IMPLICATIONS OF SPATIAL AUTOCORRELATION AND DISPERSAL
FOR THE MODELING OF SPECIES DISTRIBUTIONS

By

Volker Bahn

Dipl.-Biol. Philipps-University Marburg, 1998

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Wildlife Ecology)

The Graduate School

The University of Maine

August, 2005

Advisory Committee:

William B. Krohn, Professor of Wildlife Ecology and Leader, Maine Cooperative

Fish and Wildlife Research Unit, Co-Advisor

Raymond J. O'Connor, Professor of Wildlife Ecology, Co-Advisor

Mary K. Beard-Tisdale, Professor of Spatial Information Science and Engineering

William Halteman, Associate Professor of Mathematics

George L. Jacobson, Jr., Professor of Botany and Quaternary Science

Library Rights Statement

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at The University of Maine, I agree that the Library shall make it freely available for inspection. I further agree that permission for "fair use" copying of this thesis for scholarly purposes may be granted by the Librarian. It is understood that any copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Signature:

Date:

IMPLICATIONS OF SPATIAL AUTOCORRELATION AND DISPERSAL

FOR THE MODELING OF SPECIES DISTRIBUTIONS

By Volker Bahn

Thesis Advisors: Dr. William B. Krohn and Dr. Raymond J. O'Connor

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Doctor of Philosophy
(in Wildlife Ecology)
August, 2005

Modeling the geographical distributions of wildlife species is important for ecology and conservation biology. Spatial autocorrelation in species distributions poses a problem for distribution modeling because it invalidates the assumption of independence among sample locations. I explored the prevalence and causes of spatial autocorrelation in data from the Breeding Bird Survey, covering the conterminous United States, using Regression Trees, Conditional Autoregressive Regressions (CAR), and the partitioning of variance. I also constructed a simulation model to investigate dispersal as a process contributing to spatial autocorrelation, and attempted to verify the connection between dispersal and spatial autocorrelation in species' distributions in empirical data, using three indirect indices of dispersal.

All 108 bird species modeled showed strong spatial autocorrelation, which was significantly better modeled with CAR models than with traditional regression-based distribution models. Not all autocorrelation could be explained by spatial autocorrelation in the underlying environmental factors, suggesting another process at work, which I

hypothesized to be dispersal. In the simulation model, dispersal produced additional autocorrelation in the distribution of population abundances. The effect of dispersal on autocorrelation was modulated by the potential population growth rate, with low growth rates leading to a stronger effect. The effect of dispersal on population sizes was different between populations at the periphery and core of a range. Due to their relative isolation, peripheral populations received fewer immigrants than populations at the core, causing lower population sizes. Dispersal could therefore be an explanation for range structures independent of environmental conditions. The verification of dispersal as a partial cause of autocorrelation failed. The most plausible cause was the indirectness of the indices used to represent dispersal.

Distribution modelers should generally include space explicitly in their models, especially for species with low potential population growth rates. Dispersal has a strong potential to shape species distributions and requires more explicit consideration in distribution models and conservation plans. To reach this goal, direct research on dispersal distances and strength is urgently needed. Disruptions in natural dispersal patterns through removal of habitat isolates populations and thus may harm species beyond the effects of only direct habitat removal.

DEDICATION

This dissertation is dedicated to my wife, Deanna Newsom, my sons, Jonas and Oliver Bahn, and to Nature for its complexity and beauty.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

There has been a surge in interest in modeling the distributions of terrestrial

wildlife over the past decade (Scott et al. 1991a, Scott et al. 1991b, Scott et al. 1993,

Scott and Csuti 1997, Guisan and Zimmermann 2000, Austin 2002b, DeStefano and

Haight 2002, Scott et al. 2002). In addition to its traditional ecological use - explaining

and predicting species' occurrences, abundances and distributions - distribution modeling

has become one of the most important tools for modern conservation research and

management (Scott and Csuti 1997). Its recent popularity is due in part to the urgency of

conservation problems, but can also be attributed to increases in computing power and in

the availability of remotely sensed data and Geographic Information Systems (Austin

2002b). Accordingly, new insights into species' distributions and new distribution

modeling techniques have been developed, particularly at large extents and coarse

resolutions.

The strongest impediment to distribution modeling is the failure to include the

ecology of species in the modeling process (Austin 2002b). Despite the increasing

attention given to spatial dependencies (autocorrelation) in species occurrences (Cohen

and Levin 1991, Hanski et al. 1993, Legendre 1993, Augustin et al. 1996, Leathwick

1998, Koenig 1999, Trenham et al. 2001, Austin 2002b, Austin 2002a, Engen et al. 2002,

Lichstein et al. 2002, Keitt 2003, Peakall et al. 2003), a thorough ecological

understanding of such spatial patterns is still in its infancy. However, without a thorough

understanding of the sources and mechanisms that create such dependencies, adequate

methods for addressing them remain elusive (Austin 2002b). The goal of this dissertation

is to investigate the ecological processes causing spatial autocorrelation in species

distributions and to thus further the development of distribution modeling techniques that better incorporate the ecology of the organisms.

This dissertation consists of four chapters. In the first chapter, autocorrelation in species distributions is investigated and described using empirical data. The function of this initial exploratory research is to provide insights into patterns for inductive formation of hypotheses on the underlying causes of the patterns. In this chapter I also add improvements to established modeling techniques and develop some new techniques for spatially explicit distribution modeling. In the second chapter, I used a simulation model to quantitatively elaborate the hypothesis from Chapter 1 that spatial autocorrelation is partly caused by dispersal. The simulation model also served to investigate how sensitive the effect of dispersal was to different parameter values and scenarios. Chapter 2 provides a more detailed understanding of how dispersal could cause spatial autocorrelation patterns and which parameters it should be sensitive to. The third chapter is an extension to the second chapter, in which I ask whether the effects of dispersal on distribution patterns are constant over the range of a species or whether the relative isolation of populations at the range edge could lead to differences between population densities at the core and at the margin of a distribution. Finally, Chapter 4 attempts to confirm the connection between dispersal and autocorrelation using empirical data.

While the principles underlying this research apply broadly to distribution modeling, the focus was terrestrial vertebrates; more specifically, my empirical work was based on data from the Breeding Bird Survey (BBS)(Sauer et al. 1997). BBS data are well suited for my research because they cover many species over a large extent of space and time. The environmental conditions used as independent variables came from Very

High Resolution Radar (AVHRR) imagery classified into landcovers by Loveland et al. (1991) with additions by O'Connor (1996). Working at such a coarse scale made my research relevant to the GAP Analysis Program (Scott et al. 1991a, Scott et al. 1991b, Scott et al. 1993, Scott and Csuti 1997), which predicts vertebrate distributions by state.

The coarse scale used had several implications for distribution modeling. On the one hand, the determining factors used in such models are more likely to be indirect gradients (sensu Austin 2002b, Austin 2002a), because it is impossible to measure direct gradients such as food and shelter availability at such a scale. Using indirect gradients rather than direct factors translates into a move away from a mechanistic or causal model towards a descriptive model (Austin 2002b). On the other hand, models at coarser scales have higher predictability than those at finer scales because they integrate over much fine-scale variability. Such fine-scale variability often derives from fine-scale processes that are beyond our current ecological comprehension or beyond the level of complexity that we can effectively incorporate into distribution models. In addition, working at a coarse scale shifts the balance between external and internal factors, influencing patterns towards internal factors of the model (Goodwin and Fahrig 1998). Finally, by working at a large extent, I increased the probability of including the full range of conditions under which a species occurs. This is because the range of conditions sampled in a study (assuming an appropriate resolution and sample density) is correlated with the extent and determines the accuracy, precision, and generality of the resulting predictions (Austin 2002a).

To present a coherent picture of the approach used in this dissertation, and to accurately communicate the hypotheses and results, it is important that the reader have a

clear understanding of my use of language to describe concepts. Therefore, the following

subsections introduce and define the core concepts, issues, and expressions used in this

dissertation, in agreement with the definitions of terms in Scott *et al.* (1996) and

Morrison & Hall (2002).

Scale

Several authors have lamented the imprecise use of the concept of scale in

ecology (e.g., Goodchild and Proctor 1997, Huston 2002). Two separate concepts,

resolution and extent, are encompassed in the term scale. I use the term resolution for the

amount of detail per area captured, and the term extent for the total area covered.

Typically, research over a large extent has low resolution and research of high resolution

covers only a small extent, but this need not be the case. Therefore, I use the more precise

terms extent and resolution where appropriate. However, when both a large extent and a

low resolution are described, I still use the expression "coarse scale" and conversely "fine

scale" for a small extent and high resolution. I do not use the terms "small scale" or

"large scale," though, because they have opposite meanings in geography and ecology.

Distribution

The distribution of a species refers to the locations of its individuals. The concept

of distribution is dependent on the spatial and temporal scale of its observation and

description. At the finest resolution and smallest extent, the distribution of a species is a

snapshot of the location of every individual at a single point in time. At the coarsest scale

in space and time the distribution can be depicted as a range map that encompasses all

occurrences of the species over a long period. Clearly, spatial and temporal resolution

and extent matter when species' distributions are described and careful attention must be paid to match the scales of questions and research (Goodwin and Fahrig 1998, Huston 2002).

Distribution modeling

Distribution modeling is an important research and planning tool in ecology (Guisan and Zimmermann 2000) and conservation biology (Scott and Csuti 1997, Austin 2002b). I define a distribution model as any model that tries to explain or predict species occurrences or abundances. To date, distribution modelers have mainly used habitat associations to model species occurrences (Scott et al. 2002). To be at a place, an organism must either have been born there or have moved there, and equivalently, to leave a place it must either die or move away. Traditional distribution models, based on habitat associations, capture only the fecundity and survival part of these processes. They do not capture the spatial aspects of dispersal, as expressed in distances and resistances among patches and influences from neighboring populations. Thus, traditional habitat models do not account for patterns in distributions caused by population dynamics that are based on dispersal, such as source-sink populations and metapopulations (Pulliam 1988, Pulliam and Danielson 1991, Dias 1996, Pulliam 1996, Hanski 1998, Haydon and Pianka 1999, Hanski 2001, Johst et al. 2002). Consequently, a traditional distribution model will assign two patches of habitat with very similar physical characteristics the same probability of occupation, even if one patch is in close vicinity to many patches of excellent habitat and the other patch is very isolated.

Spatial autocorrelation

On average, the closer together two locations are, the more similar are their measures of species abundances or occurrences - a phenomenon called spatial autocorrelation (Bjørnstad et al. 1999, Selmi and Boulinier 2001, Trenham et al. 2001, Keitt et al. 2002, Schiegg 2003). Autocorrelation in abiotic and biotic resources has been observed for a long time, resulting in Tobler formulating the first law of geography as: " . . . everything is related to everything else, but near things are more related than distant things." (Tobler 1970: 236) The distribution of a species depending on these resources is also spatially autocorrelated (Legendre 1993, Lichstein et al. 2002). However, other sources of autocorrelation in species distributions may exist, a topic investigated in this dissertation.

When modeling species distributions, spatial autocorrelation has positive and negative consequences. Most authors see only the negative side. For example, spatial autocorrelation leads to dependence among samples decaying with distance, which is problematic for traditional distribution models, such as correlation and regression models, which work under the assumption of independence in the residual errors. Autocorrelated data violate this assumption and lead to inflated estimates in degrees of freedom, which lead to underestimations of variance and overestimation of significance of effects (Student 1914, Legendre and Fortin 1989, Legendre 1993, Dale and Fortin 2002). However, spatially explicit models exist that incorporate spatial autocorrelation at low cost to model complexity. These models include partialling out the spatial component in variation (Borcard et al. 1992, Meot et al. 1998), Legendre's extension of this with truncated neighborhood matrices (Legendre and Legendre 1998, Borcard and Legendre

6

2002), kriging (e.g., Legendre and Fortin 1989, van Horssen et al. 2002), autoregressive models (e.g., Augustin et al. 1996, e.g., Keitt et al. 2002, Lichstein et al. 2002), modified correlograms (Koenig and Knops 1998), and Classification and Regressions Tree (CART) models with spatial dependence (Miller and Franklin 2002). The benefit of including autocorrelation in a model is not only that assumptions are better met, but also that the values of neighbors are incorporated, which ultimately improves the predictive power of the model (Costanza and Ruth 2001). In addition, spatial models may improve variable selection (Ellner and Seifu 2002, Keitt et al. 2002). Non-spatial models cannot account for autocorrelation and thus may incorrectly select variables purely because they have a similar autocorrelation as the dependent variable, not because they are good predictors in an ecological sense (Lennon 2000, Ellner and Seifu 2002, Keitt et al. 2002).

Dispersal

I use dispersal in the sense of Lidicker (1975), which includes every movement that constitutes "leaving the home area" and excludes short-term exploratory and "round-trip" migratory movements. Dispersal can be categorized into natal and adult dispersal, with dispersal in most birds falling into the first category (Paradis et al. 1998, Gaston and Blackburn 2003). My research is concerned with the combined effect of natal and adult dispersal on coarse-scale geographical distributions of wildlife species.

Among species and even within species, dispersal distances, strategies, and motivations differ widely (Stenseth and Lidicker 1992a). These differences are not the focus of this thesis. In my investigation the cumulative effect of dispersal within a species is of primary interest.

CHAPTER 1

IMPORTANCE OF SPATIAL AUTOCORRELATION IN MODELING BIRD DISTRIBUTIONS AT A CONTINENTAL SCALE

1.1 Abstract

Spatial autocorrelation in species' distributions has been recognized as causing biases in statistics and violating the statistical assumptions of traditional distribution modeling techniques such as correlation or regression models that do not account for spatial effects. However, it remains unclear whether biases occur at all spatial resolutions and extents, and under which conditions spatially explicit modeling techniques are superior. The need to model in a spatially explicit way has been contested at large extents, where spatial autocorrelation due to animal movement is less likely than at small extents. In one case it was shown that the inclusion of all important environmental variables at a large extent alleviated all spatial autocorrelation in the distribution of the species that is due to environmental autocorrelation. I tested the performance of spatially explicit regression models in comparison to traditional non-spatial models of the distributions of 108 bird species from the Breeding Bird Survey throughout the conterminous USA. As judged by Akaike's Information Criterion, the spatially-explicit conditional autoregressive regression models strongly outperformed traditionally-used linear regression models. In addition, partialling out the purely spatial component underlying the species' distributions showed that an average of 17% of the explained variation could be attributed to purely spatial effects independent of the spatial autocorrelation induced by the underlying environmental variables. Therefore, spatially

explicit models are expected to yield better predictions especially for mobile species such as birds even in coarse-grained models with a large extent.

1.2 Introduction

Documenting and understanding the distributions of organisms in space and time are central to the fields of biogeography, ecology, and conservation biology. Ecology has been defined as the study of the distribution and abundance of organisms (Andrewartha and Birch 1954, Krebs 1972, Andrewartha and Birch 1984). In conservation biology, knowledge of the actual or potential distribution of a species is indispensable for threatened and endangered species management and protected area planning (Scott and Csuti 1997). However, at most times the actual locations of individual organisms are unknown. The discipline of distribution modeling strives to fill this void by making probabilistic statements about the geographic distribution of species (Scott et al. 2002).

Distribution models that do not include spatial location explicitly assume that species' locations are independent in space and time. Such an assumption could be violated if a) the conditions defining the niche were autocorrelated; or b) species' locations were connected through dispersal or other behaviors that lead to spatial patterning such as aggregation or regular spacing. Lichstein et al. (2002) termed the former cause of spatial dependence exogenous and the latter endogenous.

Concerning endogenous sources of spatial patterning, species generally exhibit some dispersal, be it as seeds, juveniles or adults. Such dispersal events connect populations in space and time and have the potential to create dependence at varying spatial and temporal scales (Keitt et al. 2002, Lichstein et al. 2002). Traditional habitat models do not account for population dynamics based on dispersal, such as source-sink

populations and metapopulations (Pulliam 1988, Pulliam and Danielson 1991, Dias 1996, Pulliam 1996, Hanski 1998, Haydon and Pianka 1999, Hanski 2001, Johst et al. 2002). Consequently, a traditional model will assign the same probability of occupancy to two habitat patches A and B, with similar physical characteristics, even if patch A is surrounded by excellent habitat and patch B is completely isolated from other suitable habitat. An expected consequence of dispersal among habitat patches is that the average similarity among population densities in patches decays with distance - a phenomenon called spatial autocorrelation (Bjørnstad et al. 1999, Selmi and Boulinier 2001, Trenham et al. 2001, Keitt et al. 2002, Schiegg 2003).

In addition, environmental conditions underlying a species' niche are dependent in space and time, which exogenously causes spatio-temporal dependence or autocorrelation in species' distributions (Legendre 1993). Autocorrelation in abiotic and biotic resources has been observed for a long time, resulting in Tobler formulating the first law of geography as: " . . . everything is related to everything else, but near things are more related than distant things." (Tobler 1970: 236) In following these resources, species' distributions are also spatially autocorrelated (Legendre 1993, Lichstein et al. 2002).

If only exogenous autocorrelation was present in a species' distribution, the inclusion of all environmental determinants would suffice to create a valid model because they would implicitly carry all necessary spatial information (Diniz-Filho et al. 2003). In other words, if all autocorrelation in the distribution of a species is caused by autocorrelation in the distribution of the important resources and conditions, inclusion of these conditions and resources as variables will lead to a complete model and not miss

spatial information and relationships. If, however, endogenous autocorrelation is present -

for example, due to dispersal, conspecific attraction or other behaviors leading to spatial

patterning - the inclusion of all relevant environmental and resource determinants will not

eliminate autocorrelation from residuals of the model and will lead to biases in variance

and coefficient estimates, as well as model selection (Lennon 2000, Keitt et al. 2002).

The question remains, however, whether endogenous and exogenous

autocorrelation in species distributions are of practical consequence to distribution

modeling. This question is dependent on the temporal and spatial scale of the

investigation and different authors have come to different conclusions. Typically,

researchers working at small to medium extents and fine resolution found the explicit

inclusion of spatial information beneficial or even crucial to their distribution models

(Augustin et al. 1996, Selmi and Boulinier 2001, Keitt et al. 2002, Lichstein et al. 2002).

At larger extents (in the order of hundreds of kilometers) Diniz-Filho et al. (2003) found

the inclusion of environmental variables to be sufficient to eliminate autocorrelation in

the residuals of a model for species richness of birds. Similarly, Koenig (1998) found

little evidence for spatio-temporal autocorrelation in the distribution of Californian

landbirds.

The study presented here differs from the above studies because it a) covers a

large extent (the conterminous United States); but b) concerns the distributions of single

species (in contrast to Diniz-Filho et al. 2003 who modeled species richness); and c)

deals with spatial autocorrelation only (in contrast to Koenig 1998 who investigated

spatio-temporal autocorrelation).

At small extents, the connection among populations creating spatial autocorrelation in population sizes seems to be well established (Augustin et al. 1996, Thomson et al. 1996, Lichstein et al. 2002, Peakall et al. 2003). In contrast, at large extents, most of the ecological mechanisms suggested for pattern formation at small extents are not applicable (e.g., conspecific attraction, colonialism, short distance dispersal). The most plausible mechanism that could produce spatial autocorrelation above and beyond the autocorrelation in the underlying resources is long distance dispersal.

The success of Diniz-Filho et al. (2003) in capturing spatial autocorrelation in a non-spatial model may well be attributable to their dependent variable, species richness. In contrast to single species distributions, species richness is a compound measure, which is likely to experience smoothing from the overlaying of many individual distributions. Spatial processes such as dispersal that could lead to autocorrelation in individual species' distributions are averaged across many species when concerning species richness. Because they vary from species to species in strength and extent, their pooled effect therefore may well have no discernable effect on species richness. Consequently, autocorrelation in species richness patterns is more likely to have been caused by autocorrelation in the underlying environmental factors, explaining the absence of autocorrelation in the residuals of a non-spatial model.

Spatio-temporal autocorrelation, or synchrony, requires enough exchange between populations to synchronize their population dynamics, which is a more stringent requirement than enough exchange to influence each other's population size averaged over time. While Koenig (1998) found that long distance dispersal was not strong enough

to induce synchrony in birds over large extents, it may be strong enough to induce spatial autocorrelation in distributions averaged and thus smoothed over time.

In this paper, I investigated whether spatial effects are relevant to bird distribution modeling at a coarse, national scale. Rather than using hypothesis tests to detect presence or absence of autocorrelation in model residuals at an arbitrary level, I relied on model selection through Akaike's Information Criterion (AIC) to compare the relative efficiency of distribution models that include space explicitly with those that do not. In addition, I determined the amount of variation in bird distributions that can be attributed to purely spatial effects and not to environment or environment-space interactions, following and improving upon Borcard et al.'s (1992) method for partitioning sources of variation.

