Toward a theory of abundance at large spatial scales

by

Richard Evan Feldman

Department of Biology

McGill University

Montréal, Québec, Canada

June, 2011

A thesis submitted to McGill University in partial fulfillment of the

requirements for the degree of Doctor of Philosophy.

Abstract

Fundamentally, ecology is the study of the diversity, distribution, and abundance of organisms. Recent advances in technology coupled with expanding research goals have lead to studies of how the first two of these properties vary over large spatial scales. There has been relatively few cases documenting large scale spatial variation in abundance and very little theoretical development explaining such variation. Yet a general pattern exists: a species is abundant in very few places and rare in most places in its range. Current theory suggests that such a pattern of abundance reflects underlying spatial variation in the environment. In this thesis, I used observational, experimental, theoretical, and statistical approaches to test the type of environmental variation and how such environmental variation combines with interspecific competition to generate spatial variation in abundance. For two species of hummingbirds, I found that different environmental factors related to abundance than to occupancy. Interspecific competition altered spatial variation in abundance in different ways depending on the niche differences among competing species. Interspecific competition also mediated the effect of the environment on abundance by influencing the relative costs and benefits of different hummingbird foraging strategies. I also found that abundance data can be used to predict species' response to climate change because statistical models minimize the noise inherent in abundance datasets. Despite my findings, a theory of abundance is still in its infancy. It is not known whether there is generality in the number and identity of large scale environmental gradients that affect abundance. Similarly, more work needs to be done connecting the small scale interplay between environment, species traits, behaviour, and competition to a broader geographic

context. There are also dispersal and non-niche based approaches to spatial variation in abundance that need to be reconciled with current theory. In this way, a more general theory relating macroevolutionary dynamics to macroecological patterns can be developed.

Résumé

L'écologie est l'étude de la diversité, des distributions et des abondances des organismes vivants. Les avancées technologiques récentes couplées à une expansion des objets de recherche ont permis à une étude approfondie de la variation de ces deux premières propriétés sur de très grandes échelles spatiales. Les variations en abondance sont, quant à elles, peu documentées aux grandes échelles spatiales et les développements théoriques correspondant restent limités. Il existe pourtant un pattern prévalent : une espèce donnée est généralement abondante dans une partie extrêmement réduite de sa zone géographique et rare partout ailleurs. Cette observation est aujourd'hui communément expliquée par une variation environnementale sous-jacente. Cette thèse s'appuie sur des approches à la fois empiriques et expérimentales, statistiques et théoriques pour tester le type de variation environnementale ainsi que les interactions entre environnement et compétition interspécifique pouvant générer les variations spatiales en abondances observées. Il est montré que présence-absence et abondance sont affectées par des facteurs environnementaux distincts. Il apparaît en outre que l'effet de la compétition interspécifique dépend des différences de niches entre espèces et module l'impact de l'environnement sur l'abondance en modifiant des coûts et bénéfices relatifs des différentes stratégies d'acquisition

des ressources. Finalement, la possibilité de prédire les réponses aux changements climatiques grâce aux données d'abondance et à des modèles statistiques minimisant le bruit inhérent à ce type de données est démontrée. Pour autant, une véritable théorie des distributions d'abondance reste à développer. Le nombre, et *a fortiori* l'identité, des gradients environnements affectant les abondances à grande échelle spatiale sont encore mal connus. Un effort de recherche considérable est ainsi nécessaire pour améliorer la compréhension du lien entre phénomènes locaux, dont l'interaction entre environnement, traits, comportement et compétition, et patterns à grandes échelles. Par ailleurs, l'unification entre approches basées sur la dispersion, négligeant les différences de niches, avec la théorie actuelle doit encore être accomplie pour qu'une véritable théorie générale des dynamiques macro-évolutive et patterns macro-écologiques puisse voir le jour.

Traduit par Jurgis Sapijanskas

Acknowledgements

Brian McGill, my supervisor, was a constant source of inspiration throughout my PhD. One of his words could capture the essence of my thinking. One of his ideas could send me off to explore a subject in new and deeper ways. I greatly respect his work and approach to science and I have grown as an ecologist because of him. He has spawned in me an enthusiasm for the discipline due to his clear sense of the field. My committee of Andy Gonzalez, Luc-Alain Giraldeau, and Murray Humphries kept me on track and they were always available for a quick chat about my work. Marty Lechowicz was exceptionally generous in making me feel welcome in his lab and with his lab group. One of the highlights of my PhD career was TAing ENVR 301 and for this I owe gratitude to Colin Chapman.

The McGill lab group was as good of a group of peers and friends a student could ever ask for. At times, we spanned three universities or four countries but still managed to trade jokes, advice, and critical analysis. John Donoghue always provided constructive feedback. Julie Messier has been, at times, a housemate, a travel buddy, and, always, a good friend. Peter White, you were alongside me in the whole process and I congratulate you on also finishing your PhD. Sergio Estrada Villegas, a brother in beats and beyond. Volker Bahn was a true mentor and has always been there to help me when I have been stuck with analyses or stuck in life and love.

Nearly every CEEB grad student has been a friend and peer at some point. I couldn’t have finished this PhD without the help and friendship of Shawn Leroux. He has been there for me and saved my skin on numerous occasions. More so he has been an invaluable friend through affairs related or unrelated to science. Grigoris Kylafis, Luis Fernando De Léon Reyna, and Diana Sharpe often made me forget the struggle of the PhD through good times in the Point. I would especially like to thank Neeltje Boogert, Caitlin Friesen, Aerin Jacob, Xoxo O’Farrill, and Jonathan Whiteley for their hard work and dedication to making the Biology Department a fun and stimulating academic and social environment. There are so many more and I will miss you all! A special extra thank you to Luis and Diana for submitting the thesis on my behalf while I am in Mexico. Also, thank you to Jurgis Sapijanskas for translating the thesis abstract.

In the fall of 2009, my life changed forever when I met Ivet Reyes Maturano. My now wife and love has been a constant pillar of support during the push to finish my thesis. With one smile, she eased any moment of doubt or struggle. Science comes from passion but passion comes from love. The love we share has made me feel more excited and confident about my work than ever before.

I had the good fortune to write much of this thesis while in Yalalag, Oaxaca, México. The backdrop to my laptop is the mountains of the Sierra Norte and this provided the tranquility and focus I needed to finish my thesis. I thank Tere, Juanita, Camilo, and Yunitsa Vásquez for making our stay in Yalalag so enjoyable. And of course, Coyote was there to play with when I needed a break. A huge thank also to Teresita Maturano Pérez for all she provided us when staying in Mexico City.

At the end of each chapter I provide additional acknowledgements that highlight the contributions of assistants, academics, funding agencies, and those who allowed me to work on their land. Thank you to all!

Preface

Thesis format and author contributions

This thesis is manuscript-based. There are four main chapters bookended by a general introduction and discussion. Linking paragraphs connect each of main chapters.

At the time of submission, all four chapters are under review in ecological journals. Slight differences in formatting among the chapters reflect the different journal styles. Chapters 2 - 4 are co-authored with my supervisor, Brian McGill. This acknowledges his inspiration, ideas, feedback, and financial support. The fifth chapter came out of work I did with the CC-BIO project (http://www.ccbio.uqar.ca/). I co-authored the paper with Nicolas Casajus (Université du Québec à Rimouski), Dominique Berteaux (Université du Québec à Rimouski), Volker Bahn (Wright State University), Brian McGill (University of Maine), and Jacques Larivée (Regroupement QuébecOiseaux). N. Casajus provided the code with which to run the analysis and was always available to help if I had any problems with the analysis. D. Berteaux is the PI on the CC-BIO project and provided constructive feedback on the manuscript. V. Bahn and B. McGill provided feedback on analysis and text. J. Larivée provided some of the data I used in the analysis. Alone, I came up with all the ideas and hypotheses, collated and analyzed the data, and wrote the manuscript.

Table of Contents

List of Tables

List of Figures

List of Appendices

CHAPTER 1:

General introduction

1.1. From pattern to theory

As scientists, we are inherently interested in patterns for they are the gateway to understanding. If a pattern is explainable, then it shows that we, as individuals, as humans, know something. We can be rest assured that the world is a little less mysterious than when we entered it. As scientists, and perhaps as humans, we are only seeking validation of our own knowledge and our own ability to learn and to communicate.

Ecology is the branch of science that explains patterns in the diversity, distribution, and abundance of organisms. We pick a property and a scale and seek regularity across space, time, and type. We make predictions into novel points in space or time or with novel types to test the degree of regularity. We then collect the models that made successful predictions into a theory. However, ideally, we recognize that despite regularity, there will also be variability and that part of this variability will be unpredictable. Thus, we seek to distinguish between the deterministic and stochastic contributions to our pattern (e.g. Saether et al. 2008). While a “hypothesis” is a term that embodies the deterministic predictions, a “theory” should also acknowledge the stochastic elements and clearly describe the relative contributions of each.

Scheiner & Willig (2008) distinguish three levels of theory: general, constituent, and “instantiations” of constituent theories (i.e. models). The theory I hope to contribute toward developing is the second kind: constituent theory. This level of theory does not make quantitative predictions but instead unifies the models that each predict pattern based on the particulars of scale and type. Limits to human perception mean we can only describe a part of a pattern. Thus, our models are necessarily incomplete. It is only when multiple descriptions of pattern and process are combined does generality emerge at the level of constituent theory. Likewise, constituent theory identifies and bounds the parameters used in predictive models. Consequently, there is a dynamic interplay between the two levels of theory, which hopefully create better models and better theory. Similarly, general theories integrate multiple constituent theories thereby expanding the number of patterns that can be explained with a base set of principles or statements (Fig 1.1).

In this thesis, I take one pattern – spatial variation in abundance, or, how total abundance of one species is distributed among all the populations within its range – and test models, theoretically and empirically, that can build a more comprehensive constituent theory (or more "mature" in the terminology of Scheiner & Willig [2008]). Spatial variation in abundance is considered a "fundamental principle" of a general theory by Scheiner & Willig (2008) and an "assertion" of a "unification of unified theories" by McGill (2010) (Table 1.1). Therefore, a theory of abundance is a critical link between pattern and a general theory. For example, Scheiner & Willig (2008) state their general theory in terms of seven fundamental principles while McGill (2010) uses three (Table 1.1). A theory of abundance might help reconcile these and other approaches leading to a strict set of laws. To be fair, part of the difference between Scheiner & Willig (2008) and McGill (2010) is that the latter never claims to purport a general theory of all of ecology, limiting his purview to a specific set of macroecological patterns. Similarly, I focus only on a theory at large spatial scales and is therefore still incomplete; to be truly informative, a constituent theory of abundance must apply across scales (McGill 2010).

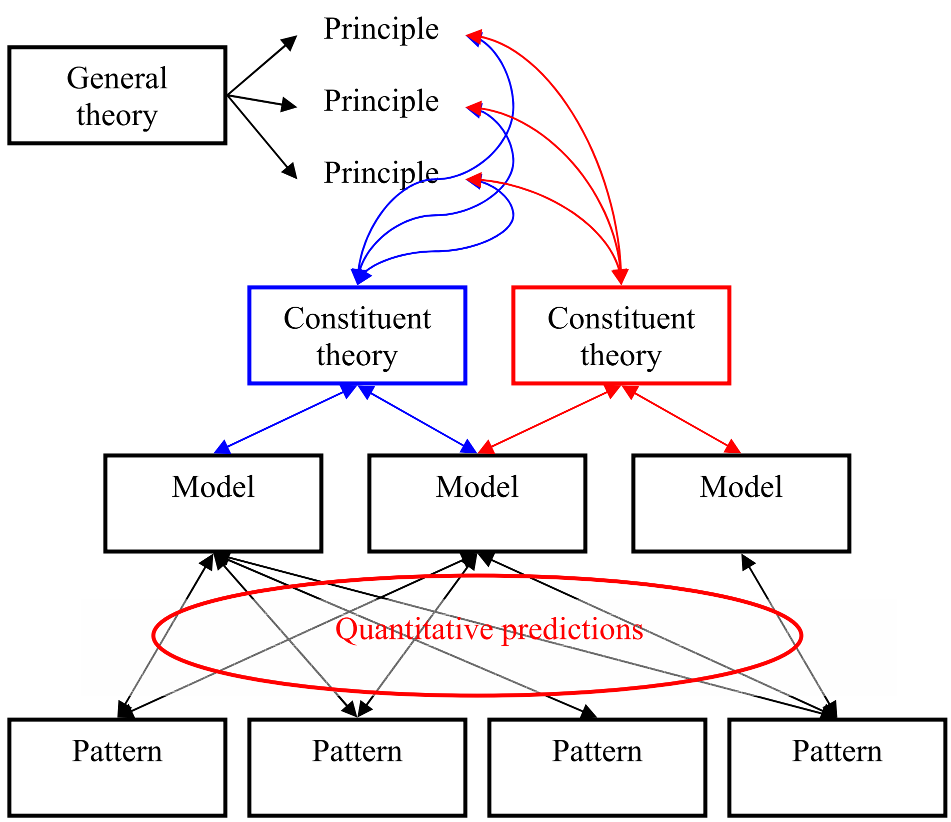


Fig. 1.1. A conceptual framework depicting the three levels of theory (inspired by Scheiner & Willig [2008]). Models are proposed to explain ecological patterns. Some models can explain more than one pattern. The models are developed and parametrized based on constituent theory, which themselves are informed by how well models quantitatively predict ecological patterns. The set of patterns (their scale and type) define the domain of a constituent theory. Multiple constituent theories share underlying principles or can be described by a series of assertions or statements. Such principles/assertions/statements make up a general theory.

Table 1.1. The "fundamental principles" of Scheiner & Willig's (2008) "general theory of ecology" as they compare to the three "assertions" of McGill's (2010) "unification of unified theories." The latter focuses only on several ecological patterns and could be considered a subset of the former. The red circle highlights that spatial variance in abundance is common to both theories.

Scheiner and Willig 2008	McGill 2010
Organisms are distributed in space and time in a heterogeneous manner	Individuals are spatially clumped within a species
Organisms interact with their abiotic and biotic environments	Abundance between species at a regional or global scale varies drastically and is roughly hollow curve in distribution
The distributions of organisms and their interactions depend on contingencies	Individuals between species can be treated as independent and placed without regard to other species
Environmental conditions are heterogeneous in space and time	
Resources are finite and heterogeneous in space and time	
All organisms are mortal	
The ecological properties of species are the result of evolution	

In this thesis, I do not propose a new theory of abundance, timidly following the current paradigm that spatial variation in abundance of a species is an outcome of spatial variation in the underlying environment. The "creators" of the theory have conceptualized spatial variation in abundance as reflecting "the way that variation in environmental conditions independently affects the local population density of each species" (Brown et al. 1995: 2040) and "a model of how spatial and temporal variations in limiting niche parameters affect local and regional population dynamics"(Brown et al. 1996: 618). The current state of the theory is as detailed as the above statements and is therefore only weakly applicable as a constituent theory. The specific targets of my thesis are the words "environment conditions/niche parameters" and "affect." In chapter 2, I test whether the energy available from food is one of these "niche parameters." In chapters 3 and 4, I test whether "affect" includes the environment acting indirectly on organisms via interspecific competition. In chapter 5, I test whether the "environment" includes noise and how this influences our ability to model relationships between environment and abundance. By helping to define these terms, sometimes in the context of a particular study system, I hope to make current theory more open to additional accumulation of evidence and more comparable to other theories. This would go a long way *toward* developing a theory of abundance.

1.2. Defining scale

Ecology is inherently a discipline of scale. The property under study – be it diversity, distribution, or abundance – can only be quantified under an explicit definition of the spatial and temporal grain and extent. After all, explaining the patterns of forest diversity in a 1 m^2 x 1 m^2 plot invokes a different set of processes than explaining diversity across an entire biome. Once the property and scale of interest are defined, we can study variation in the property, observe any pattern in that variation, and hypothesize processes that explain the pattern. As I discuss below, there are very few hypotheses explaining patterns of abundance at large scales, relative to those explaining patterns in the diversity and distribution of organisms.

For my work, I have chosen to understand patterns at large spatial scales, “large” being a necessarily vague term. Spatial scale consists of two properties: extent and grain. The first of these is the easier of the two to define. In this thesis, extent is equal to a species’ range. It is not a fixed quantity as ranges can vary from, e.g. < 100 m^2 for the Socorro Isopod (*Thermosphaeroma thermophilum*) to $> 3.0 \times 10^{11}$ m^2 for the Blue Whale (*Balaenoptera musculus*) (Brown et al. 1996). Defining the extent is also complicated by the fact that species can have disjunct ranges at different points in their life cycle, i.e. spatial extent is defined by the temporal scale of investigation. For example, if temporal extent is equal to one year, the Rufous Hummingbird’s (*Selasphorus rufus*) range extends from Alaska to Mexico. If temporal extent is defined as the northern winter, then the hummingbird’s range is limited to a small portion of central Mexico. In this thesis, I focus my studies primarily on birds and hence define spatial extent as the breeding range.

Spatial grain corresponds to an individual population because population level processes are the fundamental unit from which large scale patterns emerge (Maurer 2000; Ricklefs 2008). Defining the spatial boundaries of a population, though, is nearly impossible. A population is made up of interacting individuals but defining the spatial scale of individual interactions is dependent on temporal scale and thus difficult to measure in the field. For example, do rare, long distance dispersal events that bring two individuals into contact mean the two are from the same population? At some point, criteria for defining a population must be established, but such criteria are likely to vary with taxa and study question. Regardless, it may not be necessary to have such precise definitions of scale. It is here where subjectivity and experience rear their ugly head as we can probably do no better than having a "sense" of when scale is being used appropriately. This will necessarily lead to some disagreement and debate, but it is through such interaction that we refine our "sense" of scale.

1.3. Why do we need a theory of abundance?

Now that the spatial scale of interest has been defined – however vaguely – it is possible to look at the types of large scale patterns that have been studied. What is clear from the literature is that nearly all patterns concern diversity and distribution with relatively few focused on abundance. As such, theory has been channeled into explaining variation in diversity and distribution; there has been comparatively little development in explaining spatial variation in abundance.

Understanding diversity at various scales has been perhaps the utmost preoccupation of ecologists since the creation of the discipline. Ironically, the starting point for most studies of diversity are the Lotka-Volterra equations, which actually solve for equilibrium population size (i.e. abundance). However, the equations are more widely used as a tool to describe the conditions for coexistence. The experimental implications of the equations, i.e. competitive exclusion (Gause 1934), led Hutchinson (1961) to famously propose the paradox of the plankton, questioning how so many species can coexist on such few limiting resources. Resolving this paradox has been central to the growth of theoretical community ecology, but, at the same time, has led to answers framed mostly in terms of local scale processes (Ricklefs 2004).

As new theories of coexistence were being proposed, biogeographers and others started being interested in the latitudinal gradient in species richness (e.g. Pianka 1966). It is a simple pattern to quantify but difficult to explain. There are multiple theories but none have achieved supremacy. I will not dwell on them here instead pointing to recent reviews by Willig et al. (2003) and Currie et al. (2004). Perhaps the most influential theories will be those that attempt to resolve both the paradox of the plankton and the latitudinal gradient in species diversity, i.e. a unified theory that explains how diversity emerges at multiple scales. Given that different processes may control variation in diversity at different scales (e.g. large scales: island biogeography [MacArthur & Wilson 1967], mesoscales: metapopulation dynamics [Hanski 1991], small scales: limiting similarity [MacArthur & Levins 1967]), a unified theory of diversity might be the one that describes how feedbacks emerge from each process and how such feedbacks reinforce the scale boundaries of each process. Regardless of the current primitive state of ecology's theory of diversity, very basic observations about our world have lead to a tremendous number of questions, hypotheses, and tests that have formed the backbone of the discipline.

Likewise, there has been similar development in the attempt to understand patterns in species distributions. The majority of questions have been directed toward asking what sets species range limits. As with the diversity gradient, there is a plethora of theories explaining the why, where, and how of range limits (see reviews in Hoffmann & Blows 1994; Brown et al. 1996). These theories draw on and contribute to many other aspects of biology (e.g. quantitative genetics [Case & Taper 2000]), which therefore expands conceptual development across disciplines. Similarly, there have been many studies proposing hypotheses that account for observed range size-latitude (i.e. Rapoport's Rule [Rapoport 1982; Stevens 1989]) and range size-body size relationships (i.e. Bergmann's Rule [Meiri & Dayan 2003, Olson et al. 2009]).

There has yet to be a definitive theory of either diversity or distribution patterns at large spatial scales. Is it possible that there can be one unified theory that explains patterns in both diversity and distribution simultaneously? McGill (2010) has shown that indeed several patterns emerge from the same set of "assertions" despite the particular language and formulation of different theories. Importantly, abundance is not currently within the domain of existing theory because it is an input into current models, not an output (McGill 2010). Specifically, how a species' total abundance is divided among population in its range – the clumping of individuals – is the pattern from which other patterns emerge (see also McGill & Collins 2003). As such, a theory of abundance is an integral part of a larger theory that also explains diversity and distribution. Yet at this point in time not only are there few theories of abundance, there are barely any studies quantifying the pattern.

1.4. Spatial variation in abundance: pattern

The pattern described in this thesis is not one of local abundance, i.e. the abundance of one or more organisms at a site. Nor does the pattern directly relate to total abundance, i.e. the sum of all local abundances across a species range. These types of descriptions of abundance figure into some important theories relating abundance to range size/occupancy (Brown 1984; Gaston et al. 2000; Borregaard & Rahbek 2010) and body size (White et al. 2007). Instead the pattern I investigate is spatial variation in abundance: how and why the abundance of one species varies among all populations in a species range? Spatial variation in abundance is another measure of the species range; it is a range's texture (Fig 1.2.). Thus a unified species range theory should simultaneously describe a species' range size, shape, position, total abundance, and, importantly, how that total abundance is partitioned over locations in the range.

Spatial variation in abundance across a species range has been described for multiple species in a few instances (Brown et al. 1995; Brewer & Gaston 2002; McGeoch & Price 2004; Murphy et al. 2006) but not to the same extent as patterns in diversity and distribution. Brown (1984) was the first major attempt to quantify a general pattern and explain the pattern with theory. Brown (1984) famously described the pattern as being Gaussian, where abundance peaks in the centre of the range and declines smoothly toward range edges. Brown (1984) based this conceptualization of the range primarily from studies of environmental gradients and not species ranges. Since the publication of Brown (1984), the abundant centre and Gaussian pattern has been shown to be a poor characterization of most empirical data of species abundances (Sagarin & Gaines

2002; Samis and Eckert 2007). In a later paper, Brown himself (Brown et al. 1995) described the pattern of abundances as being roughly lognormal instead of Gaussian. In addition, this later model makes no presupposition of where in the range the peak lies.

