the representativeness of the desired habitats (Margules and Pressey, 2000; Thorne *et al.*, 2011). More recently there has been a shift towards increasing connectivity to facilitate natural adaptive responses and resilience (Williams *et al.*, 2005; Heller and Zavaleta, 2009; Hansen and Hoffman, 2011), allowing species to track their climatic niche (Heller and Zavaleta, 2009; Araújo *et al.*, 2011).

A number of empirical studies have demonstrated that habitat corridors, stepping stones and permeable matrix features can help species move through fragmented landscapes (e.g. Aars and Ims, 1999; Fischer and Lindenmayer, 2002; Haddad *et al.*, 2003; Haddad and Tewksbury, 2005; Robertson and Radford, 2009), but their effectiveness is variable and species-specific (Baum *et al.*, 2004; Prevedello and Vieira, 2010; Humphrey *et al.*, 2014). In addition, it is important to distinguish between foraging behaviour and dispersal behaviour, and between individual movements and population level benefits (which is not necessarily an implied result - Gilbert-Norton *et al.*, 2010). Hodgson *et al.* (2011a) found that evidence for the benefits of habitat corridors, stepping stones and matrix improvements was weaker in comparison to the range expansion benefits provided by increasing habitat area, quality or aggregation.

Whilst previous studies have compared alternative climate change adaptation and reserve design strategies, they have often used simplistic models of dispersal (e.g. no dispersal versus universal dispersal, (Araújo *et al.*, 2004); generic dispersal kernel across all study species, (Mokany *et al.*, 2013)), or simplistic theoretical landscapes (e.g. binary habitat classification (Kinezaki *et al.*, 2010); fractal landscapes (Hodgson *et al.*, 2012); randomly generated fragmentation (Bocedi *et al.*, 2014b); habitats represented as nodes in a network (Schoon *et al.*, 2014)). Whilst these studies provide important theoretical insights, there is also a need to combine greater detail in dispersal and population dynamics with more realistic landscape configurations. Another important consideration is for studies to broaden the representation of species, since reserve design focused on a single species is unlikely to provide community-wide benefits (Moilanen *et al.*, 2005; Carroll *et al.*, 2010). Hodgson *et al.* (2011b) studied the effects of climate change adaptation strategies on the range shifting of a selection of species types in a real landscape, using a modified version of the Incidence Function metapopulation model (Hanski, 1994). Further studies are required, using more detailed models of dispersal and population dynamics, to test these and other possible climate change adaptation strategies on a range of species in real landscapes.

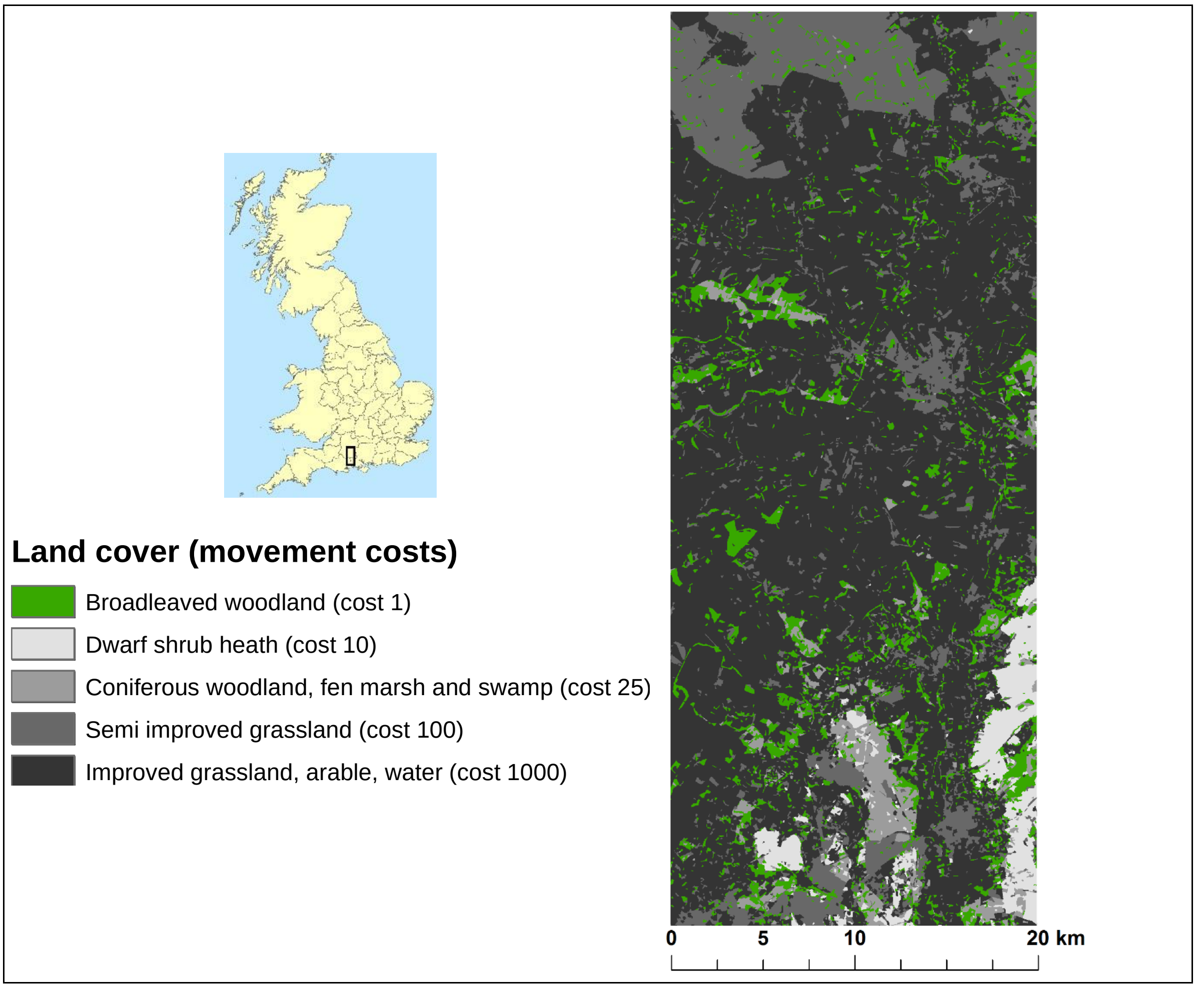
The modelling framework presented here, in contrast to many studies (although note Hodgson *et al.*, 2011b), is applied to a real landscape and aims to represent climate change adaptation strategies at achievable scales (both in terms of total area prescribed for adaptation action and the size distribution of individual actions). Multiple species are separately modelled, with realistic traits and the incorporation of population dynamics and dispersal behaviour, but without considering biotic interactions. This research aims to inform the prioritisation of landscape-scale climate change adaptation strategies in order to conserve biodiversity and allow it to adapt to a changing climate. The study determines the relative impact of different adaptation strategies on the population dynamics and range-shifting potential for a number of species. The results give insights into the species-specific nature of adaptation strategy success, the importance of the spatial location of adaptation strategies, and the influence of the quantity of habitat change on their effectiveness.

## 5.3 Methods

### 5.3.1 Landscape

The study landscape was a 20 km x 50 km region extracted from UK Landcover Map 2007 data (Morton *et al.*, 2011) and gridded at 20 m cell resolution (Figure 5.1). The landscape is dominated by agriculture (~66% by area), with broadleaved woodland making up only ~8% of the total area, and represents typical fragmentation comparable with the UK national average: 50% agriculture, 6% broadleaved woodland (Morton *et al.*, 2011). The remainder of the landscape is made up of semi-natural habitat (~16%), coniferous woodland (~4%) and built up areas (~6%). Broadleaved woodland was defined as the breeding habitat for the study species, and other habitat types formed the inter-patch matrix, each having its own associated movement cost.

*Figure 5.1: The study landscape, dominated by agriculture (~66% by area), with broadleaved woodland making up ~8% of the total area. The remainder of the landscape is made up of semi-natural habitat (~16%), coniferous woodland (~4%) and built up areas (~6%).*



### 5.3.2 Climate change adaptation strategies

A number of climate change adaptation strategies were applied to the study landscape as defined by Oliver *et al.* (2012), namely: (i) improvement of existing habitat, (ii) restoration of low quality habitat, and (iii) creation of new habitat (Table 5.1). The improvement strategy increased the carrying capacity of existing broadleaved woodlands by 10%. Although habitat quality does not always correlate with population density (Van Horne, 1983), there are many examples of quality having a positive correlation with abundance for butterflies (Pöyry *et al.*, 2009; Thomas *et al.*, 2011), small mammals (Peles and Barrett, 1996; Haughland and Larsen, 2004; Corbalán *et al.*, 2006) and birds (Lloyd, 2008). Thus the simplification and generalisation of habitat quality across species is considered a reasonable representation of current knowledge of the potential effects of improving existing breeding habitat. The restoration strategy represents the conversion of unsuitable non-broadleaved woodland (i.e. conifer), which was adjacent to broadleaved woodland, into suitable breeding habitat. The creation strategy was split into three sub-categories based on different spatial rules: (a) adjacent to existing habitat, (b) randomly within the landscape, to act as stepping stones, or (c) adjacent to small patches (defined as < 3 ha). Under each creation strategy new patches of habitat were formed from an initial cell (pixel) in the correct spatial location (Table 5.1). In order to create realistic woodlands, the new habitat patch was then expanded from these starting cells to reach the desired patch size derived from the size frequency distribution of existing broadleaved woodlands in the study landscape.

*Table 5.1: The climate change adaptation strategies, as collated by Oliver et al. (2012), which were applied to the study landscape.*

| **Name** | **Details** |
|---|---|
| i. Improve-In-situ | Existing habitat patches are improved (e.g. plant diversity increased, or non-desirable plant species removed), increasing their carrying capacity. |
| ii. Restore-Adjacent | Existing low quality patches which are not currently suitable breeding habitat and are adjacent to existing suitable breeding habitat, are improved to become suitable breeding habitat. |
| Iiia. Create-Adjacent | New habitat patches are created within improved grassland and arable landcover types, adjacent to existing suitable breeding habitat. |
| Iiib. Create-Random | New habitat patches are created within improved grassland and arable landcover types, with no rule for adjacency to existing suitable breeding habitat. |
| Iiic. Create-AdjacentSmall | New habitat patches are created within improved grassland and arable landcover types adjacent to existing suitable breeding habitat below a size threshold of 3 ha. |

Two plausible scenarios of the area prescribed for climate change adaption actions were used: (1) 500 ha (0.5% of the landscape), representing a conservative level of change; (2) 1,000 ha (1% of the landscape), representing a more ambitious level of change. These scenarios relate to the observed change in woodland area in the UK from 9% of total land area in 1980 to 12.9% in 2014 (Forestry Commission, 2014a). However, these values do not differentiate between broadleaved and conifer planting. Furthermore, due to limitations of land ownership and funding, the rate of woodland planting has decreased in recent years. Since 2009, an average of 82 km$^2$ of broadleaved woodland were planted in the UK each year, with 58% of this planting occurring in Scotland (Forestry Commission, 2014b). If this rate were maintained for the next 15 years, this would equate to 0.5% of UK land area being planted with new broadleaved woodland. Since the strategies are applied to the landscape using a stochastic spatial algorithm, ten replicates of each of the five strategies (see Table 5.1) were created. At the 1% level of prescribed change, the Restore-Adjacent strategy was not possible due to insufficient conifer woodlands adjacent to broadleaved woodlands in the study landscape.

### 5.3.3 Species

A number of artificial species were modelled, parameterised to represent a range of taxa having different population densities, stage structuring, dispersal abilities and lifespans (Table 5.2 and Appendix B). The species are not designed to represent real species accurately, but rather to represent a broad range of realistic characteristics, including density dependence and accounting for inter-specific variation in behaviour during transfer through the landscape matrix.

*Table 5.2:* Species characteristics (SMS – Stochastic movement simulator *(Palmer et al., 2011)*, a mechanistic model of dispersal; Kernel – standard dispersal kernel). For detailed RangeShifter parameter values, see *Appendix B.*

| **Group** | **Dispersal ability (D)** | **Abundance / Population density (P)** | **Reproduction (S)** | **Dispersal method** | **Name (letters and symbols indicate key species parameters)** |
|---|---|---|---|---|---|
| Invertebrates | Low ($^{--}$) | Very high ($^{++}$) | Asexual$^{a}$ ($^{-}$) | SMS | Invert_$D^{--}P^{++}S^{-}$ |
| | Medium ($^{-}$) | High ($^{+}$) | Asexual$^{a}$ ($^{-}$) | SMS | Invert_$D^{-}P^{+}S^{-}$ |
| | Medium ($^{-}$) | Very high ($^{++}$) | Asexual$^{a}$ ($^{-}$) | Kernel | Invert_$D^{-}P^{++}S^{-}$ |
| | Medium ($^{-}$) | Very high ($^{++}$) | Sexual ($^{+}$) | Kernel | Invert_$D^{-}P^{++}S^{+}$ |
| Mammals | Medium ($^{-}$) | Medium ($^{-}$) | Sexual ($^{+}$) | SMS | Mam_$D^{-}P^{-}S^{+}$ |
| | High ($^{+}$) | Low ($^{--}$) | Sexual ($^{+}$) | SMS | Mam_$D^{+}P^{--}S^{+}$ |
| Birds | High ($^{+}$) | Medium ($^{-}$) | Sexual ($^{+}$) | SMS | Bird_$D^{+}P^{-}S^{+}$ |
| | Very high ($^{++}$) | Low ($^{--}$) | Sexual ($^{+}$) | SMS | Bird_$D^{++}P^{--}S^{+}$ |

[a] In this context, an 'asexual' species does not necessarily imply asexual reproduction. This form of simulation may represent invertebrate species which mate upon emergence into the adult stage within the natal patch, and then fertilised females disperse and are able to found a new colony alone; hence dispersal of males does not need to be modelled.

For species modelled with dispersal kernels (see Table 5.2 and Appendix B), distinct breeding habitat patches were defined as contiguous areas of habitat only. For species modelled with mechanistic dispersal, for which a perceptual range was estimated, patches were defined using a least-cost network methodology (Watts *et al.*, 2010). This approach applies a cost distance analysis to generate a buffer around each distinct habitat patch, using the permeability of the surrounding matrix (taken from the Delphi analysis of Eycott *et al.* (2011)) as the cost values and the estimate of perceptual range as the maximum distance. Where multiple distinct patches were contained within a buffer, these were defined as a single home range patch.

## 5.4 The model

Species were simulated in the study landscape using RangeShifter (Bocedi *et al.*, 2014a), a platform for spatially explicit individual-based modelling of population dynamics and dispersal. An important feature of RangeShifter is that dispersal is modelled in terms of its three fundamental phases: emigration, transfer and settlement. This level of detail in dispersal is often neglected in simulation models, but is crucial for determining species responses to environmental change and therefore for conservation planning (Travis *et al.*, 2013). Moreover, RangeShifter incorporates optional mechanistic modelling of transfer limited by perceptual range using the ‘stochastic movement simulator’ (SMS; Palmer *et al.*, 2011); simulating perceptual range in individual-based models has been demonstrated as a crucial factor in differentiating movement success through a fragmented landscape (Pe’er and Kramer-Schadt, 2008).

### 5.4.1 Simulation run-in

Owing to the stochastic nature of the population dynamics and dispersal in RangeShifter, “run-in” simulations are important to determine a stable starting population for each species. For run-in simulations, the landscape was reduced to the southern 20% only, and each species was initialised at half its carrying capacity in every habitat patch. Ten replicates of the simulations were run for a period of 50 years each, and the final patch occupancy and mean density of each species was used to initialise all subsequent simulations from which the results in this paper were gathered. This initialisation in the southern 20% of the study landscape represents the population prior to a northward shift.

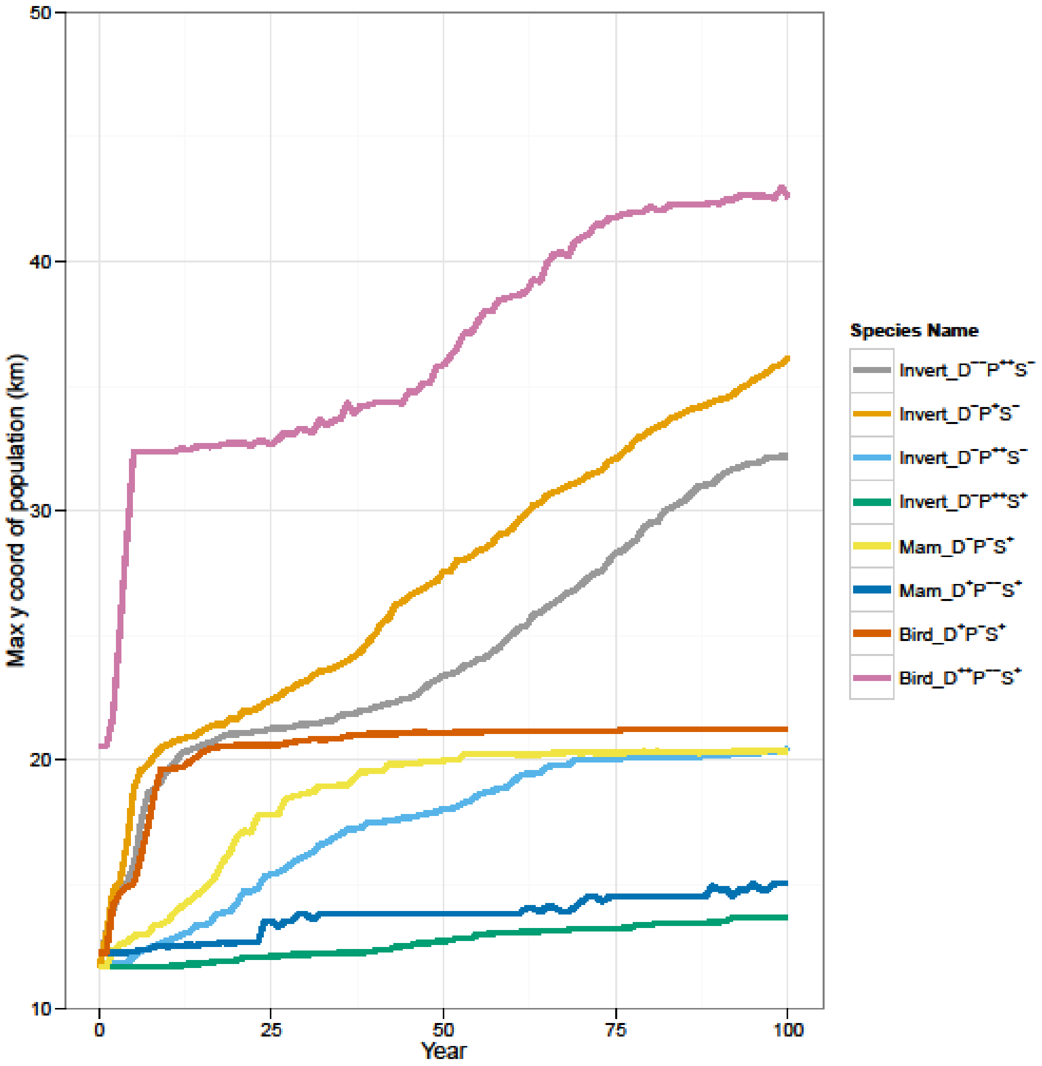
### 5.4.2 Main simulations

Ten replicate simulations were run in RangeShifter for each of the eight species on the full landscape to generate baseline measures of range shifting. Range shifting was measured as the northern edge of the most northern patch containing an individual for asexual species, or a breeding pair for sexual species. Each replicate was initialised in the specific patches and at the mean population density from the run-in simulations in the southern 20% of the landscape only, and run for 100 years. For the ninety landscape adaptation scenarios created (two quantities for area of change; five adaptation strategies at 0.5%, four adaptation strategies at 1%; ten replicates of each), and for each of the eight species, ten replicate 100-year simulations were run (initialised as above).

## 5.5 Results

The baseline simulations for each species on the original landscape demonstrated the huge disparity in range shifting potential that results from differences in species characteristics (Figure 5.2). Whilst some species were able to shift their range through almost the entire landscape (Bird_$D^{++}P^{--}S^{+}$), others barely expanded their range by more than 5 km (Mam_$D^{+}P^{--}S^{+}$, Invert_$D^{-}P^{++}S^{+}$) or 10 km (Mam_$D^{-}P^{-}S^{+}$, Bird_$D^{+}P^{-}S^{+}$, Invert_$D^{-}P^{++}S^{-}$). The species most successful at range shifting in the original landscape were those with a very high dispersal ability and low population density (Bird_$D^{++}P^{--}S^{+}$) or a high to very high population density and low to medium dispersal ability (Invert_$D^{--}P^{++}S^{-}$, Invert_$D^{-}P^{+}S^{-}$).