1.3 Methods

I compared traditional distribution models, based on environmental and climate variables only, to spatially explicit models that also included spatial position and neighborhood relationships.

I used data from the Breeding Bird Survey (BBS) for the conterminous USA from 1981 to 1990. See Robbins et al. (1986), Sauer et al. (1994), and O'Connor et al. (1996) for detailed methods and discussion of the BBS. Bird data for individual species were summarized as presence/absence over complete routes each year and then expressed as incidences over the ten years for each route. Using incidence instead of abundance has the advantage of being less sensitive to detection probabilities while being more closely related to abundance than are presence/absence data (Wright 1991, Hanski 1992).

I transformed incidence values with an arcsine transformation (Freeman and Tukey 1950, Zar 1996: 283) to move toward normal distributions. Only the 1189 routes

with the highest quality standard and at least 7 years of data were included in the analysis.

The starting points of routes were mapped to Environmental Monitoring and Assessment Program (EMAP) hexagons (White et al. 1992), which are 620 km^2 in size and approximately 27 km apart from center to center.

I selected 108 species of breeding birds for the analysis (Appendix). Criteria for the selection were good coverage over the conterminous USA (> 150 occupied routes) and sensitivity to coarse-scale predictors covered in my dataset ($R^2 > 0.5$ in initial regression tree models). Reasons for exclusion were extreme range shapes, such as long and narrow ranges along the border of the study area, or the extremely patchy distributions. Such distributions prevent meaningful spatial modeling.

I used bird ranges from Naturserve (Ridgely 2003) to determine the study area and thus the routes to be included in the models for each of the selected species. This step was necessary because including the whole study area and all 1,189 routes for all species would have meant that the many routes with zero incidences in each species would have dominated the models. Such models would have mostly modeled presence absence over the study area and not patterns of abundances within the study area. In addition, heavily skewed, zero-inflated distributions of incidence values would have led to violations in the assumptions of regression analyses and problems with the trend surfaces in the spatial models. However, because the Naturserve ranges were conservative and often excluded occupied BBS routes, I buffered all ranges by 150 km, a distance that proved to include almost all occupied BBS routes.

My independent variables stemmed from research by O'Connor et al. (1996). They comprised 159 land cover variables from Loveland et al. (1991) derived from remotely sensed Advanced Very High Resolution Radar (AVHRR) with an additional land cover type "urban." Additional variables were various measures of spatial configuration of habitat patches in hexagons (e.g., fractal dimension), climatic variables including seasonal temperatures and rainfall, and elevations from a digital elevation model. For more details on the land cover variables see O'Connor et al. (1996, 1999).

In total, there were 207 independent variables, 160 variables summarizing land cover information, 12 climate variables (January and July temperatures, precipitation, and derived variables such as seasonality), 4 variables from digital elevation models, and 31 other variables characterizing the land cover in terms of spatial configuration and fragmentation indices. Many of the land covers had a localized distribution (i.e., they did not occur at most locations) and the average number of effectively available variables at a single location was thus much smaller than 207.

The first step in the modeling process was the generation of regression tree (RT) models, which I used as a robust method for variable selection (Breiman 1984, Walker and Cocks 1991, De'ath and Fabricius 2000, Austin 2002b). These models were also used to eliminate species whose environmental determinants were not well captured at a coarse scale. RT models were built with the library RPART (Therneau and Atkinson 1997), and were pruned to final size using the 1 standard error rule after 25-fold cross-validation (Breiman 1984).

Next the selected variables were included as 3rd degree polynomials in regular linear regression models to allow for curvilinearity, which is modeled implicitly by the

RT models. To eliminate redundant variables and/or their polynomials, I used backwards step-wise model selection by Akaike's Information Criterion (AIC). Polynomial terms of lower order were kept in the model with retained higher terms of the same variable even if they had not been selected by AIC.

I built three types of regular linear regression models. The first type contained only environmental variables (ENV), the second type contained only the geographic coordinates of the hexagons (up to 3rd degree polynomial form) as a trend surface (TREND), and the third combined the first two sets of variables in one model (ENV.TREND). The last type was the model I used for the secondary variable selection by AIC as described above, while the former were hierarchical subsets of the latter.

Finally, I used conditional autoregressive regressions (CAR) for spatially explicit modeling (Cressie 1993, Lichstein et al. 2002). CAR models include information on the residuals of neighboring locations and are solved iteratively (see equation 1). Thus they capture fine-scale spatial autocorrelation, which is missed by the trend surface models. I determined the neighborhood by calculating eight models with neighborhood sizes between 50 and 400 km in 50 km steps, and selecting the neighborhood size leading to the model with the highest maximum likelihood estimate for each species. The influence of neighbors was inversely distance weighted with a spherical model (Kaluzny et al. 1996). I created CAR models with variable selections identical to the TREND model (CAR.TREND - only coordinates included) and ENV.TREND model (CAR - coordinates and environmental variables included). CAR models follow the equation:

$$\mathbf{Y} = \mathbf{X}\beta + \rho\mathbf{C}(\mathbf{Y} - \mathbf{X}\beta) + \varepsilon \qquad \text{(equation 1)}$$

Where **Y** is the vector of dependent variables; **X** is a matrix of independent variables; **C** is a symmetric neighborhood matrix; β and ρ are coefficients; and ε is a matrix of errors with the covariance matrix $\sigma^2(\mathbf{I} - \rho\mathbf{C})^{-1}$, where **I** is the identity matrix.

The log-likelihood of all regression models was calculated in S-PLUS through a likelihood ratio test, in which model components can be set to zero. The non-spatial models had the coefficient ρ (rho) in front of the neighborhood element set to zero. Akaike's Information Criterion (Akaike 1981) was calculated from these log-likelihoods and from the number of parameters included in the models (including the intercept and the spatial coefficient ρ where appropriate). The proportion of variance explained by the model (R^2) was calculated from log-likelihoods according to the formula given by Nagelkerke (1991).

I partialled out the variation that could be ascribed to the environment, space and environment/space interaction according to the method described in Borcard et al. (1992) and Legendre and Legendre (1998). My method deviated from theirs in so far as my spatial component was not restricted to the coarse-scale effects captured by a trend surface, but also included the fine-scale effects captured by the neighborhood matrix in the CAR models.

All statistical analyses were done in S-PLUS 6.2 (Insightful 2003) with the additional module SPATIAL (Kaluzny et al. 1996) and the add-on libraries RPART and MASS (Venables and Ripley 2002)(use of this product does not imply endorsement). Hypothesis tests were reported to be significant if the probability of a type I error was below 0.05, unless noted otherwise. The number given with ± after statistics is the standard error (SE), unless noted otherwise.

1.4 Results

Table 1 shows a comparison among regression trees (RTs), regular linear regression models, and spatial regression models. The sample size of included routes differed among species depending on how many routes fell within a species' range. The average sample size was 717 ± 28.7 routes per species (range: 161-1189).

Table 1. Comparison among regression tree (RT), regular linear regression models and spatial regression models. The values shown are averages of 108 individual models $\pm$ standard errors.

Model	R^2	Variables	Parameters*	AIC**
Regression Tree	0.56 ± 0.013	4.9 ± 0.30	12.3 ± 0.74	n/a
Regular regression model				
ENV	0.50 ± 0.014	4.6 ± 0.29	14.3 ± 0.68	158.8 ± 9.91
Regular regression models with trend surface				
TREND	0.40 ± 0.017	1.9 ± 0.03	7.1 ± 0.11	261.8 ± 14.09
ENV.TREND	0.56 ± 0.013	6.5 ± 0.29	19.4 ± 0.70	69 ± 5.09
Spatial regression models				
CAR	0.60 ± 0.012	6.5 ± 0.29	20.4 ± 0.70	0 ± 0
CAR.TREND	0.49 ± 0.015	1.9 ± 0.03	8.1 ± 0.11	139.4 ± 8.27

* The number of parameters is the number of splits for RTs and the number of coefficients including the intercept for linear regression models.
** Akaike's Information Criterion (AIC) scaled to the lowest value, which always was the CAR model. AIC cannot be calculated for RTs because they are not a likelihood based method.

The environmental variables passed on from the RT models were mostly retained during the AIC stepwise selection in the regression models. While 86 models retained all variables selected by the RT models, only 17 dropped 1, 4 dropped 2, and 1 dropped 3 variables. In addition, the median number of splits in the RT models (11, IQR: 7 - 15) was only slightly different from the median number of parameters (13, IQR: 8 - 18) in the environmental models (ENV), which was surprising given the very different structure and complexity selection method of the models. However, the average R^2 (%) of the RT models was 6.5 ± 0.7 higher than the average R^2 of the ENV models (49.8 ± 1.4). The

average R^2 of the RT models (56.3 ± 1.3) was almost identical to the R^2 of the ENV.TREND models (56.2 ± 1.3), which contained a trend surface based on geographic coordinates in addition to the environmental variables. Note, however, that the variable selection was optimized by the RTs but not by the linear regression models, which had only the pre-selected variables to choose from.

The full spatial regression models (CAR) were a considerable improvement over the traditional regression models, including those with environmental predictors only (ENV). The CAR models had an on average 10.2 ± 0.4 higher R^2, which is a 25.5 ± 0.02% improvement over the ENV models. However, the CAR models contained more parameters than the ENV models (median: 6, IQR: 6 - 7). The more meaningful statistic for comparing the goodness of fit between the two kinds of models is Akaike's Information Criterion (AIC), which penalizes for the number of parameters fitted in the model. The AIC values of the spatially explicit CAR models were, on average, 158.8 ± 9.912 points lower than those of the ENV models. According to the rule of thumb suggested by Burnham and Anderson (2002: 70), when comparing models, a difference in AIC of 2 or less lends substantial support to the competing model, a difference of 4-7 considerably less support and a difference >10 essentially lends no support to the inferior model.

The fully spatial CAR models also improved upon the regression models that contained a trend surface but not a neighborhood matrix (ENV.TREND). The R^2 of CAR models was on average 3.8 ± 0.3 higher than that of the ENV.TREND models, and the CAR models' AIC was on average 69.02 ± 5.09 points lower than that of the ENV.TREND models.

At the large extent of the study, using a niche based approach with environmental variables only (ENV) did not have more explanatory power than using pure spatial interpolation (CAR.TREND). Ecologically this means that the spatial position in the range and the incidences at neighboring locations are as important to the incidence value of a population as the local environmental conditions. The difference between ENV models and CAR.TREND models in R^2 was only 0.6 ± 0.9. The CAR.TREND models did not contain any environmental predictors and thus were pure spatial interpolations with fewer variables (the geographical coordinates) and parameters than the ENV models. The lower number of parameters led to a considerably lower average AIC value for the CAR.TREND models (AIC ENV - AIC CAR.TREND: 19.42 ± 11.05).

The average maximum neighborhood distance selected as giving the best model out of the 8 tested distances was 195.8 ± 7.2 km for the full CAR models and 244.4 ± 8.9 km for the CAR.TREND models, which did not contain environmental variables. The increase in distance from CAR to CAR.TREND models could be explained by the spatial information carried implicitly in the environmental variables, which accounted for a part of the spatial autocorrelation in the CAR models but not the CAR.TREND models.

Table 2 shows the results of applying Borcard et al.'s (1992) partitioning sources of variation to the data. This technique yielded estimates of the proportions of variance associated with a non-spatial effect of the environmental variables (Environment), with a purely spatial patterning in the dependent variable (Space), and with the interaction between environment and space (Interaction) due to spatial patterning in the environmental variables. In contrast to Borcard et al.'s (1992) original technique, which

20

used trend surfaces only, my results were based on a fully spatial CAR model, which captured both coarse- and fine-scale spatial patterns.

The purely environmental partition and the purely spatial partition were of similar size (Table 2: Environment and Space), 18 and 17% of the total variance explained, respectively. Approximately 65% of the explained variation in species' distributions, the largest part, however, was attributable to the spatial configuration of the environment or, as expressed here, the environment/space interaction (Table 2: Interaction).

Table 2. Partitioning of sources of variation in bird distributions according to Borcard et al.'s (1992) method. The four parts describe respectively the variation attributed to a purely local environmental effect, the spatial patterning in the dependent variable, the interaction between environment and space found in the spatial patterning of environmental variables, and the unexplained variation or error in the model. In addition to Borcard et al.'s (1992) original method, also shown is a partitioning based on fully spatial models (CAR), which captured fine-scale neighborhood effects in addition to the coarse-scale spatial effects captured in the original model's trend surfaces.

Approach	Environment	Space	Interaction	Error
Borcard et al.	0.160 ± 0.009	0.064 ± 0.004	0.337 ± 0.017	0.438 ± 0.013
Full spatial	0.109 ± 0.006	0.102 ± 0.004	0.389 ± 0.016	0.400 ± 0.012
Difference	0.052 ± 0.003	-0.038 ± 0.003	-0.052 ± 0.003	0.038 ± 0.003
P-value*	< 0.0001	< 0.0001	< 0.0001	< 0.0001

* Paired Student's t-test with 107 degrees of freedom.

Using a CAR model to determine spatial effects resulted in clear shifts in the three partitions from Borcard et al.'s original method, which uses trend surfaces only (Table 2). The partitions containing spatial elements increased (Space and Interaction) at the cost of the size of the environmental part (Environment) and the unexplained part (Error).

1.5 Discussion

When modeling species' distributions, incorporating spatial autocorrelation has positive and negative consequences. Most authors focus on the negative consequences (Student 1914, Legendre and Fortin 1989, Legendre 1993, Dale and Fortin 2002, Keitt et

al. 2002). Spatial autocorrelation leads to a dependence among samples that decays with distance. Traditional statistical models employed in distribution modeling, such as correlations and regressions, work under the assumption of independence in the residuals. Autocorrelated data violate this assumption and lead to inflated estimates in degrees of freedom, which lead to underestimates of variance and overestimation of the significance of effects (Student 1914, Legendre and Fortin 1989, Legendre 1993, Dale and Fortin 2002, Keitt et al. 2002).

However, spatially explicit models exist that can incorporate spatial autocorrelation with a low cost in terms of increased complexity. These models include truncated neighborhood matrices (Borcard and Legendre 2002), kriging (e.g., Legendre and Fortin 1989, van Horssen et al. 2002), autoregressive models (e.g., Augustin et al. 1996, Keitt et al. 2002, Lichstein et al. 2002), modified correlograms (Koenig and Knops 1998), and CART models with spatial dependence (Miller and Franklin 2002). The benefit of including autocorrelation in a model is not only that the statistical assumptions are better met, but also that the predictive power of a model is improved by incorporating additional information or predictors, such as the values at neighboring locations (Costanza and Ruth 2001). In many geostatistical applications, such as kriging, neighborhood information is the only predictor in the model, which equates to an elaborate form of spatial interpolation. In my study, models based exclusively on spatial trend and neighborhood information even outperformed the traditional models that included only environmental variables.

Spatial models may also improve variable selection (Ellner and Seifu 2002, Keitt et al. 2002). Non-spatial models cannot account for autocorrelation and thus may

incorrectly select variables purely because they have a similar autocorrelation as the dependent variable and not because they are good predictors (Lennon 2000, Ellner and Seifu 2002, Keitt et al. 2002).

While autocorrelation at fine scales has been well documented (Legendre 1993, Thomson et al. 1996, Lichstein et al. 2002), research at a coarse scale (hundreds to thousands of km) is still rare. I was able to demonstrate that spatial autocorrelation in bird distributions at such a coarse scale is important, and that spatial models are much better at handling spatially dependent data than are traditional habitat-based regression models.

In contrast to the research on bird species richness by Diniz-Filho et al. (2003), I found strong spatial effects in individual bird species' distributions that did not disappear with the inclusion of environmental variables. The difference in results may be explained by the difference in dependent variables. As a compound measurement, species richness may smooth over spatial autocorrelation in individual species' distributions caused by dispersal, leaving only environmental autocorrelation. Similarly, my finding of spatial autocorrelation effects differs from Koenig's (1998) findings from research on California birds. He only found spatio-temporal autocorrelation, or synchrony, in 1 out of 88 investigated species. However, finding synchrony in species distributions is much more demanding than finding spatial autocorrelation only. Tests of synchrony use individual observations of populations in space and time, and must accommodate variance in time as well as in space. In contrast, my focus on spatial autocorrelation in data averaged over 10 years to minimize the effects of temporal variability gave more limited but more robust results.

The power of advanced spatial modeling techniques was further demonstrated using the invaluable method of partialling out sources of variance, pioneered by Borcard et al. (1992). They used trend surface models to capture spatial patterns, which included third degree or less polynomial geographic coordinates as variables in a regression model. However, with a sensible highest polynomial inclusion of the coordinates in the third degree, trend surfaces can capture only long-wave spatial patterns and cannot account for short-range autocorrelation (Meot et al. 1998). Incorporating relatively fine-scale neighborhood effects (here at the scale of tens to hundreds of km) on top of the coarse trend surface approaches resulted in a shift in the distribution of variance across the three partitions. While the purely environmental, niche-based factors experienced a relative loss in explanatory power, the purely spatial and spatial/environmental interaction partitions gained in importance. This underscores the importance of neighborhood effects in bird distributions. Borcard and Legendre (2002) found similar shifts in partitions with an improved spatial approach to their own method. However, their method is more complicated than mine and was demonstrated only for one dimension (along a transect) in their paper.

On average, purely environmental effects and purely spatial effects each accounted for about 18% of the explained variation. In contrast, on average 65% of the explained variation in the distributions was explained by space/environment interactions. The pure environmental effect has to be understood as the immediate influence of the environmental conditions on survival and reproduction of the organism, ignoring any types of immigration and emigration, temporal movements, and influences of proximate habitats. The purely spatial component of species' distributions would then have to be

interpreted as resulting from behaviors leading to dispersal (as defined below) independent of environmental conditions. I use dispersal here in the sense of Lidicker (1975) including every movement that constitutes leaving the home area for breeding, but not short-term exploratory and "round-trip" migratory movements. This inclusive definition of dispersal includes a wide range of behaviors such as breeding aggregations, natal dispersal, adult dispersal, common-wealth breeding systems, and predator avoidance.

Interpreting the meaning of the space/environment interaction partition is difficult. This partition does not directly depend on a model but represents the difference in variances explained by the unrelated ENV and CAR.TREND models (Meot et al. 1998). The most reasonable ecological interpretation of this interaction would be the spatial configuration of required habitat elements and matrix. At the coarse scales researched in my study, the environment/space interaction could also include an isolation effect: an otherwise perfectly suitable patch may be unoccupied because of extreme isolation from other habitat. In any case, the large size of this partition drives home the point that a non-spatial view of the niche is not sufficient for understanding a species' distribution.

The selection of variables through RT models was a viable alternative to step-wise selection methods in regression models (Austin 2002b). Without RTs, variable selection including interactions and non-linear effects would have likely led to spurious results because of the high number of independent variables available compared to the number of data points (James and McCulloch 1990). Even if the large number of variables had caused the RTs to select a few spurious variables, the likelihood that they

would have been retained in the regression models would have been small because the functional relationship between dependent and independent variables is very different between the two techniques. A pre-selection among independent variables based on ecological knowledge would have been highly desirable and should be best practices for individual species (Austin 2002b). Here, however, the goal was to build numerous models with comparable and reproducible methods for statistical comparison, and manual selection was less important. This automated modeling methodology also explains the relatively low average R^2 of 60% among the models.

The variable selection had an additional caveat. Keitt et al. (2002) and Lennon (2000) found that spatial models selected different independent variables than non-spatial models, because non-spatial models tend to recover the missing spatial information by including environmental variables that happen to have a similar spatial structure. While I found that a visual comparison of spatially plotted residuals showed less spatial clustering in RT models than in regular regression models, they are not spatially explicit models and thus might be subject to the variable selection bias documented by Keitt et al. (2002).

The demonstrated superiority of spatial models has implications for conservation biology and ecology studies. Traditional distribution modeling techniques underestimate the spatial coherence of populations and thus may lead to more fragmented protected area designs that overvalue core habitats and undervalue mediocre neighboring habitats or matrix. Spatial models paint a more realistic picture of the importance of neighboring habitats and populations.

Future work is needed to identify the causal mechanisms behind autocorrelation in species' distributions over large extents. Autocorrelation over large distances is most

likely caused by some form of movement or dispersal of the organisms, be it as seeds, juveniles, or adults. The hypothesis that coarse-scale autocorrelation is caused by long distance dispersal links autocorrelation to other ecological theories based on dispersal such as source-sink populations and metapopulations (Pulliam 1988, Pulliam and Danielson 1991, Dias 1996, Pulliam 1996, Hanski 1998, Haydon and Pianka 1999, Hanski 2001, Johst et al. 2002), occupancy-abundance relationships (Gaston et al. 2000, Holt et al. 2002), range structure theory (Kirkpatrick and Barton 1997), the unified neutral theory of biodiversity and biogeography (Hubbell 2001), and synchronicity among populations (Koenig 1998). The high utility of spatial models for the investigation of the link between dispersal and autocorrelation patterns in species' distributions is, in my opinion, their most interesting contribution to ecological theory.