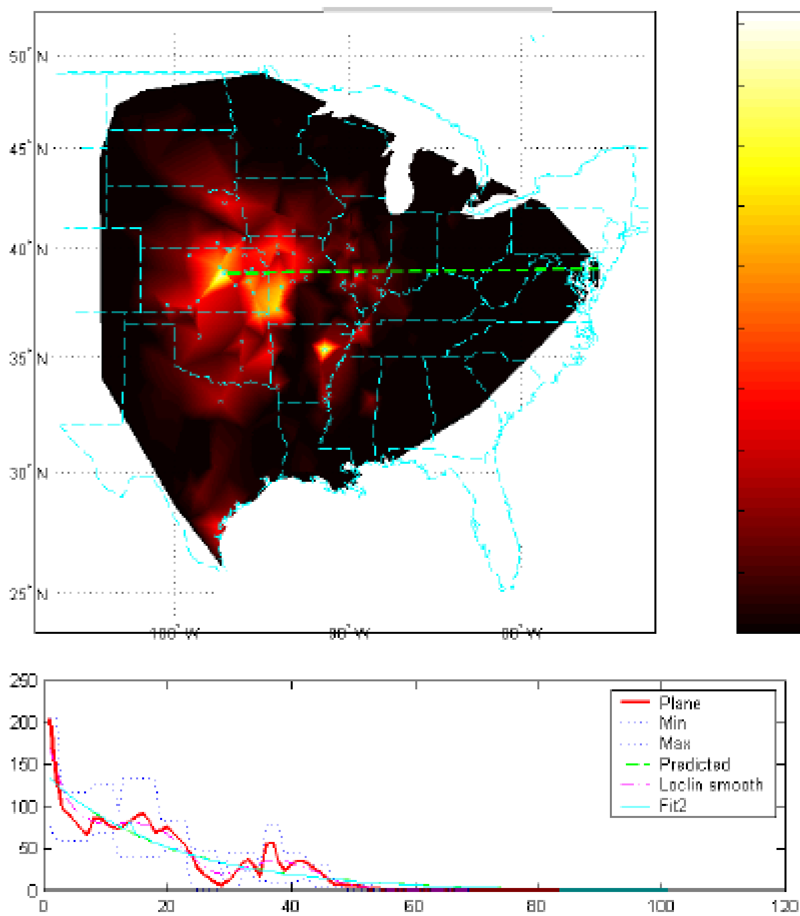


Fig. 1.2. Spatial variation in the abundance of the Dickcissel (*Spiza americana*). The range of this bird is situated in central and eastern United States. The top figure shows the distribution of abundances across the range with lighter colours representing greater abundance as indicated by the colour bar on the right. The dashed line is a transect from the point of highest abundance to the range edge. The abundances along the transect are depicted by the red line in the bottom

figure and shows the characteristic peak followed by a long tail of low abundances and absences. The other lines indicate different types of abundance models not discussed in this paper. The data is taken from the North American Breeding Bird Survey and all interpolation and analysis was conducted by B.J. McGill. Used with permission.

McGill (unpubl.), suggests that fitting an exact distribution to the pattern of abundances is untenable. The most likely specific characterization of the pattern is as a “peak-and-tail” distribution: there are few sites of high abundance and a long tail of sites where the species is rare (Fig 1.2.). In addition, abundance declines continuously and smoothly from the peak through the tail (but see McGeoch & Price (2004)). The peak-and-tail characterization frames the fundamental questions of spatial variation in abundance: why is a species abundant in so very few places in its range? Why is a species never equally abundant or rare everywhere in its range? Murphy et al. (2006) examined the ranges of 134 North American tree species and concurred with McGill’s (unpubl.) description of the peak-and-tail pattern.

The peak-and-tail pattern is aspatial in that it says nothing about where sites of different abundances are located within a range, though it does describe how sites are related to each other (i.e. spatial autocorrelation among sites). With the abundant centre hypothesis shown to be overly restrictive (see also Murphy et al. 2006), there has yet to be any theoretical development in explaining how abundance relates to position within the range. Channell & Lomolino (2000) suggested that abundances should actually be most abundant near range edges but in their case, such a pattern was contingent on the historical drivers of habitat loss and is perhaps not general.

1.5. Spatial variation in abundance: process

1.5.1 Abundance arises from spatial variation in the environment

The Brown (1984) model was an important first attempt to predict spatial variation in abundance. It began with an intuitive premise: that variation in species abundances corresponds to underlying environmental variation. To this premise was added Hutchinson's (1957) concept of the multidimensional niche. Hence, environmental variation actually represents variation in multiple individual niche factors. The species responds to each niche factor separately; persistence occurs when its abundance on all niche factors is greater than one. Abundance at a site represents the combination of the responses to each niche factor at that site. Spatial variation across a range is the sum of all sites.

Although elegant, there is considerable uncertainty about some of the model's assumptions. For example, it is not known how the responses to each niche factor should be combined. Brown, himself, switched from combining the responses additively (Brown 1984) to multiplicatively (Brown et al. 1995) thereby switching spatial variation in abundance from following a Gaussian to following a lognormal distribution. Similarly, the underlying spatial structure and interactions among individual niche factors are unknown. If the assumption of independent niche factors is violated, then neither additive nor multiplicative combinations of the niche factors would give rise to their characteristic distributions. The Brown (1984; Brown et al. 1995) models also assume that abundance changes in a

Gaussian fashion along linear gradients of each niche factor. There is no *a priori* expectation that such a description is accurate (e.g. Austin et al. 1990). More complex characterizations of species niches can be attained through mechanistic (e.g. Buckley & Roughgarden 2005) and behavioural (e.g. Gill et al. 2001b) models but such taxon-specific and information-intensive methods may not be able to inform a general theory. It may be more promising to avoid having to describe specific niche responses altogether. For example, McGill (unpubl.) was able to obtain the peak-and-tail pattern of spatial variation in abundance without needing to characterize any specific niche structure. Instead, abundance was an outcome of species traits, trade-offs, and the geographic context in which those traits are expressed (see also McGill et al. 2006). The trait and trade-off model is expanded on in the next section.

1.5.2. Abundance arises from spatial variation in the environment and interspecific interactions

The niche comprises the abiotic and biotic influences on abundance. Niche characterizations can equate the two as in Brown et al. (1995) where, for example, a species responds to a precipitation gradient as it does to a gradient in predator abundance. More likely, however, abiotic and biotic factors interact to affect abundance. In Hutchinson's (1957) original formulation of the niche, the response to abiotic niche factors describes the fundamental niche and is an outcome of a species' physiological response to the environment. Superimposed upon the fundamental niche are biotic interactions, which turn the fundamental into the realized niche. The implication is that the biotic response is constrained by the abiotic response. By not explicitly modeling abiotic and biotic responses as separate processes, Brown et al. (1995) are characterizing the fundamental niche and thus modeling the "fundamental" distribution of species abundances. Yet the pattern they purport to describe is the observed spatial variation in abundance, which necessarily includes all interactions and is thus the "realized" distribution of species abundances.

The interaction of abiotic and biotic gradients violates Brown et al.'s (1995) assumption of independent niche factors. With correlated gradients, the multiplicative combination of individual niche responses may lead to different patterns in spatial variation in abundance than those depicted. Evidence is now accumulating that some aspects of the abiotic environment and interspecific competition are inversely correlated in space: there is a trade-off between environmental tolerance and competitive ability such that a species tolerant to harsher environments is a weaker competitor (Loehle 1998; Morin & Chuine 2006). The trade-off arises because species traits that mediate how a species responds to particular environmental conditions are the same traits that mediate the outcome of interspecific interactions (Ackerly 2003). (Certainly other interactions [e.g. predation, parasitism] are subject to environmentally mediated trade-offs and equally important to abundance [e.g. Leibold 1991; Martin & Martin 2001]. However, to date, nearly all descriptions of trade-offs in the context of large scale patterns have focused on interspecific competition).

The outcome of the trade-off is that the environment may directly affect an organism's abundance or indirectly by setting the outcome of interspecific competition. In other words, an environment that is overly harsh for one species is where another species experiences competitive release (e.g. Buckley & Roughgarden 2006; Arif et al. 2007; Cadena & Loiselle 2007). Dobzhansky (1950) was the first to explain the trade-off in geographic terms: competition should dominate dynamics at low latitudes while the environment should be most influential at high latitudes. MacArthur (1972) related the gradient to species distributions: a species' northern range limit is set by its tolerance to the environment and its southern range limit is set by interspecific competition.

McGill (unpubl.) used the environmental tolerance-competitive ability trade-off to model spatial variation in abundance. He found that abundance declined from a peak to tails as increasingly harsh environments reduced survival or as increasing interspecific competition reduced fecundity. In many ways, the model and results are consistent with an earlier model that relates variation in abundance to a trade-off between interference and exploitation competitive abilities along a food availability gradient (Case & Gilpin 1974). In the Case & Gilpin (1974) model, which is based on Lotka-Volterra equations of equilibrium abundance, the species can tolerant "harsh" food-poor environments because it is a more efficient exploitation competitor. However, it declines in abundance as food becomes more plentiful because it is increasingly outcompeted by the interference competitor. The interference competitor, on the other hand, declines with decreasing food availability because it cannot persist on sparse food resources. The same kind of trade-off underlies theories of habitat selection (Brown 1971; Abramsky et al. 1990; Rosenzweig 1991, Chase 1996) and species turnover along small scale environmental gradients (Wisheu & Keddy 1992; Wisheu 1998; Greiner La Peyre et al. 2001).

1.5.3. Abundance arises from stochastic temporal processes

In the niche-based models described above, the environment has a deterministic effect on abundance. However, spatial environmental variation is not a necessary condition for generating spatial variation in abundance. An aspatial and stochastic model formulated by Ives & Klopfer (1997) was able to predict the same empirical patterns found by Brown et al. (1995). In their model, spatial variation in abundance emerged purely as an outcome of local stochastic temporal variability in survival and reproduction. Their results raise a conundrum in the quest to develop a theory of abundance: is spatial structure necessary to generate a spatial pattern? On the one hand, Ives & Klopfer (1997) suggest that spatial variation in abundance reflects the probability that any given population is at an abundant or rare point in a temporal trend. On the other hand, McGill & Collins (2003) suggest that local abundance reflects the probability that a given location is at an abundant or rare point in its range. Both perspectives likely have some validity and point to the importance of developing a theory that incorporates spatiotemporal dynamics of both resources and their consumers. I am curious whether Ives & Klopfer (1997) would have found the same results if a deterministic spatial component was added to their population dynamics model. In reality it is unlikely that temporal dynamics could be generated independent of spatial context. Regardless, the work of Ives & Klopfer (1997) represents the only challenge to a purely niche-based perspective of spatial variation in abundance.

1.6. The organization of the thesis and its contribution to theory

The title of my thesis purposely prefaces the word "theory" with the word "towards." I do not claim that this thesis has even come close to deriving a theory of abundance. Instead, I pursue four questions - four ideas - that taken together shed some light on what eventually might be a part of a theory. As I discussed above, current theory is based on questionable assumptions or, in some cases, relies on complete guesswork. In the following chapters, I attempt to etch away at some of the assumptions and add evidence where before there was none. I caution that some of the conclusions I draw pertain to particular study species at a particular point in space and time. Only with further study can such conclusions become a pillar of a constituent theory.

1.6.1. Chapter 2: Nectar production predicts breeding hummingbird abundance at large spatial scales

When deriving a niche-based theory of abundance, one of the first questions anyone would ask would be "what aspects of the environment comprise a species' niche?" If the niche could be described with only a handful of variables, i.e. if most of the variation in abundance could be explained by just a few niche axes, and these variables were consistent across species, space, and time, then we would have made a giant step toward developing a theory.

For a theory only pertaining to species distributions and range limits then, with great confidence, the answer to the above question would be "climate." (Although there is still uncertainty as to what constitutes "climate" [e.g. temperature, precipitation] and at what temporal scale it operates). There is now considerable evidence that upper latitudinal and altitudinal range limits, at least, are set by a species' climatic tolerance (Root 1988; Buckley & Roughgarden 2006; Cadena & Loiselle 2007; Morin & Chuine 2006; Arif et al. 2007; Normand et al. 2009; Busch et al. 2011). Abundance, however, is a different story. As discussed above, abundance does not generally linearly decline from a central peak outward toward northern range margins, as would be expected if climate (or temperature at least) was the primary determinant of spatial variation in abundance. Hence it is not clear whether climate is as important in shaping spatial variation in abundance as it is in shaping distributions (but see Emlen et al. 1986; Jarema et al. 2009).

Alternatively, if we were to ask any average person where a species is most abundant, they would likely reply "where its food is most abundant." Indeed, this is the hypothesis I test in my first chapter. Specifically, I ask whether abundance of Black-chinned (*Archilochus alexandri*) and Broad-tailed (*Selasphorus platycercus*) hummingbirds at different sites across a large portion of their ranges can be predicted from the energy available from their main food resource, nectar flowers. Thus, I hypothesize that spatial variation in food is one of the key niche axes underlying spatial variation in abundance. There is already some precedent for this hypothesis. One of the most well appreciated theories in ecology, the Ideal Free Distribution (IFD), predicts that spatial variation in the abundance of foraging animals at small scales (i.e. at which they can make decisions on where to forage) is matched to variation in food supply (Fretwell & Lucas 1969; Parker 1978). It is entirely possible that the IFD holds at larger spatial scales (see also Gill et al. 2001ab; Pettorelli et al. 2009), although the mechanism (i.e. the scale of individual movement) would be different.

1.6.2. Chapter 3: Interspecific niche differences affect intraspecific spatial variation in abundance

In this chapter, I address one of the major weaknesses of the Brown et al. (1995) model of spatial variation in abundance: that the response to the abiotic environment and to interspecific competitors are equivalent and independent processes. In this chapter, I expand the model by explicitly considering the responses as two separate processes. I first model a species' fundamental niche as done in Brown et al. (1995). I then add an interspecific competitor, which reduces the abundance of the focal species, i.e. turns the fundamental into the realized niche. I test how spatial variation in abundance differs between the cases with and without competition. Using the model in this way, I test a novel hypothesis: that niche differences among competing species contribute to explaining spatial variation in abundance. While it is well known that niche differences explain species abundance distributions (Sugihara 1980) via how they lead to multispecies coexistence (e.g. Chesson 2000), this is the first time they have been connected to spatial variation in abundance.

1.6.3. Chapter 4: Mechanisms of variation in hummingbird abundance along environmental gradients

In this chapter, I address in more detail how interspecific competition acts as a mechanism that links spatial variation in the environment to spatial variation in abundance. I explicitly acknowledge that environmental severity and competition gradients are inversely correlated and that abundance reflects this trade-off based on species traits. Neither of the existing trade-off models (Case & Gilpin 1974; McGill unpubl.) have been tested empirically. In this chapter I designed a field experiment to test the models. I continue using Black-chinned and Broad-tailed Hummingbirds as a model system because interference-exploitation trade-offs have been shown to explain hummingbird species distributions and turnover along elevation (Feinsinger et al. 1979; Altshuler 2006) and food availability gradients (Kodric-Brown & Brown 1978; Carpenter et al. 1993). As well, there is evidence that these patterns are rooted in interspecific differences in flight performance traits (Altshuler & Dudley 2002; Stiles et al. 2005; Altshuler 2006).

In my experiment, I manipulate food density along elevation gradients to examine the interaction of the two on abundance. Thus, I test the assumption that niche factors act independently to affect abundance. Crucially, then, I acknowledge that spatial gradients integrate all aspects of environmental variation and that each cannot be studied in isolation of each other.

1.6.4. Chapter 5: Distribution models help in combining data from divergent sources: a case study on birds in Québec under climate change

Implicit in the link between environmental variation and abundance is that temporal environmental change will lead to changes in abundance. In other words, if the spatial structure of the environment determines abundance and there is change in the former, then we would expect the latter to change as well. Climate change is one such process that can alter the spatial structure of the environment.

For example, predicted warming is not expected to happen equally everywhere. Consequently, abundance might change differently in different parts of the range, which creates heterogeneity in extinction risk (Mehlman 1997). In this chapter, my goal is to predict changes in bird abundances under future climate scenarios. While this goal does not directly inform a theory of abundance *per se*, it does make explicit how we can use abundance data in climate change and species distribution modeling, which are tools that can inform theory. Previously, nearly all models of species response to climate change use presence/absence data and focus purely on range shifts. These models do not consider what is happening inside the range.

One of the challenges in using abundance data is that it is inherently noisy. Every abundance survey has data deficiencies and biases that can obscure the true relationship between abundance and climate (Royle et al. 2007). In this chapter, I tackle this issue testing whether species distribution models remove noise in the data. If this is the case, then we can be more confident in using empirically derived abundance data to develop and test hypotheses of spatial variation in abundance.

1.7. References

Abramsky, Z., Rosenzweig, M.L., Pinshow, B., Brown, J.S., Kotler, B. & Mitchell, W.A. (1990). Habitat selection: an experimental field test with two gerbil species. *Ecology*, 71, 2358-2369.

Ackerly, D.D. (2003). Community assembly, niche conservatism, and adaptive evolution in changing environments. *International Journal of Plant Science*, 164, S165-S184.

Altshuler, D.L. (2006). Flight performance and competitive displacement of hummingbirds across elevational gradients. *American Naturalist*, 167, 216-229.

Altshuler, D.L. & Dudley, R. (2003). The ecological and evolutionary interface of hummingbird flight physiology. *Journal of Experimental Biology*, 205, 2325-2336.

Arif, S., Adams, D.C. & Wicknick, J.A. (2007). Bioclimatic modeling, morphology, and behaviour reveal alternative mechanisms regulating the distributions of two parapatric salamander species. *Evolutionary Ecology Research*, 9, 843-854.

Austin, M.P., Nicholls, A.O. & Margules, C.R. (1990). Measurement of the realized qualitative niche: environmental niches of five eucalyptus species. *Ecological Monographs*, 60, 161-177.

Borregaard, M.K. & Rahbek, C. (2010). Causality of the relationship between geographic distribution and species abundance. *Quarterly Review of Biology*, 85, 4-25.

Brewer, A.M. & Gaston, K.J. (2002). The geographical range structure of the holly leaf-miner. I. Population density. *Journal of Animal Ecology*, 71, 99-111.

Brown, J.H. (1971). Mechanisms of competitive exclusion between two species of chipmunks. *Ecology*, 52, 305-311.

Brown, J.H. (1984). On the relationship between abundance and distribution of species. *American Naturalist*, 124, 255-279.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995). Spatial variation in abundance. *Ecology,* 76, 2028-2043.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996). The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics,* 27, 597-623.

Buckley, L.B. & Roughgarden, J. (2005). Effect of species interactions on landscape abundance patterns. *Journal of Animal Ecology*, 74, 1182-1194.

Buckley, L.B. & Roughgarden, J. (2006). Climate, competition, and the coexistence of island lizards. *Functional Ecology*, 20, 315-322.

Busch, D.S., Robinson, W.D., Robinson, T.R. & Wingfield, J.C. (2011). Influence of proximity to a geographical range limit on the physiology of a tropical bird. *Journal of Animal Ecology*, 80, 640-649.

Cadena, C.D. & Loiselle, B.A. (2007). Limits to elevational disributions in two species of emberizine finches : disentangling the role of interspecific competition, autoecology, and geographic variation in the environment. *Ecography*, 30, 491-504.

Carpenter, F.L., Hixon, M.A., Temeles, E.J., Russell, R.W. & Paton, D.C. (1993). Exploitative compensation by subordinate age-sex classes of migrant Rufous Hummingbirds. *Behavioral Ecology and Sociobiology,* 33, 305-312.

Case, T. J. & Gilpin, M.E. (1974). Interference competition and niche theory. *Proceedings of the National Academy of Sciences USA*, 71, 3073-3077.

Case, T.J. & Taper, M.L (2000). Interspecific competition, environmental gradients, gene flow, and the coevolution of species borders. *American Naturalist*, 155, 583-605.

Channell, R. & Lomolino, M.V. (2000). Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *Journal of Biogeography*, 27, 169-179.

Chase, J.M. (1996). Differential competitive interactions and the included niche: an experimental analysis with grasshoppers. *Oikos*, 76, 103-112.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343-366.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegán, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121-1134.

Dobzhansky, T. (1950). Evolution in the tropics. *American Scientist*, 38, 209-221.

Emlen, J.T., DeJong, M.J., Jaeger, J.J., Moermond, T.C., Rusterholz, K.A. & White, R.P. (1986). Density trends and range boundary constraints of forest birds along a latitudinal gradient. *Auk*, 103, 791-803.

Feinsinger, P., Colwell, R.K., Terborgh, J. & Chaplin, S.B. (1979). Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. *American Naturalist*, 113, 481-497.

Fretwell, S.D. & Lucas, H.L. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica,* 19, 16-36.

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

Gause, G.F. (1934). *The Struggle for Existence.* Williams & Wilkins, Baltimore.

Gill, J.A., Norris, K., Potts, P.M., Gunnarsson, T.G., Atkinson, P.W. & Sutherland, W.J. (2001a). The buffer effect and large-scale population regulation in migratory birds. *Nature*, 412, 436-438.

Gill, J.A., Sutherland, W.J. & Norris, K. (2001b). Depletion models can predict shorebird distribution at different spatial scales. *Proceedings of the Royal Society B*, 268, 369-376.

Greiner La Peyre, M.K., Grace, J.B., Hahn, E. & Mendelssohn, I.A. (2001). The importance of competition in regulating plant species abundance along a salinity gradient. *Ecology*, 82, 62-69.

Hanski, I. (1991). Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society*, 42, 17-38.

Hoffmann, A.A. & Blows, M.W. (1994). Species borders: ecological and evolutionary perspectives. *Trends in Ecology and Evolution*, 9, 223-227.

Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415-427.

Hutchinson, G.E. (1961). The paradox of the plankton. *American Naturalist*, 95, 137-145.

Ives, A.R. & Klopfer, E.D. (1997). Spatial variation in abundance created by stochastic temporal variation. *Ecology*, 78, 1907-1913.

Jarema, S.I., Samson, J., McGill, B.J. & Humphries, M.M. (2009). Variation in abundance across a species' range predicts climate change responses in the range interior will exceed those at the edge: a case study with North American beaver. *Global Change Biology*, 15, 508-522.

Kodric-Brown, A. & Brown, J.H. (1978). Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology*, 59, 285-296.

Leibold, M.A. (1991). Trophic interactions and habitat segregation between competing *Daphnia* species. *Oecologia*, 86, 510-520.

Loehle, C. (1998). Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography*, 25, 735-742.

MacArthur, R.H. (1972). *Geographical Ecology: Patterns in the Distribution of Species.* Harper & Row, New York.