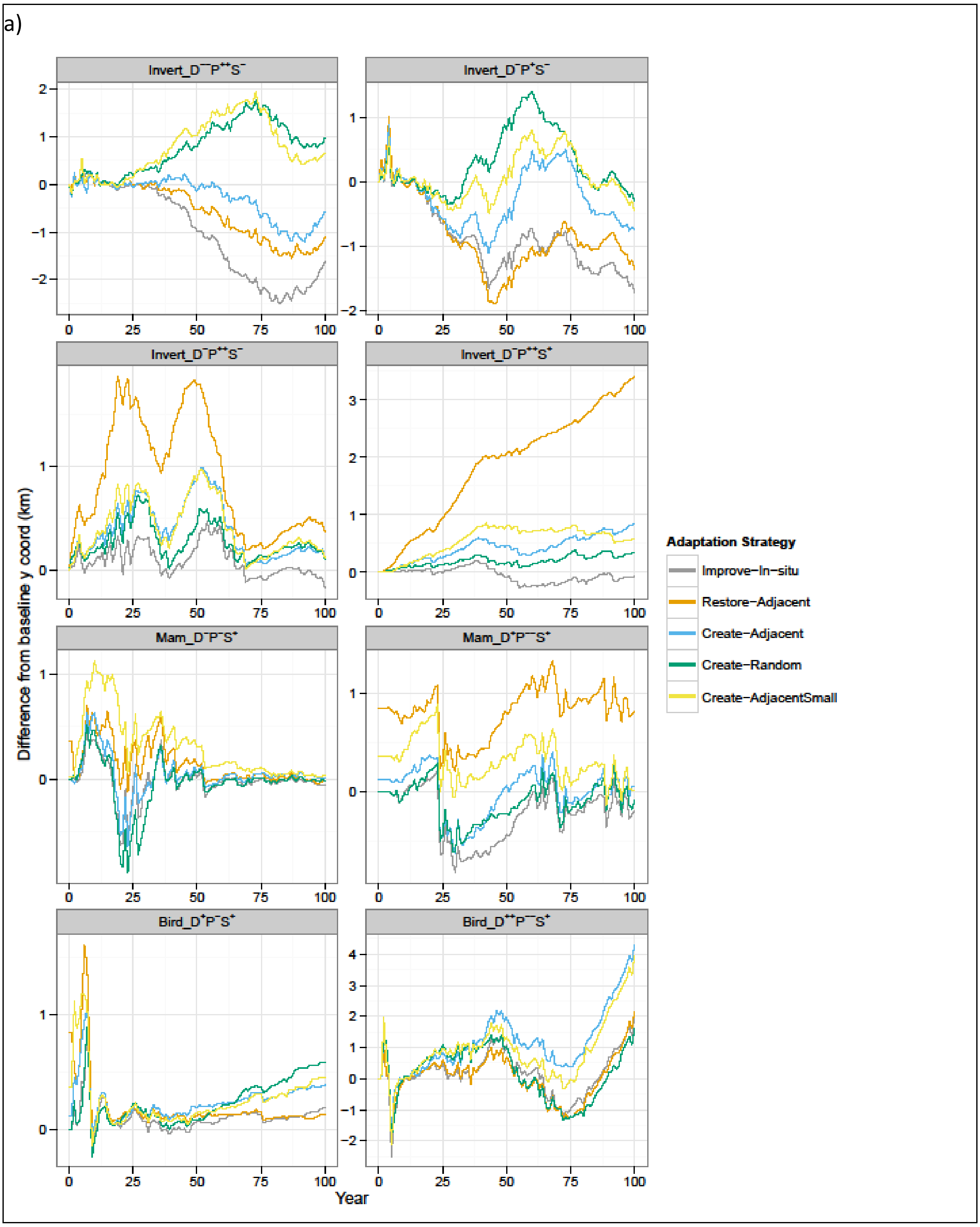
*Figure 5.2: Time series of range shifting in the baseline simulations (unchanged landscape), measured by the northern edge of the most northern patch containing an individual for asexual species, or containing a breeding pair for sexual species. Each line represents the mean of 10 replicates (replicates within RangeShifter).*



The difference between baseline range shifting and range shifting in the managed landscapes showed a variety of responses dependent on the species and management strategy (Figure 5.3). At 0.5% habitat change (Figure 5.3a), some species showed very little response to any of the adaptation strategies (Mam_D$^{-}$P$^{-}$S$^{+}$, Bird_D$^{+}$P$^{-}$S$^{+}$, Invert_D$^{-}$P$^{++}$S$^{-}$). There was evidence that the Create-AdjacentSmall strategy can be one of the best for increasing the range shifting distance for some species (Invert_D$^{--}$P$^{++}$S$^{-}$, Bird_D$^{++}$P$^{--}$S$^{+}$); Restore-Adjacent also provided a clear increase in range shifting for some species (Mam_D$^{+}$P$^{--}$S$^{+}$, Invert_D$^{-}$P$^{++}$S$^{+}$). There were also species-specific benefits from the Create-Random (Invert_D$^{--}$P$^{++}$S$^{-}$) and Create-Adjacent (Bird_D$^{++}$P$^{--}$S$^{+}$) strategies. Total gains over the baseline range shifting after 100 years were small, with the greatest gains for Bird_D$^{++}$P$^{--}$S$^{+}$ under the Create-Adjacent strategy and Create-AdjacentSmall strategy (Figure 5.3a and Figure 5.4). Invert_$D^{-}P^{++}S^{+}$ made large gains under the Restore-Adjacent strategy. All other species gained 1 km or less in range shifting from any of the habitat management strategies over the 100 years at 0.5% habitat change (Figure 5.3a and Figure 5.4).

Increasing the percentage of habitat change from 0.5% to 1% led to a consistent, but not guaranteed, increase in range shifting distance for the creation strategies (Figure 5.4). Differences were still very limited for some species (Mam_$D^{-}P^{-}S^{+}$, Invert_$D^{-}P^{++}S^{-}$), and the Create-Random strategy resulted in a lower range shifting distance for some low to medium dispersal ability species (Invert_$D^{--}P^{++}S^{-}$, Invert_$D^{-}P^{++}S^{+}$) when increasing the percentage of habitat change from 0.5% to 1% (Figure 5.4). Whilst the difference in range shifting distance from their baseline was different between species, the Create-AdjacentSmall strategy gave the greatest increase in range shifting distance for all species except Mam_$D^{-}P^{-}S^{+}$ at the higher percentage of habitat change (Figure 5.4). Create-Adjacent also increased range shifting distance for Bird_$D^{++}P^{--}S^{+}$ and Invert_$D^{-}P^{++}S^{-}$, whilst Create-Random increased range shifting distance for Bird_$D^{+}P^{-}S^{+}$ (Figure 5.3b and Figure 5.4).

*Figure 5.3: Time series (for each species) of the difference in range shifting response between the adaptation strategy (with (a) 0.5% and (b) 1% habitat change) and the baseline simulation (unchanged landscape), measured by the northern edge of the most northern patch containing an individual for asexual species, or containing a breeding pair for sexual species. Each line represents the mean of 100 replicates (10 strategy replicates x 10 RangeShifter replicates). Note that fluctutations in "Difference from baseline y coord" are the result of both baseline range shifting (where the fluctuation will be visible across every adaptation strategy in the species' graph), and adaptation strategy range shifting (where the fluctuation will only be visible in the relevant adaptation strategy in the species' graph).*



b)

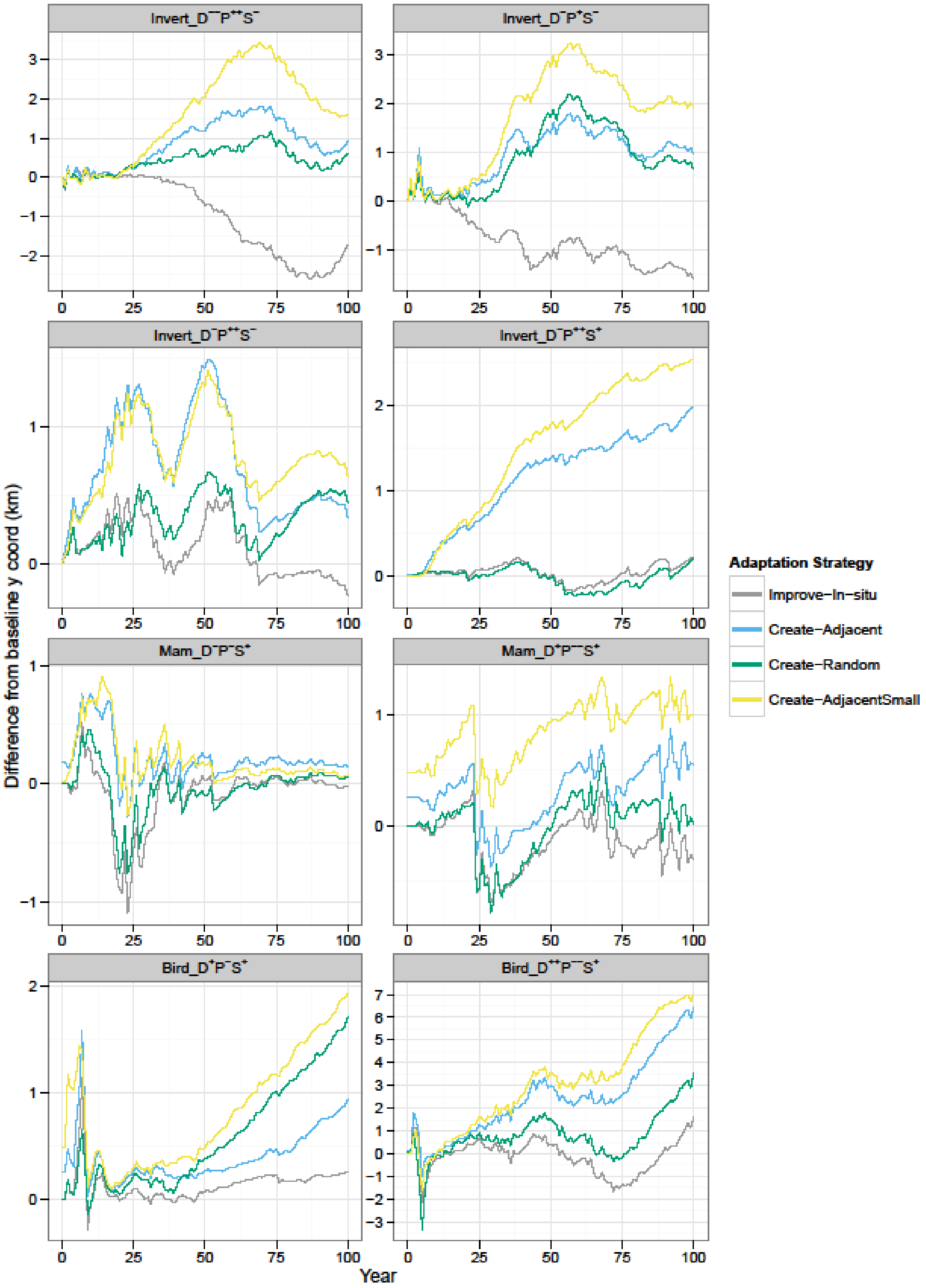
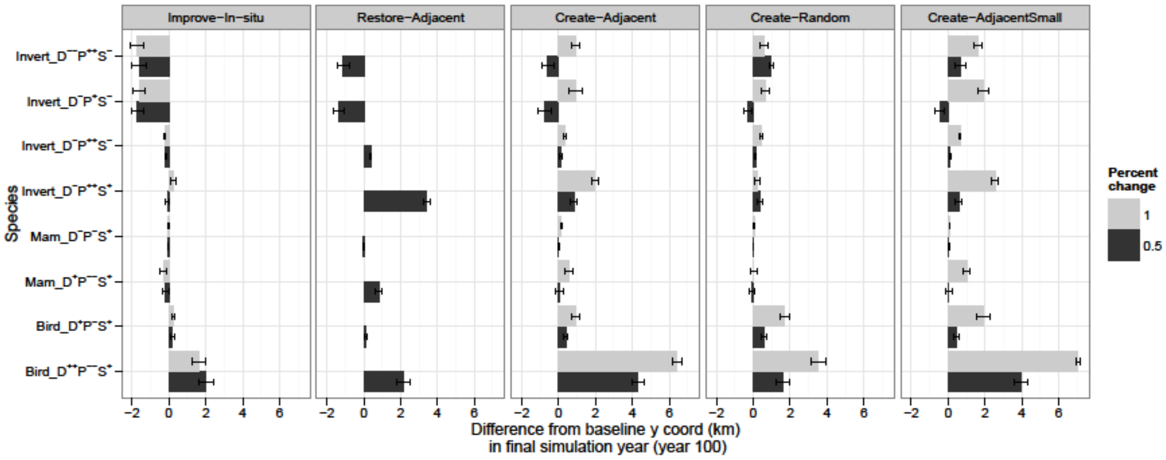

Invert_$D^{--}P^{++}S^{-}$
Invert_$D^{-}P^{+}S^{-}$
Invert_$D^{-}P^{++}S^{-}$
Invert_$D^{-}P^{++}S^{+}$
Mam_$D^{-}P^{-}S^{+}$
Mam_$D^{+}P^{--}S^{+}$
Bird_$D^{+}P^{-}S^{+}$
Bird_$D^{++}P^{--}S^{+}$
Difference from baseline y coord (km)
Year
0
25
50
75
100
−3
−2
−1
0
1
2
3
4
5
6
7
Adaptation Strategy
Improve−In−situ
Create−Adjacent
Create−Random
Create−AdjacentSmall

*Figure 5.4: Difference in range shifting response between five adaptation strategies and the baseline simulation (unchanged landscape), measured by the location after 100 years of the northern edge of the most northern patch containing an individual for asexual species, or containing a breeding pair for sexual species. Error bars represent standard error from 100 replicates (10 strategy replicates x 10 RangeShifter replicates). The Restore-Adjacent strategy was not possible with 1% prescribed for change due to insufficient conifer woodlands adjacent to broadleaved woodlands.*



## 5.6 Discussion

It is often suggested that conservation strategies and nature reserve design should aim to provide habitat and connectivity measures that will benefit as many species as possible (Moilanen *et al.*, 2005; Nicholson *et al.*, 2006; Carroll *et al.*, 2010). This work demonstrates how difficult it can be to target multiple species when resources for climate change adaptation are limited. At the 0.5% (500 hectares) level of change, the improvements in range shifting are unremarkable, with some species achieving no increase in their range. In fact, an adaptation strategy can benefit range shifting for some species, but be detrimental for others. For example, the Restore-Adjacent strategy (Figure 5.4) was beneficial for three species (Invert_D$^{-}$P$^{++}$S$^{+}$, Mam_D$^{+}$P$^{--}$S$^{+}$ and Bird_D$^{++}$P$^{--}$S$^{+}$), but detrimental for others (Invert_D$^{-}$P$^{+}$S$^{-}$ and Invert_D$^{-}$P$^{++}$S$^{-}$); the strategy was neutral or only slightly beneficial for the remaining species. When the adaptation strategy is focused on increasing the quality or area of existing habitats independent of their size (Improve-In-situ, Restore-Adjacent, Create-Adjacent), species with high to very high population density and only low to medium dispersal ability (Invert_D$^{--}$P$^{++}$S$^{-}$, Invert_D$^{-}$P$^{+}$S$^{-}$) may make smaller gains than they would have made in the unchanged landscape (Figure 5.3). No species makes more than a 4.3 km increase in their range compared with the baseline (i.e. range shifting in the unchanged landscape), and most species gain no more than 1 km over the 100 year period at the 0.5% level of change (Figure 5.4). However it is important to note that this result may illustrate one of the problems with focusing on connectivity as a measure of the success of conservation actions.

Conservation objectives strongly influence which habitat configuration will be most suitable (Margules and Pressey, 2000). Some strategies may be better suited to increasing in-situ population size, for example strategies that increase the size or quality of existing habitat. The proximity of new habitat to existing habitat can influence the lag in habitat growth and restoration, and may have a significant effect on the time it takes for new habitat to be colonised (Huxel and Hastings, 1999). This factor is rarely considered in reserve design or climate change adaptation studies, and was also not modelled in this study. Future work should incorporate habitat growth and restoration lag to determine its influence on the efficacy of different climate change adaptation strategies.

Increasing the percentage of habitat change from 0.5% to 1% leads to greater increases in range shifting distances (Figure 5.4), demonstrating that one of the key factors in improving habitat connectivity is simply increasing the amount of habitat. This suggests that there are no cheap or shortcut solutions. Stepping stones (the Create-Random strategy) proved only to be one of the best strategies for two species (Invert_$D^{--}P^{++}S^{-}$ - Figure 5.3a; Bird_$D^{+}P^{-}S^{+}$ - Figure 5.3b) that have vastly different population densities and dispersal abilities, both of which contribute towards a species' gap-crossing ability (e.g. Creegan and Osborne, 2005; Awade and Metzger, 2008; Robertson and Radford, 2009). If the total habitat area remains low, the creation of small stepping stone features cannot fix centuries of habitat fragmentation. Different species will benefit from alternative strategies and have varying thresholds for the size of gaps that they can cross, meaning that the dominant use of a single strategy will not provide connectivity for all species, especially where the amount of habitat change is low. Mokany *et al.* (2013) demonstrated the importance of using a balanced set of strategies, rather than focusing exclusively on connectivity, aggregation or representativeness. This study adds further evidence to this argument, but also demonstrates that in terms of range shifting, not all climate change adaptation strategies are equal; some provide greater benefits across broader groups of species (e.g. Create-AdjacentSmall - Figure 5.4). Even though making changes to 1% of the landscape did increase range shifting, the improvement is not huge, and species that exist in medium population densities and with medium dispersal ability will still struggle (e.g. Mam_$D^{-}P^{-}S^{+}$ - Figure 5.4). It is important to note that this study used only one landscape for all simulations so perhaps there are landscape specific effects. Landscape configuration is known to play a crucial role in determining the success of different habitat management strategies (Hodgson *et al.*, 2011a; Mokany *et al.*, 2013), so an important future area of research is to test how influential this effect was over the results of this study.

The strategy that gives the most consistent benefit across species is the creation of new habitat adjacent to existing small patches (Create-AdjacentSmall). Hodgson *et al.* (2011b), on the other hand, found that their “random” (new habitat added to cells chosen at random) and “even” (new habitat added to cells with lowest connectivity) strategies gave the most consistent increases in range expansion speed, and that “aggregation” was the least effective at facilitating range expansion. Whilst these findings are in stark contrast to the work in this chapter, it is important to note some key differences between the studies. Firstly, the two studies are based on different landscapes and at different scales; as discussed above, landscape configuration is an important factor in the success of habitat management strategies. Secondly, different adaptation strategies are used and whilst some are similar, none is identical; future work could study the effect of small variations in the way adaptation strategies are implemented. Thirdly, different models are used for the species populations; future studies to compare results from different population and dispersal models would be useful. The key is that a balanced approach should be used whereby different strategies are used for different regions and species (Mokany *et al.*, 2013). This study demonstrates that increasing the size of small patches may be the best method for improving connectivity for a number of different species simultaneously. In a world where conservation is increasingly restricted by land ownership and where budget is a limiting factor, focusing on increasing the size of small patches may be the best and most realistic option. However, landscape specific studies are crucial to ensure that the adaptation strategies chosen are best suited to the configuration of existing habitat and to the target species.

# Chapter 6: Coupled socio-ecological system modelling: feedback mechanisms, the emergence of spatial patterns and the importance of ecology in land-use change models

## 6.1 Abstract

The study of socio-ecological systems is of crucial importance for the development and usage of environmentally sustainable practices. Integrated modelling approaches are increasingly used to help us understand the interactions and feedbacks within such systems. A socio-ecological system model was developed through the coupling of two existing modelling platforms: CRAFTY, an agent-based model of land-use dynamics, and RangeShifter, an individual-based model of animal population dynamics and dispersal. A hypothetical case-study was established to simulate animal pollinators in a changing agricultural landscape, and to explore the coupled model system dynamics. The coupled model (with bi-directional system interactions) identified more severe declines in crop supply and pollinator populations than an uncoupled version (unidirectional system interactions) that ignored the interaction of pollinator ecology and population dynamics with crop productivity in the landscape. The spatial properties of the system also diverged under the two versions, with particular mechanisms in the coupled version leading to the emergence of spatial clusters of land-uses that neither support nor require animal pollinators. This study demonstrates the importance of considering species ecology in socio-ecological system modelling; ignoring it neglects a potentially crucial determinant of future land-use.

## 6.2 Introduction

The growing impact of humans on their environment is leading to an ever increasing challenge to achieve global sustainability. To move towards sustainability, it is crucial that we develop a better understanding of the complexity of human-environment interactions (Alberti *et al.*, 2011). Research and management efforts towards this goal often focus on either social or environmental issues, potentially missing crucial system interactions (Liu *et al.*, 2015). To improve our understanding, it is important that research increasingly spans multiple scientific disciplines, integrating models from different fields of research (Voinov and Shugart, 2013). This is especially true when there are dynamic interactions between multiple systems, because interventions and policy decisions may have unexpected consequences. Well-intentioned actions can sometimes have negative impacts that are difficult to predict, or even identify as a possibility (see Malawska *et al.*, 2014).

Individual- or agent-based modelling (hereafter ABM) is becoming a widely accepted method of studying underlying interactions in large systems, their impacts upon system-level properties, and decision making scenarios (at both an individual and policy level) (Farmer and Foley, 2009; Grimm and Railsback, 2013). In ecology, an important advantage of ABMs over aggregated population models is that they can utilise knowledge of mechanisms and processes at an individual level, to help us understand potential system-level outcomes (Batchelder *et al.*, 2002). Similarly in social science and land system science, ABMs have become increasingly popular in part because they have allowed for differential equations at the population level to be replaced by decision rules of low level entities (Matthews *et al.*, 2007). ABMs have also been used to study the responses of human decision making to environmental changes. For example, in a study on the Anasazi people of southwest USA, Axtell *et al.* (2002) used an ABM which simulated climatic and environmental changes to investigate possible explanations for their population decline. ABMs have also been used to study the response of farmer decision making to climate change, and the impacts on land-use (e.g. Bharwani *et al.*, 2005; Malanson *et al.*, 2014).

In ecology, ABMs are increasingly used to study animal movement in representations of real landscapes (Tang and Bennett, 2010), demonstrate that model outputs can exhibit similar patterns to field data (Watkins *et al.*, 2015), help identify threats to populations (Wiegand *et al.*, 2004), test the efficacy of conservation strategies (Synes *et al.*, 2015), and test the impacts of land-use scenarios (Gimona *et al.*, 2015). Nevertheless, few studies of species populations consider changes in landscapes through time. Instead, populations are simply simulated in landscapes with and without prescribed environmental changes (e.g. Imron *et al.*, 2011; Gimona *et al.*, 2015; Synes *et al.*, 2015). While there have been ABM studies of the ecological impacts of temporal variability in environmental conditions, these are rare and have generally focussed on direct changes to foraging and migratory behaviour rather than the long-term impacts on populations. For example Yamanaka *et al.* (2003) studied the sex-pheromone-orientated movement patterns of male moths under changing wind-direction, and Bennett and Tang (2006) studied elk *Cervus canadensis* migratory behavioural responses to changes in snow cover and vegetation biomass based on previous winter conditions.

In general, models of ecological processes incorporate a representation of the environment, but where human impacts are included, they are often based on a prescribed set of changes in land management (Bithell *et al.*, 2008; Luus *et al.*, 2013). On the other hand, models of social or land-use systems and their environmental impacts tend to incorporate a simplistic or static representation of the environment (Veldkamp and Verburg, 2004). ABMs of land-use and land-cover change often use land-use as a proxy for the available ecosystem services, and ecological processes are rarely represented as drivers of human decision making (Luus *et al.*, 2013). However, there is a growing recognition of the importance of interactions between ecological processes and the responses of humans in determining land-use (Liu *et al.*, 2007).

Previous models of land-use agents interacting with the landscape have created a human-environment link through hydrological processes (Becu *et al.*, 2003; Schreinemachers *et al.*, 2010; Hu *et al.*, 2015), soil nutrient flow (Matthews, 2006; Gaube *et al.*, 2009; Schreinemachers and Berger, 2011; Marohn *et al.*, 2012), timber harvesting (Evans and Kelley, 2008), and wildfire suppression (Hu and Sun, 2007). Socio-environmental system models have tended to focus on unidirectional interactions, with humans either acting as a driver or a user of the environment, but rarely both (Matthews and Selman, 2006; Filatova *et al.*, 2013). Bi-directional feedback between humans and their environment are crucial, particular in the context of agriculture, where farming decisions can both depend on and impact upon the environment (Altieri, 1999; Lichtenberg, 2002). Models have also been developed to study socio-ecological interactions, although these have tended to focus on modelling habitat (e.g. Linderman *et al.*, 2005; Monticino *et al.*, 2007), rather than directly modelling the study species. Some socio-ecological systems have been developed which incorporate greater ecological detail, for example, modelling farmer and hunter agents and their interactions with a wintering duck population, determined as a function of land-use, time, water availability and hunting disturbance (Mathevet *et al.*, 2003). Others have developed ABMs to study the interactions of farmer decision making with pest species, modelling the species through cellular automata (Rebaudo *et al.*, 2011) or a spatial stochastic simulation (Carrasco *et al.*, 2012). Polhill *et al.* (2013) coupled an ABM of land-use change with a species meta-community model, to investigate the effect of increasing government incentives to improve biodiversity. Their study identified non-linear responses of biodiversity to incentive policies, demonstrating the importance of coupling land-use and ecological models. For a review of applications of ABMs to environmental management, see Le Page *et al.* (2013).