CHAPTER 2

THE EFFECTS OF DISPERSAL ON ANIMAL DISTRIBUTIONS: A

SIMULATION MODEL

2.1 Abstract

Compared to population growth regulated by local conditions, dispersal has been underappreciated as a central process shaping the spatial distribution of populations. The present paper asks: 1) which conditions increase the importance of global recruits (dispersers) relative to local recruits in determining population sizes? and 2) how does dispersal influence the spatial distribution patterns of abundances among connected populations? I approached these questions with a simple, deterministic simulation model set on a landscape lattice with cells of varying habitat quality expressed as carrying capacities. Each cell contained a population with the basic dynamics of density-regulated growth, and was connected to other populations by immigration and emigration that decayed in intensity with distance. The degree to which dispersal influenced the distribution of population sizes depended most strongly on the absolute amount of dispersal, and then on the potential population growth rate. In a species with a potential population growth rate considerably larger than one, the population dynamics were dominated by local recruitment, while a rate close to one led to a strong influence of dispersal. Dispersal decaying in intensity with distance left close neighbors more alike in population size than distant populations, leading to an increase in spatial autocorrelation. The additional autocorrelation in the distribution pattern caused by dispersal cannot be modeled implicitly through environmental conditions but requires spatially-explicit

distribution models. Because species with low potential growth rates are more dependent on dispersal, conservation management of these species requires attention to factors curtailing dispersal, such as fragmentation and dispersal barriers.

2.2 Introduction

Local population dynamics are determined by birth, death, immigration, and emigration. A crucial, yet unanswered question is: what is the relative importance of local recruitment (birth and death) versus global recruitment (immigration and emigration, or dispersal) to population size locally and distribution patterns globally? The significance of this question stems from its direct relation to a central goal of ecology. Andrewartha and Birch (1954, 1984), and Krebs (1972) defined ecology as the study of the distribution and abundance of organisms. Most attempts at explaining the distribution and abundance of organisms have focused on the environmental conditions that define the fundamental niche and the biotic interactions that define the realized niche (Guisan and Zimmermann 2000). In terms of population dynamics, such approaches focus solely on the birth and death components of local population dynamics. The immigration and emigration, or dispersal part of the dynamics equation has received much less attention (Clobert et al. 2001, Bullock et al. 2002), which might be explained by the difficulty of quantifying dispersal in the field (Stenseth and Lidicker 1992b).

Dispersal connects populations across space and time, influencing persistence, size and dynamics of local populations. In a niche model, the predicted local abundance of an organism depends exclusively on the local conditions. In a spatially explicit model that includes dispersal, the predicted local abundance depends on the local conditions and the population sizes and conditions of neighboring sites because these neighboring sites

29

supply immigrants and receive emigrants from the local population. This chapter determines the conditions under which neglecting dispersal in distribution models results in misleading conclusions.

The effect of dispersal on the distribution of organisms is at the core of some important ecological theories and related research, namely metapopulation ecology (Hanski 1999), island biogeography (MacArthur and Wilson 1967), and spatial synchrony or spatio-temporal autocorrelation research (Bjørnstad et al. 1999, Hudson and Cattadori 1999, Koenig 1999, Kendall et al. 2000, Ripa 2000, Engen et al. 2002, Koenig 2002). However, the present study differs fundamentally from these fields of research by focusing on a single species, using abundance rather than presence/absence, using a spatially explicit approach, and analyzing the long-term effects of dispersal on distribution, rather than the resulting dynamic synchrony among populations.

Using abundance instead of presence/absence for determining the influence of dispersal on distribution patterns has decisive advantages. Balmer (2002) found that the use of presence/absence data rather than abundances can be misleading in ecological pattern analyses: while the absence or presence of a typically rare species does not strongly ecologically differentiate a site, the presence or absence of a typically abundant species weighs more heavily. When analyzing the effects of dispersal on a species' distribution, using presence/absence only may capture the dynamics in weak populations, which die out and are recolonized frequently, but completely miss effects in strong populations that do not die out during simulation runs but change in abundance due to dispersal. Also, McGill and Collins (2003) explained several of the most prominent macroecological patterns (the positive correlation between range size and abundance, the

30

species-area relationship, the decay of species assembly similarity with distance, and the species abundance distribution) by overlaying ranges that were randomly distributed in space and followed a "peak and tail" abundance pattern with few locations of high abundance and many of low abundance. Their work illustrated the superiority of abundance over presence/absence data in researching macroecological patterns.

The model presented here uniquely combines a landscape with a continuous distribution of habitat qualities and the simulation of abundance of populations distributed across this landscape to answer two specific questions. First, which population characteristics increase the importance of global recruits (dispersers) relative to local recruits in determining population sizes? Second, how does dispersal influence the spatial distribution patterns of abundances among connected populations?

2.3 Methods

I used a simulation model to investigate the effects of dispersal on population dynamics and abundances in connected populations. The simulation model consisted of 900 cells in a regular 30 by 30 grid, each containing a population (Figure 1a). The 900 populations experienced deterministic density-dependent growth, immigration and emigration in discrete time steps. Each population was operating with identical base rates in growth and emigration, and differed only in carrying capacity (K). The change in population size per time step was modeled with a logistic growth equation (Begon and Mortimer 1986) expanded by immigration and emigration:

$$\Delta N = N_t * (R / (1 + (R - 1) * N_t / K) - 1) + I - E;$$

where N_t = population size at time t, R = potential population growth rate (birth minus death rate not adjusted for density dependent effects), K = carrying capacity (maximum

number of individuals supported at the location before the growth rate falls to 1), $I =$
immigration (number of individuals entering the population), and $E =$ emigration
(number of individuals leaving the population).

The potential net growth rate R is the multiplier by which the population would
grow in each time step if no density dependent effects were present. R combines birth and
death rates in one value (Begon and Mortimer 1986). The realized net growth rate is R
divided by $(1 + (R - 1) * N_t / K)$, a term that approaches R when the population size N_t
approaches the carrying capacity K. Thus, the realized growth rate equals one when K is
reached. The values of R covered in the simulation encompass the range of maximum
possible R-values (1.32 - 5.23) for passeriform and piciform birds in Saether and Bakke
(2000). These maxima were derived from fecundity values assuming absence of adult or
juvenile mortality and onset of reproduction within the first time step after birth.

The carrying capacity (K) symbolized habitat quality analogous to how patch size
symbolizes habitat quality and environmental conditions in metapopulation models
(Hanski 2001). The concept of carrying capacity used here did not impose a hard ceiling
on the population size but only adjusted the realized growth rate to 1 when K was reached
and below one when the population size was larger than K. Consequently, it was possible
that a population persisted at a size larger than K, fed by higher immigration than
emigration. I chose to model K as a continuous variable because the reduction of the
landscape into a binary view of habitat and matrix may hamper the understanding of
demographic processes (Wiegand et al. 1999). K-values were selected at random for
every cell from a normal distribution with a mean of 0 and a standard deviation of 1.
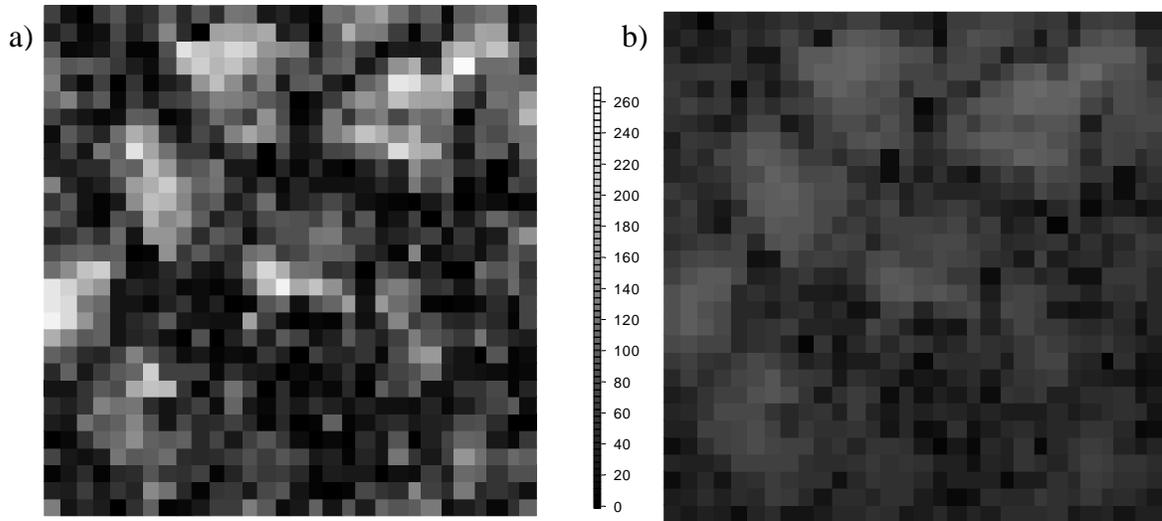
Figure 1. Distribution of population sizes before (a) and after (b) dispersal in a 30 x 30 matrix. Before dispersal, population size equals the carrying capacity (K) of the patch. K is positively autocorrelated in space up to a range of 8 cells. The population growth rate R was 1.05 and the dispersal rate in b) was 10% of the population per time step.

To introduce autocorrelation into the landscape, as is typically found in the environment (Legendre and Fortin 1989), I used the function rfsim in S-PLUS (Kaluzny et al. 1996:117-119), which calculates a covariance matrix based on a spherical function of distance with a range of eight cells. Then the random vector of K-values was multiplied with the Cholesky decomposition of this matrix. The resulting distribution of K-values over the 30 x 30 matrix was spatially positively autocorrelated up to a distance of 8 with similarities among neighbors decaying with distance according to a spherical function. Finally, I took the absolute values of the generated K-values, resulting in a distribution with many low carrying capacities and few large ones and multiplied it by 100 for realistic population sizes (which has no influence on the analytical results). A distribution of abundances with most locations having small populations and few locations having large populations is to be expected in many organisms (Brown et al. 1995, McGill and Collins 2003).

Emigration (E) was set as a fixed proportion of the population in each time step. The emigrants from each population were distributed to the other cells in proportion to their distance to the power of -2, leading to a dispersal function that declined rapidly with distance. The number of immigrants for a given population in a time step was the sum of all emigrants coming from other populations. Note that the approach to modeling dispersal in this model is deterministic and allows fractions of individuals. While dispersing individuals in a stochastic way would be more realistic, it would average out to the same result, given enough runs. Thus it would not add any qualitative insights to my model and fell victim to Occam's razor.

Dispersal comes at a cost, which is determined by the integral of the distance traveled multiplied by the local resistance encountered. In the model presented here, distance signifies total costs, including resistance, implicitly. Thus, a distance in the model signifies the total difficulty for an individual to move between two points, where a long geographic distance with low resistance could be equivalent to a short geographic distance with high resistance. Note that costs only influenced the distribution of dispersal distances among emigrants. No mortality was associated with dispersal. While this simplification is unrealistic, systematic dispersal mortality would be equivalent to a lower dispersal rate combined with a higher local mortality, which are parameter variations covered in my approach. Therefore, my experiments indirectly covered death associated with dispersal.

Other complications not considered in this model were directional bias in dispersal towards good habitat (e.g., Schooley and Wiens 2003), differential mortality associated with movement through different quality habitats (e.g., Amarasekare 1998,

34

Heino and Hanski 2001), and different dispersal strategies (e.g., density-dependent dispersal; Johst and Brandl 1997, Amarasekare 1998, Travis et al. 1999). These complications have the potential to influence the presented results but are beyond the scope of this investigation.

An important challenge was how to describe and quantify the effect of dispersal on distribution patterns in a coherent, simple, and yet powerful way. I used two different currencies to describe the observed phenomena. One is based on the change in patterns brought about by dispersal. In the absence of dispersal, the carrying capacities (K-values) explain the population sizes resulting from the simulation 100% because the simulation model is deterministic. Therefore, the change in pattern brought about by dispersal can be directly quantified as a disruption in this perfect relationship between K-values and population size. I quantified this disruption in the relationship as the R^2 of a linear regression of the population sizes on the K-values. This measure can also be seen as an indicator of the relative importance of local versus immigrant recruits. In the absence of dispersal, all population dynamics are determined by local recruitment and the R^2 is 1.0. With the introduction of dispersal, differential immigration overlays local recruitment, which is measured in the deviation of the R^2 from one because these effects are not explained in the K-values.

The second currency I used to assess the effects of dispersal was directly related to the spatial attributes of the distribution patterns. The expected effect of dispersal to neighboring populations was a correlation in population size among neighboring populations that decays with distance. Such a correlation is called positive spatial autocorrelation and can be measured with Moran's I (Legendre and Legendre 1998). I

used a standardized version of Moran's I (Haining 1990) for cell pairs one to eight cell distances apart as a measure of the effect of dispersal on autocorrelation in distributional patterns. Note that the underlying K-values were autocorrelated up to a range of eight cells as part of the landscape design, and population sizes were correspondingly autocorrelated in the absence of dispersal. I therefore measured Moran's I first in the absence of dispersal and then with the dispersal being investigated. The difference between these two values of Moran's I then gave and index of the impact of dispersal on spatial autocorrelation.

I tested the model for sensitivity to assumptions and approaches by modifying its structure, running the model on 100 randomly generated landscapes, and averaging the results. The default model was on an autocorrelated landscape as described above. First, I ran the model on landscapes without spatial autocorrelation. Second, I tested for edge effects by implementing the 30 x 30 matrix as a torus, which means that edges are eliminated by connecting them to the opposite edges. While real ranges have edges this test was useful for finding out whether the range edges played a part in the observed effects or whether similar effects could be observed within the range of a species far away from range edges. Third, I investigated the influence of my original dispersal function (Type I) on the simulation results by implementing three alternative functions: 1) uniform dispersal to the nearest eight neighbors only (Type II), 2) uniform dispersal to the nearest 15 neighbors only (Type III), and 3) dispersal with a spherical decay in intensity up to a maximum distance of 8 cells in distance (Type IV). Finally, I provided statistics for correlated and uncorrelated landscapes without dispersal for comparison.

Simulations were run up to 600 time steps or until an equilibrium was reached determined by a change smaller than 0.01 in the sum of all populations. The analyses varying the model parameters R, and the proportion of dispersal were based on a single typical random landscape, shown in Figure 1a. All simulations and statistics were programmed in S-PLUS 6.2 (Insightful 2003)(use of this product does not imply endorsement).

2.4 Results

Introducing dispersal in the population simulation model led to a systematic deviation of population sizes from their underlying carrying capacities (K) (Figure 2, Figure 3, and Table 3, line 1 and 2). Populations with below average K-values tended to exceed K and turned into sinks, while cells with above average K-values realized population sizes below K and acted as sources (*sensu* Pulliam 1988). Thus, dispersal led to a reduction in the range and variance of population sizes (Figure 1 and Figure 2). In addition, the introduction of dispersal led to an increase in positive spatial autocorrelation among population sizes (Figure 4 and Table 3, line 1 and 2). With the default parameter values (net potential local growth rate R = 1.05 and proportion of dispersers = 10%), Moran's I increased by 0.148 ± 0.005 (SE) when dispersal was introduced, while K-values lost $16.4 \pm 2.0\%$ (SE) of their explanatory power in the distribution of population sizes.

The magnitude of these effects depended on the potential population growth rate R and the proportion of dispersers (Figure 3 and Figure 4) but was not strongly influenced by the underlying model structure (Table 3). The influence of the potential population growth rate R on the changes in distribution patterns under dispersal are

shown in Figure 3 and Figure 4. With a dispersal rate of 10%, only low values of R

allowed for strong influences of immigrants on the deviation of dispersal patterns from

underlying K-values. When R was 1.3 or above, the 10% dispersal changed distribution

patterns by less than 1%. However, the increase in autocorrelation was not as dependent

on low R-values as the deviation in patterns from underlying K-values (Figure 4).
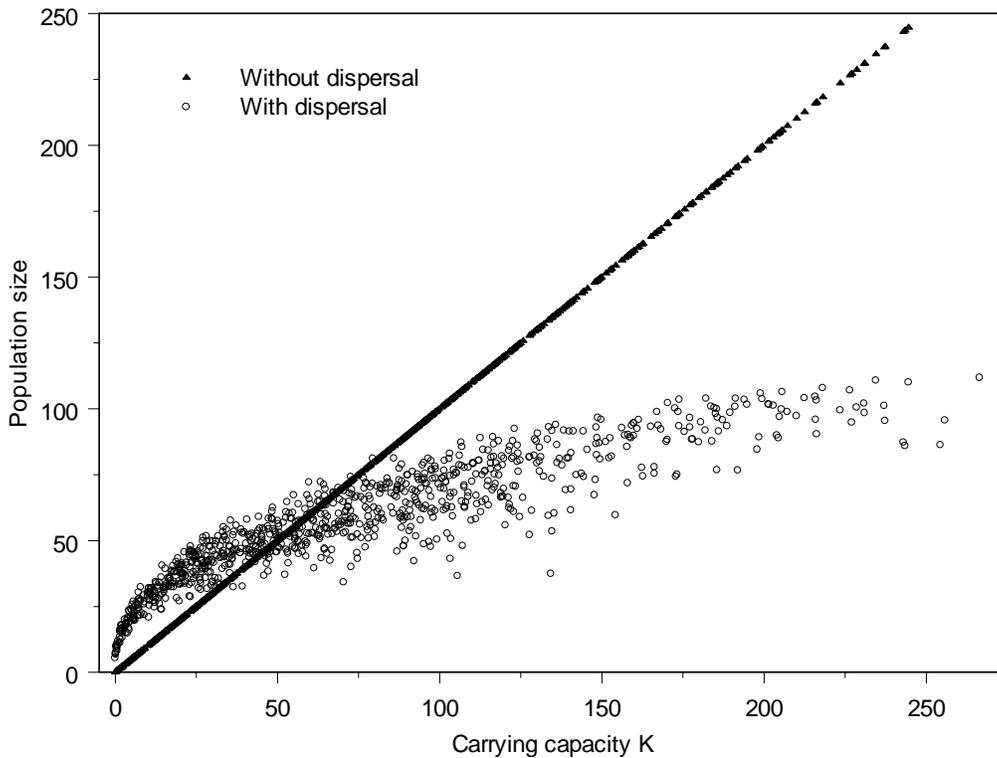
Figure 2. Deviation of population size from underlying carrying capacity (K) with and
without dispersal. Without dispersal population sizes are identical with K-values. With
dispersal populations with small K-value are larger than expected, while populations with
large K-value are smaller than expected. The population growth rate R was 1.05 and the
dispersal rate was 10% of the population per time step.

Autocorrelation increased by 23% with R = 1.3 and dispersal rate at 10%. Higher

dispersal rates caused a larger deviation in the distribution of population sizes from the

pattern of underlying K-values (Figure 3) and delayed the decrease in deviation with

higher R-values: The distribution pattern was changed by 6% and autocorrelation was

increased by 34% with a dispersal rate of 40% and an R of 1.5.
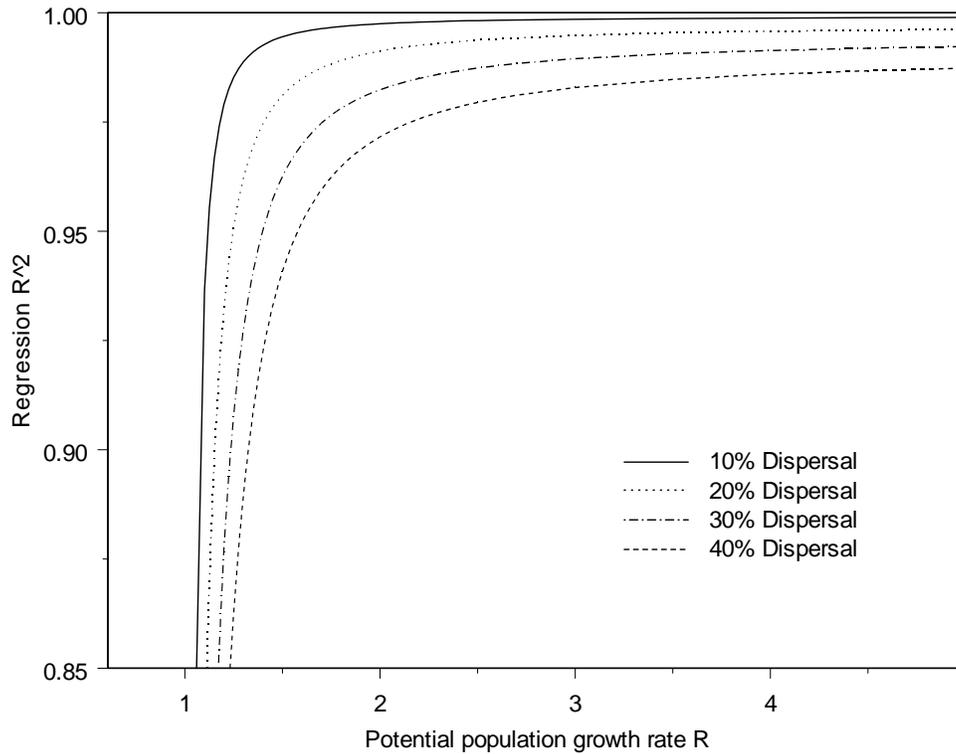
Figure 3. Effect of potential population growth rate R on distribution patterns under a range of dispersal rates. The regression R^2 is the coefficient of determination of a linear regression of the vector of 900 populations at equilibrium after dispersal against the vector of carrying capacities (K) underlying the populations. This coefficient is an expression of how strongly local population sizes are controlled by local carrying capacity rather than by immigration and emigration. R is the potential population growth rate or the factor by which the population can maximally grow in each time step before adjustment for density dependence.