MacArthur, R.H. & Levins, R. (1967). The limiting similarity, convergence and divergence of coexisting species. *American Naturalist,* 101, 377-385.

MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton.

Martin, P.R. & Martin, T.E. (2001). Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. *Ecology*, 189-206.

Maurer, B.A. (2000). Macroecology and consilience. *Global Ecology and Biogeography*, 9, 275-280.

McGeoch, M.A. & Price, P.W. (2004). Spatial abundance structures in an assemblage of gall-forming sawflies. *Journal of Animal Ecology*, 73, 506-516.

McGill, B.J. (2010). Towards a unification of unified theories of biodiversity. *Ecology Letters*, 13, 627-642.

McGill, B.J. & Collins, C. (2003). A unified theory for macroecology based on spatial patterns of abundance. *Evolutionary Ecology Research*, 5, 469-492.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21, 178-185.

Meiri, S. & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, 30, 331-351.

Mehlman, D.W. (1997). Change in avian abundance across the geographic range in response to environmental change. *Ecological Applications*, 7, 614-624.

Morin, X. & Chuine, I. (2006). Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecology Letters*, 9, 185-195.

Murphy, H.T., VanDerWal, J. & Lovett-Doust, J. (2006). Distribution of abundance across the range in eastern North American trees. *Global Ecology and Biogeography*, 15, 63-71.

Normand, S., Treier, U.A., Randin, C., Vittoz, P., Guisan, A. & Svenning, J-C. (2009). Importance of abiotic stress as a range determinant for European plants: insights from species responses to climatic gradients. *Global Ecology and Biogeography*, 18, 437-449.

Olson, V.A., Davies, R.G., Orme, C.D.L., Thomas, G.H., Meiri, S., Blackburn, T.M., Gaston, K.J., Owens, I.P.F. & Bennett, P.M. (2009). Global biogeography and ecology of body size in birds. *Ecology Letters*, 12, 249-259.

Parker, G.A. (1978). Searching for mates. In: *Behavioral Ecology: An Evolutionary Approach* (ed. Krebs, J.R. & Davies, N.B.). Blackwell, Oxford, pp. 214-244.

Pettorelli, N., Bro-Jorgensen, J., Durant, S.M., Blackburn, T. & Carbone, C. (2009). Energy availability and density estimates in African ungulates. *American Naturalist*, 173, 698-704.

Pianka, E.R. (1966). Latitudinal gradients in species diversity: a review of concepts. *American Naturalist,* 100, 33-46.

Rapoport, E.H. (1982). *Aerography: Geographical Strategies of Species*. Pergamon, Oxford.

Ricklefs, R.E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, 7, 1-15.

Ricklefs, R.E. (2008). Disintegration of the ecological community. *American Naturalist*, 172, 741-750.

Root, T. 1988. Energy constraints on avian distributions and abundances. *Ecology*, 69, 330-339.

Rosenzweig, M.L. (1991). Habitat selection and population interactions: the search for mechanism. *American Naturalist*, 137, S5-S28.

Royle, J.A., Kéry, M., Gautier, R. & Schmid, H. (2007). Hierarchical spatial models of abundance and occurrence from imperfect survey data. *Ecological Monographs*, 77, 465-481.

Sagarin, R.D. & Gaines, S.D. (2002). The ‘abundant centre’ distribution: to what extent is it a biogeographical rule? *Ecology Letters.*, 5, 137-147.

Samis, K.E. & Eckert, C.G. (2007). Testing the abundant center model using range-wide demographic surveys of two coastal dune plants. *Ecology*, 88, 1747-1758.

Scheiner, S.M. & Willig, M.R. (2008). A general theory of ecology. *Theoretical Ecology*, 1, 21-28.

Stevens, G.C. (1989). The latitudinal gradient in geographic range: how so many species coexist in the tropics. *American Naturalist*, 133, 240-256.

Stiles, F.G., Altshuler, D.L. & Dudley, R. (2005). Wing morphology and flight behavior of some North American hummingbird species. *Auk,* 122, 872-886.

Sugihara, G. (1980). Minimal community structure: an explanation of species abundance patterns. *American Naturalist*, 116, 770-787.

White, E.P., Ernest, S.K.M., Kerkhoff, A.J. & Enquist, B.J. (2007). Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution*, 22, 323-330.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology and Systematics,* 34, 273-309.

Wisheu, I.C. (1998). How organisms partition habitats: different types of community organization can produce identical patterns. *Oikos*, 83, 246-258.

Wisheu, I.C. & Keddy, P.A. (1992). Competition and centrifugal organization of plant communities: theory and tests. *Journal of Vegetation Science*, 3, 147-156.

1.8. Linking statement between Chapters 1 and 2

In the previous chapter, I placed the study in a theoretical context, described the pattern and scale of the pattern under investigation (i.e. spatial variation in abundance at large spatial scales), and then reviewed the different theoretical and empirical studies that attempt to explain the pattern. In the following chapter, I test one of the hypotheses proposed to explain the pattern: that spatial variation in abundance matches spatial variation in the underlying environment. Furthermore, I test the hypothesis that one niche factor alone (energy provided by food) may be sufficient for explaining spatial variation in abundance.

CHAPTER 2:

Nectar production predicts breeding hummingbird abundance at large spatial scales

2.1. Abstract

Aim: To test whether nectar production significantly predicts hummingbird abundances at large spatial scales

Location: Arizona, Colorado, New Mexico, Utah, USA

Methods: We surveyed nectar flowers at > 100 sites in the summer of 2008 and converted flower densities to nectar production using data obtained from the literature. We derived a model of nectar production and used this to create a nectar production map for the study region. We then tested whether nectar production significantly predicted the presence-absence and abundances of Black-chinned (*Archilochus alexandri*) and Broad-tailed (*Selasphorus platycercus*) Hummingbirds with zero-inflated Poisson regression. Abundance data was taken from the North American Breeding Bird Survey.

Results: We found that three relatively easy to obtain large-scale variables – average temperature, plant productivity, and elevation – predicted spatial variation in nectar production. We found that nectar production significantly predicted 2009 abundances of both hummingbird species. Nectar production did not predict 2008 abundances nor presence-absence in either year.

Main conclusions: Abundance and occupancy (presence-absence) do not arise from the same environmental relationships. Abundance scales with available energy only on occupied sites. Within the breeding season, hummingbird occupancy may depend on factors unrelated to nectar production and animal movement may not be sufficiently large enough to track spatial variation in nectar production.

2.2. Introduction

In the years since the publication of the treatise on the Ideal Free Distribution (Fretwell & Lucas, 1969), a multitude of theoretical and empirical studies have confirmed the importance of food supply in regulating the spatial distribution of animals (see review in Kennedy & Gray, 1993). Of particular interest is the prediction that the proportion of foraging individuals in each habitat matches each habitat's resource supply rate, a concept termed the "input-matching" or "resource-matching" rule (Parker, 1978). Although instances of "undermatching" and "overmatching" have been observed (Grand & Grant, 1994), the rule in a very general sense has been well supported (Díaz *et al.* 1998; Rodewald & Shustack, 2008).

In an ideal free context, predicting animal abundance from food supply is usually limited to the spatial scale at which individuals move and make decisions. There have been few attempts to extend resource matching to larger spatial scales. One exception is the buffer effect, which describes density-dependent changes in animal abundance across sites of varying habitat quality (Brown, 1969). The effect has been shown to operate at the scale of large islands (Iceland and Great Britain) and is driven, in part, by site variation in resource availability (Gill *et al*., 2001a, b; Gunnarsson *et al*., 2005). Aside from the buffer effect, there has been little effort dedicated to developing a theory that can explain spatial variation in abundance at large scales. In another notable exception, Brown *et al*. (1995) showed that the spatial variation in abundance at continental scales for a variety of taxa reflects the degree to which the local environment meets the niche requirements of the species. A theory of abundance consistent with Brown *et al*.

(1995), the buffer effect, and resource matching therefore predicts that food supply is a key niche factor regulating the distribution of animals across spatial scales.

The matching of animal abundance to food supply has more often been studied over time than space. For example, birds from all types of foraging guilds (i.e. fruit, insect, seed/nut, nectar) have their peak abundances occurring at similar times of the year as the food they consume (Loiselle & Blake, 1991; Inouye *et al.*, 1991; McShea, 2000; Burns, 2002; Hogstad, 2005; Cotton, 2007). Such temporal regulation suggests that a snapshot of a resource landscape across a large spatial extent would show a match between animal abundances and their food supply. Indeed, such a correspondence has been found but only over small spatial extents (< 30 km [Levey, 1988; Telléria & Pérez-Tris, 2003]) or a few study sites (6 [Abrahamczyk & Kessler, 2010]). At larger extents, the tight association between abundance and food is inconsistent among years or regions due to the effect of other environmental factors (Herrera, 1998; Koenig & Haycock, 1999). Climate, for example, is known to set species range limits (Root, 1988; Normand *et al.*, 2009) and may therefore influence how the abundance-food relationship plays out over larger scales. It may be that abundance is related to food supply only in those areas where the conditions related to distribution and occupancy are met.

Before we can test the degree to which food supply is associated with abundance across geographic ranges, we have to be able to quantify spatial variation in food resources at large spatial scales. We have been hindered from making the connection between large scale spatial variation in animal abundance and food because 1) it is often difficult to know what resources deliver the majority of an animal's energy and 2) quantifying variation in food supply at large scales requires extensive on-the-ground sampling. While many aspects of an organism's niche can be derived from easily attainable data (e.g. climate), food cannot. Our goal with this paper is to determine whether easily attainable data can be used to predict spatial variation in food availability at an extent that captures a large part of a species range. To address the problem of knowing what resources to use, we chose two species, Black-chinned (*Archilochus alexandri*) and Broad-tailed (*Selasphorus platycercus*) Hummingbirds, that obtain most of their energy from one resource, nectar. We chose these two species specifically because some information is known about their abundance and distribution and their ranges together cover a wide range of elevations, climates and habitats.

By attempting to predict hummingbird abundance from nectar production, our study fits alongside others employing a niche-based distribution modeling framework. In this context, species distributions are modeled hierarchically with resource-abundance relationships occurring at scales nested within larger scale presence-absence relationships (Guisan & Thuiller, 2005). With this study, we show that resource-abundance relationships also occur on large scales. Thus, abundance within a range should be considered a phenomenon partly independent from the range itself.

2.3. Methods

In this study we combined field data, literature data, and modeling to predict spatial variation in nectar production and hummingbird abundances at large spatial scales. We present a general overview of the steps in Appendix 1 (Fig. A2.1) and give more details below.

2.3.1. Study sites

We defined our study area as a rectangle extending from the US-Mexico border to the Colorado-Wyoming border and from 300 km to the east of the Colorado/Utah-New Mexico/Arizona border to 50 km to the west of this border (Fig. 2.1). The total extent is approximately 380000 km2. This study area captures a large portion of the US ranges of Broad-tailed and Black-chinned Hummingbirds (Ridgley *et al*. 2005, [Fig. 2.1]).

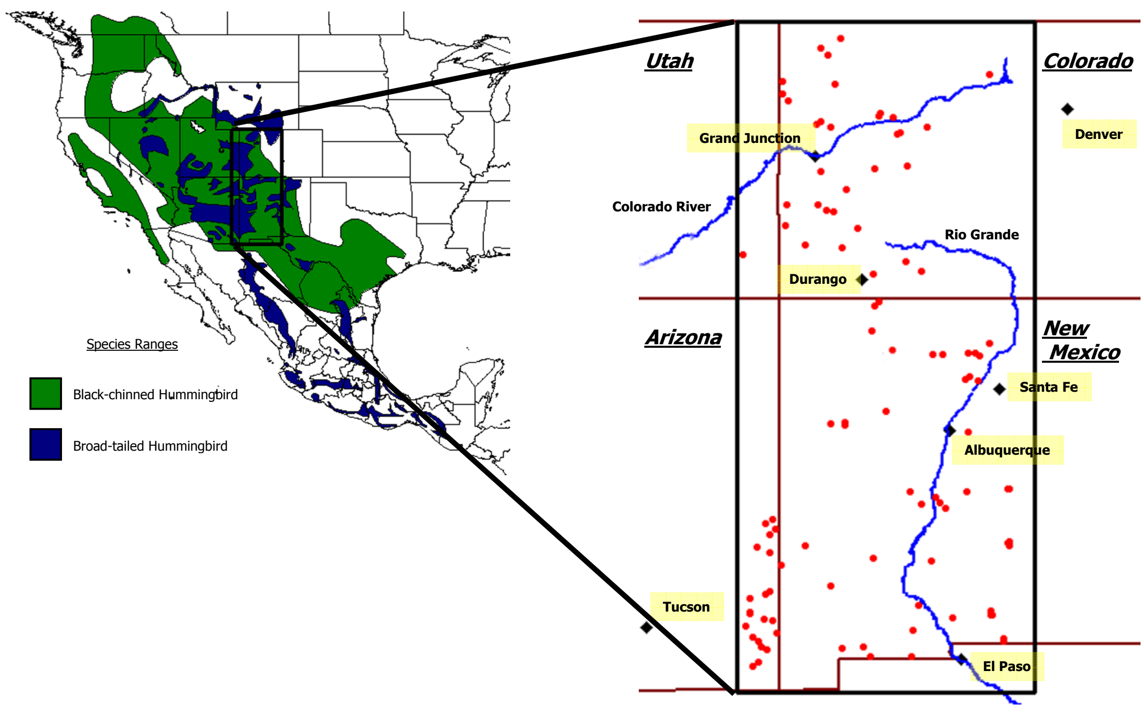


Fig. 2.1. The study region, species ranges of Black-chinned and Broad-tailed Hummingbirds, and the distribution of the 103 flower survey sites.

Within the study area we randomly chose 24 study sites using the Generate Random Points tool in HawthsTools (Byer, 2004) implemented in ArcGIS 9 (ESRI, 2009). The selection was stratified by hummingbird habitat such that eight sites occurred in Black-chinned habitat, eight sites occurred in Broad-tailed habitat and eight sites occurred in habitat where both species co-exist. "Habitat" is defined as a 240 m x 240 m pixel where a species is expected to breed based on animal-habitat models developed as part of the Southwest Regional Gap Analysis (USGS National Gap Analysis Program, 2005). We further restricted site selection such that all sites were within federal land and 2.0 km from a road. Road data were downloaded from TIGER/Line (www.census.gov/geo/www/tiger).

For each of the 24 sites, we created a 200 km radius buffer within which we randomly allocated an additional five points. This brought the total number of study sites to 144. The additional sites were also stratified by hummingbird habitat, restricted to federal land, and placed less than 2.0 km from a road. We clustered sites in this way to reduce travel among sites. We defined the grain of the study sites as 250 m x 250 m, which corresponds to the finest resolution of remotely sensed plant productivity data (i.e. the Moderate Resolution Imaging Spectroradiometer [MODIS] Vegetation Index data product).

2.3.2. Flower surveys

We surveyed each 250 m x 250 m study site once, beginning on 19 April 2008 in southern New Mexico. We arbitrarily visited one to three sites a day based partly on convenience of travel. We visited sites along a south to north trajectory and ran this trajectory twice during the field season. In this way, we visited sites late in the season that were near sites that we had visited earlier in the season. Our last survey was conducted on 28 July 2008.

From the original list of 144 sites, we surveyed 103. Fifty of the 103 sites had to be moved from their original co-ordinates because they were inaccessible due to topography or rough or non-existent roads. In these cases, we drove as close to the original site as possible and created a new point based on a direction (0 – 360°) and distance (0 – 2000 m) chosen with a random number generator. We plotted this new point in GIS to determine its latitude and longitude and used this as the middle of the relocated study plot.

Within each study site, we placed 10 m x 250 m transects at four points (50 m, 100 m, 150 m, 200 m) along a west-east axis. Each transect was oriented in a south-north direction and surveyed in this manner. (For 20 sites, we only surveyed 2 transects. We doubled flower densities from these sites before data analysis). Each transect was further subdivided into 25 m segments and it was within each 10 m x 25 m segment that we carefully counted flowers, using transect tapes or a GPS to measure the length and width of the survey section.

Within each transect segment we counted all stalks pertaining to a hummingbird pollinated species (Appendix 2). Stalks were counted when at least one flower exhibited color. We counted the number of flowers per stalk on the first stalk of each species we encountered in each 10 m x 25 m segment and applied this value to all stalks in each segment. We counted the total number of flowers (any flower exhibiting color) and the number of open flowers (indicated by a visible stamen). Dying flowers were still counted until they were dried up. In species comprised of multiple inflorescences each containing many flowers (e.g. *Fouquieria splendens*), we counted the number of flowers on one inflorescence and counted the number of inflorescences per stalk. We summed the number of flowers for each species across all transect segments in a study site to yield the total number of flowers of each species per 250 m x 250 m study site.

We only surveyed for flower species known to be pollinated by Black-chinned and Broad-tailed Hummingbirds. We created a species list by using the English and Latin names of the two hummingbird species as keywords in a literature search of Ovid BIOSIS Previews and recorded all flower species upon which observations of hummingbird foraging were made. The search returned 42 different plant species and two additional genera not specified to the species level (see Appendix 2). We expanded the field survey to include all *Agave, Aquilegia, Cirsium, Mertensia,* and *Penstemon* species that had similar corollas to the congenerics listed in Appendix 2

2.3.3. Nectar energy content

From the field surveys, we had the number of flowers of a particular genus for each 250 x 250 m study site. We wished to convert these flower density values to a measure more meaningful to hummingbird ecology: the actual amount of energy (in kJ) available over a 24 hr period in each site. To obtain this value, we used the literature to derive the nectar energy content of each genus we found on the field surveys.

Few nectar studies report energy content (J flower-1). Instead they report sucrose concentration (%), nectar production (μL), and/or sucrose production (mg). We searched the literature for studies containing at least one of these values by entering "nectar" as a keyword in Ovid BIOSIS Previews. We limited the search to the genera found on our surveys and to studies conducted in Canada, US, and Mexico. We expanded the search to other regions if no studies of a particular genus were found.

We discarded any study that did not measure "bagged" flowers. Without bagging, flowers are exposed to pollinators. Hence nectar production reflects the pollinator community, pollinator abundances and foraging pressure, which vary among studies but are rarely quantified. In addition, we only included data where bagged flowers were compared to some kind of control such that nectar production did not reflect differences in initial standing crop (e.g. studies measuring nectar production before bagging). We also only used papers that measured production over 24 hours and on more than one flower.

For studies that reported sucrose concentration, nectar volume and sucrose production, we double-checked that sucrose production was calculated following Bolten *et al*. (1979). This ensures that sucrose concentration measured as g g-1 is converted to g ml-1 before being combined with nectar volume to produce sucrose production. We corrected sucrose production values for those studies that did not follow Bolten *et al*. (1979). For papers that only reported nectar volume, we used the average sucrose concentration from all studies of the corresponding genus and calculated sucrose production. We then converted sucrose production to an energetic equivalent based on the heat combustion of sucrose, 16.48 J mg-1.

(Although nectar contains other sugars, reporting energy content in terms of sucrose is standard in hummingbird studies [see Hainsworth & Wolf, 1972]).

Our goal with the literature data was to create a distribution of plausible nectar production values for each genus by combining information from across as many studies as possible (Fig. A2.2). The literature data came in two types: they either reported the nectar content of individual flowers or they only reported the mean and variation of nectar content measured over a certain number of flowers. For the former, we used the information on each flower's nectar content. For the latter, we used the variation reported in the study to generate a distribution of values that represent each flower measured in the study. (Most studies also reported more than one mean as they were designed to compare different locations, years, color morphs, etc. In these cases, we kept all values separate. We therefore assumed that all reported measures were independent of each other).

We created a distribution of nectar production values as follows (see also Fig. A2.2). First, we converted the measure of variation in the study to standard deviation. Second, we used the mean (μ) and standard deviation (δ) reported in each study to create the shape $[(\mu\ \delta\text{-}1)2]$ and scale $(\delta 2/\mu)$ values of a gamma distribution. Third, we drew a set number of values from the gamma distribution according to the number of flowers in the study. As a result, we had nectar content for every flower measured in every study. We combined the data from all studies for each genus separately.

From the new combined data sets, we calculated means, standard deviations, scales and shapes and used these to create a new gamma distribution. Thus the new distribution captured the variation in nectar production that occurred for a genus from across a range of studies. We applied this distribution to each of our study sites. For example, if we had counted 30 *Penstemon* flowers at a site then we sampled 30 different nectar energy values from the gamma distribution we created for *Penstemon*. We then summed these 30 values to derive the total 24-hr nectar production for each study site (kJ 24 hr-1*pixel-1). We chose a gamma distribution to explicitly model the fact that not all flowers on a plant deliver equal amounts of nectar and, moreover, that most flowers deliver little nectar.

2.3.4. Environmental variables

We came up with a suite of variables that are relatively easy to obtain and reasonably expected to correlate with nectar production (Table 2.1). For the most part, these variables are self-explanatory (i.e. latitude, survey date) or are satellite based and obtainable from the internet (i.e. climate, elevation). However how we calculated some variables is explained in more detail in Appendix 4.

Table 2.1. Environmental variables used to predict spatial variation in nectar production.

Variable	Symbol	Detail
Climate: Temperature	TWARM TCOLD* TWET TDRY	Worldclim (Hijmans *et al*. 2006) temperature averages (1950-2000). Temperature was measured separately for the warmest, coldest, wettest and driest quarters of the year

Climate: Precipitation	PWARM* PCOLD PWET PDRY	Worldclim (Hijmans *et al*. 2006) precipitation averages (1950-2000). Precipitation was measured separately for the warmest, coldest, wettest and driest quarters of the year.
Weather: Temperature	TEMP TEMP3†	Spatially interpolated from daily weather station data. Temperature was measured on the survey date and as an average of the 3 months prior to the survey date.
Weather: Precipitation	PRECIP PRECIP3†	Spatially interpolated from daily weather station data. Precipitation was measured on the survey date and as an average of the 3 months prior to the survey date.
Growing degree days	GDD	Base temperature of 10°C. Days summed from first day after the last 3-day period of temperatures < 0°C (see Appendix 4).
Plant Productivity	EVI	Enhanced Vegetation Index from MODIS.
Elevation	ELEV	Taken from the Shuttle Radar Topography Mission and provided by Worldclim (Hijmans *et al*. 2005).
Latitude	LAT	
Survey date	DATE	

*The variable used in the predictive model (from PCA results)

†Three-month averages were highly correlated with daily temperature/precipitation and were not included in predictive models

2.3.5. Statistical modeling and mapping of nectar production

Preliminary analysis showed that nectar production was non-linearly related to the environmental variables. Accordingly, we used a General Additive Modeling (GAM) framework, which models non-linear relationships. GAMs are of the form $Y=\alpha + f(X_i) + \varepsilon_i$, where $f(X_i)$ represents a smoothing curve that relates the independent to the dependent variable in a non-linear fashion. We used the cubic spline smoothing term found in the package mgcv 1.5-1 (Wood, 2006) in R-2.13.0 (R Development Core Team, 2011). This package automatically chooses the optimal smoothing parameter.