Socio-ecological systems are inherently complex, often exhibiting non-linear behaviour, feedback mechanisms, time lags and shocks (Liu *et al.*, 2007; Filatova and Polhill, 2012). Their complexity necessitates that sufficiently detailed models are developed (Matthews and Selman, 2006), but caution must also be used to ensure that the model does not contain more processes, parameters and functions than is necessary (Luus *et al.*, 2013). Decision-makers have a general preference for simple explanations (Couclelis, 2002) that provide justification without needing to confront the intricacies of the system. In this context, striking an appropriate balance between simplicity and complexity is a major challenge. Evans *et al.* (2013) have recently suggested that a preference for excessively simple models may have limited progress in ecology, and that more complex models can in fact be more general.

Socio-ecological system models can be developed either by coupling existing models, or by developing the combined model from the ground up. When existing models are coupled, parameters in one part of the model may become endogenous to the system as a whole, making it more difficult to discern causal relationships (Marohn *et al.*, 2012) and to interpret results (Grimm *et al.*, 2005). However, model coupling allows for separate validations to be carried out prior to complexity being added through model integration. Whilst many simulation models have previously combined social, economic and environmental components, few have incorporated dynamic interactions (Argent, 2004) and fewer still have incorporated those between land-use and ecology. No models have yet been created that integrate individual-level farmer decision making with individual-level wildlife responses (Malawska *et al.*, 2014). The incorporation of individual-level species ecology into socio-ecological systems is important, because it is crucial in determining population dynamics and viability; the responses of species populations to farming practices can differ both between and within taxonomic groups (Malawska *et al.*, 2014).

Developing models of animal population dynamics, vegetation dynamics, land-use change or agricultural practices are significant challenges in their own right. Creating models that are integrated across these disciplines can become a huge undertaking. Broadly speaking, there are three different levels of model integration: loose coupling, where files are simply passed between the different models; tight coupling, where libraries are shared but the models remain separate; and full integration, where the models are combined into one system (Luus *et al.*, 2013). At each of these levels, there are trade-offs between model complexity, computational time, programming effort and ownership issues (Bithell and Brasington, 2009). Another key consideration in the development of a socio-ecological system model is the temporal and spatial scale at which the interacting systems operate (Malawska *et al.*, 2014). This can be a challenge as social and ecological systems often operate and interact at different (or multiple) temporal and spatial scales (Janssen and Ostrom, 2006).

In this work, two existing ABMs are loosely coupled and their application demonstrated with an abstract case study of pollinator populations in a landscape under pressure to increase food production. Previous studies on socio-ecological systems have modelled suitable habitat as a proxy for species presence (e.g. Linderman *et al.*, 2005; Monticino *et al.*, 2007); this study tests this assumption by comparing results when population dynamics are incorporated with results when only suitable habitat is considered. It is believed that this is the first study to integrate ABMs from different research disciplines, and therefore the first that demonstrates the dynamic feedback between a social land-use system and an ecological population model, both of which operate at the individual level.

## 6.3 Case study

A key socio-ecological system in the move towards sustainability is the interaction between agriculture and pollination. Approximately 75% of global food crops rely on animal pollination (Winfree, 2008). These crops account for 35% of global food crop production, and the level of animal pollinator dependence varies greatly between crops (Klein *et al.*, 2007). Global decline in pollinators is a potential concern for food production; for example, Californian orchards produce over 80% of the world’s almonds, but rely almost exclusively on managed honeybees for pollination (Klein *et al.*, 2012). Demand for food globally is projected to continue to rise, driven mainly by population growth (Valin *et al.*, 2014). To meet this demand, agricultural intensification will continue to be required, but this creates a greater risk for pollinator populations (Klein *et al.*, 2012). In particular, managed honey bee populations have been in decline in recent years (Ellis *et al.*, 2010; Potts *et al.*, 2010; vanEngelsdorp and Meixner, 2010). Balancing the need for productive agricultural land-use with the need to conserve biodiversity (including bees) is a global challenge (Tscharntke *et al.*, 2012).

The aim of this work was to test the importance of feedback mechanisms between ecology and land-use. To do this, an example study was developed, focussing on a hypothetical pollinator species in an agricultural landscape with increasing pressure from demand for food. The sensitivity of the system to both the variability in crop dependence on animal pollinators and variability in ecological parameters were assessed.

## 6.4 Methods

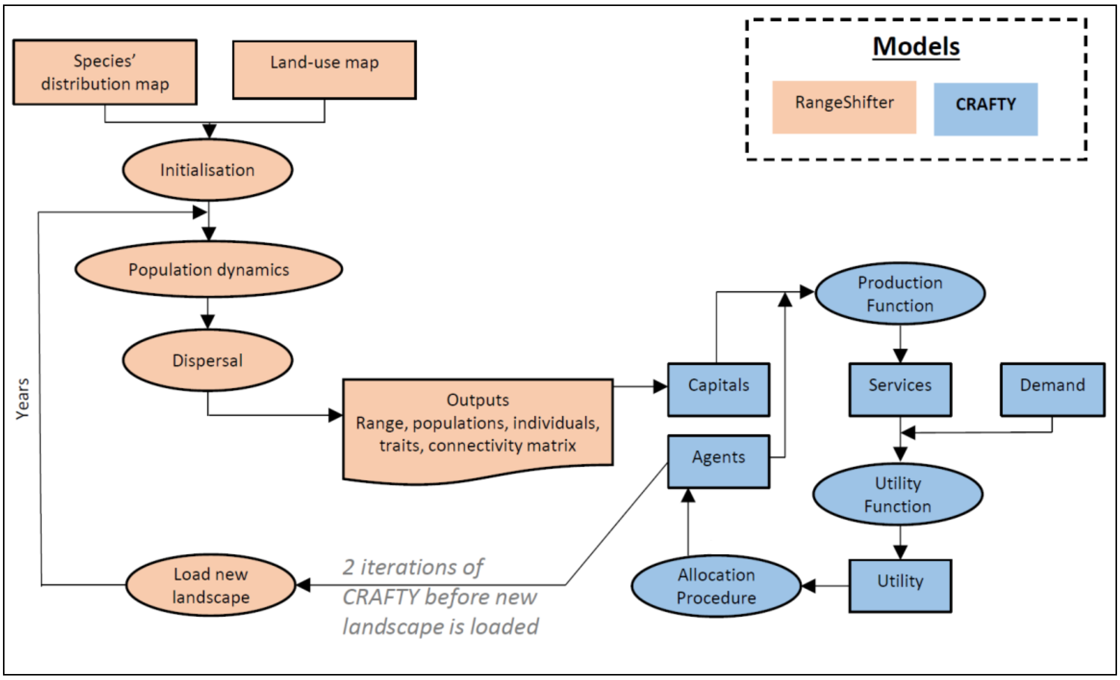
### 6.4.1 Model coupling

RangeShifter (Bocedi *et al.*, 2014a), an ABM of animal dispersal and population dynamics, was integrated with CRAFTY (Murray-Rust *et al.*, 2014), an ABM of land-use dynamics. The integration was implemented through loose coupling, i.e. the models interact through file-sharing. Loose coupling is simple to implement in terms of programming time, but runtimes are slower, since both models create output files and load input files in each time-step.

An important feature of CRAFTY is that instead of land-use types being used as proxies for ecosystem services, each pixel of land has a number of “capitals” representing the land’s potential for each available ecosystem service. Natural capitals are the stock of natural assets from which humans derive ecosystem services (Costanza *et al.*, 1997), and their representation has previously been suggested as a key feature to study feedbacks in socio-ecological systems (Luus *et al.*, 2013). The definition of a landscape through natural capitals gives greater realism, since it allows for two land parcels with the same land-use type to have different natural capitals and ecosystem service levels. It also means that agents can use ecosystem services to make decisions based on the environment, thus making CRAFTY suitable for integration with models of natural systems. For this case study, the pollinator population has a direct influence over the capital for crop productivity (i.e. crop productivity is reduced in locations without pollination). A change in crop productivity changes the competitiveness of the land-use agents, potentially leading to land-use change.

RangeShifter operates on an annual time-step, whilst one time-step of CRAFTY incorporates a full set of agent decisions about land-uses that do not have a fixed timescale. RangeShifter was modified to call CRAFTY with updated capitals (based on the species distribution – see Section 6.4.5), and to load the new landscape provided by CRAFTY each year. Two CRAFTY iterations were run for each year in RangeShifter to allow for initialisation and subsequent changes in the agent population. For the full integrated model workflow, see Figure 6.1.

Figure 6.1: *Workflow diagram for the coupled RangeShifter and CRAFTY model. For specific workflow diagrams of RangeShifter and CRAFTY see their respective papers.*



## 6.4.2 Landscape

An artificial landscape was created to allow for the simplistic representation of a scenario where demand for food (both meat and crops) is increasing but the production potential of the land has a finite limit. To define the landscape, capitals were created for each cell, selected from a uniform distribution ($0 < x \leq 1$). These capitals determine the productive potential of the land for different ecosystem services: crop productivity, livestock productivity, and forestry productivity. The "crop" is defined only as a generic crop since its reliance on pollination is one of the independent variables being tested; crop selection is not considered, and so all crop farmers produce the same crop. In this landscape of 100 x 100 cells (equating to a per-cell land unit size of 25 ha at 500 m resolution), each cell could either be managed by a unique agent implementing one type of land use or left unmanaged. Agents belonged to the following types: high intensity crop farmers, low intensity crop farmers, high intensity livestock farmers, low intensity livestock farmers, foresters. Similar to a previous application of CRAFTY (Brown *et al.*, 2014), high intensity farmers were defined with higher productivity than low intensity farmers, but greater sensitivity to the quality of the land. For the full CRAFTY parameter specification, see Appendix C.1.

### 6.4.3 Species

The study species was a hypothetical pollinator, defined as unable to breed in high intensity livestock and high intensity crop farm cells, and subject to carrying capacities dependent on land-use type (Appendix C.2). A female-only population model was used, thus assuming that males are non-limiting. Here, an 'individual' represented a single colony of pollinators rather than individual insects. The species' population dynamics were modelled at the cell scale, i.e. the individuals (colonies) present in each cell represent a distinct population, and density-dependent emigration operated at this scale. A number of species parameters were varied, in a factorial design, to study their impact on model results: maximum fecundity, carrying capacity reduction factor, and the inclusion or exclusion of long-distance dispersal in the pollinator movement model (Table 6.1). For the full RangeShifter parameter specification, see Appendix C.2.

*Table 6.1: Ecological parameter variants used for different simulation runs. These parameter variations were run in a factorial design (i.e. $2^3$ = 8 parameter combinations). See Appendix C.2 for full parameter details.*

| **Parameter** | **Parameter variant** | |
|---|---|---|
| Maximum fecundity | 1.5 | 2 |
| Carrying capacity reduction factor | 50% | 100% |
| Long-distance dispersal | Not included – only a single dispersal kernel is used | Included – 10% chance that the long distance dispersal kernel will be used |

### 6.4.4 Model type: coupled or uncoupled

To test the importance of incorporating population dynamics and the specific details of a species' ecology into socio-ecological system modelling rather than using suitable habitat as a proxy for the species, two versions of each simulation were run. The coupled models include bi-directional feedback between land-use and pollinators, meaning that land-use affects habitat suitability for pollinator populations and that pollinator distributions affect crop productivity, changing the competiveness of land-use. The uncoupled models include only unidirectional feedback, meaning that land-use affects habitat suitability for pollinator populations, but pollinator distributions do not affect crop productivity. Instead, the uncoupled model assumes that all suitable habitat will contain pollinators which will provide pollination in the neighbourhood.

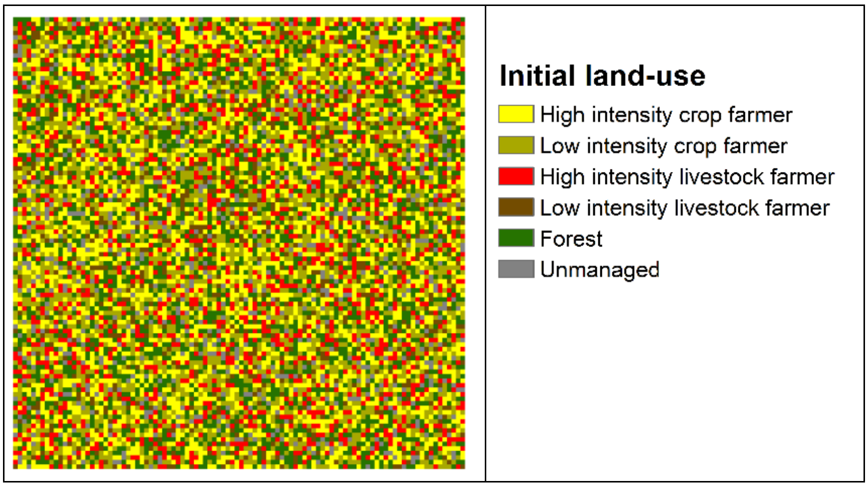
### 6.4.5 Pollination

For each cell that contains a pollinator population, that cell and its eight cell neighbourhood are pollinated (i.e. a maximum pollinator foraging distance of 500 m is assumed – in an empirical study, Osborne *et al.* (1999) found that bumble bees have a mean foraging distance of 275 m, and a range of 70-631 m). Pollinated cells retain the full crop productivity capital value that was originally assigned to that cell (Section 6.4.2). In absence of pollination, crop yield is reduced by a factor, which takes a single value for each simulation. For each species parameterisation (Section 6.4.3, Table 6.1) and each model type (Section 6.4.4), simulations were run varying the crop yield reduction factor from 0.1 (crop yield is reduced to 10% without pollination) to 0.9 in increments of 0.2. These values are representative of the variable dependence that different crops have on pollination (Klein *et al.*, 2007).

### 6.4.6 Simulation run-in

The initial demand for crop produce was set at 2.5 x initial demand for livestock produce, approximately matching the proportions of world demand for crop commodities compared to livestock commodities (Valin *et al.* (2014), using UN historical data). A ‘spin-up’ CRAFTY simulation was run for 20 years, allowing the agents to achieve a stable spatial distribution at initial demand levels. The resulting land-use map (Figure 6.2) was used to initialise all of the main simulations (Section 6.4.7). The initial demand level was below the productive capacity of the landscape, allowing for a mixture of high and low intensity farming, and for 757 of the 10,000 cells to go unmanaged (Figure 6.2).

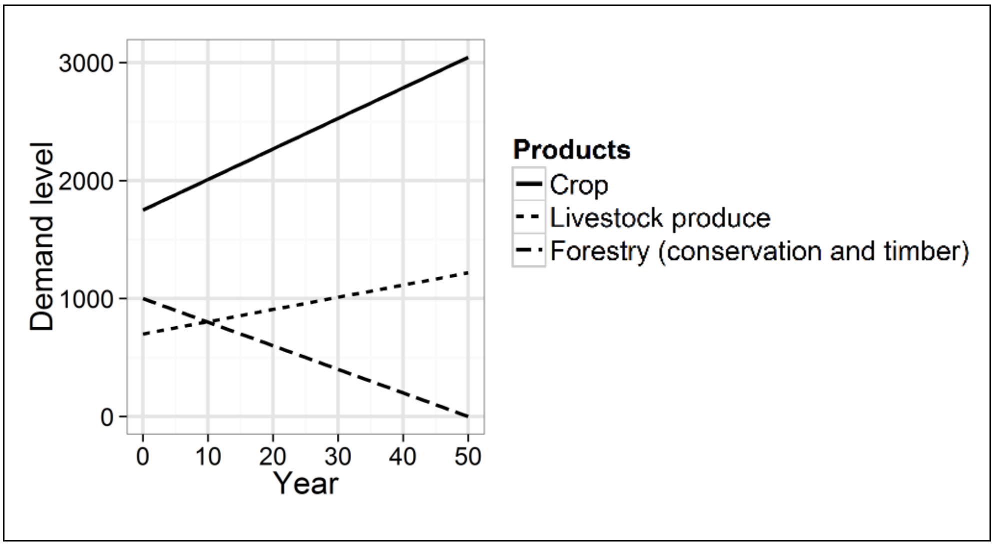
*Figure 6.2: The land-use map used to initialise each simulation. The random distribution of land-uses results from the independently randomised capital values across the cells.*



### 6.4.7 Main simulations

Demand for services is defined exogenously to CRAFTY, from an assumed non-spatial population. The same demand curve was used for every simulation in this study, beginning with 10 years of constant demand to allow the pollinator populations and land-use agents to stabilise (this was required due to the differences in crop yield in absence of pollination). The 10 years of constant demand for food were followed by 50 years of linear annual increases resulting in a 74% increase in demand for both livestock and crop produce over the 50 year period (Figure 6.3), matching the mean increase projected by Valin *et al.* (2014) for 2050. The 10 years of constant demand are not included in the results since all simulations stabilise during this initial period. Demand for forests in the case study encompasses both demand for timber and the protection of forests for conservation, and decreases to zero by the end of the 50 year period. This represents a scenario in which forest protection is gradually reduced due to the increasing demand for food. It therefore assumes that no consideration is made for the natural capital of forests, and the ecosystem services they provide.

*Figure 6.3: Demand levels used for each simulation. Demand for crop and livestock produce increase by 74% over 50 years; demand for forestry decreases to zero after 50 years.*



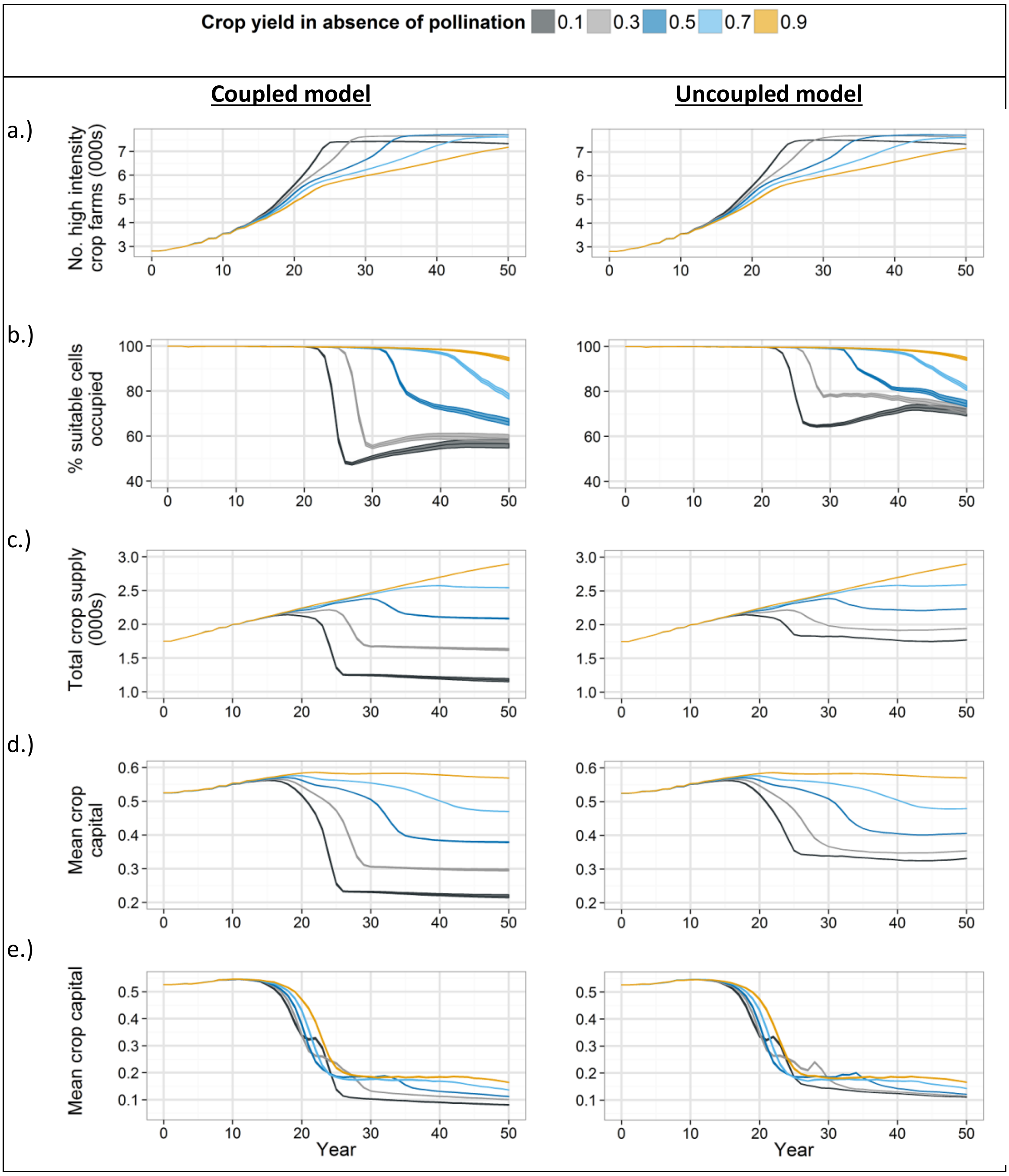
### 6.4.8 Measurement of spatial-autocorrelation

The spatial auto-correlation of high intensity livestock farmers compared to other land-uses was measured using Moran’s I statistic. Moran’s I values close to 1 indicate a high level of clustering, values close to -1 indicate a high level of dispersion, and a value of 0 indicates a random distribution. Both observed and expected values are calculated and then a z-score and p-value are computed to test for a statistically significant difference.. Moran’s I values were calculated for the final landscape of every simulation, and also for every (annual) landscape for the coupled model simulations where crop dependence on pollination was 0.9.