Table 3. Comparison of six different model structures. Means ± standard deviations of Moran's I and R^2s are given from runs on 100 randomly generated landscapes (see methods) with potential population growth rate R = 1.5, death rate d = 0.45 and dispersal rate = 0.1. See the methods section for landscape generation, dispersal types, Moran's I and R^2 calculations.

Landscape Type	Dispersal	Edge correction	Moran's I	R^2
Correlated	None	No	0.294 ± 0.102	1.000 ± 0.000
Correlated	Type I [a]	No	0.443 ± 0.115	0.835 ± 0.020
Correlated	Type II [b]	No	0.442 ± 0.115	0.828 ± 0.023
Correlated	Type III [c]	No	0.522 ± 0.110	0.783 ± 0.028
Correlated	Type IV [d]	No	0.548 ± 0.112	0.758 ± 0.030
Correlated	None	Yes	0.220 ± 0.090	1.000 ± 0.000
Correlated	Type I	Yes	0.326 ± 0.103	0.884 ± 0.010
Uncorrelated	None	No	0.071 ± 0.040	1.000 ± 0.000
Uncorrelated	Type I	No	0.228 ± 0.051	0.732 ± 0.014

[a] Dispersal decays in intensity proportional to 1/distance^2 without a maximum dispersal limit;
[b] Dispersal is uniform and only to the eight closest neighbors;
[c] Dispersal is uniform and only to the 15 closest neighbors;
[d] Dispersal decays with distance following a spherical function up to a maximum distance of eight cells.

Tests of the sensitivity of the model to its structure confirmed its adequacy. First, the variance in results introduced through the random selection of K-values during landscape creation was low (Table 3, line 1 and 2). Very few generated landscapes led to extreme results, except when all cells with high K-values were clumped around the edges of the matrix. Second, the results were sensitive to the introduction of spatial autocorrelation in the landscape. Dispersal led to a lower R^2 in uncorrelated landscapes than in correlated landscapes (Table 3, line 2 vs. line 9). However, the total autocorrelation in the distribution of population sizes was still higher in correlated landscapes than in uncorrelated landscapes after dispersal. Third, edge effects were observable in the simulation. When I implemented the 30 x 30 matrix as a torus, the observed effects of dispersal on the distribution of abundances slightly diminished (Table

40

3, line 2 vs. 7). However, autocorrelation in the distribution of K-values was also lower in

the toroidal landscape, indicating that the edge effects were not solely due to dispersal

anomalies at the edges but also computational differences in the analyses of the dispersal

patterns. The main effect of the toroidal correction was to reduce outlying population
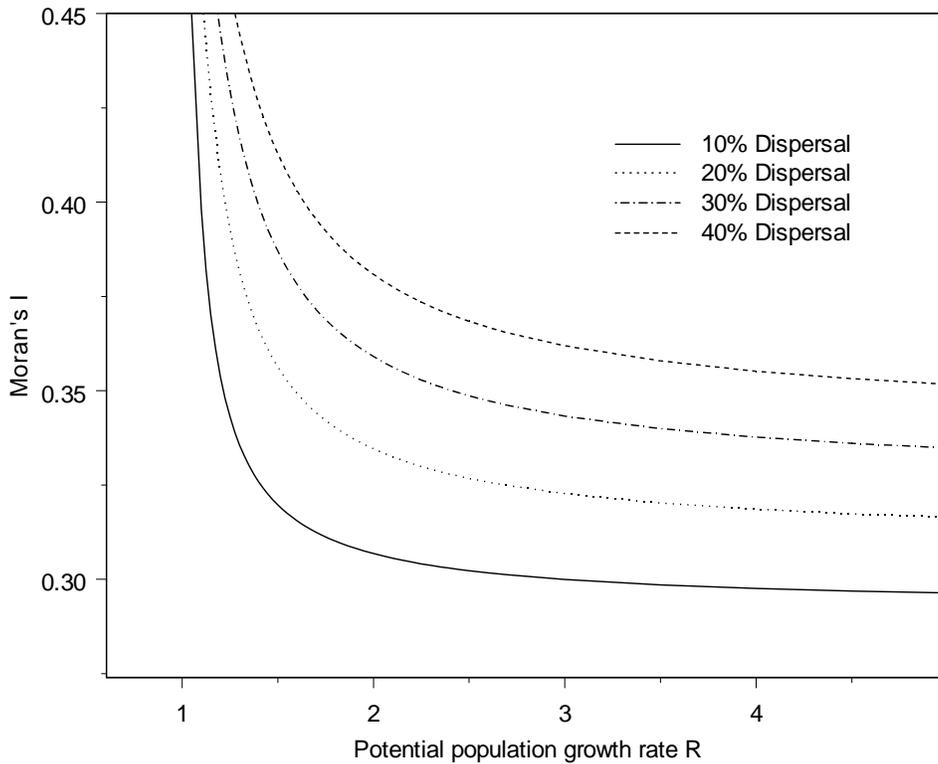
Figure 4. Effect of potential population growth rate R on autocorrelation in distribution patterns under a range of dispersal rates. Moran's I is a measure of autocorrelation based on all cell pairs with a maximum distance of eight cells. This measure is an expression of the similarity among population sizes within an eight cell distance, above and beyond the overall similarity among population sizes in the whole range. Note that the lower bottom of the graph is at the value of Moran's I for the population size distribution without dispersal. R is the potential population growth rate or the factor by which the population can maximally grow in each time step before adjustment for density dependence.

sizes due to edge effects. It did not change the main observed effect of dispersal in

changing distribution patterns (Figure 5). Fourth, the three alternate dispersal functions

(Type II-IV) led to minor quantitative differences in the overall results (Table 3, lines 3-

5), but did not influence the qualitative insights gained, so that a more detailed

investigation or a more complicated model were not justified.
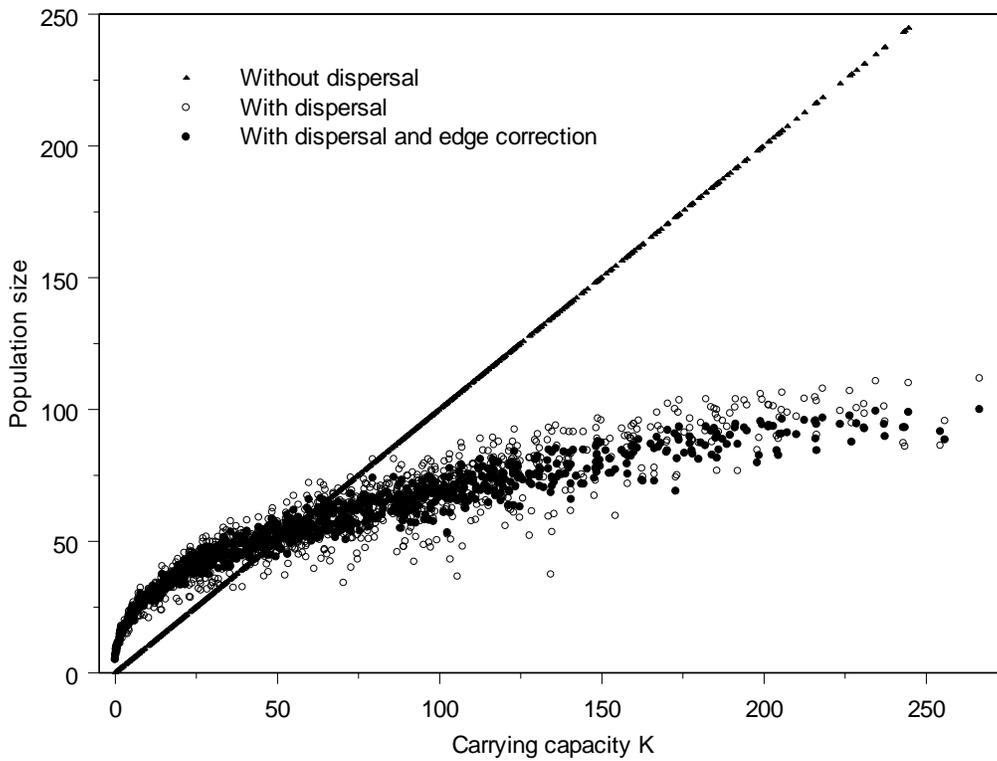
Figure 5. Deviation of population size from underlying carrying capacity (K) without dispersal, with dispersal, and with dispersal and toroidal edge correction. Without dispersal population sizes are identical with K-values. With dispersal populations with small K-value are larger than expected, while populations with large K-value are smaller than expected. The edge correction reduces the variance in the population sizes, by removing outlying population sizes due to edge effects. The population growth rate R was 1.05 and the dispersal rate was 10% of the population per time step.

2.5 Discussion

The approach presented here takes a process-based rather than habitat-centered view of spatial distributions (Thomas and Kunin 1999) by incorporating immigration and emigration into the population dynamics. The core insight of the model is that dispersal is less important for shaping the distribution of abundances in species with a large potential population growth rate than those with a small potential growth rate. In other words, the population dynamics of species that have the potential to grow quickly are dominated by local recruitment. Immigrants cannot contribute much to the local abundances of such species. Note that my model did not include local extinctions or environmental and demographic stochasticity. Both effects would likely increase the importance of migrants to overall population distribution because migrants would assume more pivotal roles by recolonizing locally extinct populations, by rescuing populations on the brink of extinction, and by spreading the risk of extinction by local environmental fluctuations (Engen et al. 2002b).

In contrast, in species with low potential population growth rates, migrants can play a very important role in the distribution of abundances. Typical species falling in this category have low numbers of offspring and a high parental investment, such as large mammals and many large birds. This result is consistent with Söndgerath & Schröder (2002), who, with a different goal and methodology, concluded that increasing the connectivity of a landscape has a noteworthy effect on spatial spread only when reproductive rates are low.

The results of this model should not be taken as numerical predictions for the parameter combinations under which dispersal has ecologically significant effects on

distribution patterns because of the necessary omission of some ecological complexities. For example, the presented effects may be weakened slightly by introducing dispersal mortality into the model, which could decrease the connection among populations. Thus, the combinations of growth and dispersal rate would have to be more extreme to come to the same effects on distribution patterns as without dispersal mortality. The lesson to be learned from this model is of a relative nature: the closer the potential population growth rate is to one, the more important are immigrants relative to local recruits and the more strongly will dispersal shape distribution patterns and cause additional positive spatial autocorrelation.

Another simplification of the model is the assumption of reaching an equilibrium in population dynamics (Pickett et al. 1994, Guisan and Zimmermann 2000). The simulation model presented here works on the assumption that an equilibrium is reached through logistic growth. I contend that the introduction of stochastic, non-equilibrial elements would not have changed the fundamental insights gained by this model and would thus have been an unnecessary complication. As long as the system is not continuously growing or shrinking, the population dynamics would have averaged out over the simulation duration of several hundred time steps and would not change the fundamental effects of dispersal on spatial distribution patterns posed as the core question of this research.

In contrast to other studies (e.g., Pulliam 2000, Keitt 2003), I did not designate source and sink populations *a priori*. Instead, I specified carrying capacities. A fixed percentage of dispersal led to a source-sink structure because the populations in cells with high K-values supplied more dispersers and the cells with low K-values accepted more

dispersers. Under this scenario the logistic growth function led to higher realized population growth rates in the source cells and lower or zero growth in the poorer habitats because the population size was closer to or even at or above K in the latter populations, although the fundamental potential population growth rates were identical. Given the fixed death rate, the cells with positive net immigration then turned into functional sinks and the ones with negative net immigration turned into sources.

The analytical approach presented here differs from the approach taken by several other ecological theories that are centered on the effects of dispersal. Island biogeography uses dispersal for colonization rates and subsequently to predict biodiversity but does not deal with abundances of individual species (MacArthur and Wilson 1967). In addition, it requires an unchanging mainland population supplying a constant stream of immigrants, which is not a model applicable to many terrestrial situations (Hanski 2001). Metapopulation ecology uses dispersal as a connection between populations for recolonizations and rescue effects, but does not analyze the spatial consequences of dispersal on the distribution of abundances. Such an approach is appropriate for discrete habitat patches such as islands or highly fragmented landscapes but is of questionable value for continuous landscapes (Hanski 1999; 2001). The analyses of synchrony in population dynamics of neighboring populations brought about by environmental synchrony (the Moran effect) or by dispersal investigates the spatio-temporal consequences of dispersal but not how these consequences change distributions over many generations (Bjørnstad et al. 1999, Hudson and Cattadori 1999, Koenig 1999, Kendall et al. 2000, Ripa 2000, Engen et al. 2002a, Koenig 2002).

The results presented here are important for the fields of distribution modeling and conservation management. Many authors assert that spatial models are a significant advance in distribution modeling and should be used whenever possible and appropriate (e.g., Legendre 1993, Augustin et al. 1996, Thomson et al. 1996, Carroll and Pearson 2000, Lennon 2000, Keitt et al. 2002, Lichstein et al. 2002). However, it is important to understand the source of spatial structure in distributions to properly apply spatial models (Austin 2002). If the only source of a spatial pattern in the form of positive spatial autocorrelation stems from the autocorrelation in the underlying environmental gradients, a model including all gradients will implicitly model the spatial structure, and more explicit spatial modeling will be an unnecessary complication (Diniz-Filho et al. 2003). If, however, another process, such as dispersal, causes spatial patterns, it is important to understand under which conditions this process may be influential enough to warrant inclusion in a distribution model. My results show that species with low to moderate potential population growth rates are most likely to exhibit ecologically significant spatial autocorrelation above and beyond the spatial autocorrelation caused by environmental gradients. These species are the most likely candidates to require spatially explicit models, whether all environmental gradients are included or not.

The spatial patterns in the distribution of species and the relative importance of dispersal to these patterns are also important to the field of wildlife conservation. Species with a high potential population growth rate are less dependent on dispersal than species with a low rate. Therefore, conservation efforts for the species with low growth rates will likely require more connectivity in the landscape and larger conservation areas than efforts for species with high growth rates.

46

CHAPTER 3

EFFECT OF DISPERSAL AT RANGE EDGES ON

THE STRUCTURE OF SPECIES' RANGES

3.1 Abstract

Range edges are of particular interest to ecology because they hold key insights into the limits of the realized niche and associated population dynamics. A recent feature of the journal *Oikos* summarized the state of the art on range edge ecology (Holt and Keitt 2005). While the typical question is what causes range edges, another important question is how range edges influence the distribution of abundances across a species' geographic range when dispersal is present? I used a single species population dynamics model on a coupled-lattice to determine the effects of dispersal on peripheral populations as compared to populations at the core of the range. In the absence of resource gradients, the isolation of populations at the range edge led to significantly lower population sizes in the periphery of the range than in the core. Lower population sizes mean higher extinction risks and lower adaptability at the range edge, which could inhibit or slow range expansions, and thus effectively stabilize range edges. While the proportion of emigrants was fixed, the number of immigrants depended on the number, proximity, and size of donor populations, which was more favorable at the core of the range than in the periphery. The strength of this effect depended on the potential population growth rate and the maximum dispersal distance. Lower potential population growth rates led to a stronger effect of dispersal resulting in a higher difference in population sizes between the two areas. The population dynamics of species with high potential population growth

rates are dominated by local recruitment and dispersal has a minor effect. The strongest differences in average population sizes between the core and the periphery were observed at medium dispersal distances, which was far enough for emigrants to disperse well into unsuitable habitat outside of the range but was short enough to avoid a strong direct connection between the periphery and the core. The differential effect of dispersal on population sizes at the core and periphery of the range in the absence of resource gradients means that traditional, habitat-based distribution models result in misleading conclusions about the habitat quality in the periphery. Lower population sizes at the periphery are also relevant to conservation, because habitat removal not only eliminates populations but also creates new edges. Populations bordering these new edges may experience declines, due to their increased isolation.

3.2 Introduction

Range edges hold a special place in the study of the distribution and abundance of species, which is at the core of ecology (Andrewartha and Birch 1954, Krebs 1972, Andrewartha and Birch 1984). Designating the transition between occupied and unoccupied habitat, range edges are a key for understanding the processes that determine the ecological and evolutionary fate of a species (Holt and Keitt 2005). In a recent feature of the journal Oikos, several authors explored the state of the knowledge on range edge ecology (Case et al. 2005, Fortin et al. 2005, Guo et al. 2005, Holt and Keitt 2005, Holt et al. 2005, Parmesan et al. 2005). These authors reviewed important processes influencing the patterns and dynamics of range edges, with the central questions being: what causes range edges, how are they maintained, and which processes control range edge dynamics? Explanations were primarily based on gradients from center to range edge in

the factors controlling population dynamics (environmental conditions and species interactions), and evolutionary factors concerning the adaptation to conditions in the range edges.

I investigated a process that fits well into the single species theoretical frame work of Holt et al. (2005), but was explored neither by them nor by Guo et al. (2005) - the two papers dealing with single species processes. I turned the original question of what causes range edges around and asked: How do range edges affect the abundance patterns within the range? The idea was that populations at range edges have fewer neighbors and thus are relatively isolated, resulting in lower immigration rates than at the range core.

Under the assumption that new species necessarily evolve in a relatively small area, every species starts out having range edges. As species adapt to the conditions in the range edges, a key question is, what keeps them from spreading further (Kirkpatrick and Barton 1997, Gaston 2003)? Initially, they will spread to all areas they can reach and that have good enough conditions to support above zero growth but will not colonize areas in which birth plus immigration is smaller than death plus emigration. Over time, though, species should adapt to conditions at the range edge, develop higher birth and/or lower death rates under these marginal conditions and colonize adjacent habitats unless they represent a "hard" physiological border such as water for terrestrial species. If populations in the periphery were systematically disadvantaged by isolation, range edges themselves could inhibit spread by furthering extinction events and suppressing adaptations and thus help perpetuating themselves.

Metapopulation models have investigated the effects of dispersal and isolation on population persistence in much detail, but with a focus on extinctions and recolonizations of populations rather than on shifts in population sizes over the range (Hanski 1999). My approach differs from classical metapopulation models in its explicit treatment of space and its investigation of abundance, not incidence. The investigation of abundance rather than incidence more directly addresses the question of the effect of range edges on range structure, because extinctions and lower genetic variability as source for adaptations are secondary consequences of low population size and introduce their own dependencies on individual species and situations that confound the question.

My main goal was to determine whether the relative isolation of populations at the periphery of a species' distribution leads to lower abundances there when dispersal is present. I did not make typical assumptions about range structures, such as better habitat or higher carrying capacities at the center of a range than in the periphery. This approach allowed an assessment of the effect of dispersal on population sizes at the edge of a range without confounding gradients in environmental conditions.

3.3 Methods

I investigated the effects of dispersal on peripheral populations using a 30 x 30 coupled lattice containing 900 individual populations (Figure 6). I simulated habitat quality through carrying capacity (K), analogous to Hanski (2001) using patch size to represent habitat quality in metapopulation models. Following Wiegand et al.'s (1999) insight that the reduction of habitat quality into the dichotomous categories "suitable" and "unsuitable" hampers the understanding of demographic processes, I sampled the K-values from a continuous normal distribution with mean 0 and standard deviation 1.