We found that the climate variables were highly correlated. Therefore, we ran a PCA (separate for temperature and precipitation) with these variables and only retained the variable that loaded most heavily onto the first axis. For all environmental variables, we did not include any correlated variables ($r \geq \pm 0.70$) in the same model. For the temporally varying data (weather and EVI) variables, we used the data corresponding to the date at which each flower survey was conducted (see Appendix 4).

To select the best predictive model, we used five-fold cross validation. We did this by dividing the data set into a training (n=54) and test (n=13) data set and repeated the procedure five times. Each time the test data set contained a different set of study sites. We used the following model selection procedure to obtain the best predictive model. First we created a full model using all nine environmental variables. From the full model containing all nine environmental variables, we dropped one variable at a time. We constructed the models separately for each training data set. We used the resulting model and the function *predict.gam* to predict new nectar energy values from the values of the environmental variables in each test data set. We then linearly regressed these predicted values onto the observed nectar energy values and reported the R2. We averaged the R2 across the five test data sets. We retained the model with the highest average R2 (or several models if the R2's were close). We also reported the AIC of the model fit to the training data sets to ensure the models we retained were also among the best fitting models. From the models we retained, we again dropped individual variables and repeated the validation. We repeated the procedure until dropping variables resulted in a drop in R2 to below 0.35. Once a final model was chosen, we added interaction terms, ran the models with cross-validation and tested whether adding the interaction term improved the R2.

We used *predict.gam* to predict new nectar production values based on the environmental variables found in each pixel of the appropriate habitat classes in our study region. We produced maps of predicted nectar production for each of the dates for which EVI data was provided (21 April, 7 May, 23 May, 8 June, 24 June, 9 July, 26 July). We classified all predictions < 0 as 0. All mapping was done in R-2.13.0 (R Development Core Team, 2011) with the rgdal 0.6-8 package (Keitt *et al*., 2009) and GRASS-6.4-SVN (GRASS Development Team 2009).

2.3.6. Predicting bird abundances

Bird abundances were taken from the Breeding Bird Survey (BBS), a volunteer-run survey that censuses all birds seen and heard along 40 km survey routes. The surveys are conducted on one day in late May or early June. We used our nectar production data from 2008 to predict bird abundances (Black-chinned and Broad-tailed Hummingbirds separately) in 2008 and 2009. We tested different years to account for any carry-over effects current year nectar production may have on the following year's population. Each BBS route was an independent sample. We limited our sample of BBS routes to our study region, for which there were 122 routes. Given that a BBS route is a linear transect, we took an average of nectar production from all the grid cells that intersected each route. We used nectar production data from 8 June, the date closest to when the BBS routes were surveyed.

To predict bird abundances from nectar production, we used zero-inflated Poisson (ZIP) regression. ZIP regression is superior to traditional Poisson regression (i.e. produces less biased parameter estimates) for count data with many zeroes (Martin et al., 2005; Wenger & Freeman, 2008). Depending on the species and year, as many as 107 of the 122 BBS routes were zeroes. ZIP has the added feature that it models two types of zeroes: those that represent true absences and those that are missed because of insufficient sampling. ZIP does this by running a binomial model distinguishing presences from absences and a Poisson model of counts (i.e. abundances) that also includes zeroes. Consequently, ZIP is not equivalent to running two separate models (i.e. one for presence-absence and one for sites where the species is present.)

By using ZIP regression, we are able to test separately whether variation in nectar production a) distinguishes occupied from unoccupied sites and b) predicts abundance in sites where the birds are expected to occur. We tested the predictive ability of nectar production in two ways. First, we compared a ZIP model with nectar production to an intercept-only model using AIC. If the former had a lower

AIC, then we looked at the significance of nectar production in the separate count and binomial models. (There is currently no way to calculate the separate AICs of the individual count and binomial components of the ZIP model). We considered nectar production a predictor of presence/absence or abundance when the slope of the parameter estimate had a p-value less than 0.05. To clearly present the relationship between nectar production and bird abundance, we used the best model to predict and graphically show bird abundances across a range of nectar production values that correspond to the values we found in the field (0 – 130 kJ 24 hr-1*pixel-1). In ZIP models, predictions are made jointly from the count and binomial models, i.e. predicted abundance is multiplied by the probability of occurrence at each nectar production value. We implemented ZIP models in the pscl package (Zeileis et al., 2008; Jackman, 2010) in R-2.13.0 (R Development Core Team, 2011).

2.3.7. Spatial autocorrelation

Prior to conducting any of the above statistical modeling, we tested for the presence and extent of spatial autocorrelation. For the 67 study sites we used to predict nectar production, the closest distance between any two sites was 0.68 km. Four sites were joined to their closest neighbour at distances of less than 1.00 km. Likewise for the 122 Breeding Bird Survey routes we used to predict bird abundances, the closest distance between any two sites was 2.24 km and four sites were connected to their closest neighbour at distances of less than 5.00 km.

To test for spatial autocorrelation we constructed a correlogram that gives the Moran's I statistic for different distance bands (Bivand et al., 2008). For both nectar production study sites and BBS routes, we chose bands of 20 km increments (i.e. 0 – 20 km, 20 – 40 km, etc.). All pairs of points connected by a distance specified by the particular band were assigned a weight of 1.00 while pairs of points at greater or lesser distances were assigned a weight of 0.00. Moran's I falls between -1 and 1 with 0 indicating a lack of spatial autocorrelation. The significance of Moran's I was calculated by bootstrapping the data 1000 times to construct 95% confidence intervals. Therefore for a particular distance band, spatial autocorrelation was significant if its Moran's I statistic had a p-value of less than 0.05. We assessed spatial autocorrelation on the residuals of the full GAM model predicting nectar production and on the residuals of the full ZIP model predicting bird abundances (for each species and year separately). All tests of spatial autocorrelation were conducted with the spdep (Bivand, 2011) and ncf (Bjornstad, 2009) packages in R-2.13.0 (R Development Core Team, 2011).

We did not find significant spatial autocorrelation in the nectar production residuals for any distance band (Fig. A2.3). When predicting bird abundances, there was significant positive spatial autocorrelation in the residuals at the smallest distance bands and, for Black-chinned Hummingbirds, significant negative spatial autocorrelation in the residuals at the largest distance bands (Fig. A2.4). Significant spatial autocorrelation indicates a lack of independence among the residuals, which violates an assumption of frequentist statistical tests (Dormann *et al.*, 2007). Even in an information-theoretic approach (i.e. AIC), spatial autocorrelation can lead to model overfitting (Diniz-Filho *et al.*, 2009). Hence, we added a spatial autocovariate term (Dormann *et al.*, 2007) to our ZIP models. The autocovariate term is an additional parameter that represents values from a set of points from a neighbourhood surrounding each sample (BBS route in this case). Although autocovariate models can bias parameter estimates (Dormann *et al.*, 2007), there is currently no practical way of running more complex spatial ZIP models.

2.4. Results

2.4.1. Flower survey

Across the 103 study sites, we found 33 different species of hummingbird-visited nectar plants corresponding to 11 genera. In any subsequent analysis, we consider only the genus level because not all species could be accurately classified and because data on nectar energy from the literature can come from several species within a genus.

Agave and *Frasera* were the least abundant plants though both contain an order of magnitude higher number of flowers per stalk compared to the other genera (Table A2.1). *Penstemon* was the most abundant plant and *Castilleja* the most common. Nearly half the sites did not contain any flowers. Most of these sites were in the Chihuahuan Desert and associated habitats.

2.4.2. Literature survey

When considering only studies that measure nectar production in the same genera we found on our surveys, that measure nectar production in a 24 hr period, and that bag flowers and compare them to a control, we ended up with 16 separate published studies covering 21 species and 9 of the 11 genera (Table A2.2). We could not find data for *Mertensia* or *Robinia* nectar production. Since these genera comprised a negligible portion of the flowers we found on our surveys, we excluded these genera from subsequent analyses. We found only one study of *Cirsium* nectar production and it came from Japan (Ohashi & Yahara, 2002). This study also only measured nectar production in a one hour period, which we multiplied by 24. We included this study in our survey despite its discrepancies with the others. Aside from the Japanese study, the others quantified different facets of 24 hr. nectar production throughout western North America and from the 1970's to the early 2000's (see Table A2.2).

2.4.3. Predicting nectar production

A preliminary analysis of nectar production data from all sites showed that TCOLD was the best predictor of spatial variation in nectar production because it best distinguished hot desert sites without flowers from cool woodland/forest sites with flowers. However, this model is not informative in predicting variation among sites that contain flowers. Hence we dropped the "hot" sites from all subsequent analyses. We decided on which sites to drop based on visual inspection of photographs of each site - it was obvious which sites could be considered "hot" and which sites "cool" based on vegetation density. This selection was substantiated by a correspondence between our visual-based habitat definition and the habitat classes as defined by the Southwest Regional Gap Analysis (USGS National Gap Analysis Program, 2005). Except for one habitat class ("Inter-Mountain Basins Semi-Desert Grassland"), there are no overlaps in the habitat classes considered "hot" and "cool" (Table A2.3). In all further analyses, we model only the “cool” sites (n=68) and limit our predictions to those habitat classes (as defined by the Gap Analysis) upon which we built the models. We dropped one other site from our analysis because it contained more than 10x the flowers (all *Penstemon*) of any other site.

We selected the best predictive model based on the R2 of the fit between predicted and observed total nectar production, averaged over five test datasets (Table 2.2). A suite of models are all candidates for the “best” model and they all contain at least TCOLD, EVI and ELEV. Given the small difference in predictive power between this three variable model and more complex models, we use the simplest model in all further predictions. Including an interaction term between TCOLD and EVI marginally improves predictive power but, again, is perhaps an unnecessary complication.

The predictions were validated by using the *predict.gam* function in the mgcv package (Wood, 2006) to produce standard errors of the predictions. Depending on the test dataset, 7-10 of the 13 observations fell within the 95% confidence interval of predictions.

Table 2.2. Summary of the top models predicting spatial variation in nectar production. The top models are chosen by the fit (R2) between observed and predicted values averaged over 5 test datasets (n=13). The fifth model shown has the lowest AIC value among models predicting spatial variation in nectar production for five training datasets (n=54). The mean and ranges for five training (AIC, ΔAIC) or test datasets (R2) are shown. Mean ΔAIC expresses the

difference among the average AIC values. The variable definitions are given in Table 2.1.

Variables in Model	R2	AIC	ΔAIC
TCOLD, EVI, ELEV, TEMP	0.45 [0.16-0.85]	582.13 [572.35-604.99]	22.39 [9.00-62.70]
TCOLD, EVI, ELEV, TCOLD*EVI	0.43 [0.10-0.48]	586.84 [570.64-600.52]	27.11 [10.92-67.08]
TCOLD, PWARM, EVI, ELEV, TEMP	0.42 [0.15-0.70]	581.12 [573.22-587.26]	21.38 [2.97-67.70]
TCOLD, EVI, ELEV	0.41 [0.14-0.76]	591.19 [576.95-600.08]	31.45 [20.31-66.63]
TCOLD, EVI, ELEV, GDD, DATE	0.22 [0.02-0.50]	559.74 [533.45-600.45]	0 [0-39.79]

Using the final model, we have created maps of the study region depicting predicted spatial variation in nectar production (Figs. 2.2A, A2.5). Much of the habitat within the study region is predicted to produce no nectar. There are some hotspots where nectar production is predicted to be > 100 kJ 24 hr-1*pixel-1. One of the major hotspots occurs in western Colorado along the western slope of the Rockies and in the San Juan Mountains including the Colorado, San Miguel, Gunnison, Piedra, Animas, La Plata, Mancos and Dolores River watersheds.

Like nectar production, the distribution of the standard error of nectar production is also patchy (Fig. 2.2B). However the areas of greatest uncertainty are not necessarily where nectar production is highest.

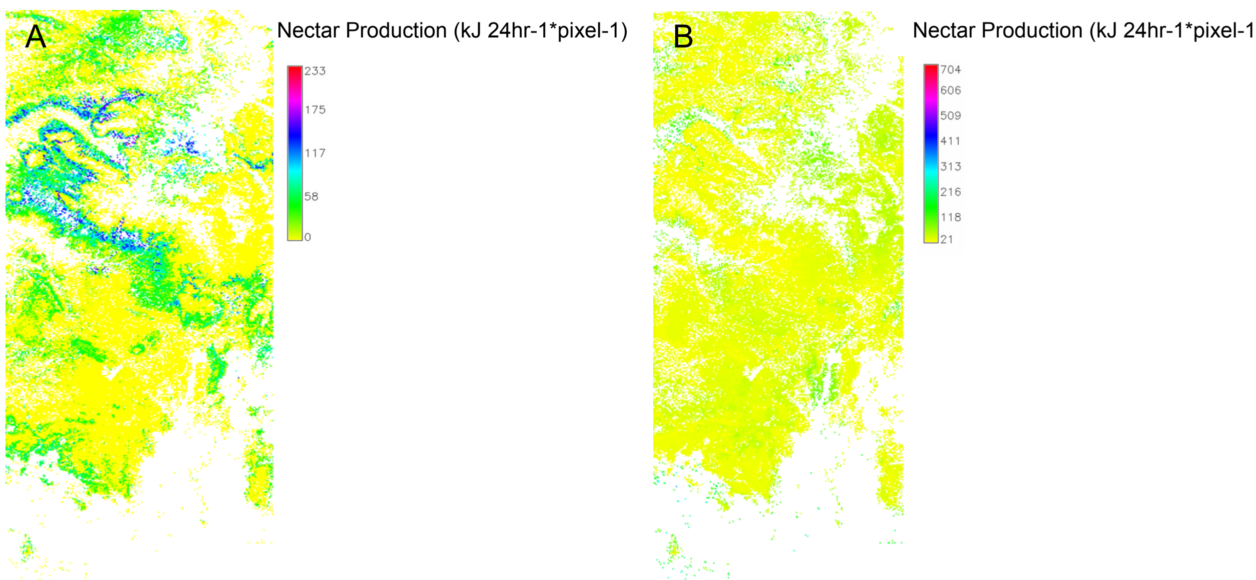


Fig. 2.2. Map of spatial variation in nectar production across the study region (A) and the associated standard error of the predictions (B). White areas indicate habitat classes not included in our surveys. The maps depict nectar production on 8 June 2008.

2.4.4. Predicting bird abundance

Nectar production predicted the abundances of Black-chinned and Broad-tailed Hummingbirds in 2009 but not in 2008. For both species in 2009, models containing nectar production had the lowest AIC and nectar production itself significantly predicted abundance (Table 2.3, Fig. 2.3). However, nectar production was not a significant predictor of presence/absence (Table 2.3). For Black-chinned Hummingbirds in 2008 the AIC of the nectar production model was only marginally lower than the intercept-only model. For Broad-tailed Hummingbirds in 2008, the lowest AIC corresponded to the autocovariate-only model (Table 2.3). For both species, the parameter estimate of nectar production was not significantly related to bird abundance or presence/absence.

Table 2.3. Results of zero inflated Poisson (ZIP) regression models relating nectar production to abundances of two hummingbird species over two years. The sample size indicates the number of Breeding Bird Survey routes the species was present out of a total of 122. The AIC and ΔAIC values compare the full model (nectar production + spatial autocovariate), the autocovariate-only, and the intercept-only models. The parameter estimates, their 95% confidence intervals, and their p-values are given for both the count and binomial components of the ZIP model. Estimates are given for the full model, regardless of whether it was the best (i.e. lowest AIC) model.

Species	Year	Model	AIC	ΔAIC	Component	Full model equation	*P*
Black-	2008	Nectar prod.	135.87	0.00	Count	abundance = (0.689 ± 0.660)	0.041
chinned	(n = 15)					– (0.0135 ± 0.0161)[nectar.prod]	0.100
						+ (2.823 ± 3.246)[spat.autocov]	0.088
		Intercept	137.13	1.26	Binomial	occupancy = (2.268 ± 0.846)	<0.001
		Autocovariate	137.90	2.02		– (0.0274 ± 0.0280)[nectar.prod]	0.056
						- (0.0262 ± 2.773)[spat.autocov]	0.985
	2009	Nectar prod.	148.99	0.00	Count	abundance = - (0.678 ± 1.043)	0.202

	(n = 20)					+ (0.0227 ± 0.0154)[nectar.prod]	0.0039
						+ (2.057 ± 2.115)[spat.autocov]	0.056
		Autocovariate	155.04	6.05	Binomial	occupancy = (1.163 ± 0.127)	0.075
		Intercept	167.39	18.4		+ (0.0004 ± 0.0202)[nectar.prod]	0.967
						- (0.141 ± 18.77)[spat.autocov]	0.141
Broad-	2008	Autocovariate	814.71	0.00	Count	abundance = (1.781 ± 0.149)	<0.001
tailed	(n = 55)					- (0.0015 ± 0.00253)[nectar.prod]	0.249
						+ (0.310 ± 0.057)[spat.autocov]	<0.001
		Nectar prod.	816.50	1.79	Binomial	occupancy = (0.949 ± 0.582)	0.001
		Intercept	937.98	123.27		- (0.0062 ± 0.0133)[nectar.prod]	0.358
						- (0.537 ± 0.337)[spat.autocov]	0.002
	2009	Nectar prod.	846.37	0.00	Count	abundance = (2.111 ± 0.121)	<0.001
	(n = 46)					+ (0.0062 ± 0.00267)[nectar.prod]	<0.001
						+ (0.247 ± 0.092)[spat.autocov]	<0.001

		Autocovariate	861.63	15.26	Binomial	occupancy = (0.844 ± 0.503)	0.001
		Intercept	920.75	74.38		+ (0.0002 ± 0.0135)[nectar.prod]	0.970
						- (1.812 ± 1.264)[spat.autocov]	0.004

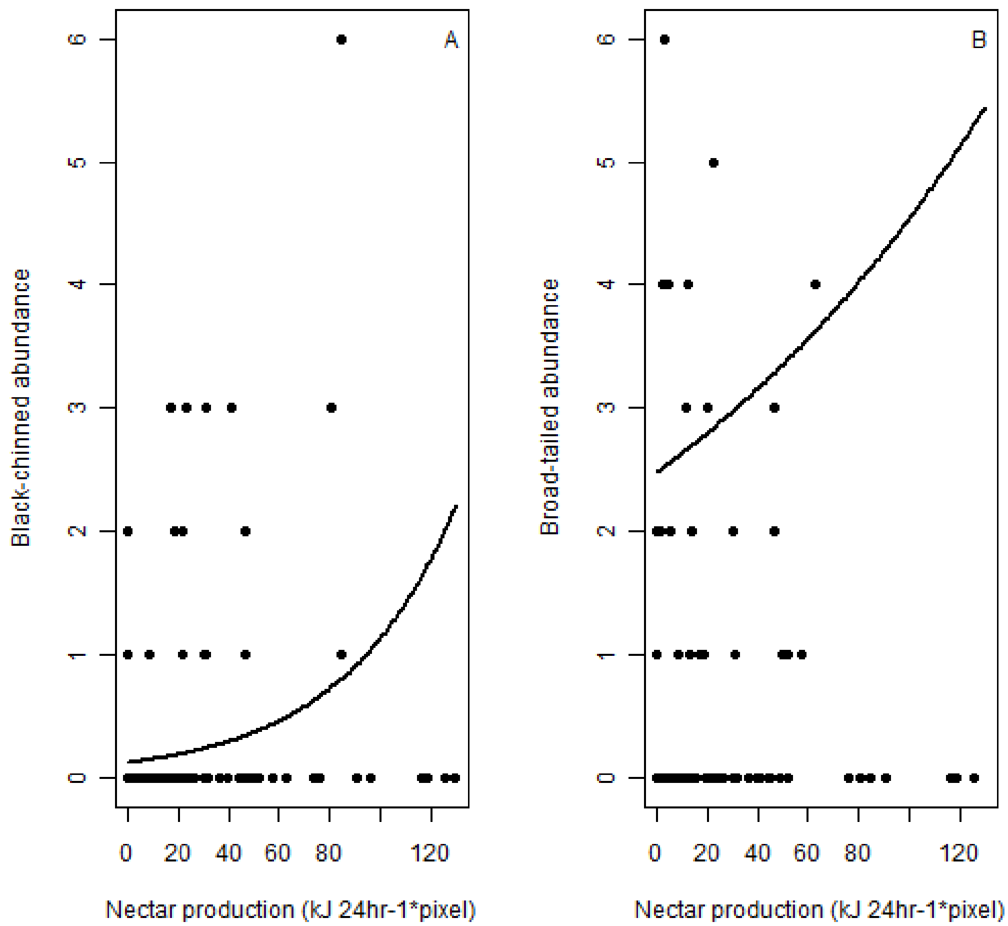


Fig. 2.3. The predicted relationship between nectar production and Black-chinned (A) and Broad-tailed (B) abundance in 2009. Predictions are made from zero-inflated Poisson regressions and include both the count and binomial models. The closed circles are the observed data.

2.5. Discussion

Using a simple model of three easy-to-obtain environmental variables, we predicted spatial variation in the energy available to hummingbirds across a large part of the Southwest USA. We then showed that energy significantly predicted the breeding abundances of two hummingbird species in the same region. Ours is the first study to show such a relationship at large spatial extents. Others have been conducted at small spatial extents (e.g. Dunning & Brown, 1982) or, if done at large scales, use temperature or primary productivity as their measure of available energy (e.g. Meehan *et al*., 2004; Pettorelli *et al*., 2009).

The scaling of abundance to energy availability is an implicit assumption of many macroecological theories, such as species energy theory (Preston, 1962; Wright, 1983). Our finding of a positive relationship between animal abundance and energy supports this assumption. In addition, two novel insights about the scaling relationship emerged from our study. First, energy from food was a significant predictor of abundance but not of presence-absence, suggesting that a species' distribution and its abundance are characterized by different environmental relationships. Second, energy from food was a better predictor of the following year's abundance than the current year, suggesting a time lag in the scaling of abundance to energy. Consequently, a theory of spatial variation in abundance at large spatial scales may only in part be a theory of spatial variation in energy availability.

2.5.1. The hummingbird-nectar relationship: abundance vs. occupancy

The positive relationship between distribution and abundance is one of the most well documented patterns in ecology (Borregaard & Rahbek, 2010). However, the two attributes are not necessarily an outcome of the same processes (Wenger & Freeman, 2008). In our study, we found that nectar production was a significant predictor of variation in abundance but not occupancy. Consequently, what is suitable and not suitable habitat for hummingbirds is determined by other factors; high nectar production alone is not sufficient for being a suitable habitat. This implies that habitat filters based on factors unrelated to nectar production constrain hummingbird distribution but once these factors are met, survival and reproduction may be most affected by nectar availability.