## 6.5 Results

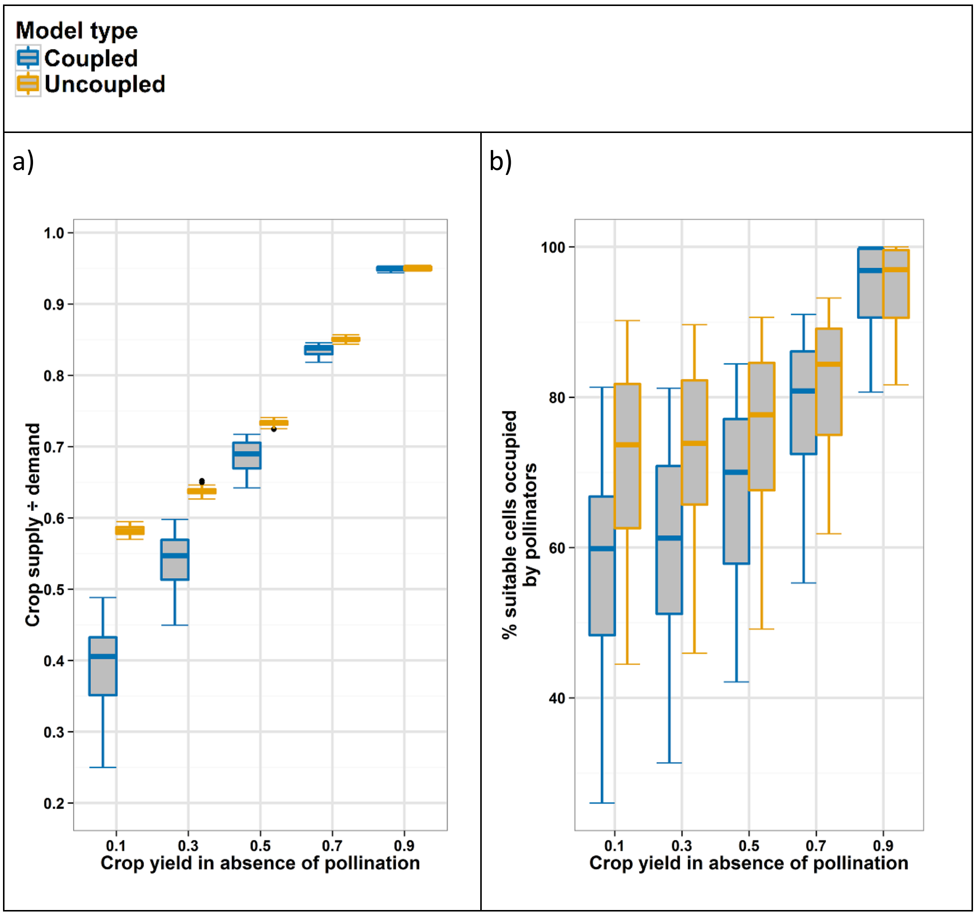
Simulation results demonstrated that both the coupled and uncoupled models captured the key dynamic of agricultural intensification driving declines in pollinator populations, with decreasing crop yield (in absence of pollination) leading to greater intensification and greater loss of pollinator populations (Figure 6.4a and b). As expected, the increasing demand for food in combination with a decreasing protection of forests led to the intensification and expansion of farming. However, this gradual intensification did not result in a steady increase in crop supply; instead, severe collapses in supply occurred as crop yield in absence of pollination decreased (Figure 6.4c). This decrease in crop supply is due to the decrease in the mean crop capital of high intensity crop farms as pollinator populations decline, again becoming more severe as crop yield in absence of pollination decreases (Figure 6.4d). The mean crop capital of low intensity crop farms also decreases for every pollination scenario, demonstrating their lack of competitiveness, and their marginalisation to lower quality land (Figure 6.4e). The decreasing crop capital, caused by loss of pollinators, drives further intensification of the landscape, reducing pollinator habitat and driving further decreases in pollinator populations in a positive feedback loop.

*Figure 6.4: Time-series behaviour of coupled and uncoupled models in terms of a) the intensification of crop farms; b) the percentage of suitable cells that are occupied by pollinator populations; c) total crop supply; d) mean crop capital of high intensity crop farms; and e) mean crop capital of low intensity crop farms. Line colours represent crop yield in absence of pollination. The shaded areas around each line represent the standard error from 80 simulations.*



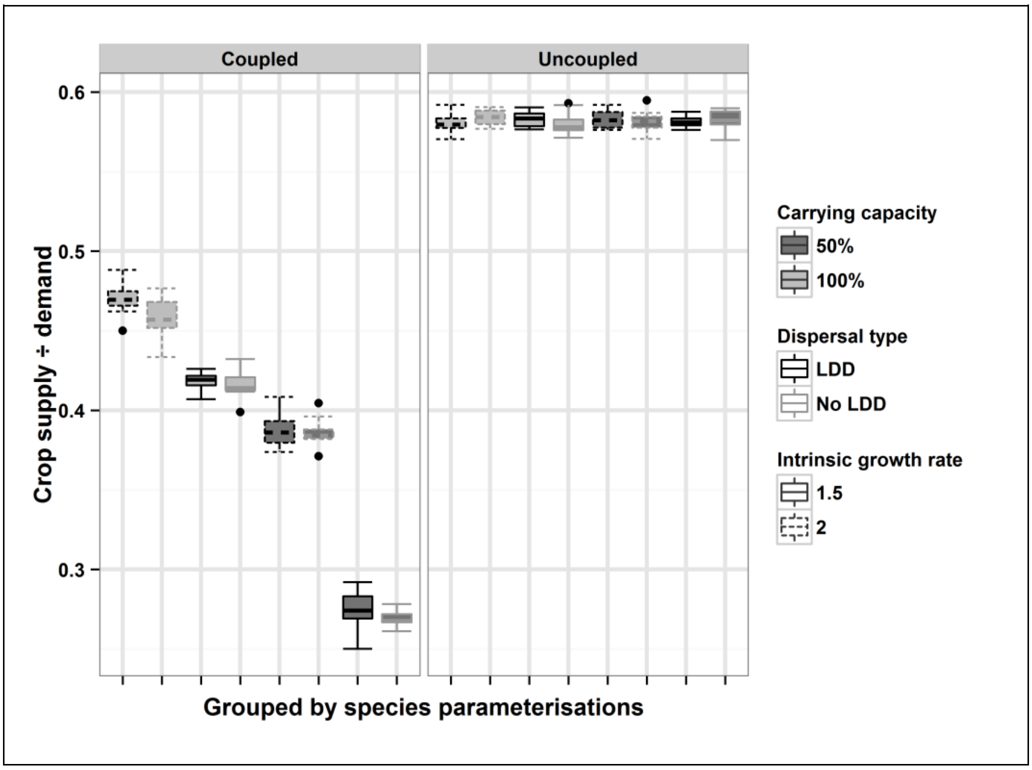
Results from the coupled and uncoupled simulations were qualitatively similar, but differed in the intensity of responses (Figure 6.4 b, c, d). When crop yield in absence of pollination is high, the coupled and uncoupled simulations provide similar outcomes in terms of the final year crop supply/demand and pollinator populations (Figure 6.5). As crop yield in absence of pollination decreases, the pollinator populations, total crop supply and the mean crop capital of high intensity crop farms all decrease at a faster rate in the coupled simulations than in the uncoupled simulations (Figure 6.4). This results in a divergence of final crop supply/demand (Figure 6.5a) and, to a lesser extent, the percentage of suitable cells occupied by pollinators (Figure 6.5b). Coupled model simulations show an increasingly wide range of final year crop supply/demand values as pollination becomes more important (Figure 6.5a).

*Figure 6.5: a) The final year crop supply/demand for each simulation and b) the percentage of suitable cells occupied by pollinators in the final year for each simulation, each grouped by crop yield in absence of pollination and model type. Each box represents 80 simulations. The ecological parameter variations were still used for the uncoupled simulations, but have no effect on the output from CRAFTY.*



The greater uncertainty shown by the coupled model compared to the uncoupled model (Figure 6.5a) was partly due to the variations used for ecological parameters (Table 6.1). When crop yield in absence of pollination is low (0.1), simulations in which the species has lower maximum fecundity and lower carrying capacity result in lower final year crop supply/demand (Figure 6.6). The number of cells occupied by pollinator populations was highly reliant on the species parameterisation, and had a strong positive correlation with crop supply/demand (Figure 6.7). By contrast and as expected, uncoupled simulations showed no differentiation in final year crop supply/demand across the different species parameterisations (Figure 6.6). The inclusion or exclusion of long distance dispersal in the coupled model had no effect on crop supply/demand gap.

*Figure 6.6: The final year crop supply/demand for simulations in which crop yield in absence of pollination was at the lowest studied level (0.1), grouped by ecological parameterisation and faceted by model type. Each box represents 10 replicates of a single parameterisation (see Table 6.1).*



Moran’s I values for the final year landscape from all simulations (both coupled and uncoupled) demonstrated a tendency for spatial-autocorrelation of livestock farmers when crop yield in absence of pollination was low (0.1), though there was greater variation in the Moran’s I values from coupled simulations (Figure 6.8). This greater variation came from the ecological parameterisations, which had no effect in the uncoupled model (Figure 6.9a). Lower maximum fecundity and lower carrying capacity resulted in lower Moran’s I values (i.e. less spatial-autocorrelation of high intensity livestock farmers), but the inclusion or exclusion of long distance dispersal had no effect. In the coupled models when crop yield in absence of pollination was low (0.1), most spatial aggregation occurred rapidly between simulation years 20 and 25, regardless of the ecological parameterisations (Figure 6.9b). After this rapid change, the level of spatial-autocorrelation diverged towards the values in Figure 6.9a, dependent on parameterisation.

*Figure 6.7: The number of cells occupied by pollinator populations in the final year in relation to crop supply/demand in the final year, crop yield in absence of pollination and ecological parameters (maximum fecundity (Rmax); carrying capacity reduction factor (K); note: the parameterisation of long distance dispersal is ignored in this graph since it had no clear influence on results).*

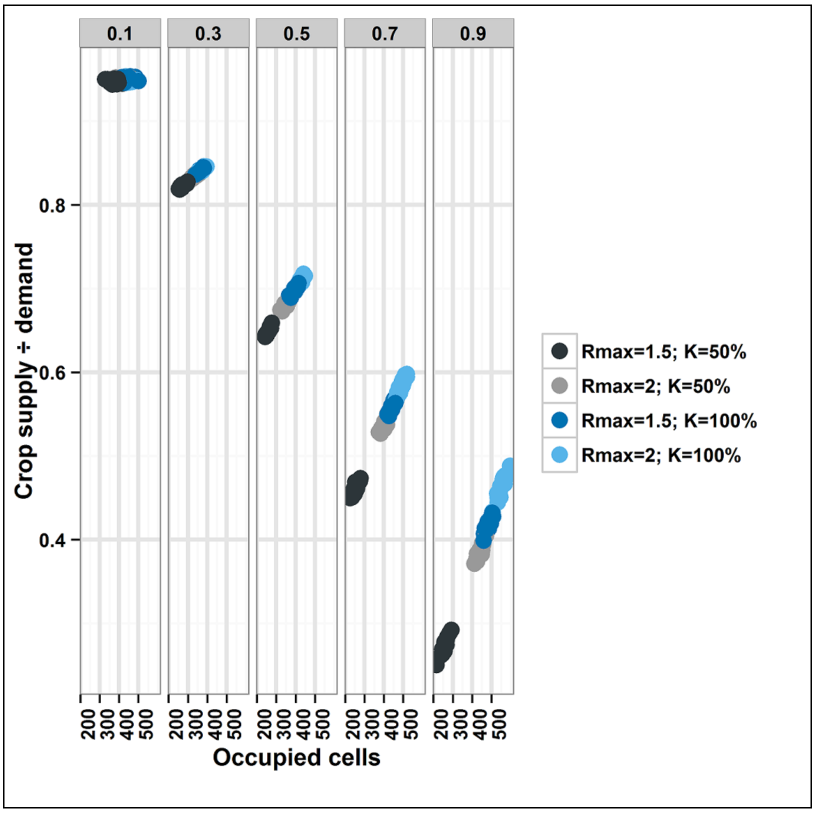


*Figure 6.8: Moran's I value for spatial aggregation of high intensity livestock farmers for each final year landscape, grouped by crop yield in absence of pollination and model type. The red dashed line represents the expected Moran's I value if the high intensity livestock farmers were randomly arranged. b) An example final year landscape, illustrating the clustering of high intensity livestock farmers.*

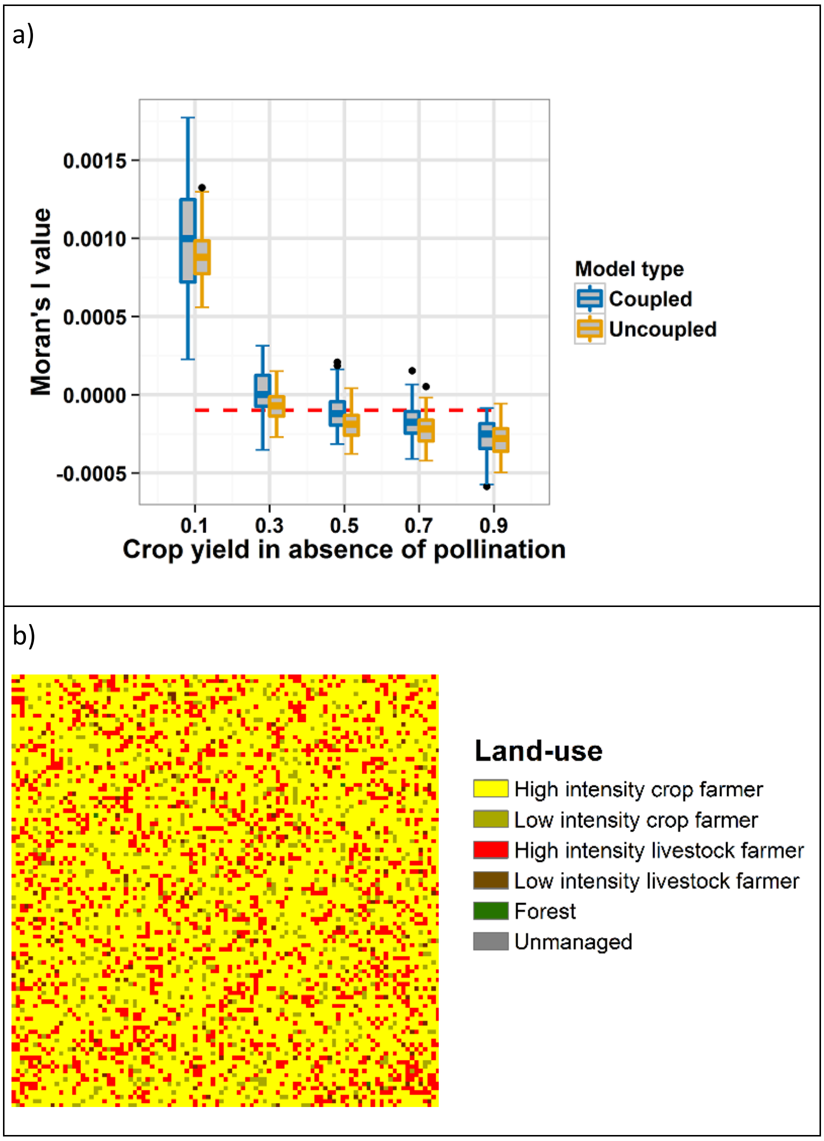
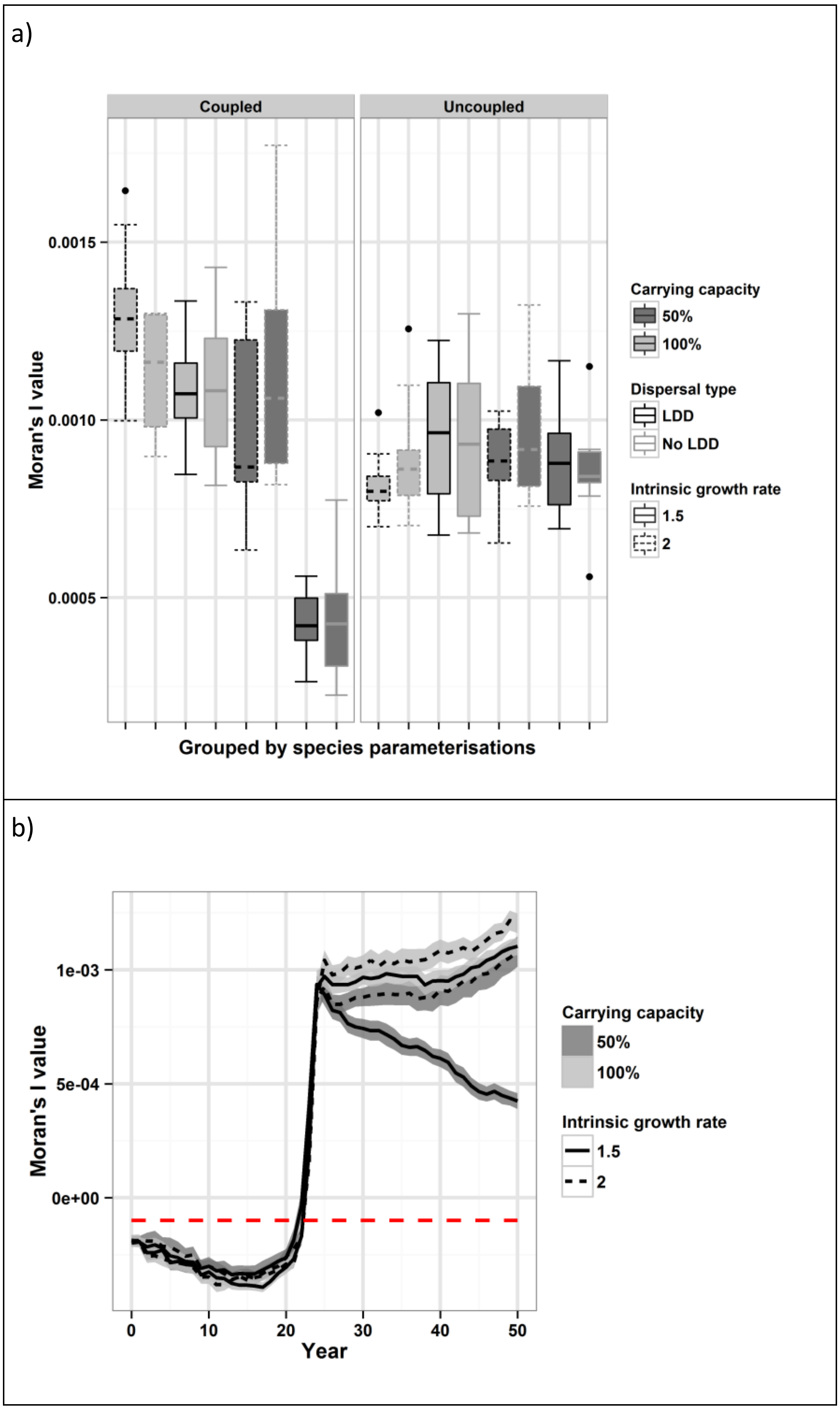


*Figure 6.9: a) Final year Moran's I value for spatial aggregation of high intensity livestock farmers for simulations in which crop yield in absence of pollination was low (0.1). Each box represents 10 replicates of a single ecological parameterisation (see Table 6.1). b) Time-series showing change in Moran's I values for high intensity livestock farmers for coupled model simulations in which crop yield in absence of pollination was low (0.1). Lines, representing the mean value from 20 replicates (10 with and 10 without long-distance dispersal) and shaded regions, representing ±1 standard error are grouped by ecological parameterisation. The red dashed line represents the expected Moran's I value if the high intensity livestock farmers were randomly arranged.*



## 6.6 Discussion

It is believed that the model integration presented in this work is the first example of a socio-ecological system model which gives equal weighting to both the social and the ecological sub-systems by using two existing agent-based modelling platforms. The integration of existing models has previously been discussed as an option for creating socio-ecological systems models (Luus *et al.*, 2013). This study demonstrates that such integration approaches are viable and useful.

The hypothetical case study, in which increasing demand for food would require an increasing intensification of agriculture, exhibits a decrease in pollinator populations as the land becomes dominated by high intensity farms which cannot support populations, a decrease in the average output of crop farmers as the pollinator populations fall, resulting in a decrease in the total crop supply which acts as a positive feedback on the need for further intensification and expansion of farming. These threshold changes occur earlier and become more severe as crop yield in absence of pollination decreases, demonstrating the increasing problem of agricultural intensification for crops reliant on animal pollinators. A key element of socio-ecological systems is that they can exhibit threshold behaviours (Liu *et al.*, 2007). It is important to note that because this study utilised an artificial landscape and hypothetical species, specific threshold values have no specific relevance to a real-world case study. However, the ability of this integrated model to identify threshold behaviours indicates the potential of this approach.

The divergence of coupled and uncoupled model supply/demand ratios as crop yield in absence of pollination decreases illustrates the importance of representing species' ecology in socio-ecological models. Whilst the range of values for the percentage of cells occupied by pollinators remains relatively consistent between coupled and uncoupled models, the associated uncertainty is not transferred to crop supply/demand in the uncoupled models. This demonstrates the potential problem in assuming that suitable habitat is a reasonable proxy for population presence. When the species' influence on the production of ecosystem services is low (e.g. high crop yield in absence of pollination), it may be reasonable to ignore population dynamics, but as their influence increases, model results become ever more reliant on the species' ecology. For the specific case study, it has been demonstrated that if the ecology and population dynamics of pollinators are not considered, projections may substantially overestimate our ability to meet future food demand levels.

The level crop yield in absence of pollination drives the strength of the interaction between pollinators and land-use agents; as pollination becomes more important, the variability in coupled model results widens. This increased variability can be attributed to the ecological parameter variations which result in wide differences in final crop supply/demand. The lowest final year crop supply/demand occurred for the ecological parameterisation with lower values for both carrying capacity and maximum fecundity, whereas the highest final supply/demand occurred for the higher values for both parameters. Population size, population growth rates and density-dependent processes are important factors in population dynamics and viability (Purvis *et al.*, 2000; Henle *et al.*, 2004), with habitat fragmentation and environmental change also impacting on population viability. Lower maximum fecundity and carrying capacity result in fewer cells being occupied, less pollination and therefore a lower crop supply/demand ratio. This illustrates the importance of the specific details of a species' ecology when studying socio-ecological systems. Due to the long processing time required for the coupled simulations, it was only possible to run the limited set of parameter variations presented here. With more time, a greater number of parameter variations could be tested, which would allow for a more systematic sensitivity analysis.

When crop yield in absence of pollination is low, there is a tendency for high intensity livestock farmers to cluster together, a result which is consistent for both coupled and uncoupled simulations. Once again, the coupled model exhibited greater sensitivity to ecological parameters. A lower maximum fecundity and carrying capacity resulted in less clustering of high intensity livestock farmers. The presence of land-uses that neither support nor require pollinators decreases the potential sources of foraging pollinators for neighbouring land-uses; this increases the likelihood that the productivity of adjacent land-uses reliant on pollination will be reduced, decreasing their competitiveness and increasing the likelihood of land-uses not requiring pollination taking over. Such a mechanism has the potential for a positive feedback loop similar to that demonstrated by Schelling's (1971) model of segregation. A very similar dynamic is at play in this more complex system, illustrating the value of agent-based modelling approaches.