However, I used the absolute of the randomly drawn values, in effect folding the negative part of the distribution onto the positive side. Brown et al. (1995) and McGill and Collins (2003) noted that species' ranges typically have relatively few locations with very high abundances and many with low abundances, which is also true for the resultant sample distribution of the K-values.
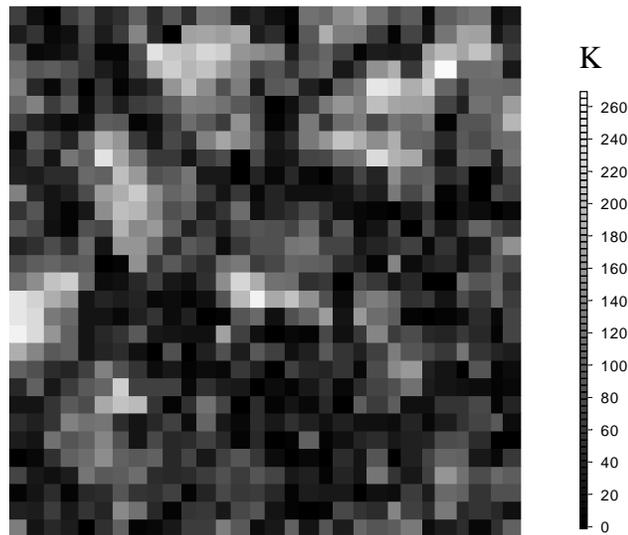
Figure 6. Randomly generated 30 x 30 grid of carrying capacities (K), which are used in the logistic growth formulas of the 900 populations - one in each grid cell. The K-values are autocorrelated with a spherical decay function up to a range of eight cells.

It is well documented that environmental conditions are autocorrelated in space (Legendre and Fortin 1989). Therefore, I introduced spatial autocorrelation in the distribution of K-values using the S-PLUS function rfsim (Kaluzny et al. 1996:117-119). This function calculates a covariance matrix based on a spherical function of distance, which I assigned a maximum range distance of eight cells. The random vector of K-values is multiplied with the Cholesky decomposition of this matrix. The resulting distribution of K-values over the 30 x 30 matrix is spatially positively autocorrelated up

to a distance of eight cells with similarities among neighbors decaying with distance according to a spherical function. I also included a test run on an uncorrelated random landscape as a null model for comparison.

Note that my method of generating landscapes did not include a bias for higher K-values at the center of the range than in the periphery. Thus, the initial external factors were identical for peripheral and central populations, which I confirmed in a t-test on the respective K-values.

Each population was governed by the basic processes of birth, death, immigration and emigration. Birth and death rates were combined in a potential population growth rate R (Begon and Mortimer 1986), which is one when no growth occurs. The formula for population change in each time step (ΔN) was based on the logistic growth formula in Begon and Mortimer (1986), which adjusts the potential population growth rate R by a density dependent term:

$$\Delta N = N_t * (R / (1 + (R - 1) * N_t / K) - 1) + I - E;$$

where N_t = population size at time t, R = potential population growth rate (birth minus death rate not adjusted for density dependent effects), K = carrying capacity (maximum number of individuals supported at the location before the realized growth rate falls to 1), I = immigration (number of individuals entering the population), and E = emigration (number of individuals leaving the population).

All cells in the model were habitable, within the limits on reproduction given by carrying capacities. However, carrying capacities were not absolute caps on the population sizes. Rather, they were the point at which the realized population growth rate

crossed from positive growth (at population sizes below K) to negative growth (at population sizes larger than K).

A fixed proportion of each population emigrated in each time step (E). This proportion was distributed to neighboring cells in reverse relationship to their distance - the further the distance between populations the lower their exchange of migrants. I implemented this dispersal pattern by replacing the distances among cells with a weight calculated as $1/\text{distance}^2$ (Figure 7). Then, I added up all weights for each population and standardized them so that they added up to the proportion of the population to be dispersed. In addition, I truncated this dispersal scheme at different distances for a series of experiments simulating different dispersal patterns.

In the model dispersers leaving the range had 100% mortality. The number of immigrants for a given population in a time step was simply the sum of all emigrants coming from other populations. Note that this approach is deterministic and allows fractions of individuals. While dispersing individuals in a stochastic way would be more realistic, it would average out to the same result given enough runs, and thus was omitted for the sake of simplicity. Also note that no mortality was associated with dispersal within the range. While this simplification is unrealistic, systematic mortality would have been equivalent to higher local mortality and a lower dispersal rate (or a different shape in the dispersal function), which are parameter variations covered in the tests below.

For a comparison between range core and periphery I had to define members of the two areas. I chose the outer two rows of cells as periphery (n = 224) and a central 16 x 16 block of cells as core (n = 256). Other designs would have been possible, but I found

this to be a good compromise between maximizing the sample size in each category and

maximizing the distance between the two groups for clear effects.
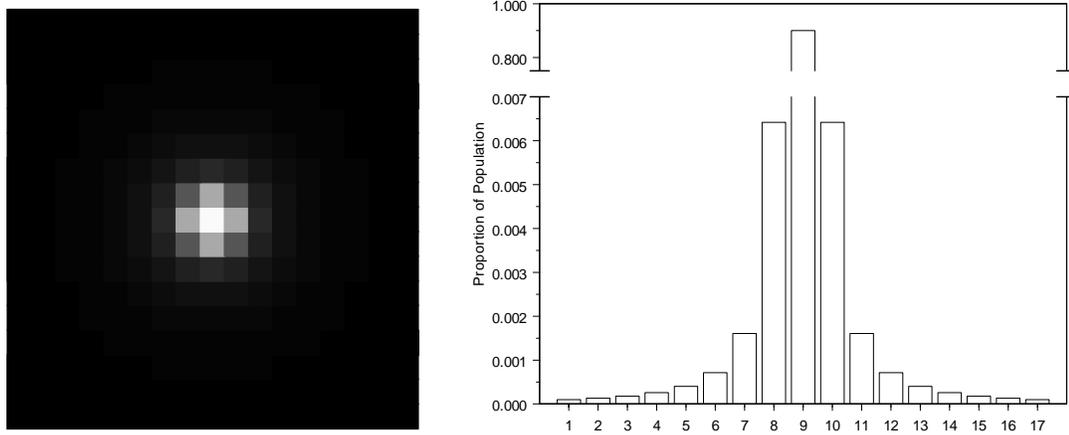
Figure 7. Graphical representation of the dispersal kernel of a single population in the center of the two graphs. In the left graph the lighter the shade of a cell, the higher the percentage of the dispersers from the center going into that cell. The right graph shows a cross section through the left graph. The center cell retained 90% of the population while 10% dispersed to neighboring cells. The proportion of dispersers decreased with $1/distance^2$. The maximum dispersal distance was eight cells in each direction from the center cell.

The dependent variable needed to capture the relative effect of dispersal on

population sizes in the periphery compared to in the core. Simply taking the difference

between the average population sizes in core and periphery would have expressed the

absolute population sizes as well as the difference in the two places. A percentage

difference in population size between the two places was the more meaningful measure

(from here on called "percent difference"), calculated as:

$$100 * (N_c - N_p) / N_p$$

where N_c = average central population size and N_p = average peripheral population size.

I tested the sensitivity of the modeling results to several variables and structures

of the model. Letting all dispersers distribute equally in all directions, be it into better or

54

inferior habitat, or even outside of the range, where they perish immediately, is a neutral approach that most closely fits the dispersal of plants. Sentient animals are more likely to make better choices. Therefore, I evaluated an alternative dispersal scheme in which all dispersers stay in the range, thus eliminating the direct loss of individuals through leaving the range and moving into inhospitable habitat. In this alternative scheme, the dispersers that would have left the range in the default dispersal scheme were redistributed to neighboring populations within the range according to the same distance weighted function used in the regular dispersal. This alternative scheme is at the other end of the spectrum than the original scheme, and represents an animal that is perfectly able to avoid habitat with a K of 0. However, I used the original scheme in most experiments because it led to clearer results and thus allowed a better depiction of the sensitivities of the model.

I varied the R-values to simulate a range of different organisms and to determine the sensitivity of the observed effects to different combinations of these two population dynamics parameters. The values of R covered in the simulation encompass the range of maximum possible R-values (1.32 - 5.23) for passeriform and piciform birds in Saether and Bakke (2000). These maxima were derived from fecundity values that assumed both absence of adult or juvenile mortality and onset of reproduction within the first time step after birth. I also varied the proportion of each population dispersing in each time step to simulate different levels of dispersal activity. Finally, I varied the maximum distance of dispersal from 1-20 cells to simulate different dispersal strategies. A maximum dispersal distance of one means that dispersal is only allowed to the four next neighbors, while a

maximum dispersal distance of 20 covers two thirds of the range width, which should

reasonably cover the existing dispersal distances among animals.

I omitted some complications in the model that may have influenced the results

but were beyond the scope of this study. Such complications include a directional bias in

dispersal towards good habitat, differential mortality associated with movement through

different quality habitats, and different dispersal strategies (e.g., density-dependent

dispersal) (Johst and Brandl 1997, Travis et al. 1999).

Simulations were run up to 600 time steps or until the sum of all populations

changed by less than 0.01. The analyses varying the model parameters reproductive rate

R, death rate d, and the proportion of dispersal were based on a single typical random

landscape shown in Figure 6, because the duration of the calculations prohibited the

repetition on 100 landscapes. To avoid biases in the selection of this typical landscape I

randomly pulled a landscape out of the 100 generated landscapes until one was identified

that was within 1 standard deviation of the average value from the 100 landscapes for

summary statistics on the difference between core and margin population sizes under

default parameter settings. Selecting a landscape that lay within 1 SD of all landscapes

was a reasonable way to avoid the random selection of an atypical outlier. All simulations

and statistics were programmed in S-PLUS 6.2 (Insightful 2003)(use of this product does

not imply endorsement).

3.4 Results

All experimental setups and parameter value combinations led to a significantly

lower average population size at the periphery of the range than the core (Table 4). This

difference existed in absence of a difference in average carrying capacities between core

and periphery (t = -0.187, df = 99, p-value = 0.853). However, the relative difference in

population sizes between the two range positions depended upon the structure of the

model and the selected parameters for potential population growth rate (R), proportion of

dispersal, and maximum dispersal distance.

Table 4. Difference in average population size between populations in the core (n = 256) and periphery (n = 224) of a range over 100 randomly generated landscapes. The average carrying capacities of each population in the two areas were not significantly different (p > 0.05). The overall average population size was 48.89. Underlying the difference were 10% dispersal per population per time step and a potential population growth rate (R) of 1.05. Confidence intervals are based on a 95% probability and the % difference is the percentage core populations (N_c) are larger than populations in the periphery (N_p): 100 * (N_c - N_p) / N_p.

Approach	Population size			
	Difference	Lower limit CI	Upper limit CI	% Difference
Standard	28.02	26.04	30.00	86.59
Stay in range	11.27	9.62	12.92	20.73
Carrying Capacity (K)	-3.10	-3.61	2.99	-

Under the default values of 10% dispersal per time step and an R-value of 1.05,

core populations were on average 86.6% (95% CI: 80.5 - 92.7%) larger than peripheral

populations. Higher rates of dispersal led to larger differences between the average

population sizes of the two areas (Figure 8) but did not change the relationship between

these differences and R-values. Smaller R-values led to larger differences in population

sizes, with a sharp increase in differences for R-values smaller than 2. In other words,

species that were unable to at least double their population size under ideal conditions

within one time step experienced strong decreases in population sizes at the margins of

their ranges. These decreases quickly intensified with further declines in potential growth

rates from two on down. In contrast, species that could at least potentially double their

population size within one time step experienced a fairly small but still observable and

consistent disadvantage in peripheral populations when dispersal was present. When R

was larger than two, its value did not have a strong influence on the difference in average

population size between core and periphery. This percentage difference then mostly

depended on the percent of dispersers in the population, being around 10% for 10%

dispersal and 20% for 40% dispersal (Figure 8).
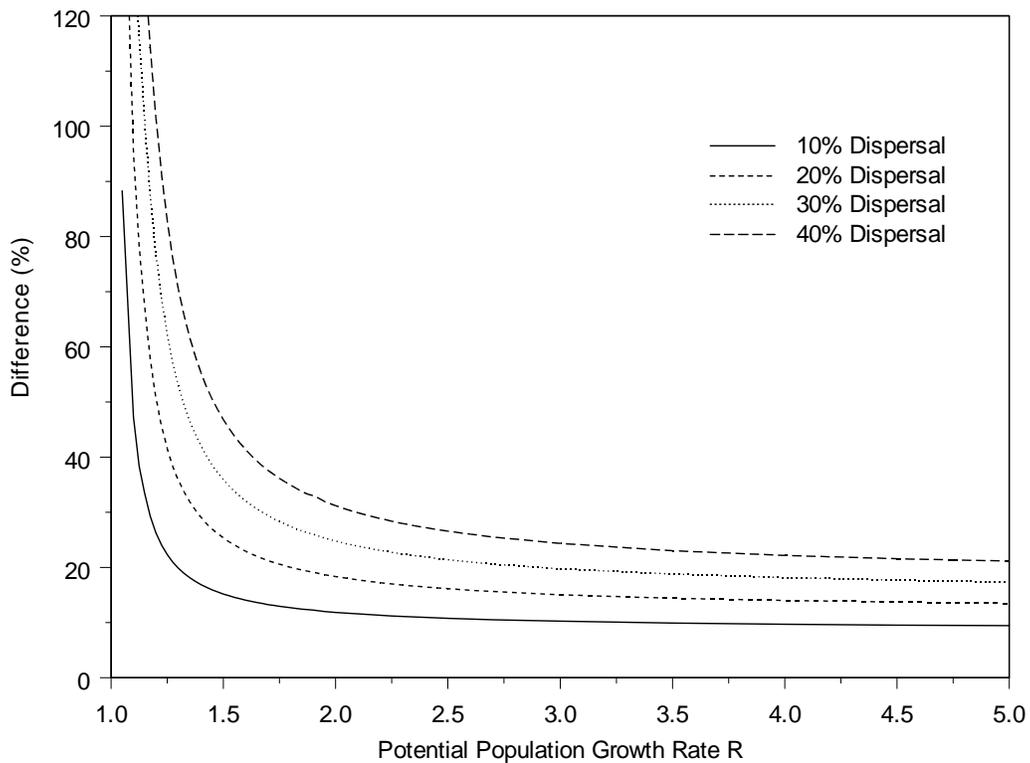
Figure 8. Connection between potential population growth rate (R), percent dispersal and
the disadvantage populations in the periphery of a range experience from dispersal.
Difference is the average percentage by which populations in the core (n = 256) of a
simulated landscape were larger than populations in the periphery (n = 224), in the
absence of differences in the average carrying capacities in the two areas. Dispersal is the
percent of individuals leaving a population in each time step. The potential population
growth rate is the factor a population can maximally grow by before adjustment to
density dependence in a logistic growth equation.

The maximum dispersal distance showed a non-monotonic relationship to the difference in population sizes between core and periphery with a single global maximum (Figure 9). The maximum difference was reached at a maximal dispersal distance of 11 cells. However, the differences were fairly similar among dispersal distances from 7 to 20 cells and only dropped sharply with dispersal distances below six cells. The gap between populations classified as peripheral and core in the experimental setup was also six cells, so that dispersal distances below six cells prevented a direct exchange of individuals between the two areas.

The observed effect - reduced population sizes in the periphery - was not only due to loss of individuals that left the range and perished. The alternative dispersal scheme, in which individuals dispersed exclusively into the range, also led to reduced population sizes in the periphery. With the standard parameter values of $R = 1.05$ and 10% dispersal, core populations were on average 20.73% larger than peripheral populations (95% CI: 17.70 - 23.77%) under the alternative dispersal scheme.
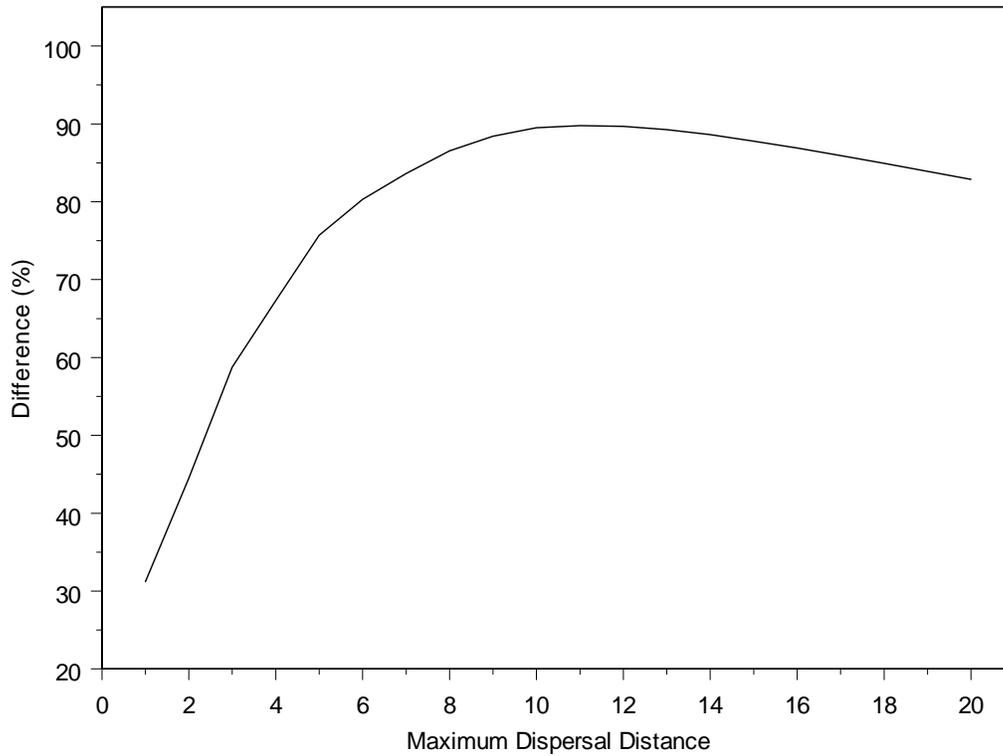
Figure 9. Influence of maximum dispersal distance (measured in cells) on the disadvantage populations in the periphery of a range experience from dispersal. Difference is the average percentage by which populations in the core (n = 256) of a simulated landscape were larger than populations in the periphery (n = 224), in the absence of differences in the average carrying capacities in the two areas. Underlying the percent difference were 10% dispersal per population per time step and a potential population growth rate (R) of 1.05.

3.5 Discussion

Isolated populations are more likely to experience a net loss of individuals to dispersal than well-connected populations because dispersers are more likely to find themselves in unfavorable habitats or perish due to longer or more difficult dispersal events. In the simulation model presented here, all populations followed the same rules with carrying capacities (K-values) randomly sampled from the same distribution and identical growth and dispersal rates. However, due to their location, peripheral populations were more isolated than populations at the core of the range. As a consequence, peripheral populations were on average smaller than core populations in absence of any systematic gradients in habitat quality, reproductive rates or other factors that could have influenced population sizes and provided an alternative explanation for the observed difference.

Lower population sizes in the periphery may have several consequences for population dynamics in the range edge and thus for the range edge itself. The model presented here did not include extinctions because fractions of individuals were allowed and all K-values were ≥ 0. Had extinctions been part of the model, the lower population size would have led to a higher likelihood of extinction (Holt et al. 2005) and the peripheral populations would have been even more isolated. The introduction of an Allee effect would have further amplified this consequence of lower population sizes. Therefore, the demonstrated effect of lower population sizes in the periphery due to dispersal could be intensified in synergism with extinctions and Allee effect, leading to more isolation and even lower population sizes in the periphery. In addition, lower population sizes bring a reduced genetic variability and thus a reduced adaptability to

range edge conditions (Holt et al. 2005). All these factors work together to inhibit range expansion and promote range contraction. Under the assumption that species typically tend to extend their range through adaptations (Kirkpatrick and Barton 1997), factors inhibiting such expansion could lead to a higher than expected stability of range edges.

The effect of lower population sizes due to isolation and dispersal need not be limited to range edges. The same model used for range edges here would be similarly valid for populations bordering unoccupied areas within the distribution or existing in highly fragmented areas. In these cases, scale and resistance of the landscape to the organism become important issues. If the unoccupied gap in the range is small relative to the dispersal distance of the species and does not represent a barrier to dispersal, populations bordering the gap will not be impacted. However, if the unsuitable gap in the range is large enough or has a high enough resistance to dispersal, it could act in a similar manner as the range edges in the model presented here and thus lead to reduced population sizes along the border of the gap. Thus the often observed peak and tail pattern in range structures (Brown et al. 1995), which is used as starting point in some important macroecological theories and models (McGill and Collins 2003, Guo et al. 2005), could partly be caused or at least amplified by the spatial arrangement of habitats, the dispersal behavior of the species and the resistance of the landscape to the species, and not solely by gradients in habitat suitability or competition.

The relation between dispersal distance and distances in the range is also important. Very short dispersal distances at a spatial extent similar to distances between populations result in low effects of dispersal on population size structure within the range. Such short dispersal distances approach the situation of no dispersal, when all

populations merely reflect the local carrying capacity. As dispersal distance increases, the lowering effects of dispersal on the size of relatively isolated populations in the range edge increase up to the point were a maximum effect is reached. The consequent decrease in effect with increase in dispersal distance owes to a direct exchange of individuals between core and periphery, which leads to an equalization in population sizes. Thus, the largest effect of isolation on population sizes can be expected in species with a medium dispersal distance that is large enough to reach well into unoccupied areas but not large enough to break the isolation effectively.