The existence of a time lag in the scaling of abundance to energy is further evidence that abundance and occupancy track different environmental relationships. Given the one year time lag, nectar production possibly affects interannual population growth, such as being associated with greater adult survival. High nectar production may enhance survival directly by ensuring that more individuals are able to meet their energetic demands (Calder, 1975). High nectar production may also indirectly affect survival by reducing interference competition and the use of aggressive behaviour (Ewald, 1985; Powers & McKee, 1994), which facilitates the co-existence of both aggressive and non-aggressive individuals and species (Carpenter & MacMillen, 1976; Dubois *et al*., 2004). High nectar production is especially important during the breeding season because of the excess energetic demands related to breeding (Powers, 1987; Clark, 2009), which leads to high breeding season mortality (Mulvihill *et al*., 1992). At the same time, hummingbirds are known to have high site fidelity (Calder et al., 1983), meaning high survival at high nectar production sites may translate to high abundances the following year.

Abundance may not reflect the current year's nectar production because the birds are constrained by the factors that influence occupancy combined with limited movement during the breeding season. Both Black-chinned and Broad-tailed Hummingbirds are migratory and arrive in our study region in early spring, before the main bloom of nectar flowers. Hence individuals may distribute themselves according to factors other than nectar availability such as insect availability (Carpenter & Castronova, 1980; Powers et al., 2010) or resources related to mate and nest-site selection (Armstrong, 1987; Baltosser, 1989). Once individuals have selected breeding habitat, subsequent movement may be insufficiently large enough to cause a redistribution of individuals to match spatial variation in nectar production. Large-scale movements allow for resource tracking but these occur seasonally as migrations (e.g. Feinsinger et al., 1985). In our study, we were interested in whether abundance matches resources solely within the breeding season. It is possible that if we could have recorded and averaged abundances across the breeding and post-breeding seasons, then a predictive relationship between nectar production and abundance might have occurred. Unfortunately, post-breeding abundance data does not exist at large spatial extents.

2.5.2. The hummingbird-nectar relationship: implications

The contrasting way in which abundance and occupancy relate to the environment affects how we understand species range patterns. Generally, the shift from occupied to unoccupied sites corresponds to a species' physiological tolerance to climate or to interspecific competition (MacArthur, 1972; Loehle, 1998). Such climate mediated shifts in occupancy happen at range limits (Normand *et al.,* 2009; Busch *et al.*, 2011) and inside ranges along elevation gradients (Buckley &

Roughgarden, 2006; Cadena & Loiselle, 2007). If spatial variation in abundance is not related to climate, then abundance would not necessarily peak in range centres nor decline smoothly to range edges, which is consistent with empirical data (Blackburn *et al.*, 1999; Sagarin & Gaines, 2002).

The contrasting way in which abundance and occupancy relate to the environment also affects how we model changes in species distributions in response to global change. Most species distribution models use presence-absence data and predict changes in occupancy (e.g. Araújo *et al*., 2005; Elith *et al*., 2006). While some have encouraged substituting inferences based on abundance for inferences based on occupancy (Pearce & Ferrier, 2001; Bahn & McGill, 2008), our study, along with just a few others (Nielsen *et al*., 2005; Wenger & Freeman, 2008) suggest that models of the two may differ. In our case, conservation decisions based on occupancy models may target those factors associated with nesting habitat or predation risk. However, important conservation decisions should also emphasize population extinction risk (Ceballos & Ehrlich, 2002), which, for hummingbirds, might be lowest in areas of high nectar production.

2.5.3. The hummingbird-nectar relationship: study limitations

Our food-abundance relationship was predicated on the notion that nectar production, from a hummingbird's perspective, can be aggregated across flower species. This was a fair assumption at least in North America. Hummingbird flowers have similar colour, size, and shape and hummingbirds do not specialize on different species (Brown & Kodric-Brown, 1979; Waser *et al.*, 1996; Dalsgaard *et al.*, 2009; but see Lange *et al*., 2000). Even if some species are not a preferred food source, they are still important when other flowers have been temporarily emptied (Stiles, 1973). Although there is a genetic component to nectar production (Leiss *et al*., 2004), this creates as much within species as among species variation (Teuber & Barnes, 1979; Hodges, 1993). Traits associated with attracting pollinators (e.g. flower size) vary geographically but this variation is an outcome of pollinator based selection (Boyd, 2002; Nattero & Cocucci, 2007). Hence, nectar production varies more among different environments (either in space or time) than among different species sampled under the same microenvironment conditions (Brown & Kodric-Brown, 1979; Lange *et al*., 2000).

The fact that nectar production is influenced by microenvironment affects how we applied nectar production to flowers within a plant. We used a gamma distribution derived from all nectar production values in the literature but disregarded the differences among studies. It would be more realistic to consider the microenvironment of our sites and from there model within and between plant variation in nectar production. Such detail would have to be built into future models. We chose a gamma distribution because it reflects the “bonanza-blank” reward schedule of some nectar plants (Feinsinger, 1978; Pleasants & Zimmerman, 1983), whereby few flowers contain high amounts of nectar and most flowers are empty.

We also used the same gamma distribution for all individuals of the same genus in a study site therefore assuming random between plant variation in nectar production. In one study of the bee pollinated *Echium vulgare*, nectar production in a patch of flowers was dominated by a few individuals and production was autocorrelated within a 1.41m radius (Leiss & Klinkhamer, 2005). In contrast, Hodges (1993) found significant between-plant differences in nectar production for *Mirabilis multiflora* but those “hot” and “cold” plants were scattered randomly throughout the study site. Regardless, by drawing from the same gamma distribution, each plant in our study sites had an equal opportunity to be “hot” or “cold”. Future models should consider using separate statistical distributions for between plant and within plant variation in nectar production.

Although the focus of our study was on spatial variation, nectar production also varies over time. We measured daily temperature and precipitation but neither of these variables were retained in the best model of nectar production, suggesting that fine scale temporal variation in nectar production is under different controls. Indeed, temperature and precipitation are more likely to be important when measured at different points in the year rather than concomitantly with nectar production. For example, temperature is known to affect snow depth and frost damage, which may be the measures mechanistically linked to changes in flower abundances at least at our higher elevation sites (Inouye & McGuire, 1991; Inouye *et al*., 2002; Miller-Rushing & Inouye, 2009). EVI, which measures plant productivity and is sampled every two weeks, was the only temporally varying variable in our model predicting nectar production. Perhaps, then, EVI captured all the necessary phenological changes in nectar production. Regardless, it is unlikely that nectar production at finer temporal scales would alter the coarse scale patterns we observed in hummingbird abundance.

Our model explains on average 40% of the variation in nectar production. Given that multiple levels of organization are involved in enumerating nectar production at the site level (i.e. nectar production per flower, number of flowers per inflorescence, number of inflorescences per plant, number of plants per site), it is surprising that so much variation can be accounted for by climate, elevation and plant productivity. This does not preclude the need for more sophisticated models that explicitly consider the controls on nectar production at each level separately. For the purposes of understanding large-scale variation in animal abundances, however, fine-scale factors may not provide any extra information.

2.5.4. Conclusions

Many organisms have populations strongly regulated by one particular resource even if this resource has restricted spatial and temporal availability (e.g. resource pulses; see review in Yang *et al*., 2008). Consequently the temporal matching of abundance to resources observed in hummingbirds (Cotton, 2007) and other birds (McShea, 2000) may have a direct spatial analogue. Just as one can pick a point in space and follow temporal fluctuations in abundance, we have shown that it is equally possible to fix a point in time, take a slice through the species range, and observe a similar form of abundance fluctuation. However, in our system, the slice representing resources and the slice representing abundance should be taken a year apart. In addition, the slice representing resources will not match the slice representing occupancy (presence-absence) regardless of when they are taken. In part, these results are an outcome of the temporal scale of our study and the taxa involved. Consequently, such dependencies would need to be incorporated into any general theory attempting to explain spatial variation in abundance.

2.6. Acknowledgements

Thank you to Amanda Barth for field assistance, Doug Armstrong, Maria Clara Castellanos, and Peter Scott for providing nectar data, and Don Powers, Peter Scott, Elizabeth Vise, Nick Waser, and Susan Wethington for help with project planning and implementation. R. Feldman was supported by an NSERC PGS-D scholarship.

2.7. References

Abrahamczyk, S. & Kessler, M. (2010) Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. *Journal of Ornithology*, **151**, 615-625.

Araújo, M.B, Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species-climate impact models under climate change. *Global Change Biology*, **11**, 1504-1513.

Armstrong, D.P. (1987) Economics of breeding territoriality in male Calliope Hummingbirds. *Auk*, **104**, 242 – 253.

Bahn, V. & McGill, B.J. (2007) Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography*, **16**, 733–742.

Baltosser, W.H. (1989) Nectar availability and habitat selection by hummingbirds in Guadalupe Canyon. *Wilson Bulletin*, **101**, 559-578.

Bivand, R. (2011) spdep: Spatial dependence: weighting schemes, statistics and models. R package version 0.5-32. http://CRAN.R-project.org/package=spdep

Bivand, R.S., Pebesma, E.J. & Gómez-Rubio, V. (2008). *Applied Spatial Data Analysis with R.* Springer, New York.

Bjornstad, O.P. (2009) ncf: spatial nonparametric covariance functions. R package version 1.1-3. http://CRAN.R-project.org/package=ncf

Blackburn, T.M., Gaston, K.J., Quinn, R.M. & Gregory, R.D. (1999) Do local abundances of British birds change with proximity to range edge? *Journal of Biogeography*, **26**, 493-505.

Bolten, A.B., Feinsinger, P., Baker, H.G. & Baker, I. (1979) On the calculation of sugar concentration in flower nectar. *Oecologia*, **41**, 301-304.

Borregaard, M.K. & Rahbek, C. (2010) Causality of the relationship between geographic distribution and species abundance. *Quarterly Review of Biology*, **85**, 4-25.

Boyd, A. (2002) Morphological analysis of Sky Island populations of *Macromeria viridiflora* (Boraginaceae). *Systematic Botany,* **27**, 116-126.

Brown, J.H. & Kodric-Brown, A. (1979) Convergence, competition, and mimicry in a temperature community of hummingbird-pollinated flowers. *Ecology,* **60**, 1022-1035.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995) Spatial variation in abundance. *Ecology,* **76**, 2028-2043.

Brown, J.L. (1969) The buffer effect and productivity in tit populations. *American Naturalist,* **103**, 347-354.

Buckley, L.B. & Roughgarden, J. (2006). Climate, competition, and the coexistence of island lizards. *Functional Ecology*, 20, 315-322.

Burns, K.C. (2002) Seed dispersal facilitation and geographic consistency in bird-fruit abundance patterns. *Global Ecology and Biogeography*, **11**, 253-259.

Busch, D.S., Robinson, W.D., Robinson, T.R. & Wingfield, J.C. (2011). Influence of proximity to a geographical range limit on the physiology of a tropical bird. *Journal of Animal Ecology*, 80, 640-649.

Byer, H.L. (2004). Hawth´s analysis tools for ArcGIS. http://www.spatialecology.com

Cadena, C.D. & Loiselle, B.A. (2007). Limits to elevational disributions in two species of emberizine finches : disentangling the role of interspecific competition, autoecology, and geographic variation in the environment. *Ecography*, 30, 491-504.

Calder, W.A. (1975) Daylength and the hummingbird's use of time. *Auk*, **92**, 81-97.

Calder, W.A., Waser, N.M., Hiebert, S.M., Inouye, D.W. & Miller, S. (1983) Site-fidelity, longevity, and population dynamics of Broad-tailed hummingbirds: a ten year study. *Oecologia*, **56**, 359-364.

Carpenter, F.L. & Castronova, J.L. (1980) Maternal diet selectivity in *Calypte anna*, *American Midland Naturalist.* **103**, 175-179.

Carpenter, F. L. & MacMillen, R.E. (1976) Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. *Science*, **194**, 639-642.

Ceballos, G. & Ehrlich, P.R. (2002) Mammal population losses and extinction crises. *Science*, **296**, 904-907.

Cotton, P.A. (2007) Seasonal resource tracking by Amazonian hummingbirds. *Ibis,* **149**, 135-142.

Dalsgaard, B., Martín González, A.M., Olesen, J.M., Ollerton, J., Timmermann, A., Andersen, L.H. & Tossas, A.G. (2009) Plant-hummingbird interactions in the West Indies: floral specialization gradients associated with environment and hummingbird size. *Oecologia*, **159**, 757-766.

Díaz, M., Illera, J.C. & Atienza, J.C. (1998) Food resource matching by foraging tits *Parus* spp. during spring-summer in a Mediterranean mixed forest; evidence for an ideal free distribution. *Ibis*, **140**, 654-660.

Diniz-Filho, J.A.F., Rangel, T.F.L.V.B. & Bini, L.M. (2008) Model selection and information theory in geographical ecology. *Global Ecology and Biogeography*, **17**, 479-488.

Dormann, C.F., McPherson, J., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P., Reineking, B., Shröeder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of distributional species data: a review. *Ecography*, **30**, 609-628.

Dubois, F., Giraldeau, L-A, Hamilton, I.M., Grant, J.W.A & Lefebvre, L. (2004) Distraction sneakers decrease the expected level of aggression within groups: a game-theoretic model. *American Naturalist*, **164**, E32-E45.

Dunning Jr., J.B & Brown, J.H. (1982) Summer rainfall and winter sparrow densities: a test of the food limitation hypothesis. *Auk*, **99**, 123-129.

Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129-151.

ESRI. (1999-2009) ArcMap 9.3.1. ESRI Inc. Redlands, CA.

Ewald, P.W. (1985) Influence of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. *Animal Behavior,* **33**, 705-719.

Feinsinger, P. (1978) Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecological Monographs,* **48**, 269-287.

Feinsinger, P., Swarm, L.A. & Wolfe, J.A. (1985) Nectar-feeding birds on Trinidad and Tobago: comparison of diverse and depauperate guilds. *Ecological Monographs*, **55**, 1-28.

Fretwell, S.D. & Lucas, H.L. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica,* **19,** 16-36.

Gill, J.A., Norris, K., Potts, P.M., Gunnarsson, T.G., Atkinson, P.W. & Sutherland, W.J. (2001a) The buffer effect and large-scale population regulation in migratory birds. *Nature*, **412**, 436-438.

Gill, J.A., Sutherland, W.J. & Norris, K. (2001b) Depletion models can predict shorebird distribution at different spatial scales. *Proceedings of the Royal Society B*, **268**, 369-376.

Grand, T.C. & Grant, J.W.A. (1994) Spatial predictability of resources and the ideal free distribution in convict cichlids, *Cichlasoma nigrofasciatum*. *Animal Behaviour*, **48**, 909-919.

GRASS Development Team. (2009) Geographic Resources Analysis Support System (GRASS) Software, Version 6.4.0. http://grass.osgeo.org

Guisan, A. & Thuiller, W. (2008) Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, **8**, 993-1009.

Gunnarsson, T.G., Gill, J.A., Petersen, A., Appleton, G.F. & Sutherland, W.J. (2005) A double buffer effect in a migratory shorebird population. *Journal of Animal Ecology,* **74**, 965-971.

Hainsworth, F.R. & Wolf, L.L. (1972) Crop volume, nectar concentration, and hummingbird energetics. *Comparative Biochemistry and Physiology A*, **42**, 359-366.

Herrera, C.M. (1998) Long-term dynamics of Mediterranean frugivorous birds and fleshy-fruits: a 12-year study. *Ecological Monographs*, **68**, 511-538.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology,* **25**, 1965-1978.

Hodges, S.A. (1993) Consistent interplant variation in nectar characteristics of *Mirabilis multiflora. Ecology*, **74**, 542-548.

Hogstad, O. (2005) Numerical and functional responses of breeding passerine species to mass occurrence of Geometrid caterpillars in a subalpine birch forest: a 30-year study. *Ibis*, **147**, 77-91.

Inouye, D.W. & McGuire, A.D. (1991) Effects of snowpack on timing and abundance of flowering in *Delphinium nelsonii* (Ranunculaceae): implications for climate change. *American Journal of Botany,* **78**, 997-1001.

Inouye, D.W., Calder, W.A. & Waser, N.M. (1991) The effect of floral abundance on feeder censuses of hummingbird populations. *Condor*, **93**, 279-285.

Inouye, D.W., Morales, M.A. & Dodge, G.J. (2002) Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Nina, in the context of climate change. *Oecologia*, **130**, 543-550.

Jackman, S. (2010) pscl: Classes and methods for R developed in the Politcal Science Computation Laboratory, Stanford University, R package version 1.03.6, http://pscl.stanford.edu/

Keitt, T.H., Bivand, R., Pebesma, E. & Rowlingson, B. (2009) rgdal: Bindings for the Geospatial Data Abstraction Library, R package version 0.6-8, http://www.gdal.org

Kennedy, M. & Gray, R.D. (1993) Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the Ideal Free Distribution, *Oikos*, **68**, 158-166.

Koenig, W.D. & Haydock, J. (1999) Oaks, acorns, and the geographical ecology of acorn woodpeckers. *Journal of Biogeography*, **26**, 159-165.

Lange, R.S., Scobell, S.A. & Scott, P.E. (2000) Hummingbird-syndrome traits, breeding system, and pollinator effectiveness in two syntopic *Penstemon* species. *International Journal of Plant Sciences,* **161**, 253-263.

Leiss, K.A. & Klinkhamer, P.G.L. (2005) Spatial distribution of nectar production in a natural *Echium vulgare* population: implications for pollinator behaviour. *Basic and Applied Ecology,* **6**, 317-324.

Leiss, K.A., Vrieling, K. & Klinkhamer, P.G.L. (2004). Heritability of nectar production in *Echium vulgare. Heredity*, **92**, 446-451.

Levey, D.J. (1988) Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs*, **58**, 251-269.

Loehle, C. (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography*, **25**, 735-742.

Loiselle, B.A. & Blake, J.G. (1991) Temporal variation in bird and fruits along an elevation gradient in Costa Rica. *Ecology*, **72**, 180-193.

MacArthur, R.H. (1972) *Geographical Ecology: Patterns in the Distribution of Species.* Harper & Row, New York.

Martin, T.G., Wintle, B.A., Rhodes, J.R., Kuhnert, P.M., Field, S.A., Low-Choy, J., Tyre, A.J. & Possingham, H.P. (2005) Zero tolerance ecology: improving ecological inference by modeling the source of zero observations. *Ecology Letters*, **8**, 1235-1246.

McShea, W.J. (2000) The influence of acorn crops on annual variation in rodent and bird populations, *Ecology*, **81**, 228-238.

Meehan, T.D, Jetz, W. & Brown, J.H. (2004) Energetic determinants of abundance in winter landbird communities, *Ecology Letters*, **7**, 532-537.

Miller-Rushing, A.J. & Inouye, D.W. (2009) Variation in the impact of climate change on flowering phenology and abundance: an examination of two pairs of closely related wildflower species, *American Journal of Botany,* **96**, 1821-1829.

Mulvihill, R.S., Leberman, R.C. & Wood, D.S. (1992) A possible relationship between reversed sexual size dimorphism and reduced male survivorship in the Ruby-throated Hummingbird. *Condor*, **94**, 480-489.

Nattero, J. & Cocucci, A.A. (2007). Geographical variation in floral traits of the tree tobacco in relation to its hummingbird pollinator fauna. *Biological Journal of the Linnean Society,* **90**, 657-667.

Nielsen, S.E., Johnson, C.J., Heard, D.C. & Boyce, M.S. (2005) Can models of presence-absence be used to scale abundance? Two case studies considering extremes in life history. *Ecology*, **28**, 197-208.

Ohashi, K. & Yahara, T. (2002). Visit larger displays but probe proportionally few flowers: counterintuitive behaviour of nectar-collecting bumble bees achieves an ideal free distribution. *Functional Ecology,* **16**, 492-503.

Parker, G.A. (1978) Searching for mates. *Behavioral Ecology: An Evolutionary Approach* (ed. by J.R. Krebs & N.B. Davies), pp 214-244. Blackwell, Oxford.

Pearce, J. & Ferrier, S. (2001) The practical value of modeling relative abundance of species for regional conservation planning: a case study. *Biological Conservation*, **98**, 33-43.

Pettorelli, N., Bro-Jorgensen, J., Durant, S.M., Blackburn, T. & Carbone, C. (2009). Energy availability and density estimates in African ungulates. *American Naturalist*, 173, 698-704.

Pleasants, J.M. & Zimmerman, M. (1983) The distribution of standing crop of nectar: what does it really tell us? *Oecologia,* **57**, 412-414.

Powers, D.R. (1987) Effects of variation in food quality on the breeding territoriality of the male Anna's hummingbird. *Condor*, **89**, 103-111.

Powers, D.R. & McKee, T. (1994) The effect of food availability on time and energy expenditures of territorial and non-territorial hummingbirds. *Condor,* 96, 1064-1075.

Powers, D.R., Van Hook, J.A., Sandlin, E.A. & McWhorter, T.J. (2010) Arthropod foraging by a Southeastern Arizona hummingbird guild. *Wilson Journal of Ornithology*, **122**, 494-502.

Preston, F.W. (1962) The canonical distribution of commonness and rarity. *Ecology*, **43**, 185-215.

R Development Core Team. (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Ridgely, R.S., Allnutt, T.F., Brooks, T., McNicol, D.K., Mehlman, D.W., Young, B.E. & Zook, J.R. (2005) Digital Distribution Maps of the Birds of the Western Hemisphere, version 2.1. NatureServe, Arlington, VA.

Rodewald, A.D. & Shustack, D.P. (2008) Consumer resource matching in urbanizing landscapes: are synanthropic species over-matching? *Ecology*, **89**, 515-521.

Root, T. (1988) Energy constraints on avian distributions and abundances. *Ecology*, **69**, 330-339.

Sagarin, R.D. & Gaines, S.D. (2002) The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters.*, **5**, 137-147.

Stiles, F.G. (1973) Food supply and the annual cycle of the Anna hummingbird. *University of California Publications in Zoology*, **97**, 1-109.

Tellería, J. L. & Pérez-Tris, J. (2003) Seasonal distribution of a migratory bird: effects of local and regional resource tracking. *Journal of Biogeography*, **30**, 1583-1591.

Teuber, L.R. & Barnes, D.K. (1979) Environmental and genetic influences on alfalfa nectar. *Crop Science*, **19**, 874-878.