There are a number of factors contributing to the reduction in pollinator populations, several of which are under ongoing research (e.g. pesticide use (Brittain *et al.*, 2010) and habitat loss (Naug, 2009)). More generally, there are numerous known impacts of human land use that affect subsequent land-use possibilities and decisions. This study demonstrates a system modelling approach that can capture the dynamics between pollinator ecology and agricultural intensification, and, in principle, other feedbacks between land use and ecology. Incorporating the key mechanisms in pollinator-agriculture relationships will allow future studies to test potential land-use and conservation policies, and improve our ability to identify, *ex ante*, unexpected undesirable outcomes.

Future research is increasingly likely to involve the coupling of models to study interacting systems. A realistic coupling of models requires that feedback mechanisms are implemented between the study systems. A model of animal movement and population dynamics will often also require a model of the landscape or environment in which the species moves. The environmental modelling requirement can vary greatly depending on the species, and may include models of land-use, climate, vegetation, hydrology, or even finer scale environments. Such model pairs can be integrated simplistically by creating a sequence of landscapes to be loaded in a time-series by spatial models of animal movement. However, a one-way integration such as this makes the assumption that the animal has no influence over the landscape upon which it exists, an assumption that is rarely, if ever true in reality. As this study has shown, the impact of pollinators on crop yield can radically change the speed of agricultural intensification, and the spatial configuration of the landscape. Grazing animals interact with vegetation dynamics, the presence of endangered or protected species may lead to habitat designation and the presence of invasive species can disrupt local biodiversity and vegetation. Such feedbacks between animals and their environment require two-way integration of environmental, social and ecological models. It is believed that the coupled model described in this study is the first to couple two individual-based social and ecological models. Both CRAFTY and RangeShifter are case-study independent modelling platforms, so this integrated model has great flexibility for applications to other socio-ecological interactions, and with greater detail than the case study presented here.

# Chapter 7: Discussion

This thesis has aimed to investigate approaches for improving species distribution modelling methods. A broad range of approaches have been studied, both in the pre-processing and the modelling phases of the work. A framework to integrate the approaches presented in this thesis would be a significant undertaking, and was not within the scope of this work. Furthermore, the advances made in this thesis will not always be required or feasible, and should only be incorporated into existing SDM approaches when appropriate for the aims of the study.

Many SDM studies obtain species location data from historical inventories, but this can lead to biases since the data is often collated from multiple sources, and different sampling methods may have been used. This can make it difficult to account for variability in sampling effort and detectability. Chapter 2 demonstrated the potential benefits of utilising a distance sampling methodology when collecting species occurrence data. Whilst distance sampling is already an established methodology, species and habitat covariates have rarely been used. The lesson from Chapter 2 is that when conducting field surveys, it is important to consider the potential impact that different habitat types will have on the detectability of the study species. Whilst the influence of distance on detectability has been widely discussed, the influence of habitat has received far less consideration (but see Sillett *et al.,* (2012)). Future field surveys should collect information on habitat at each data collection point to help parameterise the observation model. Clearly such a methodology requires a significant amount of fieldwork, an undertaking that is rarely possible, particularly over large study regions. However, where feasible, data collection and pre-processing should utilise methods that account for errors in observation (in particular, related to distance, species and habitat). Where such data is subsequently used in an SDM, a state-space or hierarchical modelling approach should be used to ensure that parameters related to observability are estimated separately from the parameters related to the processes being studied (Royle and Kéry, 2007; Patterson *et al.*, 2008; Kéry and Royle, 2010; Hostetler and Chandler, 2014).

Whilst Chapter 2 demonstrated the potential to share information from multiple species to improve the modelling of species detectability (prior to inclusion in a SDM), Chapter 3 demonstrated a potential method for sharing information on multiple competing species within a

SDM. Some SDM studies have incorporated the distributions of co-occurring species (Araújo and Luoto, 2007; Heikkinen *et al.*, 2007; Sutherst *et al.*, 2007; Hof *et al.*, 2012; le Roux *et al.*, 2012; Giannini *et al.*, 2013), but such studies are rare. Although Chapter 3 did not identify improved model performance from the inclusion of competing species, this may be due to the limited number of species variations used, the focus on only one type of interaction (resource competition) and the use of only one species distribution modelling algorithm (MaxEnt). Future work on this topic may be able to use a similar methodology over a broader range of biotic interactions and spatial scales to identify those factors that influence the suitability of interacting species as predictor variables.

Chapter 4 presents the toolbox developed to create the landscape strategies used in Chapter 5. This toolbox has flexibility beyond the examples presented in Chapter 4 and Chapter 5, and can easily be transferred to other study landscapes and systems. Furthermore, the simulations presented in Chapter 5 form only a small subset of the total number of simulation results. Chapter 5 focussed on a single landscape and two conservative levels of prescribed change; the entire dataset includes simulation data from six landscapes and four levels of prescribed change (two additional more ambitious levels of prescribed change). Ongoing work is utilising this additional data to test for landscape effects on species range shifting ability and climate change adaptation strategy success. As discussed in Chapter 4, the STeLMAG toolbox can also be used to generate temporal habitat quality transitions. There is often a time-lag between conservation actions and the generation of functioning habitat (Morris *et al.*, 2006; Maron *et al.*, 2012), and this can lead to a lag in the responses of species that utilise the habitat (e.g. Cosentino *et al.*, 2014). Seed bank availability can also be an important factor in the restoration and regeneration of habitat (Pakeman and Small, 2005; Metsoja *et al.*, 2014), meaning that the proximity of restoration efforts to existing or former habitat may play a role in the speed of restoration. Future work can develop upon the methodology of Chapter 5 to consider the time-lag between the different climate change adaptation actions. Whilst Chapter 4 does not directly address SDM methods, no landscape simulation tools were identified that were appropriate for the questions addressed by Chapter 5.

The methodology used in Chapter 5 does not consider the potential effects of a changing climate on species life history or on habitat suitability; the focus of the work is on a mechanistic approach. The use of RangeShifter (Bocedi *et al.*, 2014a) allows this chapter to make a number of advances over previous studies on the range shifting potential of species, particularly by explicitly accounting for the three stages of dispersal, and the costs associated with dispersal, which have rarely been considered in dispersal models (Travis *et al.*, 2012). A number of “hybrid” models exist which incorporate process-based ecological processes such as population dynamics and dispersal into SDMs (Keith *et al.*, 2008; Engler and Guisan, 2009; Kearney and Porter, 2009; Conlisk *et al.*, 2013). Whilst RangeShifter can facilitate such an approach by loading habitat suitability maps, this approach was not taken since Chapter 5 already makes a number of advances over previous studies on range shifting. Furthermore, parameterisation of these hybrid models remains a significant challenge (Franklin, 2010; Schurr *et al.*, 2012). In particular, knowledge on how the growth rates, fecundity levels and mortality risk of species change under different environmental conditions is still limited; without this knowledge, the results from hybrid models must be treated with caution.

Chapter 6 incorporates another feature that has rarely been considered in previous SDM studies: two-way interactions between social systems and ecological systems. In fact, no other studies were found that have modelled both the social and ecological system at an individual level. Malawska *et al.* (2014) also found that no previous studies had integrated an individual-based model of farmer decision making with an individual-based model of wildlife responses. Since Chapter 6 is so novel, it is still a long way from integration with existing SDM approaches. However, the divergence of the coupled and uncoupled model results illustrates the importance of considering coupled interactions when modelling the distributions of certain species (i.e. those that have a strong link to a social capital). Without coupled interactions, positive feedback mechanisms which drive population declines may be underestimated. Whilst some species may have little interaction with social or economic systems, many species are fundamentally connected to these systems through their interaction with the landscape. Such interactions should be considered in future species distribution modelling studies. Such an approach may be particularly useful to study the spread of invasive species, and to identify potential policy interventions. Furthermore, due to its cross-disciplinary nature, Chapter 6 also highlights the importance of the approach for future social system studies. Without consideration of potential ecological interactions, social issues such as food security may be underestimated.

Developing a socio-ecological system model can be an enormous challenge, requiring multi-disciplinary collaborative work (Luus *et al.*, 2013; Malawska *et al.*, 2014). However, as Chapter 6 demonstrates, the coupling of existing models can be a viable alternative if suitable and compatible models exist. The methodology is currently being developed further in preparation for publication. The existing results will remain, but additional simulations are being developed to incorporate institutional interventions. The ability to test policies and their potential impacts is a key benefit of coupled socio-ecological system modelling (Malawska *et al.*, 2014; Liu *et al.*, 2015). Since CRAFTY already allows for the incorporation of institutional agents (Brown *et al.*, 2014), policies can be implemented within the existing framework whilst maintaining the mechanistic individual-based approach. The planned work will incorporate an institutional agent which can provide subsidies to low intensity farmers based on the monitoring of pollinator populations. This work can help identify to what extent such policies can alleviate potential food security issues related to pollinator population declines.

The research chapters in this thesis do not all directly address whether the approaches taken can improve SDM methods. However, all (except Chapter 4 which is a necessary precursor to Chapter 5) have utilised novel methods which advance the science and with further study may provide improvements to existing SDM methods. The use of habitat and species covariates as with the distance sampling approach in Chapter 2 is directly applicable to species distribution modelling, and could be implemented using a state-space or hierarchical Bayesian approach. The novel approach for including species interactions in Chapter 3 is also directly applicable to existing SDM methods. Whilst no improvements were found, future work could widen this study to include different interactions at different scales. The use of an individual-based model with detailed representation of the three stages of dispersal and population dynamics to study range shifting in Chapter 5 illustrates the potential of such modelling platforms. Such a methodology could be incorporated into existing SDMs with a hybrid model approach. However, such models still have many limitations, and so this is left for future work. Finally, the methodology of Chapter 6 demonstrates the potential importance of including socio-ecological interactions when modelling species distributions. Where species are tightly coupled with social systems through a shared landscape, future species distribution modelling studies should incorporate an approach such as that presented in Chapter 6.

# Appendices

# Appendix A

*Table A.1: Parameters available in the ExistingPatches tool within the STeLMAG toolbox.*

| **Parameter label** | **Explanation** | **Data type** |
|---|---|---|
| Output folder | The directory location to which all outputs are saved. It is recommended that a new directory is used each time a *STeLMAG tool is run.* | Folder |
| Number of replicates | The number of replicate landscapes to create (through the stochastic allocation procedure) from this rule set. | Long |
| Land-cover raster | The raster-based study landscape. | Raster dataset |
| Study habitat ID | The study habitat ID value (from the study landscape raster) that represents the habitat type to be managed. | Long |
| Total management area (# cells) | The total number of cells from the raster-based study landscape to allocate for management action. | Long |
| Use habitat quality transition data | Select this option if temporal habitat quality transitional data should be applied to the land management actions. If this option is selected, then *Habitat quality (CSV file)*, *Habitat transitions (CSV file)* and *Habitat transition strategy name* will be required. | Boolean |
| Habitat quality (CSV file) | A comma-separated values (CSV) file which defines the habitat quality for each habitat type in the study landscape.<br>This file should be of the form:<br>**ID,Quality**<br>**<Habitat ID value>,<quality value>**<br>**... , ...**<br>Habitat ID values should be from the study landscape, quality values can be any floating point number. | File |
| Habitat transitions (CSV file) | A comma-separated values (CSV) file which defines the temporal habitat quality transitions. These transitions should represent the change in*Study habitat ID* quality as management is applied.<br>This file should be of the form:<br>**Year,<strategy name 1>,<strategy name 2>,...**<br>**<year>,<strategy 1 quality value>,<strategy 2 quality value>**<br>**... , ... , ...**<br>Strategy names should be an alpha-numeric string. Any number of strategies can be defined in the *Habitat transitions file*; the specific strategy used each time the tool is run is selected from the *Habitat transition strategy namedrop-down menu. The year values can be any integer value, over any interval. Quality values can be any floating point number.* | File |

*… Table A.1 continued: Parameters available in the ExistingPatches tool within the STeLMAG toolbox.*

| **Parameter label** | **Explanation** | **Data type** |
|---|---|---|
| Habitat transition strategy name | The strategy name for the temporal habitat quality transitions which should be applied to the land management actions. Strategies can be selected from a drop-down box, filled with the strategy names for temporal habitat quality transitions as defined in the *Habitat transitions CSV file*. | String |
| Region group patch neighbourhood rule | The region group patch neighbourhood rule used to define habitat patch cohesion (default is Moore's 8-cell neighbourhood). | String |
| Existing patch minimum size (# cells) | The minimum size (in terms of number of cells) of existing patches of the study habitat (as defined by the *Study habitat ID* parameter) which should be considered for management. | Long |
| Existing patch maximum size (# cells) | The maximum size (in terms of number of cells) of existing patches of the study habitat (as defined by the *Study habitat ID* parameter) which should be considered for management. | Long |

*Table A.2: Parameters available in the CustomPatches_Adjacent tool within the STeLMAG toolbox.*

| **Parameter label** | **Explanation** | **Data type** |
|---|---|---|
| Output folder | The directory location to which all outputs are saved. It is recommended that a new directory is used each time a *STeLMAG tool is run.* | Folder |
| Number of replicates | The number of replicate landscapes to create (through the stochastic allocation procedure) from this rule set. | Long |
| Land-cover raster | The raster-based study landscape. | Raster dataset |
| Study habitat ID | The study habitat ID value (from the study landscape raster) that represents the habitat type to be created. | Long |
| Total management area (# cells) | The total number of cells from the raster-based study landscape to allocate for management action. | Long |
| Habitat ID(s) to be modified | The habitat ID value(s) (from the study landscape raster) of habitat types in which management actions should take place. | Multiple value |
| Use habitat quality transition data | Select this option if temporal habitat quality transitional data should be applied to the land management actions.<br>If this option is selected, then *Habitat quality (CSV file)*, *Habitat transitions (CSV file)* and *Habitat transition strategy name* will be required. | Boolean |
| Habitat quality (CSV file) | A comma-separated values (CSV) file which defines the habitat quality for each habitat type in the study landscape.<br>This file should be of the form:<br><br>**ID,Quality**<br>**<Habitat ID value>,<quality value>**<br>**… , …**<br><br>Habitat ID values should be from the study landscape, quality values can be any floating point number. | File |
| Habitat transitions (CSV file) | A comma-separated values (CSV) file which defines the temporal habitat quality transitions. These transitions should represent the transition of habitat quality as it changes from the *Habitat ID(s) to be modified* to the *Study habitat ID*.<br>This file should be of the form:<br><br>**year,<strategy name 1>,<strategy name 2>,…**<br>**<year>,<strategy 1 quality value>,<strategy 2 quality value>**<br>**… , … , …**<br><br>Strategy names should be an alpha-numeric string. Any number of strategies can be defined in the *Habitat transitions file*; the specific strategy used each time the tool is run is selected from the *Habitat transition strategy name* drop-down menu. The year values can be any integer value, over any interval. Quality values can be any floating point number. | File |

*… Table A.2 continued: Parameters available in the CustomPatches_Adjacent tool within the STeLMAG toolbox.*

| **Parameter label** | **Explanation** | **Data type** |
|---|---|---|
| Habitat transition strategy name | The strategy name for the temporal habitat quality transitions which should be applied to the land management actions.<br>Strategies can be selected from a drop-down box, filled with the strategy names for temporal habitat quality transitions as defined in the *Habitat transitions CSV file*. | String |
| Existing patch minimum size (# cells) | The minimum size (in terms of number of cells) of existing patches of the study habitat (as defined by the *Study habitat ID* parameter) which should be available for expansion by the creation of new adjacent habitat patches. | Long |
| Existing patch maximum size (# cells) | The maximum size (in terms of number of cells) of existing patches of the study habitat (as defined by the *Study habitat ID* parameter) which should be available for expansion by the creation of new adjacent habitat patches. | Long |
| New patch minimum size (# cells) | The minimum size (in terms of number of cells) of the new adjacent patches of the study habitat (as defined by the *Study habitat ID* parameter). | Long |
| New patch maximum size (# cells) | The maximum size (in terms of number of cells) of the new adjacent patches of the study habitat (as defined by the *Study habitat ID* parameter). | Long |
| Region group patch neighbourhood rule | The region group patch neighbourhood rule used to define habitat patch cohesion (default is Moore's 8-cell neighbourhood). | String |
| Beta distribution parameters: alpha | The Beta distribution is defined by two positive parameter values: alpha and beta. This parameter defines alpha. Alpha must be a positive floating point number (default value is 1.5). | Double |
| Beta distribution parameters: beta | The Beta distribution is defined by two positive parameter values: alpha and beta. This parameter defines beta. Beta must be a positive floating point number (default value is 5). | Double |

*Table A.3: Parameters available in the CustomPatches_ExSitu tool within the STeLMAG toolbox.*

| **Parameter label** | **Explanation** | **Data type** |
|---|---|---|
| Output folder | The directory location to which all outputs are saved. It is recommended that a new directory is used each time a *STeLMAG tool is run.* | Folder |
| Number of replicates | The number of replicate landscapes to create (through the stochastic allocation procedure) from this rule set. | Long |
| Land-cover raster | The raster-based study landscape. | Raster dataset |
| Study habitat ID | The study habitat ID value (from the study landscape raster) that represents the habitat type to be created. | Long |
| Total management area (# cells) | The total number of cells from the raster-based study landscape to allocate for management action. | Long |
| Habitat ID(s) to be modified | The habitat ID value(s) (from the study landscape raster) of habitat types in which management actions should take place. | Multiple value |
| Use habitat quality transition data | Select this option if temporal habitat quality transitional data should be applied to the land management actions.<br>If this option is selected, then *Habitat quality (CSV file)*, *Habitat transitions (CSV file)* and *Habitat transition strategy name* will be required. | Boolean |
| Habitat quality (CSV file) | A comma-separated values (CSV) file which defines the habitat quality for each habitat type in the study landscape.<br>This file should be of the form:<br>**ID,Quality**<br>**<Habitat ID value>,<quality value>**<br>**… , …**<br>Habitat ID values should be from the study landscape, quality values can be any floating point number. | File |
| Habitat transitions (CSV file) | A comma-separated values (CSV) file which defines the temporal habitat quality transitions. These transitions should represent the transition of habitat quality as it changes from the *Habitat ID(s) to be modified* to the *Study habitat ID*.<br>This file should be of the form:<br>**year,<strategy name 1>,<strategy name 2>,…**<br>**<year>,<strategy 1 quality value>,<strategy 2 quality value>**<br>**… , … , …**<br>Strategy names should be an alpha-numeric string. Any number of strategies can be defined in the *Habitat transitions file*; the specific strategy used each time the tool is run is selected from the *Habitat transition strategy name* drop-down menu. The year values can be any integer value, over any interval. Quality values can be any floating point number. | File |

*… Table A.3 continued: Parameters available in the CustomPatches_ExSitu tool within the STeLMAG toolbox.*

| **Parameter label** | **Explanation** | **Data type** |
|---|---|---|
| Habitat transition strategy name | The strategy name for the temporal habitat quality transitions which should be applied to the land management actions.<br>Strategies can be selected from a drop-down box, filled with the strategy names for temporal habitat quality transitions as defined in the *Habitat transitions CSV file*. | String |
| Existing patch minimum size (# cells) | The minimum size (in terms of number of cells) of existing patches of the study habitat (as defined by the *Study habitat ID* parameter). Only those patches within the given size restrictions will be considered when either *Minimum distance* or *Maximum distance* are set. | Long |
| Existing patch maximum size (# cells) | The maximum size (in terms of number of cells) of existing patches of the study habitat (as defined by the *Study habitat ID* parameter). Only those patches within the given size restrictions will be considered when either *Minimum distance* or *Maximum distance* are set. | Long |
| New patch minimum size (# cells) | The minimum size (in terms of number of cells) of the new patches of the study habitat (as defined by the *Study habitat ID* parameter). | Long |
| New patch maximum size (# cells) | The maximum size (in terms of number of cells) of the new patches of the study habitat (as defined by the *Study habitat ID* parameter). | Long |
| Minimum distance between existing and new habitats | The minimum distance (in the units of the study landscape) between existing study habitat patches (within the size restrictions) and new study habitat patches. If left blank, then *Minimum distance* = 0, i.e. no minimum distance. | Long |
| Maximum distance between existing and new habitats | The maximum distance (in the units of the study landscape) between existing study habitat patches (within the size restrictions) and new study habitat patches. If left blank, there is no *Maximum distance* restriction. | Long |
| Region group patch neighbourhood rule | The region group patch neighbourhood rule used to define habitat patch cohesion (default is Moore's 8-cell neighbourhood). | String |
| Beta distribution parameters: alpha | The Beta distribution is defined by two positive parameter values: alpha and beta. This parameter defines alpha. Alpha must be a positive floating point number (default value is 1.5). | Double |
| Beta distribution parameters: beta | The Beta distribution is defined by two positive parameter values: alpha and beta. This parameter defines beta. Beta must be a positive floating point number (default value is 5). | Double |

# Appendix B

Tables of RangeShifter parameter values follow on the next pages.