Another parameter important to the magnitude in the difference of population sizes was the potential population growth rate R. The lower the R-value, the more local populations were influenced by dispersal. A high R-value, in contrast, meant that local recruitment was strong and dispersers had but a small influence on population sizes. Thus, species with a low potential of population growth under ideal conditions are expected to suffer more dire consequences from isolation and fragmentation. In addition, their populations in the periphery are expected to be relatively weak, inhibiting range expansion and furthering range contraction. Examples for species with a low potential for population growth are large mammals and long-lived bird species. However, even species with high R-values showed 10-20% larger core populations (depending on the percent of dispersal).

The determination of R-values from empirical data is problematic. Realized R-values are necessarily close to 1 - otherwise, the population would be expanding or contracting rapidly. However, potential R-values used in the growth equation require knowledge on how fast a population could grow under ideal circumstances. A maximum

is given through maximum fecundity. For example, a bird that is only able to lay a clutch of 2 eggs cannot have an R larger than 2. However, it could have a much smaller R when effective population size, proportion of juveniles, natural mortality under ideal conditions and similar factors are considered. Therefore, R-values are likely lower than clutch sizes may suggest and effects of dispersal on peripheral populations may be considerable.

A part of the observed effect was due to the model structure selected. The death of all individuals that left the range contributed substantially to the lower population sizes in the periphery. When individuals were not allowed to leave the range and perish, but dispersed exclusively into the range, the difference in average population size between periphery and core dropped from 86.6% to 20.7%. These two extremes cover most dispersal strategies, from plants that have no control over habitat selection during passive dispersal to intelligent animals, which exclusively disperse into habitats with a carrying capacity > 0. Most animals are likely to be found somewhere in between these two extremes. The more capable a species is in selecting habitat during dispersal, the weaker the effect of dispersal on population sizes in the periphery or in fragmented habitats is expected to be.

The most direct and strongest explanations for range structure and range edges are undoubtedly a species' niche and interspecific interactions (Holt and Keitt 2005). The effect of dispersal on range structure studied here is neither to be seen as competing with these processes nor as an alternative process; rather, it augments existing insights by describing an important effect that is independent of suitability gradient or interspecific interactions.

The results presented here have implications for the modeling of the geospatial distributions of species. The population sizes in the periphery were lower than in the core in the absence of systematic difference in habitat quality. Traditional distribution models, based on habitat associations but not spatial information, would not be able to interpret this situation correctly. Based on the lower population sizes, they would associate the habitat conditions in the periphery with a lower value than they actually have, distorting the actual resource preferences of the analyzed species. Or, alternatively, if the model was based on sample locations mostly from the core of the range, the population sizes or probability of occurrence would be over-predicted at the periphery of range. A spatially explicit model may remedy such a bias.

Lower population sizes in the periphery imply additional stress on the populations and individuals located there. However, when the range becomes fragmented at a sensitive spatial scale, similar stresses can occur within the range. The processes demonstrated here thus reemphasize the importance of connectivity for the survival of a species. In particular, additional habitat fragmentation in the periphery could lead to increased population extinction and thus to range contraction. The new periphery after range contraction would then again experience population decreases because of new isolation. An important lesson for conservation from this study is that habitat conversion not only decreases the total population by the equivalent of lost carrying capacity but also by jeopardizing populations at the newly formed edge. These effects are particularly important in species with low R-values and medium dispersal distances.

CHAPTER 4

POTENTIAL RELATIONSHIP BETWEEN SPATIAL AUTOCORRELATION IN SPECIES DISTRIBUTIONS AND DISPERSAL

4.1 Abstract

Spatial autocorrelation in species distributions indicates a lack of independence between sample locations and causes problems in distribution modeling. Knowing the cause of such spatial autocorrelation is vital to selecting the best suited modeling methods. Most autocorrelation in distributions is caused by autocorrelation in the underlying environmental conditions. However, it has been hypothesized that dispersal can cause additional autocorrelation, necessitating different modeling techniques. In this study, I tested the connection between autocorrelation and dispersal at a coarse scale on data from 107 species of the Breeding Bird Survey. Because no direct information on the dispersal of these species was available, dispersal indices were derived from three ecological theories: the deviation from an abundance-occupancy relationship, the spatial exponent of Taylor's power law, and density dependence. Spatial autocorrelation was captured in conditional autoregressive regression models (CAR) and measured with a standardized version of the regression coefficient rho, the extent of the included neighborhood, and the additional variance explained in CAR models over traditional regression models. No association between these measures of autocorrelation and the indices for dispersal was found. I therefore conclude that indirect ecological indices for dispersal carry too much noise and too little information for successful analysis.

4.2 Introduction

Dependence between observations across geographic space has long been identified as a source of error in statistical analyses (Student 1914). In geography, the universal spatial dependence or autocorrelation in measurements of a variable collected at different spatial locations has been termed the First Law of Geography (Tobler 1970). Ecologists have also recognized the problem for decades (Legendre 1993), but only recently has the number of studies addressing spatial autocorrelation proliferated (Augustin et al. 1996, Leathwick 1996, Overton 1996, Thomson et al. 1996, Koenig 1999, Lennon 2000, Koenig 2001, Trenham et al. 2001, Keitt et al. 2002, Lichstein et al. 2002, Diniz-Filho et al. 2003, Peakall et al. 2003).

In the field of distribution modeling, spatial autocorrelation has been widely identified in species' occurrences and distributions (Legendre 1993) and statistical techniques have been developed to address the problem (Dale et al. 2002, Dale and Fortin 2002, Keitt et al. 2002, Lichstein et al. 2002). However, as Austin (2002b) points out, an understanding of the ecological processes that underlie spatial autocorrelation in species distributions is a prerequisite to the creation of adequate models. When all autocorrelation in a species' distribution is due to autocorrelation in the underlying environmental factors, and all factors are included in a distribution model, spatially explicit modeling is unnecessary (Austin 2002b). Only when a major environmental factor is missed or when ecological processes lead to additional autocorrelation in a species' distribution are spatial models necessary. The questions thus become which ecological processes could lead to spatial autocorrelation in species distributions, and is there any empirical evidence for the effects of such processes?

The ecological process most likely to cause spatial autocorrelation in species distributions is dispersal in the widest sense (Austin 2002b). I use dispersal in the sense of Lidicker (1975), including every movement that constitutes leaving the home area for breeding, but not short-term exploratory and "round-trip" migratory movements. The exchange of individuals between populations may synchronize population sizes (Paradis et al. 1998, Bjørnstad et al. 1999), an effect that is thought to decay with distance because dispersal strength also typically decays with distance. The behavioral motivations for dispersal vary widely (Stenseth and Lidicker 1992a). While it would be interesting and ultimately important to gain a detailed understanding of such motivations, I considered the motivation for dispersal a secondary question in this study and I focused solely on the consequences of dispersal.

Dispersal is difficult to study, particularly at large extents (Stenseth and Lidicker 1992b). Accordingly, very little information on long-distance dispersal is found in the literature. I therefore developed an indirect approach to predict the dispersal activity of bird species and compared this dispersal index to autocorrelation found in their distributions. Because some of the most prominent ecological fields and theories – for example metapopulation dynamics, island biogeography, and studies on population synchrony – have dispersal at their core, I used such theories to develop indirect predictors of dispersal. While such indirect predictors are not well-suited to determining unequivocal cause and effect, the use of several unrelated theories and approaches can still make a strong case (Levins 1966).

The goal of this study was to determine whether dispersal was related to spatial autocorrelation in species distributions above and beyond what can be explained through

spatial autocorrelation in underlying environmental factors. To answer this question, it was necessary to find a consistent way to predict dispersal activity and to determine the amount of spatial autocorrelation in species distributions that could not be explained by autocorrelation in underlying environmental conditions.

4.3 Methods

The methods of this study have two distinct components. First, I needed to analyze the spatial autocorrelation patterns present in each species' distribution. This required finding suitable measures that could characterize both the strength and extent of autocorrelation. In addition, these measures needed to differentiate between autocorrelation caused by autocorrelation in underlying environmental conditions and autocorrelation due to other ecological processes. Second, I needed indices of dispersal strength, derived indirectly from ecological or life history characteristics of the species. Ideally, these dispersal indices would encompass dispersal strength (or volume) and dispersal distance. However, given their indirect nature, they were rather vague, purely comparative measures of dispersal without the concreteness of a dispersal kernel or strategy. The measures of autocorrelation and indices of dispersal are explained in detail below.

4.3.1. Measures of autocorrelation

The source of data, the creation of the spatial models, and the partitioning of sources of variation were described in detail in Chapter 1. However, the sample size of bird species was reduced by one to 107 because of missing data for one species (Appendix). I derived three measures for autocorrelation from these models and the partitioning of variances according to Borcard et al.'s (1992) method. The first measure

was the extent of the neighborhood included in the spatial model (from here on just "Extent"), which was optimized during the modeling process. The second measure was the variation in distribution identified as purely spatial effect during the partitioning of variation following Borcard et al. (1992), from here on called "Space." The third measure was a standardized version of ρ (from here on called "Rho.std"), which was the regression coefficient in front of the neighborhood matrix in the conditional autoregressive models (CAR).

Extent is the maximum distance at which a significant autocorrelation effect can be measured. Extent does not give any indication of the strength of autocorrelation. Note that the way the maximum extent was determined here was not identical to the range of a variogram. In general, the optimal extents of neighborhoods were smaller than the range in variograms on the same data. However, this issue was not a research focus and was not investigated in detail.

The spatial partition of variation in species distributions (Space) was the R^2 of the CAR model minus the R^2 of the traditional environmental model. It describes the variation explained in the CAR model that is attributable neither to the environmental predictors nor to the spatial information implicit in the environmental predictors. Thus, it does not necessarily measure spatial autocorrelation *per se*, but is an indirect index for purely spatial variation in the distribution patterns that could not be explained through environmental variables.

The coefficient ρ indicates the strength of inclusion of the neighborhood matrix in the CAR model, and thus indirectly captures both the strength and the extent of spatial autocorrelation. However, as in other regression coefficients, ρ was also dependent on the

magnitude of and variation in the dependent and independent variables, and the neighborhood matrix. Therefore, I standardized ρ analogously to the standardization of regular regression coefficients (Zar 1996: 420): $b_i' = b_i * s_{X_i} / s_Y$ where b_i' is the standardized regression coefficient of the ith independent variable, b_i is the non-standardized regression coefficient, s_{X_i} is the standard deviation of the independent variable X_i, and s_Y is the standard deviation of the dependent variable Y. In the case of the coefficient ρ in CAR regressions, X is not simply a variable but an expression describing neighborhood effects: $\mathbf{C}(\mathbf{Y} - \mathbf{X}\beta)$, where $\mathbf{C}$ is the neighborhood matrix, $\mathbf{Y}$ is the dependent variable, $\mathbf{X}$ is a matrix of all independent variables and β is a vector of regression coefficients for the independent variables. In practice, I used the observed values of the dependent variable $\mathbf{Y}$ minus the predictions from the purely environmental part of the model $\mathbf{X}\beta$ minus the residuals ε to calculate the spatial signal $\rho\mathbf{C}(\mathbf{Y} - \mathbf{X}\beta)$ (Kaluzny et al. 1996). Taking the standard deviation of the spatial signal is equal to the $b_i * s_{X_i}$ part of the standardized coefficient equation because ρ is a constant multiplier. Therefore, I only needed to divide this value by the standard deviation of $\mathbf{Y}$ to arrive at the standardized coefficient Rho.std.

4.3.2. Independent Variables

4.3.2.1 Density dependence

The first index of dispersal activity was based on density dependence. I assumed that an increase in density dependence would correlate with an increase in dispersal because dispersal was identified as one of the mechanisms through which density dependence is attained (Taylor and Taylor 1977). Boone (1991) derived density dependence scores for breeding birds of the conterminous United States using Pollard et

71

al's (1987) Monte Carlo randomization estimate (from here called "Poll"). In this measure, higher values meant less density dependence. Therefore, I expected this measure to correlate negatively with my measures of autocorrelation.

4.3.2.2. Spatio-temporal Population Dynamics

The second index for dispersal activity used population dynamics characterized by Taylor's Power Law. McArdle et al. (1990) used Taylor's power law to characterize species according to their spatial and temporal variation in population densities. In particular the spatial exponent is relevant to dispersal. This exponent is estimated by the equation: $s^2 = a\ m^b$ (Taylor 1961), where s^2 is the variance in abundance at all locations in a given year, a is a scaling coefficient thought to be related to sampling or computing, m is the mean in abundance across all locations in a given year, and b is the spatial exponent. The exponent b is determined as the slope of a log-log regression of variance vs. mean with individual data points stemming from different years.

When the mean and variance are independent, the expected spatial exponent is two (McArdle et al. 1990). That means that the variance quadruples when the mean doubles across sites. If the exponent is larger than two, the variance more than quadruples, which means that the high-density sites must be extremely packed and the low density sites must stay disproportionately sparsely populated in a good year. In contrast, if the exponent is lower than two, the variance across space increases less than expected with mean abundance meaning that high-density sites are not very high and low density sites are higher than expected. Taylor and Taylor (1977) and Taylor et al. (1983) attributed the variation in the power coefficient to aggregation and dispersal. Accordingly, an exponent smaller than two suggests a reduction in variance among sites

potentially through more dispersal from high-density sites to low-density sites than an exponent larger than two. Alternatively, a similar reduction in variance among sites could be achieved with other mechanisms of density dependence such as reduced birth or increased death rates weakening the connection between the exponent and dispersal. Nevertheless, my prediction is that species with a spatial exponent > 2 will have lower indicators of autocorrelation than species with a spatial exponent ≤ 2. I used the spatial exponent (from here called "Bspatial") calculated by Oyler (1993) for birds of the United States and correlated them with the three measures of autocorrelation using Spearman's rank correlation and expecting a negative correlation.

4.3.2.3. Hanski's deviation from abundance-occupancy relationship

The third indirect index for dispersal activity was derived according to a hypothesis put forward by Hanski et al. (1993). They presented possible explanations for the positive abundance-occupancy relationship, which is a widely documented macroecological pattern within homogenous taxonomic assemblages (Gaston et al. 2000, Holt et al. 2002). One of the explanations was based on metapopulation dynamics and, additionally to explaining the relationship, led to the expectation of a deviation from the relationship. According to their equations, they expected that species with low dispersal activity (i.e., a relatively low percentage of individuals dispersing over a relatively low average distance) would be above the predicted abundance-occupancy relationship, while those with high dispersal (i.e., a relatively high percentage of individuals dispersing over a relatively high average distance) would fall below. I turned the relationship around so that abundance was on the x-axis and range size was on the y-axis (Figure 10) because high average abundance causing a large range is more plausible than a large range

73

causing high average abundance. In my version, species that failed to achieve large

ranges despite high average abundances were assumed to be poor dispersers while

species that had unusually large ranges compared to their average abundances were

assumed to be very active dispersers (Figure 10). In this theory and layout of the

relationship, positive residuals signified active dispersers, while negative residuals stood

for poor dispersers. Therefore, the working hypothesis was that the residuals of a simple

linear regression between abundance and range size (from here called "Ao.resid") would

correlate positively with measures of spatial autocorrelation.
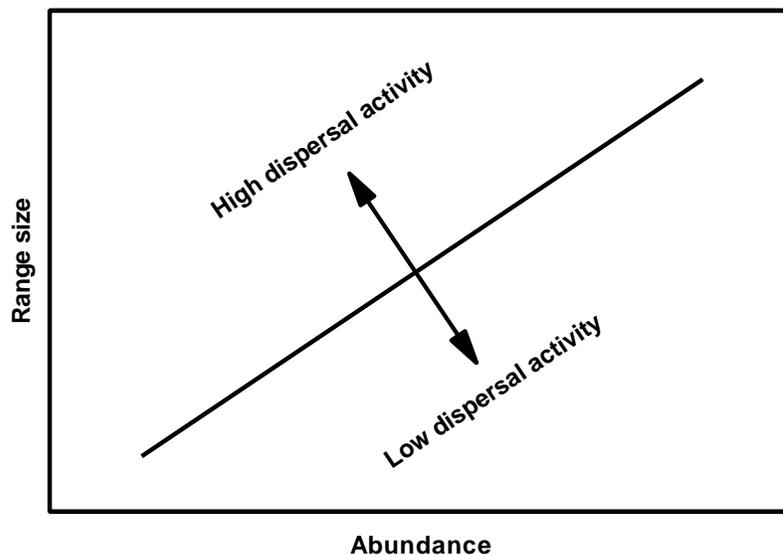
Figure 10. Relationship between average abundance and occupancy (here labeled distribution). While the main relationship is attributed to niche width, deviations from it are caused by rates of dispersal. Adapted from Hanski et al. (1993)

Incidence values are more robust than abundance measures (O'Connor et al. 1996)

but are expected to correlate well with abundance (Wright 1991). Therefore, I used

incidence values over 10 years rather than abundance in the calculation of Ao.resid. I

calculated the average incidence values for each species only across sites with non-zero

incidence values (Gaston et al. 2000). Range size was derived from the Naturserve maps

(Ridgely 2003), also used in the range determination for the distribution models.

4.3.3. Confounding variables

Two variables deserved attention because of their potentially confounding effects

on the relation between dispersal and autocorrelation. The first one was the number of

sampling locations. Species with larger ranges also had more sampling locations and thus

larger sample sizes. Several of the independent and dependent variables described above

were substantially correlated with sample size. These correlations were taken into

consideration by using partial correlations, controlling for the sample size. The second

potentially confounding variable was the potential population growth rate R. I showed in

Chapter 2 that R influences the relationship between dispersal and spatial autocorrelation

in species distributions. Here clutch size (hereafter called "Max.clutch") taken from

Ehrlich et al. (1988) was used as a proxy for R.

All statistics were programmed in S-PLUS 6.2 (Insightful 2003)(use of this

product does not imply endorsement). Rather than presenting hypotheses tests on the

Spearman rank correlations I calculated bootstrap bias-corrected, adjusted 95%

confidence limits (Efron and Tibshirani 1998) to give the reader an impression of the

uncertainty in the regression coefficients. The number of bootstrap resamples was 10,000.

4.4 Results

The three measures of autocorrelation only showed partial agreement (Table 5).

While the standardized regression coefficient for neighborhood inclusion (Rho.std) and

the pure spatial partition (Space) correlated fairly well (r = 0.513, 95% CI: 0.366 - 0.641),

the two measures did not correlate meaningfully with the maximum neighborhood extent.

This result underscores the lack of any systematic relationship between the overall

strength of autocorrelation and its extent.

Table 5. Spearman rank correlation coefficient among three different measures of
autocorrelation. Confidence intervals are bootstrap bias-correct, adjusted 95% probability
limits. N = 107.

Variable 1	Variable 2	r	Lower CI	Upper CI
Space	Extent	0.111	-0.081	0.297
Space	Rho.std	0.513	0.366	0.641
Extent	Rho.std	0.124	-0.086	0.320

The confounding variables had few effects on the three measures of

autocorrelation (Table 6). The only moderately strong correlation was between extent and

the sample size of locations (n). Larger n occur in larger ranges, which can accommodate

larger neighborhoods. In addition, larger n allowed better models, which were more

capable of profiting from small effects caused by distant neighbors. Another weak but

interesting positive correlation existed between the maximum clutch size (Max.clutch)

and Rho.std. When Max.clutch is seen as an index for potential population growth rate,

such a correlation was predicted in Chapter 2.

The three indices for dispersal were only weakly correlated with each other, with

some of the correlations having the opposite sign than expected (Table 7). I expected

Ao.resid to correlate positively with dispersal, while Poll and Bspatial were assumed to

correlate negatively with dispersal. According to these expectations, Poll and Bspatial should have correlated positively, but correlated negatively instead. Poll and Ao.resid should have correlated negatively, but did not show any consistent correlation pattern within the confidence limits. Bspatial and Ao.resid were expected to correlate negatively. While the point estimate for the regression coefficient was consistent with this expectation, the direction of the correlation was inconclusive within the confidence interval. The abundance-occupancy relationship held up fairly well in the Breeding Bird Survey data ($R^2 = 0.11$, F-statistic = 12.33 on 1 and 105 degrees of freedom, p-value = 0.0007).

Table 6. Spearman rank correlation coefficient among three confounding variables and three measures of dispersal. Confidence intervals are bootstrap bias-correct, adjusted 95% probability limits. N = 107.