USGS National Gap Analysis Program (2005) Provisional Digital Animal-Habitat Models for the Southwestern United States, version 1.0. Center for

Applied Spatial Ecology, New Mexico Cooperative Fish and Wildlife Research Unit and New Mexico State University, Las Cruces, NM.

Waser, N.M., Chittka, L., Price, M.W., Williams, N.M. & Ollerton, J. (1996) Generalization in pollination systems, and why it matters. *Ecology*, **77**, 1043-1060.

Wood, S.N. (2006) *Generalized Additive Models: An Introduction with R*. Chapman and Hall/CRC.

Wright, D.H. (1983) Species-energy theory: an extension of species-area theory. *Oikos*, **41**, 496-506.

Yang, L.H. Bastow, J.L., Spence, K.O. & Wright, A.N. (2008) What can we learn from resource pulses? *Ecology*, **89**, 621-634.

Zeileis, A., Kleiber, C. & Jackman, S. (2008) Regression models for count data in R, *Journal of Statistical Software*, **27**, np.

2.8. Appendix 1

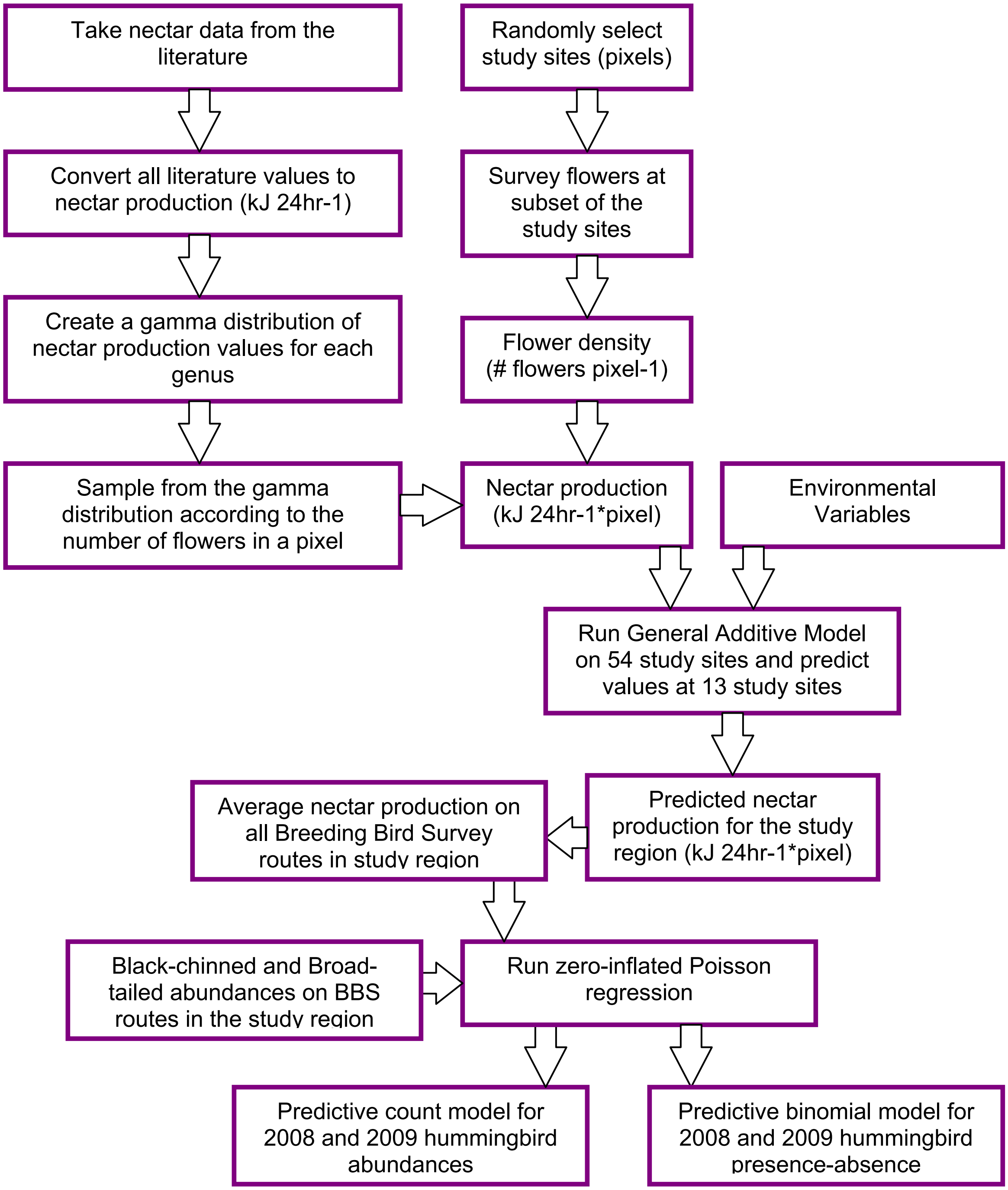


Fig. A2.1. Multiple steps were required to combine literature, field, and satellite data into a predictive model of nectar production across 67 study sites. Nectar production was then used to predict Black-chinned and Broad-tailed Hummingbird abundances across 122 Breeding Bird Survey Routes.

2.9. Appendix 2: List of species searched for on the flower surveys

Agave sp.

Anisacanthus thuberi

Aquilegia sp.

Arctostaphylos pungens

Bouvardia glaberrima

Bouvardia ternifolia

Caesalpinia gilliesii

Campsis sp.

Castilleja sp.

Chilopsis linearis

Cirsium sp.

Delphinium barbeyi

Delphinium geranioides

Delphinium nutallianum

Echinocereus triglochidiatus

Epilobium canum

Erythrina flabelliformis

Erythronium gradniflorum

Fouquieria splendens

Frasera speciosa

Heuchera sanguinea

Hydrophyllum capitatum

Ipomopsis aggregate

Justica californica

Lonicera involucrate

Mertensia sp.

Mimulus cardinalis

Nicotiana glauca

Penstemon sp.

Ribes cereum

Robinia neomexicana

Salvia lemmonii

Salvia regla

Silene laciniata

Stachys coccinea

2.10. Appendix 3

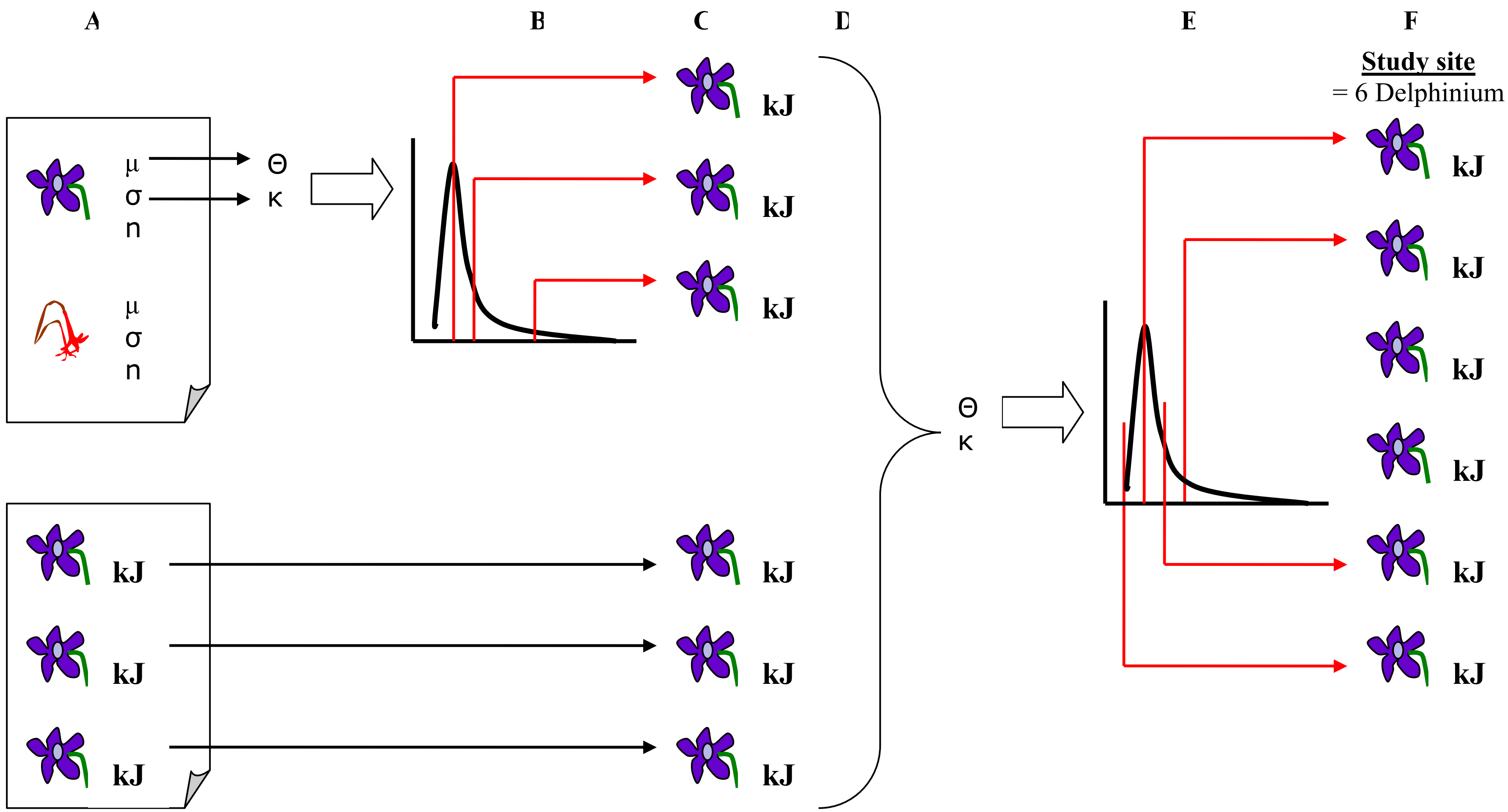


Fig A2.2. We surveyed the literature to find studies reporting nectar production for a set of plant genera found in our study region (a). For some studies we were able to obtain nectar data for all flowers in their survey (a-bottom). Other studies only reported the mean (μ), standard deviation (σ), and sample size (n) (a-top). We converted these measures to scale (θ) and shape (κ) parameters to create a gamma distribution of nectar production values (b). We drew from the gamma distribution with the number of times equal to the sample size of the flower survey to give nectar production values for each flower in the survey (c). We created gamma distributions for every study and for every genus separately (*Delphinium* in this example). We then combined the nectar data for all flowers of the same genus (d). From all the flower data, we created new scale (θ) and shape (κ) parameters and a new gamma distribution (e). We drew from the gamma distribution with the number of times equal to the number of flowers counted for the genus on a study site (6 *Delphinium* flowers were counted at this hypothetical study site). The result was the nectar production for each flower for each genus at each study site (f), which could be summed to give overall nectar production at each study site.

2.11. Appendix 4. Details on how we measured the environmental variables used in the predictive models

Weather

To obtain temperature and precipitation data for our study sites on the date they were surveyed, we spatially interpolated weather station data. We downloaded daily temperature and precipitation data from the National Climate Data Centre (www.ncdc.noaa.gov) that corresponded to the study area enlarged by 300 km in all directions. This corresponded to 150 - 427 weather stations (depending on date and data required) from Colorado, New Mexico, Utah, Arizona, Texas, Wyoming and northern Mexico. Since elevation and temperature are highly correlated, any interpolation must account for this trend. The Kriging with External Drift (KED) technique removes this trend by regressing elevation onto climate and uses the residuals in the construction of the semivariogram (Goovaerts, 2000). Therefore when kriging models temperature/precipitation based on nearby locations it does so with the effect of elevation removed. We used KED to predict temperature and precipitation at the extent of the enlarged study region and at a grain corresponding to the elevation data (i.e. 250m x 250m) for every day from January 1st - July 31st, 2008. We implemented KED using the gstat package (Pebesma, 2004) in R-2.8.1 (R Development Core Team, 2008). We used the gstat default setting of interpolating a pixel based on a neighborhood of the 12 closest weather stations. When modeling the variogram, we used a spherical model with the sill set to the variance in weather station data, the range as the square root of one-quarter of the size of the prediction grid and the nugget as zero (Hengl et al., www.spatial-analyst.net). We further tested the validity of the interpolation and our choice of variogram model by using a ten-fold cross-validation procedure in gstat. We ran this cross-validation for 25 randomly chosen dates and used the cross-validation to compare spherical, Bessian, linear and exponential variogram models. We used two metrics (prediction variance, correlation) to compare observed and predicted values and found that our predictions were adequate regardless of model type or date.

Growing Degree Days

Growing degree days (GDD) is the accumulation of temperature experienced by a plant over a given amount of time. It has predicted plant distribution (Prentice *et al.*, 1992; Thuiller *et al.*, 2005) and was strongly correlated with alkaloid concentration in the hummingbird pollinated *Delphinium barbeyi* in Utah (Ralphs *et a*l., 2002). We calculated degree days (per study sites) as

$$GDD = \sum_{i=k}^{n} (t - t_{base}),$$

where t is average daily temperature and t_{base} = 10°C. The start of the growing period (k) corresponds to the day after the last 3-day period of temperatures below 0°C and ends (n) on the date at which the site was surveyed. If $t < t_{base}$, then GDD = 10 for that day and if $t > 30$°C then GDD = 20 for that day.

Enhanced Vegetation Index (EVI)

Vegetation indices express the reflectance of the Earth's surface in the green spectrum and thus are used as a measure of plant productivity. The most common index is the Normalized Difference Vegetation Index (NDVI). EVI is similar to NDVI but is a better indicator of plant productivity in sparsely vegetated regions. MODIS EVI is provided every 16 days and measured in 250 x 250 m pixels (www.lpdaac.usgs.gov/lpdaac/products/modis_products_table).

2.12. Appendix 5. Spatial autocorrelation in model residuals

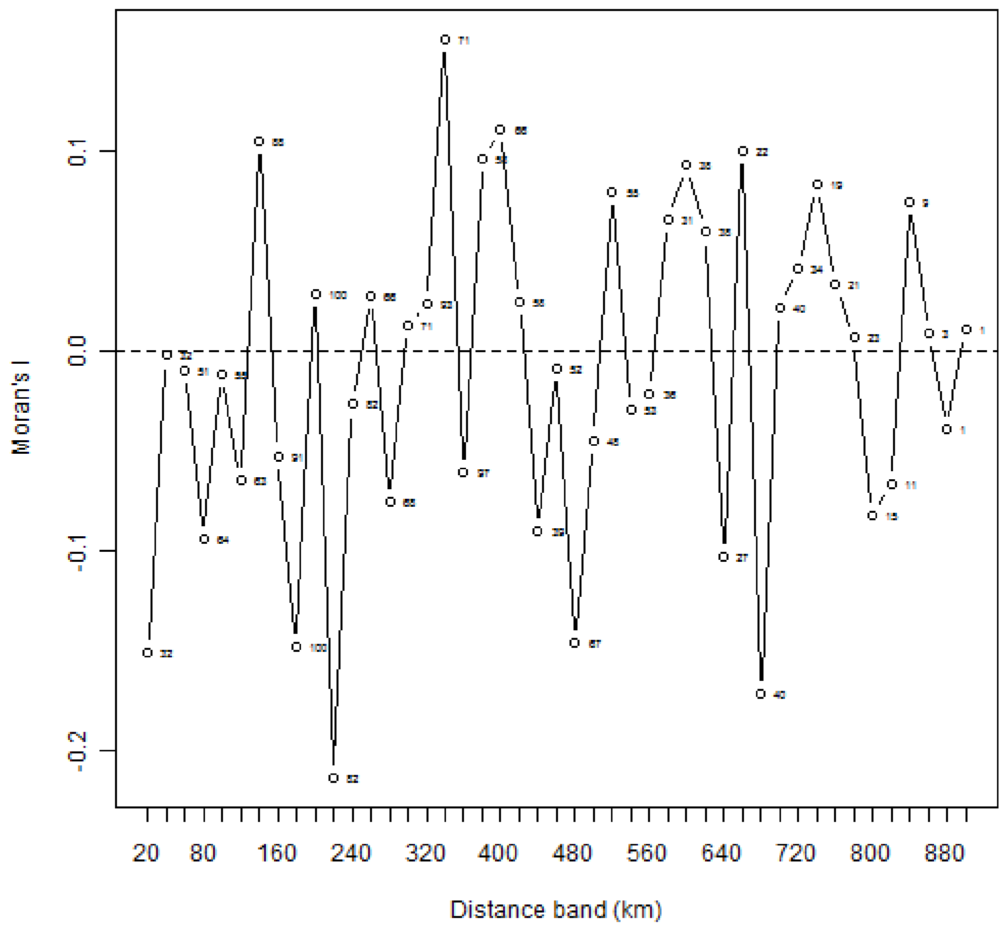


Fig. A2.3. A correlogram depicting the extent of spatial autocorrelation in the residuals from a General Additive Model relating environmental variables to nectar production at 67 study sites. Moran's I was calculated for all pairs of points in each 20 km distance band. The number of points is given. Moran's I values greater than zero indicate positive spatial autocorrelation and values below zero indicate negative spatial autocorrelation. Dark circles indicate significant spatial autocorrelation ($P < 0.05$). Hollow circles indicate non-significant spatial autocorrelation ($P > 0.05$).

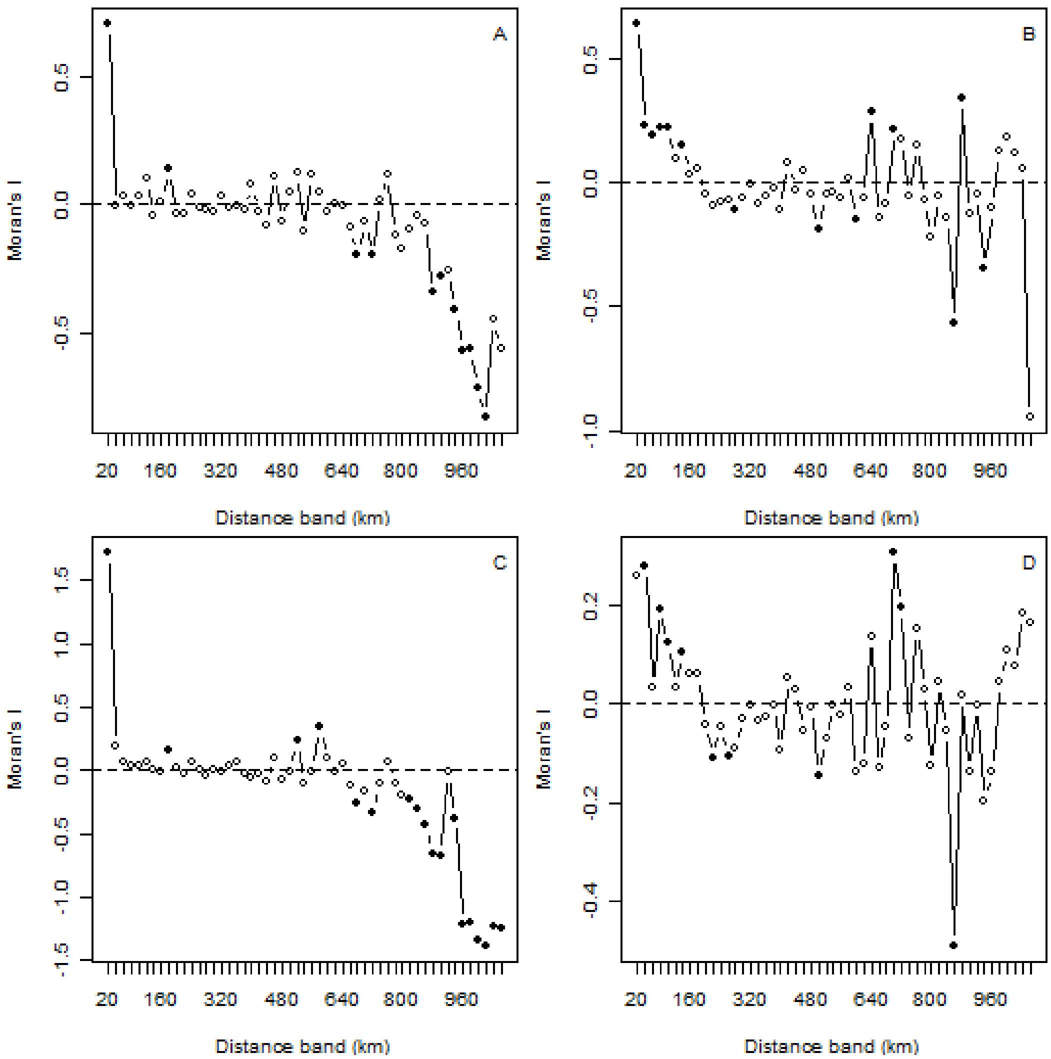


Fig. A2.4. A correlogram depicting the extent of spatial autocorrelation in the residuals from a zero-inflated Poisson regression relating nectar production to the abundance of Black-chinned Hummingbirds in 2008 (a), Broad-tailed Hummingbirds in 2008 (b), Black-chinned Hummingbirds in 2009 (c), and Broad-tailed Hummingbirds in 2009 (d) across 122 Breeding Bird Survey routes. Moran's I was calculated for all pairs of points in each 20 km distance band. Moran's I values greater than zero indicate positive spatial autocorrelation and values below zero indicate negative spatial autocorrelation. Dark circles indicate significant spatial autocorrelation ($P < 0.05$). Hollow circles indicate non-significant spatial autocorrelation ($P > 0.05$).

2.13. Appendix 6

Table A2.1. The frequency of occurrence and average abundance of each genus across 103 study sites. Also, the average number of flowers per stalk is given.

		Stalks	Flowers
Genus	# sites	mean ± standard deviation	mean ± standard deviation
Agave	1	7.000	252.000
Castilleja	28	106.036 ± 169.755	4.118 ± 2.842
Cirsium	6	13.000 ± 14.642	1.786 ± 1.929
Delphinium	18	440.389 ± 1171.283	3.733 ± 3.193
Echinocereus	9	49.417 ± 83.823	0.900 ± 0.303
Fouquieria	4	11.400 ± 11.653	159.833 ± 163.904
Frasera	1	3.000	25.000 ± 2.828
Ipomopsis	12	68.000 ± 178.442	6.859 ± 6.810
Mertensia	3	22.667 ± 29.771	10.300 ± 11.036
Penstemon	21	688.619 ± 2515.601	9.218 ± 6.497
Robinia	1	17.000	5.000 ± 4.243

2.14. Appendix 7

Table A2.2. Studies used to derive nectar production values.