*Table B.1: RangeShifter parameter values for simulated invertebrate species*

| **Parameter** | **Invert_$D^{--}P^{++}S^{-}$** | **Invert_$D^{-}P^{+}S^{-}$** | **Invert_$D^{-}P^{++}S^{-}$** | **Invert_$D^{-}P^{++}S^{+}$** |
|---|---|---|---|---|
| **Population dynamics** | | | | |
| Reproduction | Asexual / female only | Asexual / female only | Asexual / female only | Sexual model (simple) |
| Stage structure | No | No | No | No |
| Intrinsic growth rate (*Rmax*) | 10 | 25 | 10 | 10 |
| Competition coefficient ($b_c$) | 1 | 1 | 1 | 1 |
| Carrying capacity (*K*) | 50 | 20 | 50 | 50 |
| **Dispersal - emigration** | | | | |
| Emigration probability | Density-dependent | Density-dependent | Density-dependent | Density-dependent |
| Max. emigration probability ($D_0$) | 0.7 | 0.7 | 0.7 | 0.7 |
| Slope at inflection point (α) | 10 | 10 | 10 | 10 |
| Inflection point (β) | 0.5 | 0.5 | 0.5 | 0.5 |
| **Dispersal – transfer** | | | | |
| Movement model | SMS | SMS | Dispersal kernel | Dispersal kernel |
| Kernel type | | | Negative exponential | Negative exponential |
| Mean distance (metres) | | | 100 | 100 |
| Perceptual range (metres) | 40 | 120 | | |
| Directional persistence | 5 | 8 | | |
| **Habitat dependent movement costs / per-step mortality** | | | | |
| Improved grassland, arable, water | 1000 / 0.1 | 1000 / 0.1 | | |
| Semi improved grassland | 100 / 0.05 | 100 / 0.05 | | |
| Coniferous woodland, FMS | 25 / 0.01 | 25 / 0.01 | | |
| Dwarf shrub heath | 10 / 0.005 | 10 / 0.005 | | |
| Broadleaved woodland | 1 / 0 | 1 / 0 | | |
| **Dispersal - settlement** | | | | |
| Settle-if | Find a suitable patch (not the natal one) | Find a suitable patch (not the natal one) | Die | Die |

*Table B.2: RangeShifter parameter values for simulated vertebrate species*

| **Parameter** | **Mam_$D^-P^-S^+$** | **Mam_$D^+P^{--}S^+$** | **Bird_$D^+P^-S^+$** | **Bird_$D^{++}P^{--}S^+$** |
|---|---|---|---|---|
| **Population dynamics** | | | | |
| Reproduction | Sexual model (simple) | Sexual model (simple) | Sexual model (simple) | Sexual model (simple) |
| Stage structure | Yes | Yes | Yes | Yes |
| Number of stages | 2 | 3 | 2 | 2 |
| Maximum age | 4 | 10 | 5 | 8 |
| Minimum age (stage 2) | | 2 | | |
| Fecundity: juvenile ($\varphi_0$) | 0 | 0 | 0 | 0 |
| Fecundity: stage 1 ($\varphi_1$) | 4 | 0 | 5 | 3 |
| Fecundity: stage 2 ($\varphi_2$) | | 4 | | |
| Development probability: juvenile ($\gamma_0$) | 1 | 1 | 1 | 1 |
| Development probability: stage 1 ($\gamma_1$) | | 1 | | |
| Survival probability: juvenile ($\sigma_0$) | 1 | 1 | 1 | 1 |
| Survival probability: stage 1 ($\sigma_1$) | 0.6 | 0.7 | 0.5 | 0.5 |
| Survival probability: stage 1 ($\sigma_2$) | | 0.9 | | |
| Density-dependence in fecundity | Yes | Yes | Yes | Yes |
| Strength of dens. dep. in fecundity ($1/b$) | 3 | 1 | 5 | 1.5 |
| **Dispersal – emigration** | | | | |
| Emigration probability | Density-dependent | Density-dependent | Density-dependent | Density-dependent |
| Stage-dependent | Yes | Yes | Yes | Yes |
| **Juvenile stage (stage 0)** | | | | |
| Maximum emigration probability ($D_0$) | 0.55 | 0.4 | 0.5 | 0.5 |
| Slope at the inflection point ($\alpha$) | 5 | 2 | 3 | 3 |
| Inflection point ($\beta$) | 0.5 | 0.5 | 0.5 | 0.5 |

| **Parameter** | **Mam_D$^{-}$P$^{-}$S$^{+}$** | **Mam_D$^{+}$P$^{--}$S$^{+}$** | **Bird_D$^{+}$P$^{-}$S$^{+}$** | **Bird_D$^{++}$P$^{--}$S$^{+}$** |
|---|---|---|---|---|
| **Dispersal – transfer** | | | | |
| Movement model | SMS | SMS | SMS | SMS |
| Perceptual range (metres) | 300 | 400 | 400 | 1000 |
| Directional persistence | 10 | 15 | 15 | 50 |
| **Habitat dependent movement costs** | | | | |
| Improved grassland, arable, water | 1000 | 1000 | 1000 | 1000 |
| Semi improved grassland | 100 | 100 | 100 | 100 |
| Coniferous woodland, FMS | 25 | 25 | 25 | 25 |
| Dwarf shrub heath | 10 | 10 | 10 | 10 |
| Broadleaved woodland | 1 | 1 | 1 | 1 |
| **Habitat dependent per-step mortality** | | | | |
| Improved grassland, arable, water | 0.08 | 0.08 | 0.05 | 0.01 |
| Semi improved grassland | 0.04 | 0.04 | 0.025 | 0.005 |
| Coniferous woodland, FMS | 0.008 | 0.008 | 0.005 | 0.0005 |
| Dwarf shrub heath | 0.004 | 0.004 | 0.001 | 0.0001 |
| Broadleaved woodland | 0 | 0 | 0 | 0 |
| **Dispersal - settlement** | | | | |
| Sex-dependent | Yes | Yes | Yes | Yes |
| Males settle if | Find a suitable patch + mating requirements | Find a suitable patch + mating requirements | Find a suitable patch + mating requirements | Find a suitable patch + mating requirements |
| Females settle if | Find a suitable patch (not the natal one) | Find a suitable patch (not the natal one) | Find a suitable patch (not the natal one) | Find a suitable patch (not the natal one) |

FMS - Fen, marsh and swamp
SMS - Stochastic movement simulator (Palmer *et al.*, 2011)

# Appendix C

## C.1 CRAFTY parameter values

*Table C.1.1: Giving-up and giving-in thresholds of each agent type.*

| **Agent type** | **Giving-up threshold** | **Giving-in threshold** |
|---|---|---|
| Forestry | 0 | 0.01 |
| High intensity crop farmer | 0 | 0.01 |
| High intensity livestock farmer | 0 | 0.01 |
| Low intensity crop farmer | 0 | 0.001 |
| Low intensity livestock farmer | 0 | 0.001 |

*Table C.1.2: Capital sensitivities and production levels of each agent type.*

| **Agent type** | **Sensitivity to productivity of:** | | | **Service production** |
|---|---|---|---|---|
| | **Crop** | **Livestock** | **Forestry** | |
| Forestry | 0 | 0 | 1 | 1 (Forestry services) |
| High intensity crop farmer | 1 | 0 | 0 | 1 (Crop) |
| High intensity livestock farmer | 0 | 1 | 0 | 1 (Livestock) |
| Low intensity crop farmer | 0.8 | 0 | 0 | 0.5 (Crop) |
| Low intensity livestock farmer | 0 | 0.5 | 0 | 0.5 (Livestock) |

## C.2 RangeShifter parameter values

*Table C.2.1: RangerShifter parameter values for hypothetical pollinator species.*

| **Parameter** | **Value** |
|---|---|
| **Population dynamics** | |
| Model type | Cell-based |
| Reproduction | Asexual / female only |
| Stage structure | No |
| Maximum fecundity | VARIED: 2; 1.5 |
| Competition coefficient ($b_c$) | 1 |
| **Habitat dependent carrying capacity ($K$)** | |
| Carrying capacity reduction factor | VARIED: 100%; 50% |
| High intensity crop farm | 0 individuals/ha (an individual represents a colony) |
| Low intensity crop farm | 1.1 individuals/ha |
| High intensity livestock farm | 0 individuals/ha |
| Low intensity livestock farm | 1.1 individuals/ha |
| Forest | 2.3 individuals/ha |
| Unmanaged land | 1.4 individuals/ha |
| **Dispersal - emigration** | |
| Emigration probability | Density-dependent |
| Max. emigration probability ($D_0$) | 0.7 |
| Slope at inflection point (α) | 10 |
| Inflection point (β) | 0.5 |
| **Dispersal - transfer** | |
| Movement model | Dispersal kernel |
| Kernel type | VARIED: negative exponential; double negative exponential |
| Mean distance I (metres) | 500 |
| Mean distance II (metres) | VARIED: 1500 if Kernel type = double negative exponential; else null. |
| Probability of kernel II | VARIED: 10% if Kernel type = double negative exponential; else null. |
| **Dispersal - settlement** | |
| If the arrival cell is unsuitable | Die |

# Bibliography

Aars, J., Ims, R.A., 1999. The effect of habitat corridors on rates of transfer and interbreeding between vole demes. Ecology 80, 1648–1655.

Akber, M.A., Shrestha, R.P., 2015. Land use change and its effect on biodiversity in Chiang Rai province of Thailand. Journal of Land Use Science 10, 108–128.

Alberti, M., Asbjornsen, H., Baker, L.A., Brozovic, N., Drinkwater, L.E., Drzyzga, S.A., Jantz, C.A., Fragoso, J., Holland, D.S., Kohler, T. (Tim) A., 2011. Research on coupled human and natural systems (CHANS): approach, challenges, and strategies. Bulletin of the Ecological Society of America 92, 218–228.

Alldredge, M.W., Pollock, K.H., Simons, T.R., Shriner, S.A., 2007a. Multiple-species analysis of point count data: a more parsimonious modelling framework. Journal of Applied Ecology 44, 281–290.

Alldredge, M.W., Simons, T.R., Pollock, K.H., 2007b. A field evaluation of distance measurement error in auditory avian point count surveys. The Journal of Wildlife Management 71, 2759–2766.

Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems & Environment 74, 19–31. doi:10.1016/S0167-8809(99)00028-6

Amundson, C.L., Royle, J.A., Handel, C.M., 2014. A hierarchical model combining distance sampling and time removal to estimate detection probability during avian point counts. The Auk 131, 476–494.

Andersen, M.C., Ewald, M., Northcott, J., 2005. Risk analysis and management decisions for weed biological control agents: Ecological theory and modeling results. Biological Control 35, 330–337. doi:10.1016/j.biocontrol.2005.05.003

Anderson, R.P., 2012. Harnessing the world's biodiversity data: promise and peril in ecological niche modeling of species distributions. Annals of the New York Academy of Sciences 1260, 66–80.

Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., J Hijmans, R., Huettmann, F., R Leathwick, J., Lehmann, A., Li, J., G Lohmann, L., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.

# Bibliography

Anderson, R.P., Peterson, A.T., Gómez-Laverde, M., 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. Oikos 98, 3–16.

Applegate, R.D., Kissell Jr, R.E., Moss, E.D., Warr, E.L., Kennedy, M.L., 2011. Problems with Avian Point Counts for Estimating Density of Northern Bobwhite-A Case Study. Journal of Fish and Wildlife Management 2, 117–121.

Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. Ecology letters 14, 484–492.

Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L., Williams, P.H., 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology 10, 1618–1626.

Araújo, M.B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography 33, 1677–1688. doi:10.1111/j.1365-2699.2006.01584.x

Araújo, M.B., Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16, 743–753.

Araújo, M.B., Thuiller, W., Pearson, R.G., 2006. Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography 33, 1712–1728. doi:10.1111/j.1365-2699.2006.01482.x

Araújo, M.B., Whittaker, R.J., Ladle, R.J., Erhard, M., 2005. Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography 14, 529–538.

Argent, R.M., 2004. An overview of model integration for environmental applications—components, frameworks and semantics. Environmental Modelling & Software 19, 219–234.

Aukema, B.H., Carroll, A.L., Zhu, J., Raffa, K.F., Sickley, T.A., Taylor, S.W., 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. Ecography 29, 427–441. doi:10.1111/j.2006.0906-7590.04445.x

Austin, M.P., Belbin, L., Meyers, J.A., Doherty, M.D., Luoto, M., 2006. Evaluation of statistical models used for predicting plant species distributions: role of artificial data and theory. Ecological Modelling 199, 197–216.

Austin, M.P., Smith, T.M., 1990. A new model for the continuum concept, in: Progress in Theoretical Vegetation Science. Springer, pp. 35–47.

Awade, M., Metzger, J.P., 2008. Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. Austral Ecology 33, 863–871. doi:10.1111/j.1442-9993.2008.01857.x

Axtell, R.L., Epstein, J.M., Dean, J.S., Gumerman, G.J., Swedlund, A.C., Harburger, J., Chakravarty, S., Hammond, R., Parker, J., Parker, M., 2002. Population growth and collapse in a multiagent model of the Kayenta Anasazi in Long House Valley. Proceedings of the National Academy of Sciences of the United States of America 99, 7275–7279.

Bächler, E., Liechti, F., 2007. On the importance of g (0) for estimating bird population densities with standard distance-sampling: implications from a telemetry study and a literature review. Ibis 149, 693–700.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M., Turlure, C., 2013. Individual dispersal, landscape connectivity and ecological networks. Biological Reviews 88, 310–326.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012a. Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution 3, 327–338.

Barbet-Massin, M., Thuiller, W., Jiguet, F., 2012b. The fate of European breeding birds under climate, land-use and dispersal scenarios. Global Change Biology 18, 881–890.

Batchelder, H.P., Edwards, C.A., Powell, T.M., 2002. Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention. Progress in Oceanography 53, 307–333.

Baum, K.A., Haynes, K.J., Dillemuth, F.P., Cronin, J.T., 2004. The matrix enhances the effectiveness of corridors and stepping stones. Ecology 85, 2671–2676.

Beatley, T., 2014. Habitat conservation planning: endangered species and urban growth. University of Texas Press.

Beck, J., Böller, M., Erhardt, A., Schwanghart, W., 2014. Spatial bias in the GBIF database and its effect on modeling species’ geographic distributions. Ecological Informatics 19, 10–15. doi:10.1016/j.ecoinf.2013.11.002

# Bibliography

Becu, N., Perez, P., Walker, A., Barreteau, O., Le Page, C., 2003. Agent based simulation of a small catchment water management in northern Thailand: description of the CATCHSCAPE model. Ecological Modelling 170, 319–331.

Bennett, D.A., Tang, W., 2006. Modelling adaptive, spatially aware, and mobile agents: Elk migration in Yellowstone. International Journal of Geographical Information Science 20, 1039–1066.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18, 182–188. doi:10.1016/S0169-5347(03)00011-9

Best, A.S., Johst, K., Münkemüller, T., Travis, J.M.J., 2007. Which species will succesfully track climate change? The influence of intraspecific competition and density dependent dispersal on range shifting dynamics. Oikos 116, 1531–1539. doi:10.1111/j.0030-1299.2007.16047.x

Bharwani, S., Bithell, M., Downing, T.E., New, M., Washington, R., Ziervogel, G., 2005. Multi-agent modelling of climate outlooks and food security on a community garden scheme in Limpopo, South Africa. Philosophical Transactions of the Royal Society B: Biological Sciences 360, 2183–2194.

Bibby, C.J., Marsden, S., Jones, M., 1998. Bird surveys. Expedition Advisory Centre.

Bithell, M., Brasington, J., 2009. Coupling agent-based models of subsistence farming with individual-based forest models and dynamic models of water distribution. Environmental Modelling & Software 24, 173–190.

Bithell, M., Brasington, J., Richards, K., 2008. Discrete-element, individual-based and agent-based models: Tools for interdisciplinary enquiry in geography? Geoforum 39, 625–642.

Bocedi, G., Palmer, S.C.F., Pe’er, G., Heikkinen, R.K., Matsinos, Y.G., Watts, K., Travis, J.M.J., 2014a. RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species’ responses to environmental changes. Methods in Ecology and Evolution 5, 388–396.

Bocedi, G., Pe’er, G., Heikkinen, R.K., Matsinos, Y., Travis, J.M.J., 2012. Projecting species’ range expansion dynamics: sources of systematic biases when scaling up patterns and processes. Methods in Ecology and Evolution 3, 1008–1018. doi:10.1111/j.2041-210X.2012.00235.x

Bocedi, G., Zurell, D., Reineking, B., Travis, J.M., 2014b. Mechanistic modelling of animal dispersal offers new insights into range expansion dynamics across fragmented landscapes. Ecography.

Bonte, D., Hovestadt, T., Poethke, H.-J., 2010. Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. Oikos 119, 560–566. doi:10.1111/j.1600-0706.2009.17943.x

Brady, M., Sahrbacher, C., Kellermann, K., Happe, K., 2012. An agent-based approach to modeling impacts of agricultural policy on land use, biodiversity and ecosystem services. Landscape ecology 27, 1363–1381.

Brewster, J.P., Simons, T.R., 2009. Testing the importance of auditory detections in avian point counts. Journal of Field Ornithology 80, 178–182.

Brittain, C.A., Vighi, M., Bommarco, R., Settele, J., Potts, S.G., 2010. Impacts of a pesticide on pollinator species richness at different spatial scales. Basic and Applied Ecology 11, 106–115. doi:10.1016/j.baae.2009.11.007

Brooker, R.W., 2006. Plant–plant interactions and environmental change. New Phytologist 171, 271–284.

Brotons, L., Thuiller, W., Araújo, M.B., Hirzel, A.H., 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27, 437–448. doi:10.1111/j.0906-7590.2004.03764.x

Brown, C., Murray-Rust, D., van Vliet, J., Alam, S.J., Verburg, P.H., Rounsevell, M.D., 2014. Experiments in Globalisation, Food Security and Land Use Decision Making.

Buchanan, G.M., Pearce-Higgins, J.W., Grant, M.C., 2006. Observer variation in estimates of Meadow Pipit Anthus pratensis and Skylark Alauda arvensis abundance on moorland: Capsule Counts least susceptible to observer effects were those within 25 m of a transect and the total number along a transect, with observer effects greater for distance sampling. Bird Study 53, 92–95.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., 2005. Distance sampling. Wiley Online Library.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to distance sampling: estimating abundance of wildlife populations. Introduction to distance sampling: estimating abundance of wildlife populations.

Buckland, S.T., Marsden, S.J., Green, R.E., 2008. Estimating bird abundance: making methods work. Bird Conservation International 18, S91–S108.

Buckland, S.T., Rexstad, E.A., Marques, T.A., Oedekoven, C.S., 2015. Designing Distance Sampling Experiments, in: Distance Sampling: Methods and Applications, Methods in Statistical Ecology. Springer International Publishing, pp. 29–34.

Cabeza, M., Moilanen, A., 2003. Site-Selection Algorithms and Habitat Loss. Conservation Biology 17, 1402–1413.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D., Cook, B.J., 2002. Positive interactions among alpine plants increase with stress. Nature 417, 844–848. doi:10.1038/nature00812

Cambui, E.C.B., Nogueira de Vasconcelos, R., Boscolo, D., Bernardo da Rocha, P.L., Miranda, J.G.V., 2015. GradientLand Software: A landscape change gradient generator. Ecological Informatics 25, 57–62. doi:10.1016/j.ecoinf.2014.12.001

Carrasco, L.R., Cook, D., Baker, R., MacLeod, A., Knight, J.D., Mumford, J.D., 2012. Towards the integration of spread and economic impacts of biological invasions in a landscape of learning and imitating agents. Ecological Economics 76, 95–103. doi:10.1016/j.ecolecon.2012.02.009

Carroll, C., Dunk, J.R., Moilanen, A., 2010. Optimizing resiliency of reserve networks to climate change: multispecies conservation planning in the Pacific Northwest, USA. Global Change Biology 16, 891–904.

Cassey, P., McArdle, B.H., 1999. An assessment of distance sampling techniques for estimating animal abundance. Environmetrics 10, 261–278.

Cerasale, D.J., Guglielmo, C.G., 2010. An integrative assessment of the effects of tamarisk on stopover ecology of a long-distance migrant along the San Pedro River, Arizona. The Auk 127, 636–646.

Chamberlain, D.E., Wilson, A.M., Browne, S.J., Vickery, J.A., 1999. Effects of habitat type and management on the abundance of skylarks in the breeding season. Journal of Applied Ecology 36, 856–870. doi:10.1046/j.1365-2664.1999.00453.x

Chávez-León, G., Velázquez, A., 2004. Abundance and distribution of the Long-tailed Wood-Partridge (Dendrortyx macroura) in a temperate coniferous forest. Journal of Field Ornithology 75, 345–352.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026.

Chipperfield, J.D., Dytham, C., Hovestadt, T., 2011. An updated algorithm for the generation of neutral landscapes by spectral synthesis. PloS one 6, e17040.

Cimprich, D.A., 2009. Effect of count duration on abundance estimates of Black-capped Vireos. Journal of Field Ornithology 80, 94–100.

Conlisk, E., Syphard, A.D., Franklin, J., Flint, L., Flint, A., Regan, H., 2013. Uncertainty in assessing the impacts of global change with coupled dynamic species distribution and population models. Global change biology 19, 858–869.

Corbalán, V., Tabeni, S., Ojeda, R.A., 2006. Assessment of habitat quality for four small mammal species of the Monte Desert, Argentina. Mammalian Biology - Zeitschrift für Säugetierkunde 71, 227–237. doi:10.1016/j.mambio.2006.02.002

Cosentino, B., Schooley, R., Bestelmeyer, B., Kelly, J., Coffman, J., 2014. Constraints and time lags for recovery of a keystone species (Dipodomys spectabilis) after landscape restoration. Landscape Ecol 29, 665–675. doi:10.1007/s10980-014-0003-5

Costanza, R., d'Arge, R., de Groot, R., Faber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., Van den Belt, M., 1997. The value of the world's ecosystem services and natural capital. Nature 387, 253–260.

Couclelis, H., 2002. Modeling frameworks, paradigms, and approaches. Geographic information systems and environmental modelling, Prentice Hall, London.

Creegan, H.P., Osborne, P.E., 2005. Gap-crossing decisions of woodland songbirds in Scotland: an experimental approach. Journal of Applied Ecology 42, 678–687.

Crooks, K.R., Sanjayan, M., 2006. Connectivity Conservation. Cambridge University Press, Cambridge.

Dallimer, M., King, T., 2008. Habitat preferences of the forest birds on the island of Principe, Gulf of Guinea. African Journal of Ecology 46, 258–266.

Dallimer, M., King, T., Atkinson, R.J., 2009. Pervasive threats within a protected area: conserving the endemic birds of São Tomé, West Africa. Animal Conservation 12, 209–219.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B., Wood, S., 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391, 783–786.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Beyond Predictions: Biodiversity Conservation in a Changing Climate. Science 332, 53–58.

Debinski, D.M., Holt, R.D., 2000. A Survey and Overview of Habitat Fragmentation Experiments. Conservation Biology 14, 342–355. doi:10.1046/j.1523-1739.2000.98081.x

Delgado, A., Moreira, F., 2000. Bird assemblages of an Iberian cereal steppe. Agriculture, ecosystems & environment 78, 65–76.

Diefenbach, D.R., Brauning, D.W., Mattice, J.A., Thompson III, F.R., 2003. Variability in grassland bird counts related to observer differences and species detection rates. The Auk 120, 1168–1179.

Doerr, V.A.J., Barrett, T., Doerr, E.D., 2011. Connectivity, dispersal behaviour and conservation under climate change: a response to Hodgson et al. Journal of Applied Ecology 48, 143–147. doi:10.1111/j.1365-2664.2010.01899.x

Dormann, C.F., 2007. Promising the future? Global change projections of species distributions. Basic and Applied Ecology 8, 387–397.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. doi:10.1111/j.1600-0587.2012.07348.x

Drielsma, M., Ferrier, S., 2009. Rapid evaluation of metapopulation persistence in highly variegated landscapes. Biological conservation 142, 529–540.

Dullinger, S., Dirnböck, T., Grabherr, G., 2004. Modelling climate change-driven treeline shifts: relative effects of temperature increase, dispersal and invasibility. Journal of ecology 92, 241–252.

Ekblom, R., 2010. Evaluation of the analysis of distance sampling data: a simulation study. Ornis Svecica 20, 43–53.

Elith, J., Leathwick, J., 2007. Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. Diversity and distributions 13, 265–275.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40, 677.

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77, 802–813. doi:10.1111/j.1365-2656.2008.01390.x

Ellis, J.D., Evans, J.D., Pettis, J., 2010. Colony losses, managed colony population decline, and Colony Collapse Disorder in the United States. Journal of Apicultural Research 49, 134–136. doi:10.3896/IBRA.1.49.1.30

Elphick, C.S., 2008. How you count counts: the importance of methods research in applied ecology. Journal of Applied Ecology 45, 1313–1320.