Variable 1	Variable 2	r	Lower CI	Upper CI
n	Space	-0.030	-0.218	0.168
n	Extent	0.376	0.175	0.538
n	Rho.std	0.025	-0.190	0.233
Max.clutch	Space	0.098	-0.097	0.292
Max.clutch	Extent	0.042	-0.161	0.231
Max.clutch	Rho.std	0.210	0.008	0.381

Table 7. Spearman rank correlation coefficient among three different indices for dispersal derived from three different ecological theories. Confidence intervals are bootstrap bias-correct, adjusted 95% probability limits. N = 107

Variable 1	Variable 2	r	Lower CI	Upper CI
Poll	Bspatial	-0.221	-0.378	-0.039
Poll	Ao.resid	0.140	-0.060	0.313
Bspatial	Ao.resid	-0.114	-0.292	0.085

The three indices of dispersal showed some correlations with confounding variables (Table 8). All three indices correlated with sample size (n), but only Ao.resid correlated strongly. Poll and Bspatial had different signs in front of their correlation

coefficients with n, which may partly explain why they unexpectedly correlated

negatively with each other. Weight and maximum clutch size (Max.clutch) did not show

strong correlations with the three indices.

Table 8. Spearman rank correlation coefficient among three confounding variables and three measures of dispersal. Confidence intervals are bootstrap bias-correct, adjusted 95% probability limits. N = 107.

Variable 1	Variable 2	r	Lower CI	Upper CI
n	Poll	0.321	0.120	0.490
n	Bspatial	-0.234	-0.414	-0.033
n	Ao.resid	0.787	0.688	0.858
Max.clutch	Poll	0.009	-0.178	0.197
Max.clutch	Bspatial	0.033	-0.158	0.228
Max.clutch	Ao.resid	0.013	-0.185	0.207

No meaningful correlations between measures of autocorrelation and indices of

dispersal were found (Table 9). I found only one moderately strong correlation, which

was between Extent and Ao.resid. The most likely cause for this positive correlation was,

however, the positive correlation of both variables with n. Partial correlations controlling

for n lowered regression coefficient in this relationship but left the other correlation

coefficients virtually unchanged (Table 10).

Table 9. Spearman rank correlation coefficient among three measures of spatial autocorrelation and three indices of dispersal. Confidence intervals are bootstrap bias-correct, adjusted 95% probability limits. N = 107.

Variable 1	Variable 2	r	Lower CI	Upper CI
Space	Poll	0.048	-0.146	0.227
Space	Bspatial	0.082	-0.103	0.260
Space	Ao.resid	0.051	-0.145	0.243
Extent	Poll	0.107	-0.092	0.296
Extent	Bspatial	-0.144	-0.328	0.045
Extent	Ao.resid	0.488	0.319	0.632
Rho.std	Poll	0.123	-0.083	0.303
Rho.std	Bspatial	-0.094	-0.271	0.094
Rho.std	Ao.resid	0.075	-0.128	0.262

Table 10. Partial Spearman rank correlation coefficients among three measures of spatial autocorrelation and three indices of dispersal. The correlations are controlled in respect to sample size n. Confidence intervals are bootstrap bias-correct, adjusted 95% probability limits. N = 107.

Variable 1	Variable 2	r	Lower CI	Upper CI
Space	Poll	0.061	-0.146	0.246
Space	Bspatial	0.077	-0.116	0.255
Space	Ao.resid	0.121	-0.072	0.314
Extent	Poll	-0.016	-0.195	0.191
Extent	Bspatial	-0.062	-0.248	0.133
Extent	Ao.resid	0.336	0.162	0.504
Rho.std	Poll	0.121	-0.075	0.320
Rho.std	Bspatial	-0.091	-0.267	0.121
Rho.std	Ao.resid	0.089	-0.078	0.254

4.5 Discussion

This study was unable to find a connection between autocorrelation and indirect indices of dispersal. The absence of correlations prevented conclusions about a possible relationship between dispersal and spatial autocorrelation in species distributions above and beyond what can be explained through spatial autocorrelation in underlying environmental factors. The failure to find the predicted correlations could have had multiple causes, which can be broadly assigned to two categories: the hypothesized relationship did not exist, or, the relationship existed but the selected methods were unsuitable for detecting it. Given that the selected methods were very indirect and that a connection between dispersal and spatial autocorrelation was shown in theory in Chapter 2 and hypothesized by several authors (e.g., Paradis et al. 1998, Bjørnstad et al. 1999, Trenham et al. 2001), I interpret the results predominately as a failure of the methods and not as strong evidence for the absence of an effect.

Despite the failure to find meaningful correlations, there are some lessons to be learned from this study. Therefore, I will discuss the methods in detail, and elucidate the

parts that were most likely responsible for the failure and the parts that seemed to be valuable methodological contributions and offer interesting insights.

A mismatch in scale between the observed effect and the investigated process can prevent meaningful results in ecology (Levin 1992). The data used for deriving the autocorrelation measures were of large spatial extent and coarse grain (the North American Breeding Bird Survey). Thus, the study was set at a coarse scale. The first two indices of dispersal, density dependence (Poll) and the spatial exponent of Taylor's power law (Bspatial) were calculated from the same dataset. Therefore, the scale should have matched, although sometimes the scale at which a phenomenon can be observed is coarser than the scale at which the underlying processes take place (Huston 2002). The last index for dispersal, the deviation from an abundance-occupancy relationship, was not an unequivocal scale match. Abundance-occupancy relationships have been shown at coarse scales that would match the present study (Bock and Ricklefs 1983, Gaston et al. 1999, Gaston et al. 2000). However, Hanski et al.'s (1993) hypothesis concerning the relationship between the residuals from the abundance-occupancy regression and dispersal was based on metapopulation dynamics equations, which are typically concerned with smaller extents than covered here. At these smaller extents, considerable dispersal connects populations. However, overall, a mismatch in scale was likely not a major flaw of this study.

A more obvious weakness of the approach was the indirect nature of the indices of dispersal. How well did the selected measures express dispersal? In the case of dispersal being responsible for the deviation from the abundance-occupancy relationship hypothesized by Hanski et al. (1993), Matter et al. (1993) found some support, while

Gaston and Blackburn (2002) failed to support this theory. Also in disagreement with Hanski et al.'s (1993) theory, Paradis et al. (1998) found in a study of dispersal that wide-spread and abundant species exhibited lower dispersal activity than species with small ranges and low abundances. In addition, the ranges of many of the bird species investigated were only partly in the study area of the conterminous United States. Therefore, some of the range sizes entered in the abundance-occupancy relationship were considerably smaller than the species' entire range. Hanski et al. (1993) considered this point but concluded that partial ranges should also work in this relationship. It remains unclear, though, whether the predicted dispersal is dependent on the proportion of range included in the relationship. In addition, the relationship between dispersal and spatial autocorrelation may be dependent on the specific part of the range included in the study area.

The connection between density-dependence and dispersal has, to my knowledge, no direct empirical support. Population regulation dependent on density is a well supported and universally documented phenomenon (Murdoch 1994). However, it is unclear whether the mechanisms of regulation are mostly local, through birth and death rates, or whether dispersal among populations, as in metapopulation dynamics, is mainly responsible for density-dependence (Murdoch 1994). Although most models implement density-independent dispersal (Amarasekare 2004), organisms typically exhibit density-dependent dispersal (Sutherland et al. 2002). If dispersal is density-dependent, it is fair to assume that dispersal is also at least part of the population density regulation mechanism (Taylor and Taylor 1977). Therefore, using density-dependence as a proxy for dispersal activity is likely not wrong but may be a weak approach dependent on how important

local mechanisms of density-dependence are compared to dispersal. For example, Rodenhouse et al's (1997) theory of density-dependence through site dependence relies on dispersal as the primary mechanism. However, the dispersal exhibited in the context of density-dependence may be of relatively short range and thus may be a scale mismatch to the observed spatial autocorrelation. In addition, an improvement to Pollard et al's (1987) method became available (Link and Hoover 1991) after Boone (1991) used it to calculate density dependence indices for North American breeding birds.

My hypothesis on the negative correlation between the spatial exponent b_s in Taylor's power law and dispersal agrees with Taylor and Taylor's (1977) view, although they called what I defined as dispersal migration. My approach agreed with their concept of dispersal as a process generally counteracting aggregation and thus leading to more uniformly distributed population sizes (see also Chapter 2). However, Taylor and Taylor (1977) also introduced another form of dispersal that leads to more aggregation, which they called congregatory migration and which is caused by intraspecific attraction. In addition, they note that many behaviors, such as the search for food, mates and shelter, antagonistic interactions, and predator avoidance, can lead to movements that obscure the effects of dispersal. Other species-specific characteristics that potentially influence b_s independently of dispersal are the spatial and temporal patterns of relevant environmental conditions, and population growth rate. Therefore, while the basic hypothesis was probably correct, there are many reasons why the connection could have been weak.

A final issue that could have caused the lack of meaningful correlations was the variability in sample size n among species. Each species had a different range size and accordingly a different number of included sample points. While I did consider

82

correlations with n (Table 6 and Table 8) and controlled for n where appropriate (Table 10), not all problems arising from differences in sample size were obvious or easily controlled. Most importantly, sample size influenced the quality of the models and thus variable selection, efficiency of models in differentiating between noise and signal, and parameter estimates. In brief, the uncertainty encompassed in the models of the different species varied because n varied, and this additional variation may well have weakened existing correlations between indices of dispersal and measures of autocorrelation.

In conclusion, the selected indices for dispersal were likely neither inappropriate, nor at a wrong scale. The most likely explanation for the absence of results was the indirect nature of the ecological indices. The noise in the data overwhelmed the information in these approaches, a conclusion supported by the absence of correlation among the three indices. Future research needs to be based on direct, empirical dispersal information such as used for British birds in Paradis et al. (1998).

CONCLUSION

Chapter 1 of this dissertation revealed strong autocorrelation patterns at the national level in bird distributions. While spatial autocorrelation in environmental variables accounted for most of the explained variation (65%), 17% of the explained variation was due to neighborhood effects and spatial position within the range of the bird abundances themselves (from here on called "residual autocorrelation"). In other words, the observed bird abundances deviated consistently from the values predicted through environmental conditions, depending on the position in the range and the abundances of neighboring populations.

If neighboring populations influence each other's abundances independently of environmental conditions, some exchange among the populations must exist. Certainly, many different mechanisms, behaviors and motivations may be responsible for such exchange, but all explanations have one thing in common: movement of individuals through the landscape and therefore dispersal in the broadest sense.

The preceding results inspired the use of a simulation model (Chapter 2) to explore the mechanics and sensitivities of the hypothesized effects of dispersal on autocorrelation. I constructed the model such that populations on a regular grid were connected by dispersal. In this model, dispersal caused residual autocorrelation in the distribution of abundances above and beyond the autocorrelation that was already built into the underlying carrying capacities. The effect was dependent on the potential population growth rate of the simulated species. A high growth rate led to a dominance of local recruitment and a low effect of dispersal. In contrast, a low growth rate led to strong

influences of migrants and thus a large increase in autocorrelation in abundances even with moderate levels of dispersal. Thus, from an ecological standpoint, species with low potential population growth rates are more dependent on neighborhood effects than those with high growth rates. These neighborhood effects cause them to deviate from the distribution that would be expected if environmental conditions were the only predictors.

While Chapter 2 covered the spatial effects of neighborhood relationships, the simulation modeling of Chapter 3 focused on the position in the range as an explanation for residual autocorrelation. I established in Chapter 2 that residual autocorrelation in species distributions could be caused by position in the range or neighborhood effects. The trend surface used in the spatial models is mostly able to capture long-waved spatial patterns, which most closely correspond to "position in the range," while the neighborhood matrix included in the spatial regression models captures short-waved patterns or "neighborhood effects." It is important to understand that the different environmental conditions typically found throughout the range have already been accounted for and that only the purely spatial residual effect of the "position in the range" is the focus of this research. Therefore, environmental conditions expressed as carrying capacities in the simulation model of Chapter 3 were randomly sampled from the same distribution throughout the range. The resultant abundance structure in the range was caused exclusively by dispersal. Populations at the periphery of the range had smaller population sizes than those at the core because the isolation of populations at the periphery caused them to lose more individuals to emigration than they gained through immigration. In contrast, the populations in the core had a neutral dispersal balance. Again, the magnitude of this effect was dependent on the potential population growth

rate, with a lower rate leading to higher differences in population sizes between the core and the periphery than high growth rates. The ecological lesson of Chapter 3 was that the typical peak and tail range structure observed in many species need not be caused exclusively by environmental conditions or competition, but may also be caused by the dispersal and relative isolation of populations at range edges. Thus, position in the range could cause deviations from the distribution predicted by environmental conditions only.

Chapter 4 attempted to verify the connection between residual autocorrelation and dispersal in empirical data. Because no dispersal data were available for the modeled bird species at the coarse scale of the Breeding Bird Survey (BBS), I used indirect predictions of dispersal strength through indices based on metapopulation ecology, Taylor's Power Law and density dependence. The empirical verification was unsuccessful, most likely because the selected indices carried too much noise and too little information.

While empirical testing of the link between dispersal and autocorrelation remained inconclusive, a solid theoretical and methodological foundation for future research on this link and its significance to distribution modeling has been established. Building on this foundation will require better information on the dispersal characteristics of individual species if the consequences of dispersal to the species' distribution are to be fully understood. In addition, further consideration of the behavior and autecology of each individual species would allow models to better account for residual variance. In particular, different dispersal behaviors may lead to different dispersal kernels and dispersal strengths, with very different consequences to distributions of individual species. While it may be scientifically more satisfying to establish the underlying core relationship or law of a phenomenon first and investigate the deviations from the law

86

later, an earlier control for residual variance may often be necessary in ecology if a weak

signal is to be extracted from noise.

BIBLIOGRAPHY

Akaike, H. 1981. Modern development of statistical methods. Pages 169-184 *in* P. Eykhoff, editor. Trends and progress in systems identification. Pergamon Press, Oxford, England.

Amarasekare, P. 1998. Interactions between local dynamics and dispersal: Insights from single species models. Theoretical Population Biology 53:44-59.

_____. 2004. Spatial variation and density-dependent dispersal in competitive coexistence. Proceedings of the Royal Society of London - Series B: Biological Sciences 271:1497-1506.

American Ornithologists' Union. 1998. Checklist of North American Birds. 7th edition. American Ornithologists' Union, Washington, DC, USA.

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, IL, USA.

_____. 1984. The ecological web: More on the distribution and abundance of animals. University of Chicago Press, Chicago, IL, USA.

Augustin, N. H., M. A. Muggleston, and S. T. Buckland. 1996. An autologistic model for the spatial distribution of wildlife. Journal of Applied Ecology 33:339-347.

Austin, M. P. 2002a. Case studies of the use of environmental gradients on vegetation and fauna modelling: Theory and practice in Australia and New Zealand. Pages 73-82 *in* M. J. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington, DC, USA.

_____. 2002b. Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. Ecological Modelling 157:101-118.

Balmer, O. 2002. Species lists in ecology and conservation: Abundances matter. Conservation Biology 16:1160-1161.

Begon, M., and M. Mortimer. 1986. Population ecology: A unified study of animals and plants. 2nd edition. Blackwell Scientific, Oxford, UK.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: Analyzing patterns and processes of population synchrony. Trends in Ecology & Evolution 14:427-432.

Bock, C. E., and R. E. Ricklefs. 1983. Range size and local abundance of some North American songbirds: A positive correlation. American Naturalist 122:295-299.

Boone, R. B. 1991. Construction of a database used in analyses of bird populations and agriculture, with a study of density dependence. M.S., University of Maine, Orono, ME.

Borcard, D., and P. Legendre. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. Ecological Modelling 153:51-68.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the Spatial Component of Ecological Variation. Ecology 73:1045-1055.

Breiman, L. 1984. Classification and regression trees. Wadsworth International Group, Belmont, CA, USA.

Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. Ecology 76:2028-2043.

Bullock, J. M., R. Kenward, and R. Hails, editors. 2002. Dispersal ecology: The 42nd symposium of the British Ecological Society held at the University of Reading, 2-5 April 2001. 1st edition. Blackwell Publishing, Malden, MA, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, NY, USA.

Case, T. J., R. D. Holt, M. A. McPeek, and T. H. Keitt. 2005. The community context of species' borders: Ecological and evolutionary perspectives. Oikos 108:28.

Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nicholas, editors. 2001. Dispersal. Oxford University Press, Oxford, UK.

Cohen, D., and S. A. Levin. 1991. Dispersal in patchy environments the effects of temporal and spatial structure. Theoretical Population Biology 39:63-99.

Costanza, R., and M. Ruth. 2001. Dynamic systems modeling. Pages 21-29 *in* R. Costanza, B. S. Low, E. Ostrom, and J. Wilson, editors. Institutions, Ecosystems, and Sustainability. Lewis Publishers, Boca Raton, FL, USA.

Cressie, N. A. C. 1993. Statistics for spatial data. Wiley, New York, NY, USA.

Dale, M. R. T., P. Dixon, M.-J. Fortin, P. Legendre, D. E. Myers, and M. S. Rosenberg. 2002. Conceptual and mathematical relationships among methods for spatial analysis. Ecography 25:558-577.

Dale, M. R. T., and M.-J. Fortin. 2002. Spatial autocorrelation and statistical tests in ecology. Ecoscience 9:162-167.

De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. Ecology 81:3178-3192.

DeStefano, S., and R. G. Haight. 2002. Forest wildlife-habitat relationships: Population and community responses to forest management. Society of American Foresters, Bethseda, MD, USA.

Dias, P. C. 1996. Sources and sinks in population biology. Trends in Ecology & Evolution 11:326-330.

Diniz-Filho, J. A. F., L. M. Bini, and B. A. Hawkins. 2003. Spatial autocorrelation and red herrings in geographical ecology. Global Ecol Biogeography 12:53-64.

Efron, B., and R. Tibshirani. 1998. An introduction to the bootstrap. Volume 57. Chapman & Hall/CRC, Boca Raton, FL, USA.

Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook: A field guide to the natural history of North American birds: Including all species that regularly breed north of Mexico. Simon & Schuster, New York, NY, USA.

Ellner, S. P., and Y. Seifu. 2002. Using spatial statistics to select model complexity. Journal of Computational & Graphical Statistics 11:348-369.

Engen, S., R. Lande, and B.-E. Saether. 2002. Migration and spatiotemporal variation in population dynamics in a heterogeneous environment. Ecology 83:570-579.

Fortin, M. J., T. H. Keitt, B. A. Maurer, M. L. Taper, D. M. Kaufman, and T. M. Blackburn. 2005. Species' geographic ranges and distributional limits: Pattern analysis and statistical issues. Oikos 108:7.

Freeman, M. F., and J. W. Tukey. 1950. Transformations related to the angular and the square root. The Annals of Mathematical Statistics 21:607-611.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, UK.

Gaston, K. J., and T. M. Blackburn. 2003. Dispersal and the interspecific abundance-occupancy relationship in British birds. Global Ecol Biogeography 12:373-379.

Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance-occupancy relationships. Journal of Applied Ecology 37:39-59.

Gaston, K. J., T. M. Blackburn, and R. D. Gregory. 1999. Intraspecific abundance-occupancy relationships: Case studies of six bird species in Britain. Diversity & Distributions 5:197-212.

Goodchild, M. F., and J. Proctor. 1997. Scale in a digital geographic world. Geographical and Environmental Modelling 1:5-23.

Goodwin, B. J., and L. Fahrig. 1998. Spatial scaling and animal population dynamics. Pages 193-206 *in* D. L. Peterson, and V. T. Parker, editors. Complexity in Ecological Systems; Ecological scale: Theory and applications. Columbia University Press, New York, NY, USA.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135:147-186.

Guo, Q., M. Taper, M. Schoenberger, and J. Brandle. 2005. Spatial-temporal population dynamics across species range: From centre to margin. Oikos 108:47.

Haining, R. P. 1990. Spatial data analysis in the social and environmental sciences. Cambridge University Press, Cambridge, UK.

Hanski, I. 1992. Inferences from ecological incidence functions. American Naturalist 139:657-662.

_____. 1998. Metapopulation dynamics. Nature 396:41-49.

_____. 1999. Metapopulation ecology. Oxford University Press, Oxford, UK.

_____. 2001. Spatially realistic theory of metapopulation ecology. Naturwissenschaften 88:372-381.

Hanski, I., J. Kouki, and A. Halkka. 1993. Three explanations of the positive relationship between distribution and abundance of species. Pages 108-116 *in* R. E. Ricklefs, and D. Schluter, editors. Species diversity in ecological communities: Historical and geographical perspectives. University of Chicago Press, Chicago, IL, USA.

Haydon, D. T., and E. R. Pianka. 1999. Metapopulation theory, landscape models, and species diversity. Ecoscience 6:316-328.

Heino, M., and I. Hanski. 2001. Evolution of migration rate in a spatially realistic metapopulation model. American Naturalist 157:495-511.

Holt, A. R., K. J. Gaston, and F. He. 2002. Occupancy-abundance relationships and spatial distribution: A review. Basic & Applied Ecology 3:1-13.

Holt, R. D., and T. H. Keitt. 2005. Species' borders: A unifying theme in ecology. Oikos 108:3.