Reference	Flower Species	Location	Lat/Long	Elevation (m)	Reported Values	Data Type	Sample size	Sampling dates
Armstrong, 1987	*Castilleja miniata*	Ashnola Forest, 25km sw of Penticton, BC	49.30N, 119.78W	800	Energy content	Raw data	25	June, 1985
	Delphinium nuttallianum						1	
	Penstemon nitidus						35	
	Penstemon procerus						67	
Brown & Kodric-Brown, 1979	*Castilleja austromontana*	Nutrioso, AZ	33.953N, 109.209W	> 2500	Sucrose Concentration, Nectar Volume, Sucrose Production	Mean	100	July - September, 1975
	Castilleja integra			< 2500			131	July - September, 1973, 1975
	Ipomopsis aggregata			2000 - 3000			191	July - September, 1973, 1974, 1975

	Penstemon barbatus			1800 - 3000			203	July - September, 1973, 1974, 1975
Castellanos, Wilson & Thomson, 2002	*Penstemon speciosus*	Southern Sierra Nevadas, California	N/A (Southern Sierra Nevadas, California)	2000	Sucrose concentration, Nectar Volume	Raw data	21	July 27, 1999
Elam & Linhart, 1988	*Ipomopsis aggregata*	Newton Park and Pine Junction, CO	39.47N, 105.39W	2450 - 2500	Nectar volume	Mean	333	July 21, 1985
Gass, Angehr & Centa, 1976	*Castilleja miniata*	Grizzly Lake, Northwest California	N/A	2200 - 2400	Sucrose production	Mean	30	Aug 4, 1972; Aug 22, 1973
Hixon, Carpenter & Paton, 1983	*Castilleja linariaefolia*	Bishop, CA	37.5N, 118.5W	1700	Sucrose Production	Mean	50	August, 1979

Kuban, Lawley & Neill, 1983	*Agave havardiana*	Big Bend National Park, TX	29.25N, 103.3W	1410 - 1560	Sucrose concentration, Nectar volume	Mean, Standard Error of the Mean	35	Summer, 1975, 1976, 1980
Lange & Scott, 1999	*Castilleja lanata* *Penstemon pseudospectabilis*	Horshoe Canyon - Chiricahuas	31.78N, 109.17W	1485	Sucrose Concentration, Nectar Volume, Sucrose Production	Mean, Standard Deviation	7 17	April 22, 1997
Lange, Scobell & Scott, 2000	*Penstemon barbatus* *Penstemon pinifolius*	Rustler Park - Chiricahuas	31.88N, 109.28W	2630	Sucrose concentration, sucrose production	Raw Data	N/A	July 5-6, 1997 July 6-7, 1997
Norment, 1988	*Frasera speciosa*	Clay Butte, Beartooth Mountains, WY	44.94N, 109.63W	3050	Sucrose concentration, Nectar volume	Mean, Standard Deviation	72	July 4 - Aug 15, 1984

Ohashi & Yahara, 2002	*Cirsium purpuratum*	Kinu River, Tochigi Prefecture, Japan	N/A (Kinu River, Tochigi Prefecture, Japan)	N/A	Sucrose production	Mean, Standard Error of the Mean	38	September, 1997
Scobell & Scott, 2002	*Echinocereus coccineus*	Horseshoe Canyon, Cave Creek, Long Park, Morse Canyon, Barfoot Peak - Chiricahuas	31.78N, 109.17W	1550 - 2680	Sucrose Concentration, Nectar Volume, Sucrose Production	Mean, Standard Deviation	56	June, 1997
Scott, Buchmann & O'Rourke,	*Fouquieria splendens*	Big Bend National Park, TX	20.25N, 103.25W	860 - 1560	Sucrose Concentration, Sucrose Production	Mean	14	Spring 1988

1993								
Slauson, 2000	*Agave chrysantha*	Peppersauce - Santa Catalina Mountains, AZ	31.55N, 110.72W	1432	Sucrose concentration, Nectar volume	Mean, Standard Error of the Mean	60	July 5-11, 1994
	Agave palmeri	Mustang Mountains, AZ	31.72N, 110.5W	1500			60	August 1-7, 1994
Waser, 1978	*Delphinium nuttallianum*	Rocky Mountain Biological Laboratory, Colorado	38.96N, 106.99W	2900	Sucrose Concentration, Nectar Volume, Sucrose Production	Mean, Standard Error of the Mean	25	July 9, 1975; June 21, 1976
	Ipomopsis aggregata						63	
Wright, 1985	*Delphinium barbeyi*	Rocky Mountain Biological Laboratory, Colorado	38.96N, 106.99W	N/A	Sucrose Concentration, Nectar Volume	Mean, Standard Deviation	94	July - August, 1981
	Frasera speciosa						58	

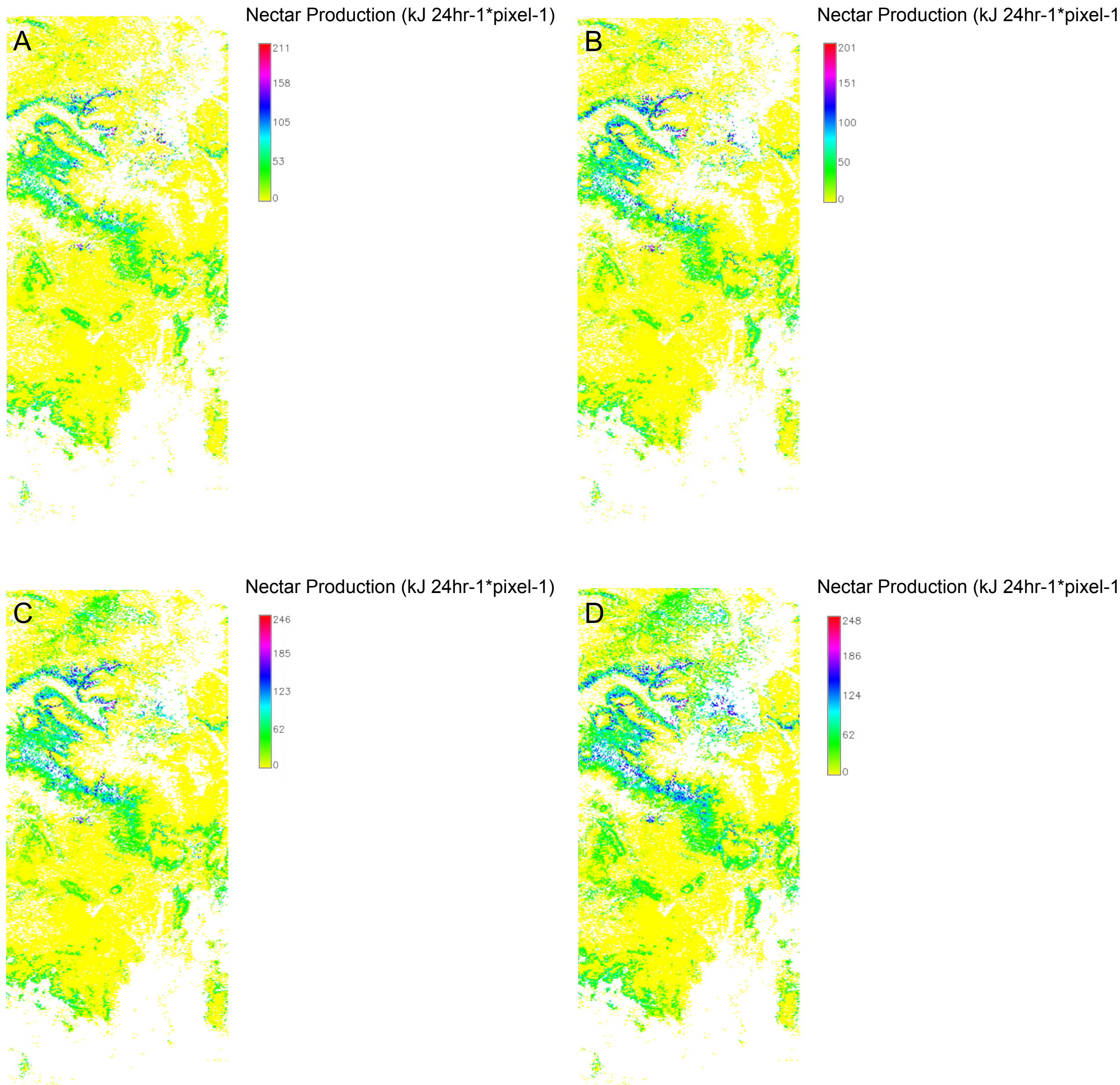
2.15. Appendix 8

Table A2.3. Habitat classes of our study sites. Only "cool" sites were used in the analysis. Consequently, predictions of nectar production were made only for the "cool" habitat classes. All habitat classifications are from the Southwest Regional Gap Analysis (USGS National Gap Analysis Program, 2005).

Habitat Class	# of sites
Hot	
Apacherian-Chihuahuan Mesquite Upland Scrub	8
Apacherian-Chihuahuan Piedmont Semi-Desert Grassland and Steppe	6
Chihuahuan Creosotebush, Mixed Desert and Thorn Scrub	9
Chihuahuan Mixed Salt Desert Scrub	2
Chihuahuan Stabilized Coppice-Dune and Sand Flat Scrub	3
Inter-Mountain Basins Semi-Desert Grassland	1
Madrean Encinal	3
Madrean Pinyon-Juniper Woodland	3
Cool	
Colorado Plateau Pinyon-Juniper Shrubland	5
Colorado Plateau Pinyon-Juniper Woodland	19
Inter-Mountain Basins Big Sagebrush Shrubland	4
Inter-Mountain Basins Greasewood Flat	1
Inter-Mountain Basins Semi-Desert Grassland	2

Inter-Mountain Basins Semi-Desert Shrub Steppe	1
Madrean Pine-Oak Forest and Woodland	3
Madrean Upper Montane Conifer-Oak Forest and Woodland	2
Mogollon Chaparral	1
North American Warm Desert Lower Montane Riparian Woodland and Shrubland	1
Rocky Mountain Aspen Forest and Woodland	7
Rocky Mountain Gambel Oak-Mixed Montane Shrubland	1
Rocky Mountain Montane Dry-Mesic Mixed Conifer Forest and Woodland	1
Rocky Mountain Montane Mesic Mixed Conifer Forest and Woodlands	1
Rocky Mountain Ponderosa Pine Woodland	13
Southern Rocky Mountain Montane-Subalpine Grassland	1
Southern Rocky Mountain Pinyon-Juniper Woodland	3
Western Great Plains Foothill and Piedmont Grassland	2

2.16. Appendix 9



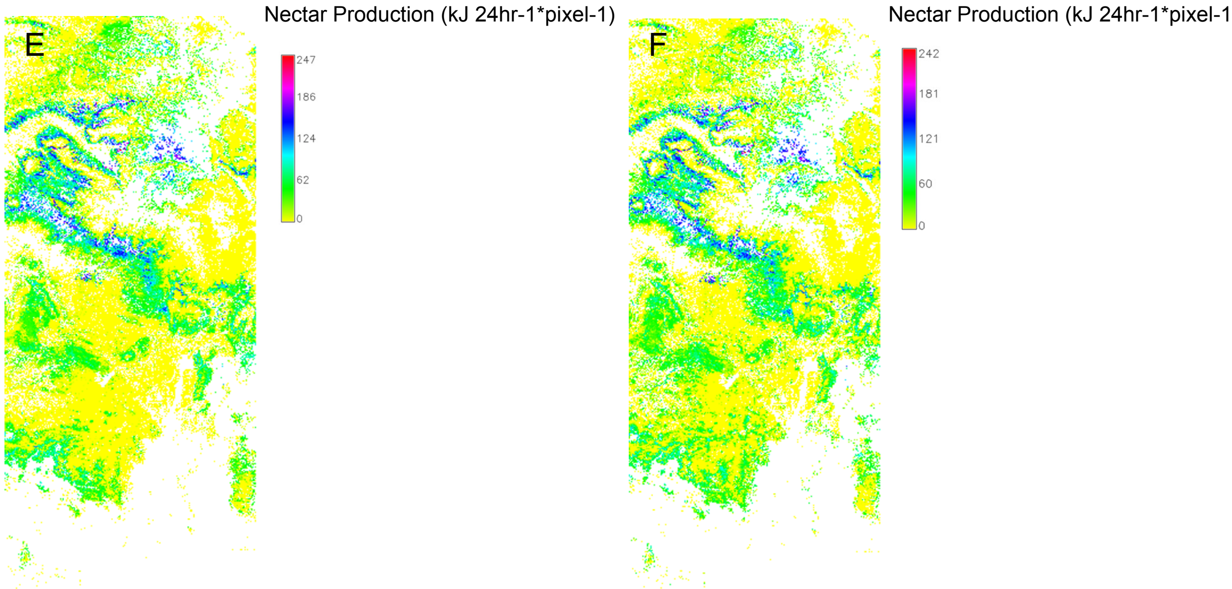


Fig. A2.5. Maps of spatial variation in nectar production across the study region for 21 April (a), 07 May (b), 23 May (c), 24 June (d), 09 July (e), and 26 July (f). White areas indicate habitat classes not included in our surveys. The dates correspond to the dates for which EVI data are provided.

2.17. Appendix 10: References for citations in the appendices

Armstrong, D.P. (1987) Economics of breeding territoriality in male Calliope Hummingbirds. *Auk*, **104**, 242 – 253.

Brown, J.H. & Kodric-Brown, A. (1979) Convergence, competition, and mimicry in a temperature community of hummingbird-pollinated flowers. *Ecology*, **60**, 1022-1035.

Castellanos, M.C., Wilson, P. & Thomson, J.D. (2002) Dynamic nectar replenishment in flowers of Penstemon (Scrophulariaceae). *American Journal of Botany*, **89**, 111-118.

Elam, D.R. & Linhart, Y.B. (1988) Pollination and seed production in *Ipomopsis aggregatra*: differences among and within flower color morphs. *American Journal of Botany*, **75**, 1262-1274.

Gass, C.L., Angehr, G. & Centa, J. (1976) Regulation of food supply by feeding territoriality in the rufous hummingbird. *Canadian Journal of Zoology*, **54**, 2046-2054.

Goovaerts, P. (2000) Geostatistical approaches for incorporating elevation into the spatial interpolation of rainfall. *Journal of Hydrology*, **228**, 113-129.

Hixon, M.A., Carpenter, F.L. & Paton, D.C. (1983) Territory area, flower density, and time budgeting in hummingbirds: an experimental and theoretical analysis. *American Naturalist,* **122**, 366-391.

Kuban, J.F., Lawley, J. & Neill, R.L. (1983) The partitioning of flowering century plants by Black-chinned and Lucifer Hummingbirds. *Southwestern Naturalist*, **28**, 143-148.

Lange, R.S., Scobell, S.A. & Scott, P.E. (2000) Hummingbird-syndrome traits, breeding system, and pollinator effectiveness in two syntopic *Penstemon* species. *International Journal of Plant Sciences,* **161**, 253-263.

Lange. R.S., & Scott, P.E. (1999) Hummingbird and bee pollination of *Penstemon pseudospectabilis*. *Journal of the Torrey Botanical Society*, **126**, 99-106.

Norment, C.J. (1988) The effect of nectar-thieving ants on the reproductive success of *Frasera speciosa* (Gentianaceae). *American Midland Naturalist*, **120**, 331-336.

Ohashi, K. & Yahara, T. (2002) Visit larger displays but probe proportionally few flowers: counterintuitive behaviour of nectar-collecting bumble bees achieves an ideal free distribution. *Functional Ecology*, **16**, 492-503.

Pebesma, E.J. (2004) Multivariable geostatistics in S: the gstat package. *Computers and Geosciences,* **30**, 683-691.

Prentice, I.C., Cramer, W., Harrison, S.P., Leeman, R., Monserud, R.A. & Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography,* **19**, 117-134.

R Development Core Team. (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Ralphs, M.H., Gardner, D.R., Turner, D.L., Pfister, J.A. & Thacker, E. (2002) Predicting toxicity of tall larkspur (*Delphinium barbeyi*): measurement of the variation in alkaloid concentration among plants and among years. *Journal of Chemical Ecology,* **28**, 2327-2341.

Scobell, S.A. & Scott, P.E. (2002) Visitors and floral traits of a hummingbird-adapted cactus (*Echinocereus coccineus*) show only minor variation along an elevational gradient. *American Midland Naturalist,* **147**, 1-15.

Scott, P.E., Buchmann, S.L. & O'Rourke, M.K. (1993) Evidence for mutualism between a flower-piercing carpenter bee and ocotillo: use of pollen and nectar by nesting bees. *Ecological Entomology,* **18**, 234-240.

Slauson, L.A. (2000) Pollination biology of two Chiropterophilous Agaves in Arizona. *American Journal of Botany*, **87**, 825-836.

Thuiller, W., Lavorel, S., Araujo, M.B., Sykes, M.T. & I.C. Prentice. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America,* **102**, 8245-8250.

USGS National Gap Analysis Program. (2005) Provisional Digital Animal-Habitat Models for the Southwestern United States, version 1.0. Center for Applied Spatial Ecology, New Mexico Cooperative Fish and Wildlife Research Unit and New Mexico State University, Las Cruces, NM.

Waser, N.M. (1978). Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology*, **59**, 934-944.

Wright, D.H. (1985) Patch dynamics of a foraging assemblage of bees. *Oecologia*, **65**, 558-565.

2.18. Linking statement between Chapters 2 and 3

The results of the previous chapter show that variation in an environmental factor at large spatial scales predicts variation in animal abundance. The results do not say anything about mechanism: the pathway whereby environment affects abundance. One possibility is that the environment affects an organism's abundance directly and also indirectly via interspecific competition. Moreover, differences in how interspecific competition plays out due to interspecific niche differences affects spatial variation in abundance. In the next chapter, I use a simulation model to test this hypothesis.

CHAPTER 3:

Interspecific niche differences modify how abundance is distributed across a species range

3.1. Abstract

Current models of spatial variation in abundance – how a species' total abundance is partitioned among sites within its range – do not explicitly consider the effects of interspecific competition. Yet competition is a key mechanism that turns the fundamental into the realized niche, the latter of which describes spatial variation in abundance. We model abundance as an outcome of abiotic environmental variation and competition based on the niche differences between a focal species and a competitor. We measure spatial variation in abundance through a variety of metrics previously used to describe species abundance distributions. We found that when competing with generalists, spatial variation in abundance was more evenly distributed than when competing with specialists. In a second simulation we found that increasing phylogenetic relatedness among species in a multispecies community also affected spatial variation in abundance. The results of both simulations suggest that observed differences among species in their patterns of abundance may be attributed to evolved niche differences among species.

3.2. Introduction

Studies at large spatial scales have been invaluable in documenting new ecological phenomenon. For example, a large scale perspective has lead to the idea that the species range is a unique entity shaped by processes acting over large spatial and temporal gradients. In turn, such an understanding has lead to advancements across biological disciplines (e.g. quantitative genetics [Case & Taper 2000]). Most studies of species ranges have focused on understanding their size, shape, and location (Brown et al. 1996). Comparatively few studies have focused on their texture: how the abundance of a species varies among sites within its range. Yet it is an understanding of abundance that tells us the capacity of species to respond to habitat fragmentation (Gonzalez et al. 1998) and climate change (Murphy et al. 2010).

Spatial variation in abundance (SVA) refers to how the total abundance of one species is partitioned among multiple sites in its range (Brown 1984; Brown et al. 1995). This is different from the species abundance distribution (SAD), which describes how the total abundance at one site is partitioned among multiple species (McGill et al. 2007). Across a species range, SVA takes on a characteristic pattern: there are few sites of high abundance, many sites of low abundance, and many sites within the range where the species is absent (Brown et al. 1995). The specific distribution likely varies from lognormal to logseries as has been found with SADs (McGill et al. 2007). The SVA pattern has been shown to be general across taxa including birds (Brown et al. 1995), insects from the family Agromyzidae (Brewer & Gaston 2002) and Tenthredinidae (McGeoch & Price 2004), trees (Murphy et al. 2006), and beavers (*Castor canadensis* [Jarema et al. 2009]).

Brown (1984) was the first to create a predictive model of SVA. In the model, abundance is matched to underlying environmental variation. Specifically, abundance is normally distributed along multiple independent environmental gradients. A site is a random point on each of the environmental gradients and abundance at a site is the sum of these individual responses. The process is repeated multiple times to obtain a distribution of abundances at multiple sites within a range. The model predicts a Gaussian-shaped SVA pattern with an abundance peak in the center of the range. In a later model, Brown et al. (1995) multiplicatively combined the individual responses producing a roughly lognormal SVA, which is more consistent with empirical data. Importantly, the model did not necessarily predict that the abundance peak is in the center of the range, which has been shown to be an inaccurate characterization of SVA (Sagarin & Gaines 2002; Samis & Eckert 2007).

The Brown (1984; Brown et al. 1995) models are grounded in the concept of the Hutchinsonian niche where a species' population growth rate at a particular location depends on the environmental conditions, or niche factors, at that location (Hutchinson 1957). Using the niche concept to explain small scale variation in abundance is nothing new; the ideal free distribution essentially formalizes the abundance-environment relationship into a predictive tool (Fretwell & Lucas 1969). There is considerably less theory connecting niche theory to large scale species distributions (but see Pulliam 2000). Even empirically, SVA has been related to underlying variation in niche factors in only a few instances (e.g. Mehlman 1997; Gill et al. 2001). Yet developing and testing theory is crucial to predicting the response of species and ecosystems to global change (Kerr et al. 2007).

The principles of niche theory have been more commonly applied to explaining SADs. While there are many hypotheses explaining the occurrence of the SAD (McGill et al. 2007), nearly all are grounded in the concepts of competitive exclusion and limiting similarity (MacArthur and Levins 1967). Consequently, each points to niche differences among species being a key influence on how total abundance within a community is partitioned among member species. While there are non-niche hypotheses for the SAD (e.g. Hubbell 2001), empirical evidence strongly suggests that niche differences matter (McGill et al. 2006; Kraft et al. 2008; Adler et al. 2010). Given that the pattern of SVA is similar in form to the SAD, it is possible that niche differences among competing species are also important in generating SVA.