Engler, R., Guisan, A., 2009. MigClim: predicting plant distribution and dispersal in a changing climate. Diversity and Distributions 15, 590–601.

ESRI, 2013. ArcGIS Desktop and Spatial Analyst Extension: Release 10.2. Environmental Systems Research Institute, Redlands, CA.

Etherington, T.R., Holland, E.P., O'Sullivan, D., 2015. NLMpy: a python software package for the creation of neutral landscape models within a general numerical framework. Methods in Ecology and Evolution 6, 164–168. doi:10.1111/2041-210X.12308

Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C.M., Merz, M., O'Malley, M.A., Orzack, S.H., Weisberg, M., 2013. Do simple models lead to generality in ecology? Trends in ecology & evolution 28, 578–583.

Evans, T.P., Kelley, H., 2008. Assessing the transition from deforestation to forest regrowth with an agent-based model of land cover change for south-central Indiana (USA). Geoforum 39, 819–832.

Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81, 117–142.

Eycott, A.E., Marzano, M., Watts, K., 2011. Filling evidence gaps with expert opinion: The use of Delphi analysis in least-cost modelling of functional connectivity. Landscape and Urban Planning 103, 400–409.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual review of ecology, evolution, and systematics 487–515.

Farmer, J.D., Foley, D., 2009. The economy needs agent-based modelling. Nature 460, 685–686.

Farnsworth, G.L., Pollock, K.H., Nichols, J.D., Simons, T.R., Hines, J.E., Sauer, J.R., Brawn, J., 2002. A removal model for estimating detection probabilities from point-count surveys. The Auk 119, 414–425.

Fewster, R.M., Buckland, S.T., Siriwardena, G.M., Baillie, S.R., Wilson, J.D., 2000. Analysis of population trends for farmland birds using generalized additive models. Ecology 81, 1970–1984.

Filatova, T., Polhill, G., 2012. Shocks in coupled socio-ecological systems: what are they and how can we model them? iEMSs.

Filatova, T., Verburg, P.H., Parker, D.C., Stannard, C.A., 2013. Spatial agent-based models for socio-ecological systems: challenges and prospects. Environmental Modelling & Software 45, 1–7.

Fischer, J., Lindenmayer, D.B., 2002. The conservation value of paddock trees for birds in a variegated landscape in southern New South Wales. 2. Paddock trees as stepping stones. Biodiversity & Conservation 11, 833–849.

Forestry Commission, 2014a. Forestry Statistics 2014 [WWW Document]. URL http://www.forestry.gov.uk/website/forstats2014.nsf/TopContents?Open&ctx=5BFAF7169C6D2E038025735D00349319 (accessed 12.2.14).

Forestry Commission, 2014b. Forestry Statistics 2014 - New planting and restocking [WWW Document]. URL http://www.forestry.gov.uk/website/forstats2014.nsf/0/4F09640F0B6F8C27802573760033DE64?open&RestrictToCategory=1 (accessed 12.2.14).

Franklin, J., 2010. Moving beyond static species distribution models in support of conservation biogeography. Diversity and Distributions 16, 321–330.

Fraterrigo, J.M., Pearson, S.M., Turner, M.G., 2009. Joint effects of habitat configuration and temporal stochasticity on population dynamics. Landscape ecology 24, 863–877.

Freeman, S.N., Noble, D.G., Newson, S.E., Baillie, S.R., 2007. Modelling population changes using data from different surveys: the Common Birds Census and the Breeding Bird Survey: Capsule A method for producing and validating long-term population indices using data from the Common Birds Census and its successor, the Breeding Bird Survey, is described. Bird Study 54, 61–72.

Fuller, R.J., Langslow, D.R., 1984. Estimating numbers of birds by point counts: how long should counts last? Bird Study 31, 195–202.

Gardner, R.H., Milne, B.T., Turnei, M.G., O’Neill, R.V., 1987. Neutral models for the analysis of broad-scale landscape pattern. Landscape ecology 1, 19–28.

Gaube, V., Kaiser, C., Wildenberg, M., Adensam, H., Fleissner, P., Kobler, J., Lutz, J., Schaumberger, A., Schaumberger, J., Smetschka, B., 2009. Combining agent-based and stock-flow modelling approaches in a participative analysis of the integrated land system in Reichraming, Austria. Landscape Ecology 24, 1149–1165.

Gaucherel, C., 2008. Neutral models for polygonal landscapes with linear networks. Ecological Modelling 219, 39–48. doi:10.1016/j.ecolmodel.2008.07.028

Giannini, T.C., Chapman, D.S., Saraiva, A.M., Alves-dos-Santos, I., Biesmeijer, J.C., 2013. Improving species distribution models using biotic interactions: a case study of parasites, pollinators and plants. Ecography 36, 649–656.

Gilbert-Norton, L., Wilson, R., Stevens, J.R., Beard, K.H., 2010. A Meta-Analytic Review of Corridor Effectiveness. Conservation Biology 24, 660–668.

Gimona, A., Poggio, L., Polhill, J.G., Castellazzi, M., 2015. Habitat networks and food security: promoting species range shift under climate change depends on life history and the dynamics of land use choices. Landscape Ecology 1–19.

Godsoe, W., Harmon, L.J., 2012. How do species interactions affect species distribution models? Ecography 35, 811–820.

Gottschalk, T., Huettmann, F., 2011. Comparison of distance sampling and territory mapping methods for birds in four different habitats. J Ornithol 152, 421–429. doi:10.1007/s10336-010-0601-1

Graham, C.H., Elith, J., Hijmans, R.J., Guisan, A., Townsend Peterson, A., Loiselle, B.A., The Nceas Predicting Species Distributions Working Group, 2008. The influence of spatial errors in species occurrence data used in distribution models. Journal of Applied Ecology 45, 239–247. doi:10.1111/j.1365-2664.2007.01408.x

Graham, C.H., Ferrier, S., Huettman, F., Moritz, C., Peterson, A.T., 2004. New developments in museum-based informatics and applications in biodiversity analysis. Trends in Ecology & Evolution 19, 497–503. doi:10.1016/j.tree.2004.07.006

Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84, 2809–2815.

Granholm, S.L., 1983. Bias in density estimates due to movement of birds. Condor 243–248.

Grimm, V., Railsback, S.F., 2013. Individual-based modeling and ecology. Princeton university press.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T., DeAngelis, D.L., 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310, 987–991.

Guisan, A., Edwards Jr, T.C., Hastie, T., 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecological Modelling 157, 89–100. doi:10.1016/S0304-3800(02)00204-1

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecology letters 8, 993–1009.

Gutiérrez, D., Fernández, P., Seymour, A.S., Jordano, D., 2005. Habitat distribution models: are mutualist distributions good predictors of their associates? Ecological applications 15, 3–18.

Gu, W., Swihart, R.K., 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. Biological Conservation 116, 195–203. doi:10.1016/S0006-3207(03)00190-3

Haddad, N.M., Baum, K.A., 1999. An experimental test of corridor effects on butterfly densities. Ecological Applications 9, 623–633.

Haddad, N.M., Bowne, D.R., Cunningham, A., Danielson, B.J., Levey, D.J., Sargent, S., Spira, T., 2003. Corridor use by diverse taxa. Ecology 84, 609–615.

Haddad, N.M., Tewksbury, J.J., 2005. Low-quality habitat corridors as movement conduits for two butterfly species. Ecological Applications 15, 250–257.

Hansen, L.J., Hoffman, J.R., 2011. The Role of Connectivity, in: Climate Savvy. Springer, pp. 136–146.

Hanski, I., 1994. A practical model of metapopulation dynamics. Journal of animal ecology 151–162.

Haselmayer, J., Quinn, J.S., 2000. A comparison of point counts and sound recording as bird survey methods in Amazonian southeast Peru. The Condor 102, 887–893.

Hastie, T.J., Tibshirani, R.J., 1990. Generalized additive models. CRC Press.

Haughland, D.L., Larsen, K.W., 2004. Ecology of North American red squirrels across contrasting habitats: relating natal dispersal to habitat. Journal of Mammalogy 85, 225–236.

Heikkinen, R.K., Luoto, M., Virkkala, R., Pearson, R.G., Körber, J.-H., 2007. Biotic interactions improve prediction of boreal bird distributions at macro-scales. Global Ecology and Biogeography 16, 754–763.

Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological conservation 142, 14–32.

Henle, K., Sarre, S., Wiegand, K., 2004. The role of density regulation in extinction processes and population viability analysis. Biodiversity & Conservation 13, 9–52.

Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12, 450–455.

Hiebeler, D., 2000. Populations on fragmented landscapes with spatially structured heterogeneities: landscape generation and local dispersal. Ecology 81, 1629–1641.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. International journal of climatology 25, 1965–1978.

Hirzel, A., Guisan, A., 2002. Which is the optimal sampling strategy for habitat suitability modelling. Ecological modelling 157, 331–341.

Hirzel, A.H., Helfer, V., Metral, F., 2001. Assessing habitat-suitability models with a virtual species. Ecological modelling 145, 111–121.

Hodgson, J.A., Moilanen, A., Wintle, B.A., Thomas, C.D., 2011a. Habitat area, quality and connectivity: striking the balance for efficient conservation. Journal of Applied Ecology 48, 148–152.

Hodgson, J.A., Thomas, C.D., Cinderby, S., Cambridge, H., Evans, P., Hill, J.K., 2011b. Habitat re-creation strategies for promoting adaptation of species to climate change. Conservation Letters 4, 289–297. doi:10.1111/j.1755-263X.2011.00177.x

Hodgson, J.A., Thomas, C.D., Dytham, C., Travis, J.M., Cornell, S.J., 2012. The speed of range shifts in fragmented landscapes. PloS one 7, e47141.

Hodgson, J.A., Thomas, C.D., Wintle, B.A., Moilanen, A., 2009. Climate change, connectivity and conservation decision making: back to basics. Journal of Applied Ecology 46, 964–969.

Hof, A.R., Jansson, R., Nilsson, C., 2012. How biotic interactions may alter future predictions of species distributions: future threats to the persistence of the arctic fox in Fennoscandia. Diversity and Distributions 18, 554–562.

Hof, C., Araújo, M.B., Jetz, W., Rahbek, C., 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature 480, 516–519.

Hoffmann, A.A., Sgro, C.M., 2011. Climate change and evolutionary adaptation. Nature 470, 479–485. doi:10.1038/nature09670

Hortal, J., Jiménez-Valverde, A., Gómez, J.F., Lobo, J.M., Baselga, A., 2008. Historical bias in biodiversity inventories affects the observed environmental niche of the species. Oikos 117, 847–858.

Hostetler, J.A., Chandler, R.B., 2014. Improved state-space models for inference about spatial and temporal variation in abundance from count data. Ecology 96, 1713–1723. doi:10.1890/14-1487.1

Humphrey, J.W., Watts, K., Fuentes-Montemayor, E., Macgregor, N.A., Peace, A.J., Park, K.J., 2014. What can studies of woodland fragmentation and creation tell us about ecological networks? A literature review and synthesis. Landscape Ecology 1–30.

Huntley, B., Collingham, Y.C., Willis, S.G., Green, R.E., 2008. Potential impacts of climatic change on European breeding birds. PloS one 3, e1439.

Hutchinson, G.E., 1978. An introduction to population ecology.

Huxel, G.R., Hastings, A., 1999. Habitat loss, fragmentation, and restoration. Restoration Ecology 7, 309–315.

Hu, X., Sun, Y., 2007. Agent-based modeling and simulation of wildland fire suppression, in: Simulation Conference, 2007 Winter. IEEE, pp. 1275–1283.

Hu, Y., Cai, X., DuPont, B., 2015. Design of a web-based application of the coupled multi-agent system model and environmental model for watershed management analysis using Hadoop. Environmental Modelling & Software 70, 149–162. doi:10.1016/j.envsoft.2015.04.011

Ibáñez, I., Clark, J.S., Dietze, M.C., Feeley, K., Hersh, M., LaDeau, S., McBride, A., Welch, N.E., Wolosin, M.S., 2006. Predicting biodiversity change: outside the climate envelope, beyond the species-area curve. Ecology 87, 1896–1906.

Imron, M.A., Herzog, S., Berger, U., 2011. The influence of agroforestry and other land-use types on the persistence of a Sumatran Tiger (Panthera tigris sumatrae) population: An individual-based model approach. Environmental management 48, 276–288.

Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M.P., 2011. Lessons learned while integrating habitat, dispersal, disturbance, and life-history traits into species habitat models under climate change. Ecosystems 14, 1005–1020.

Janssen, M.A., Ostrom, E., 2006. Chapter 30 Governing Social-Ecological Systems, in: L. Tesfatsion and K.L. Judd (Ed.), Handbook of Computational Economics. Elsevier, pp. 1465–1509.

Jiménez-Valverde, A., Lobo, J.M., 2007. Threshold criteria for conversion of probability of species presence to either–or presence–absence. Acta oecologica 31, 361–369.

Johnston, A., Newson, S.E., Risely, K., Musgrove, A.J., Massimino, D., Baillie, S.R., Pearce-Higgins, J.W., 2014. Species traits explain variation in detectability of UK birds. Bird Study 61, 340–350. doi:10.1080/00063657.2014.941787

Joseph, L.N., Field, S.A., Wilcox, C., Possingham, H.P., 2006. Presence–absence versus abundance data for monitoring threatened species. Conservation biology 20, 1679–1687.

Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology letters 12, 334–350.

Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araújo, M.B., Rebelo, T.G., 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biology Letters 4, 560–563.

Kéry, M., Royle, J.A., 2010. Hierarchical modelling and estimation of abundance and population trends in metapopulation designs. Journal of Animal Ecology 79, 453–461. doi:10.1111/j.1365-2656.2009.01632.x

Kinezaki, N., Kawasaki, K., Shigesada, N., 2010. The effect of the spatial configuration of habitat fragmentation on invasive spread. Theoretical population biology 78, 298–308.

King, A.W., With, K.A., 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? Ecological Modelling 147, 23–39. doi:10.1016/S0304-3800(01)00400-8

Kissling, W.D., Field, R., Korntheuer, H., Heyder, U., Böhning-Gaese, K., 2010. Woody plants and the prediction of climate-change impacts on bird diversity. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365, 2035–2045. doi:10.1098/rstb.2010.0008

Klein, A.-M., Brittain, C., Hendrix, S.D., Thorp, R., Williams, N., Kremen, C., 2012. Wild pollination services to California almond rely on semi-natural habitat. Journal of Applied Ecology 49, 723–732. doi:10.1111/j.1365-2664.2012.02144.x

Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B: Biological Sciences 274, 303–313.

Lawson, D.M., Regan, H.M., Zedler, P.H., FRANKLIN, J., 2010. Cumulative effects of land use, altered fire regime and climate change on persistence of Ceanothus verrucosus, a rare, fire-dependent plant species. Global Change Biology 16, 2518–2529.

Leathwick, J.R., Austin, M.P., 2001. Competitive interactions between tree species in New Zealand’s old-growth indigenous forests. Ecology 82, 2560–2573.

Lee, D.C., Marsden, S.J., 2008. Adjusting count period strategies to improve the accuracy of forest bird abundance estimates from point transect distance sampling surveys. Ibis 150, 315–325.

Legendre, P., Dale, M.R., Fortin, M.-J., Gurevitch, J., Hohn, M., Myers, D., 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 25, 601–615.

Le Page, C., Bazile, D., Becu, N., Bommel, P., Bousquet, F., Etienne, M., Mathevet, R., Souchere, V., Trébuil, G., Weber, J., 2013. Agent-based modelling and simulation applied to environmental management, in: Simulating Social Complexity. Springer, pp. 499–540.

Le, Q.B., Park, S.J., Vlek, P.L.G., Cremers, A.B., 2008. Land-Use Dynamic Simulator (LUDAS): A multi-agent system model for simulating spatio-temporal dynamics of coupled human–landscape system. I. Structure and theoretical specification. Ecological Informatics 3, 135–153. doi:10.1016/j.ecoinf.2008.04.003

le Roux, P.C., Virtanen, R., Heikkinen, R.K., Luoto, M., 2012. Biotic interactions affect the elevational ranges of high-latitude plant species. Ecography 35, 1048–1056. doi:10.1111/j.1600-0587.2012.07534.x

Lichtenberg, E., 2002. Chapter 23 Agriculture and the environment, in: Handbook of Agricultural Economics. Elsevier, pp. 1249–1313.

Lindenmayer, D.B., Fischer, J., 2013. Habitat fragmentation and landscape change: an ecological and conservation synthesis. Island Press.

Linderman, M.A., An, L., Bearer, S., He, G., Ouyang, Z., Liu, J., 2005. Modeling the spatio-temporal dynamics and interactions of households, landscapes, and giant panda habitat. Ecological Modelling 183, 47–65.

Liu, C., White, M., Newell, G., Griffioen, P., 2013. Species distribution modelling for conservation planning in Victoria, Australia. Ecological Modelling 249, 68–74. doi:10.1016/j.ecolmodel.2012.07.003

Liu, J., Dietz, T., Carpenter, S.R., Alberti, M., Folke, C., Moran, E., Pell, A.N., Deadman, P., Kratz, T., Lubchenco, J., 2007. Complexity of coupled human and natural systems. Science 317, 1513–1516.

Liu, J., Mooney, H., Hull, V., Davis, S.J., Gaskell, J., Hertel, T., Lubchenco, J., Seto, K.C., Gleick, P., Kremen, C., 2015. Systems integration for global sustainability. Science 347, 1258832.

Li, X., He, H.S., Wang, X., Bu, R., Hu, Y., Chang, Y., 2004. Evaluating the effectiveness of neutral landscape models to represent a real landscape. Landscape and Urban Planning 69, 137–148. doi:10.1016/j.landurbplan.2003.10.037

Lloyd, H., 2008. Influence of within-patch habitat quality on high-Andean Polylepis bird abundance. Ibis 150, 735–745. doi:10.1111/j.1474-919X.2008.00843.x

Lobo, J.M., Jiménez-Valverde, A., Hortal, J., 2010. The uncertain nature of absences and their importance in species distribution modelling. Ecography 33, 103–114.

Lo, Y.-H., Blanco, J.A., Kimmins, J.P., 2010. A word of caution when planning forest management using projections of tree species range shifts. The Forestry Chronicle 86, 312–316.

Luoto, M., Virkkala, R., Heikkinen, R.K., 2007. The role of land cover in bioclimatic models depends on spatial resolution. Global Ecology and Biogeography 16, 34–42. doi:10.1111/j.1466-8238.2006.00262.x

Luus, K.A., Robinson, D.T., Deadman, P.J., 2013. Representing ecological processes in agent-based models of land use and cover change. Journal of Land Use Science 8, 175–198.

Malanson, G.P., Verdery, A.M., Walsh, S.J., Sawangdee, Y., Heumann, B.W., McDaniel, P.M., Frizzelle, B.G., Williams, N.E., Yao, X., Entwisle, B., Rindfuss, R.R., 2014. Changing crops in response to climate: Virtual Nang Rong, Thailand in an agent based simulation. Applied Geography 53, 202–212. doi:10.1016/j.apgeog.2014.06.010

Malawska, A., Topping, C.J., Nielsen, H.Ø., 2014. Why do we need to integrate farmer decision making and wildlife models for policy evaluation? Land Use Policy 38, 732–740. doi:10.1016/j.landusepol.2013.10.025

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.

Marohn, C., Schreinemachers, P., Quang, D.V., Siripalangkanont, P., Hörhold, S., Berger, T., Cadisch, G., 2012. Interpreting outputs of a landscape-scale coupled social-ecological system, in: International Congress on Environmental Modelling and Software Managing Resources of a Limited Planet, Sixth Biennial Meeting, Leipzig.

Maron, M., Hobbs, R.J., Moilanen, A., Matthews, J.W., Christie, K., Gardner, T.A., Keith, D.A., Lindenmayer, D.B., McAlpine, C.A., 2012. Faustian bargains? Restoration realities in the context of biodiversity offset policies. Biological Conservation 155, 141–148. doi:10.1016/j.biocon.2012.06.003

Marques, F.F., Buckland, S.T., Goffin, D., Dixon, C.E., Borchers, D.L., Mayle, B.A., Peace, A.J., 2001. Estimating deer abundance from line transect surveys of dung: sika deer in southern Scotland. Journal of Applied Ecology 38, 349–363.

Marques, T., 2009. Distance sampling: estimating animal density. Significance 6, 136–137.

Marques, T.A., 2004. Predicting and correcting bias caused by measurement error in line transect sampling using multiplicative error models. Biometrics 60, 757–763.

Marques, T.A., Thomas, L., Fancy, S.G., Buckland, S.T., Handel, C.M., 2007. Improving estimates of bird density using multiple-covariate distance sampling. The Auk 124, 1229–1243.

Marsden, S.J., 1999. Estimation of parrot and hornbill densities using a point count distance sampling method. Ibis 141, 327–390.

Marsden, S.J., Whiffin, M., Galetti, M., Fielding, A.H., 2005. How well will Brazil's system of Atlantic forest reserves maintain viable bird populations? Biodiversity & Conservation 14, 2835–2853.

Martínez, M.L., Pérez-Maqueo, O., Vázquez, G., Castillo-Campos, G., García-Franco, J., Mehltreter, K., Equihua, M., Landgrave, R., 2009. Effects of land use change on biodiversity and ecosystem services in tropical montane cloud forests of Mexico. Forest Ecology and Management 258, 1856–1863. doi:10.1016/j.foreco.2009.02.023

Mathevet, R., Bousquet, F., Le Page, C., Antona, M., 2003. Agent-based simulations of interactions between duck population, farming decisions and leasing of hunting rights in the Camargue (Southern France). Ecological modelling 165, 107–126.

Matthews, R., 2006. The People and Landscape Model (PALM): Towards full integration of human decision-making and biophysical simulation models. Ecological Modelling 194, 329–343.

Matthews, R.B., Gilbert, N.G., Roach, A., Polhill, J.G., Gotts, N.M., 2007. Agent-based land-use models: a review of applications. Landscape Ecology 22, 1447–1459.

Matthews, R., Selman, P., 2006. Landscape as a focus for integrating human and environmental processes. Journal of Agricultural Economics 57, 199–212.

McRae, B.H., Schumaker, N.H., McKane, R.B., Busing, R.T., Solomon, A.M., Burdick, C.A., 2008. A multi-model framework for simulating wildlife population response to land-use and climate change. Ecological Modelling 219, 77–91.

Meiyappan, P., Dalton, M., O’Neill, B.C., Jain, A.K., 2014. Spatial modeling of agricultural land use change at global scale. Ecological Modelling 291, 152–174. doi:10.1016/j.ecolmodel.2014.07.027

Metsoja, J.-A., Neuenkamp, L., Zobel, M., 2014. Seed bank and its restoration potential in Estonian flooded meadows. Applied Vegetation Science 17, 262–273. doi:10.1111/avsc.12057

Meynard, C.N., Quinn, J.F., 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. Journal of Biogeography 34, 1455–1469.