Holt, R. D., T. H. Keitt, M. A. Lewis, B. A. Maurer, and M. L. Taper. 2005. Theoretical models of species' borders: Single species approaches. Oikos 108:18.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ, USA.

Hudson, P. J., and I. M. Cattadori. 1999. The Moran effect: A cause of population synchrony. Trends in Ecology & Evolution 14:1-2.

Huston, M. A. 2002. Ecological context for predicting occurrences. Pages 7-21 *in* M. J. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington, DC, USA.

Insightful. 2003. S-PLUS version 6.2. Seattle, WA, USA.

James, F. C., and C. E. McCulloch. 1990. Multivariate Analysis in Ecology and Systematics Panacea or Pandora's Box? Pages 129-166 *in* R. F. Johnston, editor. Annual Review of Ecology and Systematics. Annual Reviews Inc., Palo Alto, CA, USA.

Johst, K., and R. Brandl. 1997. The effect of dispersal on local population dynamics. Ecological Modelling 104:87-101.

Johst, K., R. Brandl, and S. Eber. 2002. Metapopulation persistence in dynamic landscapes: The role of dispersal distance. Oikos 98:263-270.

Kaluzny, S. P., S. C. Vega, T. P. Cardoso, and A. A. Shelly. 1996. S+SPATIALSTATS User's Manual, Version 1.0. MathSoft, Inc., Seattle, WA, USA.

Keitt, T. H. 2003. Spatial autocorrelation, dispersal and the maintenance of source-sink populations. Pages 225-238 *in* G. A. Bradshaw, P. A. Marquet, and K. L. Ronnenberg, editors. How landscapes change: Human disturbance and ecosystem fragmentation in the Americas. Springer-Verlag, Berlin, Germany.

Keitt, T. H., O. N. Bjornstad, P. M. Dixon, and S. Citron-Pousty. 2002. Accounting for spatial pattern when modeling organism-environment interactions. Ecography 25:616-625.

Kendall, B. E., O. N. Bjornstad, J. Bascompte, T. H. Keitt, and W. F. Fagan. 2000. Dispersal, environmental correlation, and spatial synchrony in population dynamics. American Naturalist 155:628-636.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. American Naturalist 150:1-23.

Koenig, W. D. 1998. Spatial autocorrelation in California land birds. Conservation Biology 12:612-620.

_____. 1999. Spatial autocorrelation of ecological phenomena. Trends in Ecology & Evolution 14:22-25.

_____. 2001. Spatial autocorrelation and local disappearances in wintering North American birds. Ecology 82:2636-2644.

_____. 2002. Global patterns of environmental synchrony and the Moran effect. Ecography 25:283-288.

Koenig, W. D., and J. M. H. Knops. 1998. Testing for spatial autocorrelation in ecological studies. Ecography 21:423-429.

Krebs, C. J. 1972. Ecology: The experimental analysis of distribution and abundance. Harper & Row, New York, NY, USA.

Leathwick, J. R. 1996. Use of spatial autocorrelation analysis to test predictive spatial models of New Zealand forest tree species. *in* Proceedings of 1996 Annual Combined Meeting of the Ecological Society of America on Ecologists/Biologists as Problem Solvers, Providence, RI, USA.

_____. 1998. Are New Zealand's Nothofagus species in equilibrium with their environment? Journal of Vegetation Science 9:719-732.

Legendre, P. 1993. Spatial autocorrelation: Trouble or new paradigm? Ecology 74:1659-1673.

Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio 80:107-138.

Legendre, P., and L. Legendre. 1998. Numerical ecology. 2nd English edition. Elsevier, Amsterdam, Netherlands.

Lennon, J. J. 2000. Red-shifts and red herrings in geographical ecology. Ecography 23:101-113.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943-1967.

Levins, R. 1966. The strategy of model building in population ecology. American Scientist 54:421-431.

Lichstein, J. W., T. R. Simons, S. A. Shriner, and K. E. Franzreb. 2002. Spatial autocorrelation and autoregressive models in ecology. Ecological Monographs 72:445-463.

Lidicker, W. Z. J. 1975. The role of dispersal in the demography of small mammals. Pages 103-128 *in* F. B. Golley, K. Petrusewicz, and L. Ryszkowski, editors. Small Mammals: Their Productivity and Population Dynamics. Cambridge University Press, Cambridge, England.

Link, W. A., and B. A. Hoover. 1991. The detection of density-dependence from a series of annual census: A comment. Ecology 72:1514-1515.

Loveland, T. R., J. W. Merchant, D. O. Ohlen, and J. F. Brown. 1991. Development of a land-cover characteristics database for the conterminous U.S. Photogrammetric Engineering and Remote Sensing 57:1453-1463.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ, USA.

Matter, S. F., I. Hanski, and M. Gyllenberg. 2002. A test of the metapopulation model of the species-area relationship. Journal of Biogeography 29:977-983.

McArdle, B. H., K. J. Gaston, and J. H. Lawton. 1990. Variation in the size of animal populations patterns problems and artifacts. Journal of Animal Ecology 59:439-454.

McGill, B., and C. Collins. 2003. A unified theory for macroecology based on spatial patterns of abundance. Evolutionary Ecology Research 5:469-492.

Meot, A., P. Legendre, and D. Borcard. 1998. Partialling out the spatial component of ecological variation: Questions and propositions in the linear modelling framework. Environmental & Ecological Statistics 5:1-27.

Miller, J., and J. Franklin. 2002. Modeling the distribution of four vegetation alliances using generalized linear models and classification trees with spatial dependence. Ecological Modelling 157:227-247.

Morrison, M. L., and L. S. Hall. 2002. Standard terminology: Toward a common language to advance ecological understanding and applications. Pages 43-52 *in* M. J. Scott, P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington, DC, USA.

Murdoch, W. W. 1994. Population Regulation in Theory and Practice. Ecology 75:271-287.

Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination. Biometrika 78:691-692.

O'Connor, R. J., M. T. Jones, R. B. Boone, and T. B. Lauber. 1999. Linking continental climate, land use, and land patterns with grassland bird distribution across the conterminous United States. Studies in Avian Biology 19:45-59.

O'Connor, R. J., M. T. Jones, D. White, C. Hunsaker, T. Loveland, B. Jones, and E. Preston. 1996. Spatial partitioning of environmental correlates of avian biodiversity in the conterminous United States. Biodiversity Letters 3:97-110.

Overton, J. M. 1996. Spatial autocorrelation and dispersal in mistletoes: Field and simulation results. Vegetatio 125:83-98.

Oyler, S. J. 1993. Avian bioindicator dynamics. M.S., University of Maine, Orono, ME.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns of natal and breeding dispersal in birds. Journal of Animal Ecology 67:518-536.

Parmesan, C., S. Gaines, L. Gonzalez, D. M. Kaufman, J. Kingsolver, A. T. Peterson, and R. Sagarin. 2005. Empirical perspectives on species borders: From traditional biogeography to global change. Oikos 108:58.

Peakall, R., M. Ruibal, and D. B. Lindenmayer. 2003. Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. Evolution 57:1182-1195.

Pollard, E., K. H. Lakhani, and P. Rothery. 1987. The detection of density-dependence from a series of annual censuses. Ecology 68:2046-2055.

Pulliam, H. R. 1988. Sources sinks and population regulation. American Naturalist 132:652-661.

_____. 1996. Sources and sinks: Empirical evidence and population consequences. Pages 45-69 *in* O. E. Rhodes, Jr., R. K. Chesser, and M. H. Smith, editors. Population dynamics in ecological space and time. University of Chicago Press, Chicago, IL, USA.

Pulliam, H. R., and B. J. Danielson. 1991. Sources behavior and density regulation in house mice living in large enclosures. American Naturalist 137:S50-S66.

Ridgely, R. S., T.F. Allnutt, T. Brooks, D.K. McNicol, D.W. Mehlman, B.E. Young, and J.R. Zook. 2003. Digital distribution maps of the birds of the western hemisphere, version 1.0. NatureServe, Arlington, VA, USA.

Ripa, J. 2000. Analysing the Moran effect and dispersal: Their significance and interaction in synchronous population dynamics. Oikos 89:175-187.

Robbins, C. S., D. Bystrak, and P. H. Geissler. 1986. The breeding bird survey: Its first fifteen years. Fish Wildlife Service. Resource Publication 177.

Rodenhouse, N. L., T. W. Sherry, and R. T. Holmes. 1997. Site-dependent regulation of population size: A new synthesis. Ecology 78:2025-2042.

Saether, B.-E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642-653.

Sauer, J. R., J. E. Hines, G. Gough, I. Thomas, and B. G. Peterjohn. 1997. The North American Breeding Bird Survey Results and Analysis. Version 96.4. Patuxent Wildlife Research Center.

Sauer, J. R., B. G. Peterjohn, and W. A. Link. 1994. Observer differences in the North American breeding bird survey. Auk 111:50-62.

Schiegg, K. 2003. Environmental autocorrelation: Curse or blessing? Trends in Ecology & Evolution 18:212-214.

Schooley, R. L., and J. A. Wiens. 2003. Finding habitat patches and directional connectivity. Oikos 102:559-570.

Scott, J. M., H. Anderson, F. Davis, S. Caicoo, B. Csuti, Edwards Thomas C, Jr., R. Noss, J. Ulliman, C. Groves, and R. G. Wright. 1993. Gap analysis: A geographic approach to protection of biological diversity. Wildlife Monographs 123:1-41.

Scott, J. M., and B. Csuti. 1997. Gap analysis for biodiversity survey and maintenance. Pages 321-340 *in* M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, editors. Biodiversity, II. Understanding and protecting our biological resources. Joseph Henry Press, Washington, DC, USA.

Scott, J. M., B. Csuti, and S. Caicco. 1991a. Gap analysis assessing protection needs. Pages 15-26 *in* W. E. Hudson, editor. Landscape linkages and biodiversity: Defenders of wildlife. Island Press, Washington, DC, USA.

Scott, J. M., B. Csuti, and F. Davis. 1991b. Gap analysis an application of geographic information systems for wildlife species. Pages 167-180 *in* D. J. Decker, editor. Challenges in the conservation of biological resources: A practitioner's guide. Westview Press, Boulder, CO, USA.

Scott, M. J., P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. 2002. Predicting species occurrences: Issues of accuracy and scale. Island Press, Washington, DC, USA.

Scott, M. J., T. H. Tear, and F. W. Davis, editors. 1996. GAP analysis: A landscape approach to biodiversity planning. American Society for Photogrammetry and Remote Sensing, Bethesda, MD, USA.

Selmi, S., and T. Boulinier. 2001. Ecological biogeography of Southern Ocean islands: The importance of considering spatial issues. American Naturalist 158:426-437.

Stenseth, N. C., and W. Z. Lidicker, Jr., editors. 1992a. Animal dispersal: Small mammals as a model. Chapman and Hall, London, England.

_____. 1992b. The study of dispersal a conceptual guide. Pages 5-20 *in* N. C. Stenseth, and W. Z. Lidicker, Jr., editors. Animal dispersal: Small mammals as a model. Chapman and Hall, London, England.

Student. 1914. The elimination of spurious correlation due to position in time or space. Biometrika 10:179-181.

Sutherland, W. J., J. A. Gill, and K. Norris. 2002. Density-dependent dispersal in animals: Concepts, evidence, mechanisms and consequences. Pages 134-151 *in* J. M. Bullock, R. E. Kenward, and R. S. Hails, editors. Dispersal ecology. Blackwell Science, Oxford, UK.

Taylor, L. R. 1961. Aggregation, variance and the mean. Nature 189:732-735.

Taylor, L. R., and R. A. J. Taylor. 1977. Aggregation migration and population mechanics. Nature 265:415-421.

Taylor, L. R., R. A. J. Taylor, I. P. Woiwod, and J. N. Perry. 1983. Behavioural dynamics. Nature 303:801-804.

Therneau, T. M., and E. J. Atkinson. 1997. An introduction to recursive partitioning using the rpart routines. Department of Health Science Research, Mayo Clinic, Rochester, MN, USA.

Thomson, J. D., G. Weiblen, B. A. Thomson, S. Alfaro, and P. Legendre. 1996. Untangling multiple factors in spatial distributions: Lilies, gophers, and rocks. Ecology 77:1698-1715.

Tobler, W. R. 1970. A computer movie simulating urban growth in the detroit region. Economic Geography 46:234-240.

Travis, J. M. J., D. J. Murrell, and C. Dytham. 1999. The evolution of density-dependent dispersal. Proceedings of the Royal Society of London - Series B: Biological Sciences 266:1837-1842.

Trenham, P. C., W. D. Koenig, and H. B. Shaffer. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. Ecology 82:3519-3530.

van Horssen, P. W., E. J. Pebesma, and P. P. Schot. 2002. Uncertainties in spatially aggregated predictions from a logistic regression model. Ecological Modelling 154:93-101.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. 4th edition. Springer, New York, NY, USA.

Walker, P. A., and K. D. Cocks. 1991. HABITAT: A procedure for modelling a disjoint environmental envelope for a plant or animal species. Global Ecology and Biogeography Letters 1:108-118.

White, D., A. J. Kimmerling, and W. S. Overton. 1992. Cartographic and geometric components of a global sampling design for environmental monitoring. Cartography and Geographic Information Systems 19:5-21.

Wiegand, T., K. A. Moloney, J. Naves, and F. Knauer. 1999. Finding the missing link between landscape structure and population dynamics: A spatially explicit perspective. American Naturalist 154:605-627.

Wright, D. H. 1991. Correlations between incidence and abundance are expected by chance. Journal of Biogeography 18:463-466.

Zar, J. H. 1996. Biostatistical analysis. 3rd edition. Prentice Hall, Upper Saddle River, NJ, USA.

APPENDIX

LIST OF STUDY SPECIES

Table A.1. List of common and scientific names of the 108 bird species used in this dissertation. Names from the 7th edition of the Checklist of North American Birds (American Ornithologists' Union 1998).

Common name	Scientific Name
Little Blue Heron	*Egretta caerulea*
Cattle Egret	*Bubulcus ibis*
Green Heron	*Butorides virescens*
Common Snipe	*Gallinago delicata*
Northern Bobwhite	*Colinus virginianus*
California Quail	*Callipepla californica*
Black Vulture	*Coragyps atratus*
Burrowing Owl	*Athene cunicularia*
Yellow-billed Cuckoo	*Coccyzus americanus*
Black-billed Cuckoo	*Coccyzus erythropthalmus*
Downy Woodpecker	*Picoides pubescens*
Yellow-bellied Sapsucker	*Sphyrapicus varius*
Pileated Woodpecker	*Dryocopus pileatus*
Red-headed Woodpecker	*Melanerpes erythrocephalus*
Red-bellied Woodpecker	*Melanerpes carolinus*
Chuck-will's-widow	*Caprimulgus carolinensis*
Common Nighthawk	*Chordeiles minor*
Chimney Swift	*Chaetura pelagica*
Western Kingbird	*Tyrannus verticalis*
Western Wood-Pewee	*Contopus sordidulus*
Acadian Flycatcher	*Empidonax virescens*
Least Flycatcher	*Empidonax minimus*
Blue Jay	*Cyanocitta cristata*
Fish Crow*	*Corvus ossifragus*
Bobolink	*Dolichonyx oryzivorus*
Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*
Eastern Meadowlark	*Sturnella magna*
Western Meadowlark	*Sturnella neglecta*
Orchard Oriole	*Icterus spurius*
Bullock's Oriole	*Icterus bullockii*
Brewer's Blackbird	*Euphagus cyanocephalus*
Common Grackle	*Quiscalus quiscula*
Evening Grosbeak	*Coccothraustes vespertinus*
Purple Finch	*Carpodacus purpureus*
House Finch	*Carpodacus mexicanus*

* Omitted in Chapter 4.

Table A.1. Continued.

Common name	Scientific Name
American Goldfinch	*Carduelis tristis*
Lesser Goldfinch	*Carduelis psaltria*
Pine Siskin	*Carduelis pinus*
Vesper Sparrow	*Pooecetes gramineus*
Savannah Sparrow	*Passerculus sandwichensis*
Grasshopper Sparrow	*Ammodramus savannarum*
Lark Sparrow	*Chondestes grammacus*
White-throated Sparrow	*Zonotrichia albicollis*
Chipping Sparrow	*Spizella passerina*
Clay-colored Sparrow	*Spizella pallida*
Field Sparrow	*Spizella pusilla*
Song Sparrow	*Melospiza melodia*
Swamp Sparrow	*Melospiza georgiana*
Eastern Towhee	*Pipilo erythrophthalmus*
Northern Cardinal	*Cardinalis cardinalis*
Rose-breasted Grosbeak	*Pheucticus ludovicianus*
Black-headed Grosbeak	*Pheucticus melanocephalus*
Blue Grosbeak	*Passerina caerulea*
Indigo Bunting	*Passerina cyanea*
Painted Bunting	*Passerina ciris*
Dickcissel	*Spiza americana*
Lark Bunting	*Calamospiza melanocorys*
Western Tanager	*Piranga ludoviciana*
Scarlet Tanager	*Piranga olivacea*
Summer Tanager	*Piranga rubra*
Purple Martin	*Progne subis*
Tree Swallow	*Tachycineta bicolor*
Violet-green Swallow	*Tachycineta thalassina*
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*
Cedar Waxwing	*Bombycilla cedrorum*
Loggerhead Shrike	*Lanius ludovicianus*
Red-eyed Vireo	*Vireo olivaceus*
Warbling Vireo	*Vireo gilvus*
White-eyed Vireo	*Vireo griseus*
Black-and-white Warbler	*Mniotilta varia*
Prothonotary Warbler	*Protonotaria citrea*
Nashville Warbler	*Vermivora ruficapilla*
Orange-crowned Warbler	*Vermivora celata*

Table A.1. Continued.

Common name	Scientific Name
Yellow Warbler	*Dendroica petechia*
Magnolia Warbler	*Dendroica magnolia*
Chestnut-sided Warbler	*Dendroica pensylvanica*
Blackburnian Warbler	*Dendroica fusca*
Black-throated Green Warbler	*Dendroica virens*
Pine Warbler	*Dendroica pinus*
Prairie Warbler	*Dendroica discolor*
Ovenbird	*Seiurus aurocapilla*
Mourning Warbler	*Oporornis philadelphia*
MacGillivray's Warbler	*Oporornis tolmiei*
Common Yellowthroat	*Geothlypis trichas*
Yellow-breasted Chat	*Icteria virens*
Hooded Warbler	*Wilsonia citrina*
Canada Warbler	*Wilsonia canadensis*
American Redstart	*Setophaga ruticilla*
Northern Mockingbird	*Mimus polyglottos*
Gray Catbird	*Dumetella carolinensis*
Brown Thrasher	*Toxostoma rufum*
Carolina Wren	*Thryothorus ludovicianus*
Bewick's Wren	*Thryomanes bewickii*
House Wren	*Troglodytes aedon*
Winter Wren	*Troglodytes troglodytes*
Sedge Wren	*Cistothorus platensis*
White-breasted Nuthatch	*Sitta carolinensis*
Red-breasted Nuthatch	*Sitta canadensis*
Brown-headed Nuthatch	*Sitta pusilla*
Tufted Titmouse	*Baeolophus bicolor*
Black-capped Chickadee	*Poecile atricapillus*
Carolina Chickadee	*Poecile carolinensis*
Blue-gray Gnatcatcher	*Polioptila caerulea*
Wood Thrush	*Hylocichla mustelina*
Veery	*Catharus fuscescens*
Hermit Thrush	*Catharus guttatus*
American Robin	*Turdus migratorius*
Eastern Bluebird	*Sialia sialis*

BIOGRAPHY OF THE AUTHOR

Volker Bahn was born in Munich, Germany. He grew up in Taufkirchen and graduated from Gymnasium Unterhaching in 1988. He attended Philipps-University Marburg, Germany, and graduated in 1998 with a "Diplom Biologe" degree (M.S. equivalent), majoring in conservation biology and minoring in botany, ecology, and cultural anthropology. During his degree program, he spent a year abroad as a visiting student at the University of Victoria, British Columbia, Canada.

Before coming to Maine, Volker worked for the British Columbia Ministry of Environment, Lands, and Parks and the University of Victoria. He also was a visiting research scholar at Auburn University and consulted for Albert-Ludwigs-University Freiburg, Germany, and Yale University. He published four articles in peer-reviewed journals and three in a peer-reviewed government publication. Volker is member of the Society for Conservation Biology and the Ecological Society of America.

Volker entered the Wildlife Ecology graduate program in January 2002, and was awarded the Outstanding Graduate Student Award from the Department of Wildlife Ecology in 2005. After receiving his degree, he will commence a postdoctoral position at McGill University, Montreal, Quebec, Canada. Volker is a candidate for the Doctor of Philosophy degree in Wildlife Ecology from the University of Maine in August, 2005.