Midgley, G.F., Davies, I.D., Albert, C.H., Altwegg, R., Hannah, L., Hughes, G.O., O’Halloran, L.R., Seo, C., Thorne, J.H., Thuiller, W., 2010. BioMove–an integrated platform simulating the dynamic response of species to environmental change. Ecography 33, 612–616.

Minchin, P.R., 1987. Simulation of multidimensional community patterns: towards a comprehensive model. Vegetatio 71, 145–156.

Moilanen, A., Franco, A.M., Early, R.I., Fox, R., Wintle, B., Thomas, C.D., 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proceedings of the Royal Society B: Biological Sciences 272, 1885–1891.

Moisen, G.G., Frescino, T.S., 2002. Comparing five modelling techniques for predicting forest characteristics. Ecological Modelling 157, 209–225.

Mokany, K., Harwood, T.D., Ferrier, S., 2013. Comparing habitat configuration strategies for retaining biodiversity under climate change. Journal of Applied Ecology 50, 519–527.

Monticino, M., Acevedo, M., Callicott, B., Cogdill, T., Lindquist, C., 2007. Coupled human and natural systems: A multi-agent-based approach. Environmental Modelling & Software 22, 656–663.

Moreira, F., 1999. Relationships between vegetation structure and breeding bird densities in fallow cereal steppes in Castro Verde, Portugal. Bird Study 46, 309–318.

Moreira, F., Leitão, P.J., Morgado, R., Alcazar, R., Cardoso, A., Carrapato, C., Delgado, A., Geraldes, P., Gordinho, L., Henriques, I., 2007. Spatial distribution patterns, habitat correlates and population estimates of steppe birds in Castro Verde. Airo 17, 5–30.

Moreira, F., Leitão, P.J., Synes, N.W., Alcazar, R., Catry, I., Carrapato, C., Delgado, A., Estanque, B., Ferreira, R., Geraldes, P., Gomes, M., Guilherme, J., Henriques, I., Lecoq, M., Leitão, D., Marques, A.T., Morgado, R., Pedroso, R., Prego, I., Reino, L., Pedro, R., Tomé, R., Zina, H., Osborne, P.E., 2012. Population trends in the steppe birds of Castro Verde in the period 2006-2011: consequences of a drought event and land use changes? Airo 22, 79–89.

Morris, R.K.A., Alonso, I., Jefferson, R.G., Kirby, K.J., 2006. The creation of compensatory habitat—Can it secure sustainable development? Journal for Nature Conservation 14, 106–116.

Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R., Simpson, I., 2011. Final Report for LCM2007-the new UK land cover map. Countryside Survey Technical Report No 11/07.

Murray-Rust, D., Brown, C., van Vliet, J., Alam, S.J., Robinson, D.T., Verburg, P.H., Rounsevell, M., 2014. Combining agent functional types, capitals and services to model land use dynamics. Environmental Modelling & Software 59, 187–201. doi:10.1016/j.envsoft.2014.05.019

Nathan, R., Horvitz, N., He, Y., Kuparinen, A., Schurr, F.M., Katul, G.G., 2011. Spread of North American wind-dispersed trees in future environments. Ecology Letters 14, 211–219.

Naug, D., 2009. Nutritional stress due to habitat loss may explain recent honeybee colony collapses. Biological Conservation 142, 2369–2372. doi:10.1016/j.biocon.2009.04.007

Nicholson, E., Westphal, M.I., Frank, K., Rochester, W.A., Pressey, R.L., Lindenmayer, D.B., Possingham, H.P., 2006. A new method for conservation planning for the persistence of multiple species. Ecology Letters 9, 1049–1060.

Norvell, R.E., Howe, F.P., Parrish, J.R., Thompson III, F.R., 2003. A seven-year comparison of relative-abundance and distance-sampling methods. The Auk 120, 1013–1028.

Noss, R.F., O'Connell, M., Murphy, D.D., 1997. The science of conservation planning: habitat conservation under the Endangered Species Act. Island Press.

Oksanen, J., Minchin, P.R., 2002. Continuum theory revisited: what shape are species responses along ecological gradients? Ecological Modelling 157, 119–129.

Oliver, T.H., Smithers, R.J., Bailey, S., Walmsley, C.A., Watts, K., 2012. A decision framework for considering climate change adaptation in biodiversity conservation planning. Journal of Applied Ecology 49, 1247–1255.

Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological conservation 117, 285–297.

Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R., Edwards, A.S., 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. Journal of Applied Ecology 36, 519–533. doi:10.1046/j.1365-2664.1999.00428.x

Osborne, P.E., Leitão, P.J., 2009. Effects of species and habitat positional errors on the performance and interpretation of species distribution models. Diversity and Distributions 15, 671–681. doi:10.1111/j.1472-4642.2009.00572.x

Otto, M.C., Pollock, K.H., 1990. Size bias in line transect sampling: a field test. Biometrics 239–245.

Pagel, J., Anderson, B.J., O'Hara, R.B., Cramer, W., Fox, R., Jeltsch, F., Roy, D.B., Thomas, C.D., Schurr, F.M., 2014. Quantifying range-wide variation in population trends from local abundance surveys and widespread opportunistic occurrence records. Methods in Ecology and Evolution 5, 751–760. doi:10.1111/2041-210X.12221

Pakeman, R.J., Small, J.L., 2005. The role of the seed bank, seed rain and the timing of disturbance in gap regeneration. Journal of Vegetation Science 16, 121–130. doi:10.1111/j.1654-1103.2005.tb02345.x

Palmer, S.C.F., Coulon, A., Travis, J.M.J., 2011. Introducing a "stochastic movement simulator" for estimating habitat connectivity. Methods in Ecology and Evolution 2, 258–268.

Parker, J.D., Torchin, M.E., Hufbauer, R.A., Lemoine, N.P., Alba, C., Blumenthal, D.M., Bossdorf, O., Byers, J.E., Dunn, A.M., Heckman, R.W., Hejda, M., Jarošík, V., Kanarek, A.R., Martin, L.B., Perkins, S.E., Pyšek, P., Schierenbeck, K., Schlöder, C., van Klinken, R., Vaughn, K.J., Williams, W., Wolfe, L.M., 2013. Do invasive species perform better in their new ranges? Ecology 94, 985–994. doi:10.1890/12-1810.1

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399, 579–583.

Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O., Matthiopoulos, J., 2008. State–space models of individual animal movement. Trends in Ecology & Evolution 23, 87–94. doi:10.1016/j.tree.2007.10.009

Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global ecology and biogeography 12, 361–371.

Pearson, R.G., Dawson, T.P., Liu, C., 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. Ecography 27, 285–298.

Pearson, R.G., Thuiller, W., Araújo, M.B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T.P., Lees, D.C., 2006. Model-based uncertainty in species range prediction. Journal of Biogeography 33, 1704–1711. doi:10.1111/j.1365-2699.2006.01460.x

Peele, A.M., Marra, P.M., Sillett, T.S., Sherry, T.W., 2015. Combining survey methods to estimate abundance and transience of migratory birds among tropical nonbreeding habitats. The Auk 132, 926–937.

Pe’er, G., Henle, K., Dislich, C., Frank, K., 2011. Breaking functional connectivity into components: a novel approach using an individual-based model, and first outcomes. PloS one 6, e22355.

Pe’er, G., Kramer-Schadt, S., 2008. Incorporating the perceptual range of animals into connectivity models. Ecological Modelling 213, 73–85. doi:10.1016/j.ecolmodel.2007.11.020

Pe’er, G., Zurita, G.A., Schober, L., Bellocq, M.I., Strer, M., Müller, M., Pütz, S., 2013. Simple process-based simulators for generating spatial patterns of habitat loss and fragmentation: A review and introduction to the G-RaFFe model. PloS one 8, e64968.

Peles, J.D., Barrett, G.W., 1996. Effects of vegetative cover on the population dynamics of meadow voles. Journal of Mammalogy 857–869.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological modelling 190, 231–259.

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175.

Pimentel, D., Zuniga, R., Morrison, D., 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52, 273–288. doi:10.1016/j.ecolecon.2004.10.002

Piquer-Rodríguez, M., Kuemmerle, T., Alcaraz-Segura, D., Zurita-Milla, R., Cabello, J., 2012. Future land use effects on the connectivity of protected area networks in southeastern Spain. Journal for Nature Conservation 20, 326–336. doi:10.1016/j.jnc.2012.07.001

Polhill, J.G., Gimona, A., Gotts, N.M., 2013. Nonlinearities in biodiversity incentive schemes: a study using an integrated agent-based and metacommunity model. Environmental Modelling & Software 45, 74–91.

Pompe, S., Hanspach, J., Badeck, F., Klotz, S., Thuiller, W., Kühn, I., 2008. Climate and land use change impacts on plant distributions in Germany. Biology Letters 4, 564–567.

Ponder, W.F., Carter, G.A., Flemons, P., Chapman, R.R., 2001. Evaluation of Museum Collection Data for Use in Biodiversity Assessment. Conservation Biology 15, 648–657. doi:10.1046/j.1523-1739.2001.015003648.x

Potts, S.G., Roberts, S.P.M., Dean, R., Marris, G., Brown, M.A., Jones, R., Neumann, P., Settele, J., 2010. Declines of managed honey bees and beekeepers in Europe. Journal of Apicultural Research 49, 15–22. doi:10.3896/IBRA.1.49.1.02

Pöyry, J., Paukkunen, J., Heliölä, J., Kuussaari, M., 2009. Relative contributions of local and regional factors to species richness and total density of butterflies and moths in semi-natural grasslands. Oecologia 160, 577–587. doi:10.1007/s00442-009-1328-7

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A., Solomon, A.M., 1992. Special paper: a global biome model based on plant physiology and dominance, soil properties and climate. Journal of biogeography 117–134.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., Wilson, K.A., 2007. Conservation planning in a changing world. Trends in ecology & evolution 22, 583–592.

Prevedello, J.A., Vieira, M.V., 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation 19, 1205–1223.

Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proceedings of the Royal Society of London B: Biological Sciences 267, 1947–1952.

Ramsey, F.L., Wildman, V., Engbring, J., 1987. Covariate adjustments to effective area in variable-area wildlife surveys. Biometrics 1–11.

Rebaudo, F., Crespo-Pérez, V., Silvain, J.-F., Dangles, O., 2011. Agent-based modeling of human-induced spread of invasive species in agricultural landscapes: insights from the potato moth in Ecuador. Journal of Artificial Societies and Social Simulation 14, 7.

Reutter, B.A., Helfer, V., Hirzel, A.H., Vogel, P., 2003. Modelling habitat-suitability using museum collections: an example with three sympatric Apodemus species from the Alps. Journal of Biogeography 30, 581–590. doi:10.1046/j.1365-2699.2003.00855.x

Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. The American Naturalist 158, 87–99.

Ricotta, C., Carranza, M.L., Avena, G., Blasi, C., 2002. Are potential natural vegetation maps a meaningful alternative to neutral landscape models? Applied Vegetation Science 5, 271–275.

Rissman, A.R., Lozier, L., Comendant, T., Kareiva, P., Kiesecker, J.M., Shaw, M.R., Merenlender, A.M., 2007. Conservation Easements: Biodiversity Protection and Private Use. Conservation Biology 21, 709–718. doi:10.1111/j.1523-1739.2007.00660.x

Robertson, O.J., Radford, J.Q., 2009. Gap-crossing decisions of forest birds in a fragmented landscape. Austral Ecology 34, 435–446. doi:10.1111/j.1442-9993.2009.01945.x

Rodrigues, A.S.L., Gaston, K.J., 2002. Optimisation in reserve selection procedures—why not? Biological Conservation 107, 123–129. doi:10.1016/S0006-3207(02)00042-3

Rosenstock, S.S., Anderson, D.R., Giesen, K.M., Leukering, T., Carter, M.F., Thompson III, F., 2002. Landbird counting techniques: current practices and an alternative. The Auk 119, 46–53.

Royle, J.A., Kéry, M., 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology 88, 1813–1823. doi:10.1890/06-0669.1

Royle, J.A., Kéry, M., Gautier, R., Schmid, H., 2007. Hierarchical spatial models of abundance and occurrence from imperfect survey data. Ecological Monographs 77, 465–481. doi:10.1890/06-0912.1

Schelling, T.C., 1971. Dynamic models of segregation. Journal of mathematical sociology 1, 143–186.

Schloss, C.A., Nuñez, T.A., Lawler, J.J., 2012. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences 109, 8606–8611.

Schoon, M., Baggio, J.A., Salau, K.R., Janssen, M., 2014. Insights for managers from modeling species interactions across multiple scales in an idealized landscape. Environmental Modelling & Software 54, 53–59.

Schreinemachers, P., Berger, T., 2011. An agent-based simulation model of human–environment interactions in agricultural systems. Environmental Modelling & Software 26, 845–859. doi:10.1016/j.envsoft.2011.02.004

Schreinemachers, P., Potchanasin, C., Berger, T., Roygrong, S., 2010. Agent-based modeling for ex ante assessment of tree crop innovations: litchis in northern Thailand. Agricultural Economics 41, 519–536.

Schurr, F.M., Pagel, J., Cabral, J.S., Groeneveld, J., Bykova, O., O'Hara, R.B., Hartig, F., Kissling, W.D., Linder, H.P., Midgley, G.F., 2012. How to understand species' niches and range dynamics: a demographic research agenda for biogeography. Journal of Biogeography 39, 2146–2162.

Selmi, S., Boulinier, T., 2003. Does time of season influence bird species number determined from point-count data? A capture-recapture approach. Journal of Field Ornithology 74, 349–356.

Sillett, T.S., Chandler, R.B., Royle, J.A., Kéry, M., Morrison, S.A., 2012. Hierarchical distance-sampling models to estimate population size and habitat-specific abundance of an island endemic. Ecological Applications 22, 1997–2006. doi:10.1890/11-1400.1

Soberón, J., 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecology letters 10, 1115–1123.

Soberón, J.M., 2010. Niche and area of distribution modeling: a population ecology perspective. Ecography 33, 159–167.

Stockman, A.K., Beamer, D.A., Bond, J.E., 2006. An evaluation of a GARP model as an approach to predicting the spatial distribution of non-vagile invertebrate species. Diversity and Distributions 12, 81–89. doi:10.1111/j.1366-9516.2006.00225.x

Stockwell, D., 1999. The GARP modelling system: problems and solutions to automated spatial prediction. International journal of geographical information science 13, 143–158.

Sutherst, R.W., Maywald, G.F., Bourne, A.S., 2007. Including species interactions in risk assessments for global change. Global change biology 13, 1843–1859.

Synes, N.W., Osborne, P.E., 2011. Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. Global Ecology and Biogeography 20, 904–914.

Synes, N.W., Watts, K., Palmer, S.C.F., Bocedi, G., Bartoń, K.A., Osborne, P.E., Travis, J.M.J., 2015. A multi-species modelling approach to examine the impact of alternative climate change adaptation strategies on range shifting ability in a fragmented landscape. Ecological Informatics 30, 222–229. doi:10.1016/j.ecoinf.2015.06.004

Tang, W., Bennett, D.A., 2010. Agent-based Modeling of Animal Movement: A Review. Geography Compass 4, 682–700.

Templeton, A.R., Shaw, K., Routman, E., Davis, S.K., 1990. The Genetic Consequences of Habitat Fragmentation. Annals of the Missouri Botanical Garden 77, 13–27. doi:10.2307/2399621

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F., De Siqueira, M.F., Grainger, A., Hannah, L., 2004. Extinction risk from climate change. Nature 427, 145–148.

Thomas, J.A., Simcox, D.J., Hovestadt, T., 2011. Evidence based conservation of butterflies. Journal of Insect Conservation 15, 241–258.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Strindberg, S., Hedley, S.L., Bishop, J.R., Marques, T.A., Burnham, K.P., 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47, 5–14.

Thorne, J.H., Huber, P.R., Harrison, S., 2011. Systematic conservation planning. Serpentine: the evolution and ecology of a model system 309.

Thuiller, W., 2004. Patterns and uncertainties of species' range shifts under climate change. Global Change Biology 10, 2020–2027. doi:10.1111/j.1365-2486.2004.00859.x

Thuiller, W., Albert, C., Araújo, M.B., Berry, P.M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G.F., Paterson, J., Schurr, F.M., 2008. Predicting global change impacts on plant species' distributions: future challenges. Perspectives in Plant Ecology, Evolution and Systematics 9, 137–152.

Thuiller, W., Araujo, M.B., Lavorel, S., 2004. Do we need land-cover data to model species distributions in Europe? Journal of Biogeography 31, 353–361.

Thuiller, W., Lavorel, S., Sykes, M.T., Araújo, M.B., 2006. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. Diversity and Distributions 12, 49–60. doi:10.1111/j.1366-9516.2006.00216.x

Travis, J.M.J., 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proceedings of the Royal Society of London B: Biological Sciences 270, 467–473.

Travis, J.M.J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J.A., Kubisch, A., Penteriani, V., 2013. Dispersal and species' responses to climate change. Oikos 122, 1532–1540.

Travis, J.M.J., Mustin, K., Bartoń, K.A., Benton, T.G., Clobert, J., Delgado, M.M., Dytham, C., Hovestadt, T., Palmer, S.C.F., Van Dyck, H., 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. Methods in Ecology and Evolution 3, 628–641.

Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biological conservation 151, 53–59.

Václavík, T., Meentemeyer, R.K., 2009. Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions? Ecological Modelling 220, 3248–3258. doi:10.1016/j.ecolmodel.2009.08.013

Valin, H., Sands, R.D., van der Mensbrugghe, D., Nelson, G.C., Ahammad, H., Blanc, E., Bodirsky, B., Fujimori, S., Hasegawa, T., Havlik, P., Heyhoe, E., Kyle, P., Mason-D'Croz, D., Paltsev, S., Rolinski, S., Tabeau, A., van Meijl, H., von Lampe, M., Willenbockel, D., 2014. The future of food demand: understanding differences in global economic models. Agricultural Economics 45, 51–67. doi:10.1111/agec.12089

Vandermeer, J., Carvajal, R., 2001. Metapopulation dynamics and the quality of the matrix. The American Naturalist 158, 211–220.

Van der Putten, W.H., Macel, M., Visser, M.E., 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365, 2025–2034. doi:10.1098/rstb.2010.0037 vanEngelsdorp, D., Meixner, M.D., 2010. A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. Journal of Invertebrate Pathology 103, Supplement, S80–S95. doi:10.1016/j.jip.2009.06.011

Van Horne, B., 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 893–901.

Vaughan, I.P., Ormerod, S.J., 2005. The continuing challenges of testing species distribution models. Journal of Applied Ecology 42, 720–730.

Veldkamp, A., Verburg, P.H., 2004. Modelling land use change and environmental impact. Journal of Environmental Management 72, 1–3.

Verburg, P.H., Overmars, K.P., 2009. Combining top-down and bottom-up dynamics in land use modeling: exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. Landscape ecology 24, 1167–1181.

Villard, M.-A., Metzger, J.P., 2014. REVIEW: Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology 51, 309–318. doi:10.1111/1365-2664.12190

Visser, H., De Nijs, T., 2006. The map comparison kit. Environmental Modelling & Software 21, 346–358.

Voinov, A., Shugart, H.H., 2013. “Integronsters”, integral and integrated modeling. Environmental Modelling & Software 39, 149–158.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Wang, Q., Malanson, G.P., 2008. Neutral Landscapes: Bases for Exploration in Landscape Ecology. Geography Compass 2, 319–339. doi:10.1111/j.1749-8198.2008.00090.x

Watkins, A., Noble, J., Foster, R.J., Harmsen, B.J., Doncaster, C.P., 2015. A spatially explicit agent-based model of the interactions between jaguar populations and their habitats. Ecological Modelling 306, 268–277. doi:10.1016/j.ecolmodel.2014.10.038

Watts, K., Eycott, A.E., Handley, P., Ray, D., Humphrey, J.W., Quine, C.P., 2010. Targeting and evaluating biodiversity conservation action within fragmented landscapes: an approach based on generic focal species and least-cost networks. Landscape Ecology 25, 1305–1318.

Wieczorek, J., Guo, Q., Hijmans, R., 2004. The point-radius method for georeferencing locality descriptions and calculating associated uncertainty. International journal of geographical information science 18, 745–767.

Wiegand, T., Knauer, F., Kaczensky, P., Naves, J., 2004. Expansion of brown bears (Ursus arctos) into the eastern Alps: a spatially explicit population model. Biodiversity & Conservation 13, 79–114.

Wilcox, B.A., Murphy, D.D., 1985. Conservation strategy: the effects of fragmentation on extinction. American naturalist 879–887.

Wilcox, C., Cairns, B.J., Possingham, H.P., 2006. The role of habitat disturbance and recovery in metapopulation persistence. Ecology 87, 855–863. doi:10.1890/05-0587

Williams, N.S., Hahs, A.K., Morgan, J.W., 2008. A dispersal-constrained habitat suitability model for predicting invasion of alpine vegetation. Ecological applications 18, 347–359.

Williams, P., Hannah, L., Andelman, S., Midgley, G., Araújo, M., Hughes, G., Manne, L., Martinez-Meyer, E., Pearson, R., 2005. Planning for Climate Change: Identifying Minimum-Dispersal Corridors for the Cape Proteaceae. Conservation Biology 19, 1063–1074.

Wilson, H.B., Kendall, B.E., Possingham, H.P., 2011. Variability in population abundance and the classification of extinction risk. Conservation Biology 25, 747–757.

Wilson, R.J., Davies, Z.G., Thomas, C.D., 2009. Modelling the effect of habitat fragmentation on range expansion in a butterfly. Proceedings of the Royal Society of London B: Biological Sciences rspb. 2008.0724.

Winfree, R., 2008. Pollinator-dependent crops: an increasingly risky business. Current Biology 18, R968–R969.

Wintle, B.A., Bardos, D.C., 2006. Modeling species-habitat relationships with spatially autocorrelated observation data. Ecological Applications 16, 1945–1958.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biological Reviews 88, 15–30. doi:10.1111/j.1469-185X.2012.00235.x

With, K.A., Cadaret, S.J., Davis, C., 1999. Movement responses to patch structure in experimental fractal landscapes. Ecology 80, 1340–1353. doi:10.1890/0012-9658(1999)080[1340:MRTPSI]2.0.CO;2

Wu, X., Hu, Y., He, H.S., Bu, R., Onsted, J., Xi, F., 2009. Performance evaluation of the SLEUTH model in the Shenyang metropolitan area of northeastern China. Environmental modeling & assessment 14, 221–230.

Yamanaka, T., Tatsuki, S., Shimada, M., 2003. An individual-based model for sex-pheromone-oriented flight patterns of male moths in a local area. Ecological Modelling 161, 35–51.