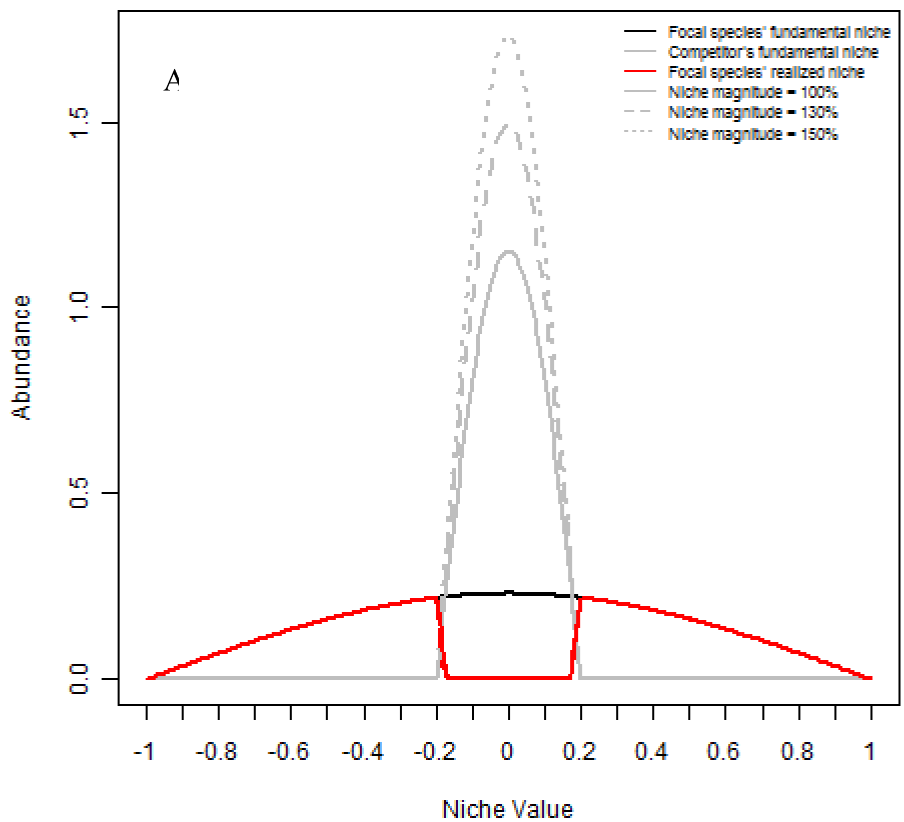
While the Brown et al. (1995) model is a first approximation connecting the multidimensional niche to SVA, it does not explicitly consider niche differences or interspecific interactions. In the model there is only one species and it responds to competitors in the same way as it responds to abiotic niche factors. However, the responses to the abiotic environment and to competitors are two distinct processes (Cavender-Bares et al. 2004; Kraft et al. 2008). Environmental tolerance-competitive ability trade-offs mean that some abiotic and competition gradients are inversely correlated in space (MacArthur 1972; Chase 1996), which violates the model’s assumption of independent niche factors. Moreover, the model assumes a Gaussian response of the organism to each niche factor. Such a response corresponds to the expected physiological response, e.g. thermal performance curves (Kingsolver 2009). Consequently, when the responses to each niche factor are combined into an overall abundance, the result is a distribution of abundances based purely on physiology, i.e. the fundamental niche. However, the goal of the model is to explain empirical distribution patterns, i.e. the realized niche.

Niche differences are often characterized by where along an environmental gradient niches are located and the degree to which they overlap (e.g. Cavender-Bares et al. 2004; Kraft et al. 2008). Such properties are an outcome of interspecific differences in niche breadth (MacArthur & Levins 1967). However, niche differences can arise in other ways. In particular, recent theories of coexistence are predicated on competitive ability trade-offs (reviewed in Kneitel & Chase 2004), which require differences in niche magnitude. Niche breadth and magnitude are often traded-off meaning that niche differences express relative differences in physiological specialization (McNaughton & Wolf 1970). Niches can also differ based on phylogeny with niches being conserved among more closely related species (Wiens & Graham 2005). Consequently, overall niche similarity can be decomposed into the number of niche axes upon which two species overlap and the extent of overlap where overlap occurs (Lovette and Hochachka 2006). Each of these types of niche differences can have an influence on abundance whether within or among communities. Yet neither the effect of competing with generalists or specialists nor in competing with related or unrelated species on abundance has ever been explored.

Our goal with this paper is to test how interspecific niche differences lead to different patterns of SVA compared to what is expected if species are only responding to the abiotic environment. We use the Brown et al. (1995) model as a template but explicitly introduce an interspecific competitor. We run two simulations to test how niche differences lead to differences in how the abundance of a focal species is distributed across its range. First, we test how the degree of the competitor's physiological specialization affects the focal species' SVA and whether there is an additional effect of increasing niche magnitude. Second, we simulate a multispecies community to test how the degree of niche conservatism among competitors affects the focal species' SVA.

3.3. Methods

In our simulation model, the abundance of a focal species is reduced by a competitor at sites that occur in both species' fundamental niche. The mechanism by which abundance is reduced, i.e. interference or exploitation competition, is not specified. We model the two species as having inclusive niches: the fundamental niche optimum for both species occurs at the same point on a niche axis and niche overlap occurs in the niche's center (McNaughton & Wolf 1970; Colwell & Fuentes 1975). The extent of overlap is determined by the competitor's niche breadth (Fig. 3.1). The amount by which the competitor reduces the focal species' abundance depends on the competitor's niche magnitude (see below). Inclusive niches differ from reciprocal niches where overlap occurs in the niche's tails (Colwell & Fuentes 1975). Inclusive niche structure has been shown to characterize how species are distributed among different habitats (Brown 1971; Abramsky et al. 1990; Rosenzweig 1991) and along small (Wisheu & Keddy 1992; Wisheu 1998; Greiner La Peyre et al. 2001) and large scale (MacArthur 1972; Anderson et al. 2002; Cadena & Loiselle 2007) environmental gradients. In the absence of competition, two or more species attain their highest abundances in the same habitat or portion of the environmental gradient. In reality, however, one species is competitively dominant, which limits inferior competitors to the less preferred habitat or portion of the gradient (Chase 1996). At the same time, the inferior competitor is more tolerant (i.e. has a wider niche breadth), which allows it to persist in environments where the superior competitor could not (Connell 1961). In our model, the focal species refers to the species with the wider niche breadth and the competitor's niche is included within the focal species' niche. Consequently, the competitor always affects the abundance of the focal species but not vice versa (but see Chase 1996). We assume that competition does not alter the fundamental niche of either species.



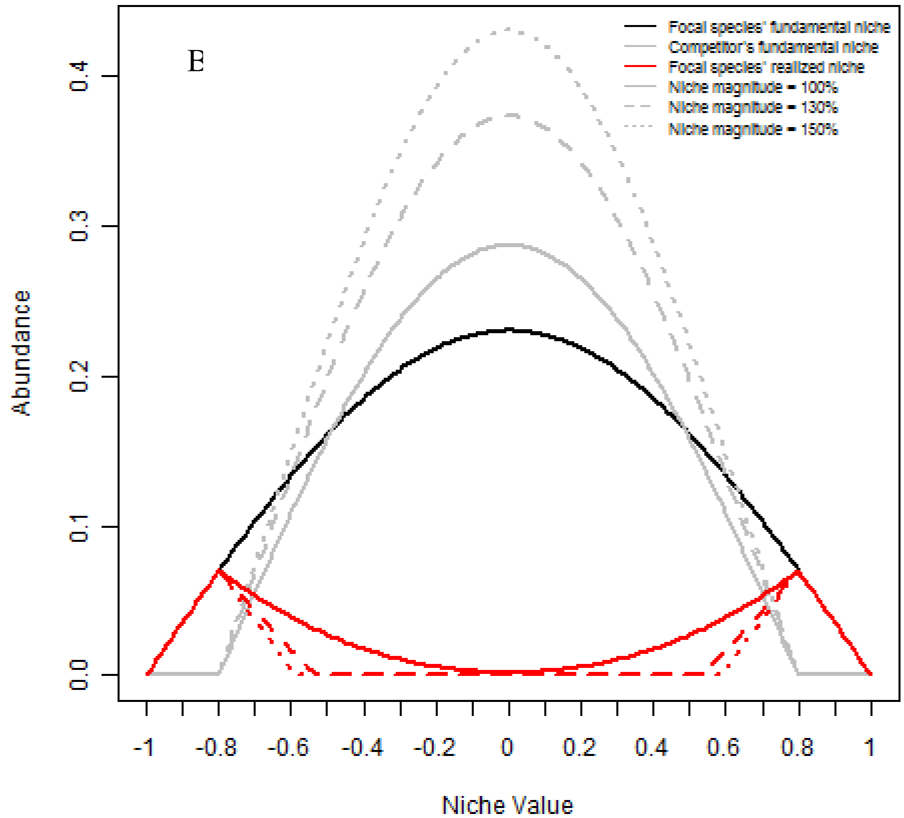


Fig. 3.1. How interspecific competition turns the focal species' fundamental niche into a realized niche. The fundamental niche of the focal species (black curve) and the competitor (grey curve) are both Gaussian responses to a linear environmental gradient (x-axis). As the competitor's abundance increases, the abundance of the focal species declines in proportion, which gives the realized niche (red curve). A competitor with a niche breadth equal to 20% of the focal species' niche breadth (a) and 80% of the focal species' niche breadth (b) are shown. For each case, three levels of niche magnitude are shown.

3.3.1. Simulating the focal species' fundamental niche

We create niches following Brown et al. (1995). In the model, a focal species' niche consists of all the biotic and abiotic factors that influence abundance. This multivariate niche is decomposed into multiple univariate niche axes. Abundances at different points along the niche axis follow a Gaussian distribution. The species response is a normal curve with a mean of zero, standard deviation of one, and is truncated to zero at +/- one standard deviation from the mean. One point is chosen randomly (between the truncation points) for each niche axis. This point is a "site" within the geographic range. The abundance at the site is determined for each niche axis and then the results for all niche axes are multiplied together, yielding a total abundance at a particular site. Brown et al. (1995) repeat this process 594 times, representing a species range that consists of 594 sites. We round up to 600 sites.

3.3.2. Simulating the competitor's fundamental niche

In our version of the simulation, we added a second species that also has a Gaussian response to (some or all of) the same niche axes as the focal species. However, we altered the response curve to reflect differences in niche breadth and magnitude. To vary these niche properties, we modified the standard deviation and truncation points of the Gaussian curve (Fig. 3.1). We also varied the number of axes upon which the two species overlap and compete, hereafter called "niche divergence".

We ran a full factorial design with nine niche breadth, five niche magnitude, and five niche divergence levels. We varied niche breadth from 10% -

90% of the focal species' niche, increasing at 10% intervals. A narrow niche indicates greater physiological specialization: less niche overlap but a greater niche magnitude. Within each niche breadth level, we varied niche magnitude by subtracting a term from the standard deviation such that niche magnitude increased in 10% increments above the "base" niche magnitude (up to a maximum of 150%). We varied niche divergence by allowing competition to take place on 0, 1, 2, 3, or 4 niche axes. With zero axes, there is, in effect, no competition. As such the results of this simulation correspond to the fundamental distribution of abundances as modeled by Brown et al. (1995).

3.3.3. Simulating interspecific competition

Modeling competition begins by drawing a random number from a uniform distribution between -1 and +1. This value corresponds to a hypothetical "site". If this site falls outside the competitor's niche, then the focal species' abundance is determined by the Gaussian response as described above and in Brown et al. (1995). If the site falls within the competitor's niche, we first calculate the competitor's abundance based on its fundamental niche. We then modify the focal species' abundance by the competitor's abundance such that the decline in the former is proportional to the increase in the latter (Fig. 3.1):

$N_r = N_f - Ce^{-N_f}$, where

N_r = the focal species' abundance after competition

N_f = the focal species' abundance before competition

C = the competitor species' abundance

We repeat this process for four niche axes and 600 sites: we calculate the focal species' abundance (possibly modified by competition) for each niche axis at each site and then multiply the abundances from each of the four niche axes together at each site to give an overall abundance at each of the 600 sites. Any negative abundance values are automatically assigned a value of zero.

3.3.4. Simulating variation in phylogenetic relatedness

In this simulation, we varied levels of relatedness by varying niche divergence. A community of closely related species should have highly conserved niches and thus overlap on multiple niche axes. When species are not highly related they should overlap only on a few axes. We tested the effect of variation in phylogenetic relatedness by simulating a community consisting of one focal species and three competitor species. Preliminary analysis showed that patterns in SVA did not differ among communities with greater than three competitors. In the community, we assigned each species a different niche breadth (0.3, 0.5, 0.7) so that the community consisted of a range of specialists and generalists. The focal species was the most general. We also increased the total number of niche axes to 11.

We modeled three levels of niche divergence. For the lowest levels of relatedness, the focal species overlapped with each competitor on 1-3 of the 11 niche axes. For intermediate levels of relatedness, the focal species overlapped with the competitors on 5-7 of the 11 niche axes. For a community where the species are highly related, the focal species overlapped with the competitors on 9-11 of the 11 axes. For each competitor species, we randomly chose the number of niche axes on which it overlapped with the focal species restricted by the treatment values. When more than one competitor occurred at a site, we reduced the focal species' abundance by the maximum competitor abundance at the site. Due to computing limitations, the focal species' range consisted of 300 sites.

3.3.5. Analyzing spatial variation in abundance

We calculate five measures of SVA: total abundance, occupancy, dominance, evenness, and skewness. While these measures typically describe the distribution of abundances for multiple species at one site they can easily be applied to describing the abundances of one species across multiple sites. We refer the reader to McGill (2011) for tests and discussions comparing different measures of species abundance distributions. Briefly, we measure dominance as the proportion of total abundance at the most abundant site. We measure evenness using the Shannon/Pielou metric (McGill 2011). Skewness characterizes the distribution of log abundances (see also McGill 2003). A negative skew indicates a distribution with more sites that have low abundance. A positive skew indicates a distribution where there are more sites that have high abundance. In both cases, lognormal is the reference distribution. For both evenness and skewness measures, we only include sites that have abundance greater than zero. Consequently, we also measure the total number of occupied sites (i.e. abundance greater than zero).

For each of our simulations (niche breadth vs. magnitude vs. divergence; high vs. moderate vs. low phylogenetic relatedness) we calculate each of the above metrics. We then run a full-factorial MANOVA in R 2.10.1 (R

Development Core Team 2009) to test for significant differences in the metrics among each treatment. Treatments are significant when $p \leq 0.05$.

3.4. Results

3.4.1. Niche differences

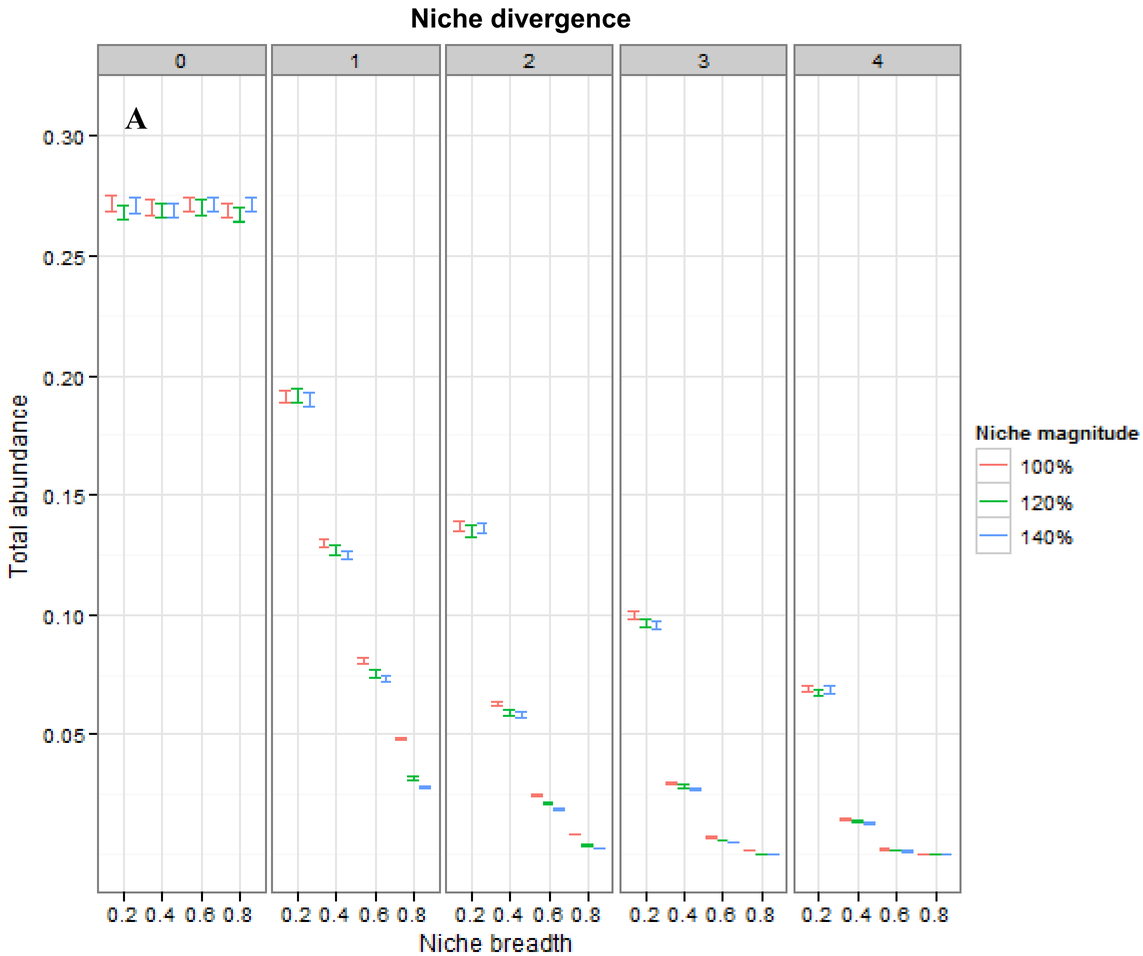
We found that adding interspecific competition to the Brown et al. (1995) model significantly changed the pattern of abundance across a species range compared to a model without competition (Table 3.1). With competition, SVA was significantly more even and the site with the highest abundance contained an even higher proportion of the total abundance (Fig. 3.2). However, SVA was only marginally less skewed toward sites of low abundance. Overall, the focal species had a lower abundance and occupied fewer sites when competition was included.

The effect of interspecific competition was greater when the competitor was a generalist than a specialist and when competition took place on an increasing number of niche axes. Most measures of SVA exponentially increased (dominance, evenness) or decreased (occupancy, total abundance) as the competitor increasingly became a generalist. The steepness of the relationship increased as competition took place on more niche axes (Fig. 3.2). However, the exponential relationship was not observed when the competitor's niche magnitude was at its lowest level (100%) because extreme competitor generality combined with low niche magnitude lead to different results. In this competitive scenario, the focal species occupied all 600 sites in its range and had a distribution more uneven than without competition.

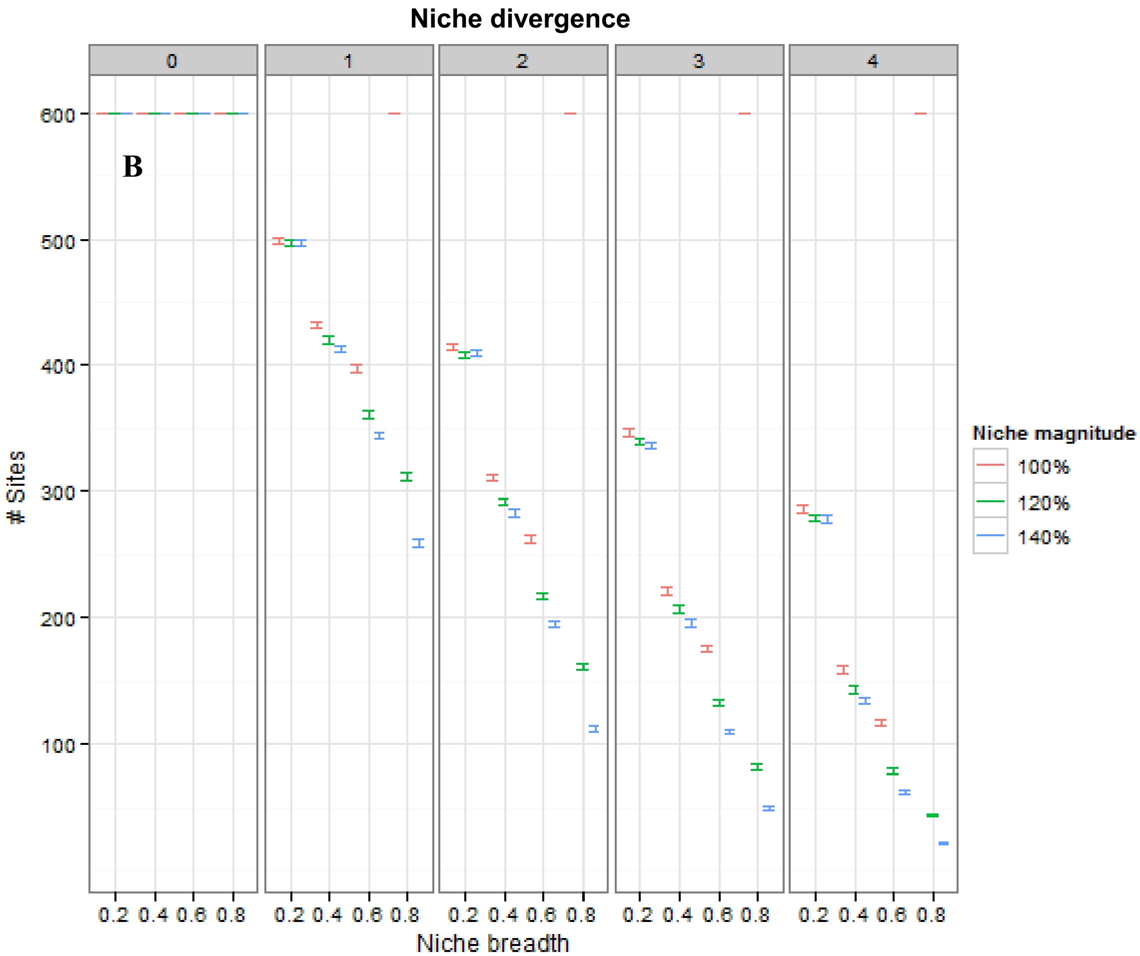
Table 3.1. MANOVA and ANOVA results for the five measures of spatial variation in abundance with a full interaction design three treatments and their interactions. Residual degrees of freedom = 18625.

Factor	df	All	Occupancy	Total abundance	Dominance	Evenness	Skewness
Breadth	8	F = 164.2	F = 148160.4	F = 79377.0	F = 3359.4	F = 6142.0	F = 118.5
		P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001
Magnitude	5	F = 1131.0	F = 83454.8	F = 116.5	F = 1242.2	F = 3202.3	F = 44.5
		P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001
Divergence	4	F = 4346.3	F = 1269554.2	F = 609820.0	F = 8420.0	F = 16429.6	F = 434.8
		P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001
Breadth x	40	F = 241.6	F = 26529.8	F = 5.5	F = 465.9	F = 996.2	F = 113.9
magnitude		P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001
Breadth x	32	F = 626.2	F = 12023.9	F = 6577.6	F = 975.6	F = 1445.2	F = 16.5
divergence		P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001
Magnitude x	20	F = 379.5	F = 5801.8	F = 33.0	F = 367.1	F = 740.1	F = 20.8

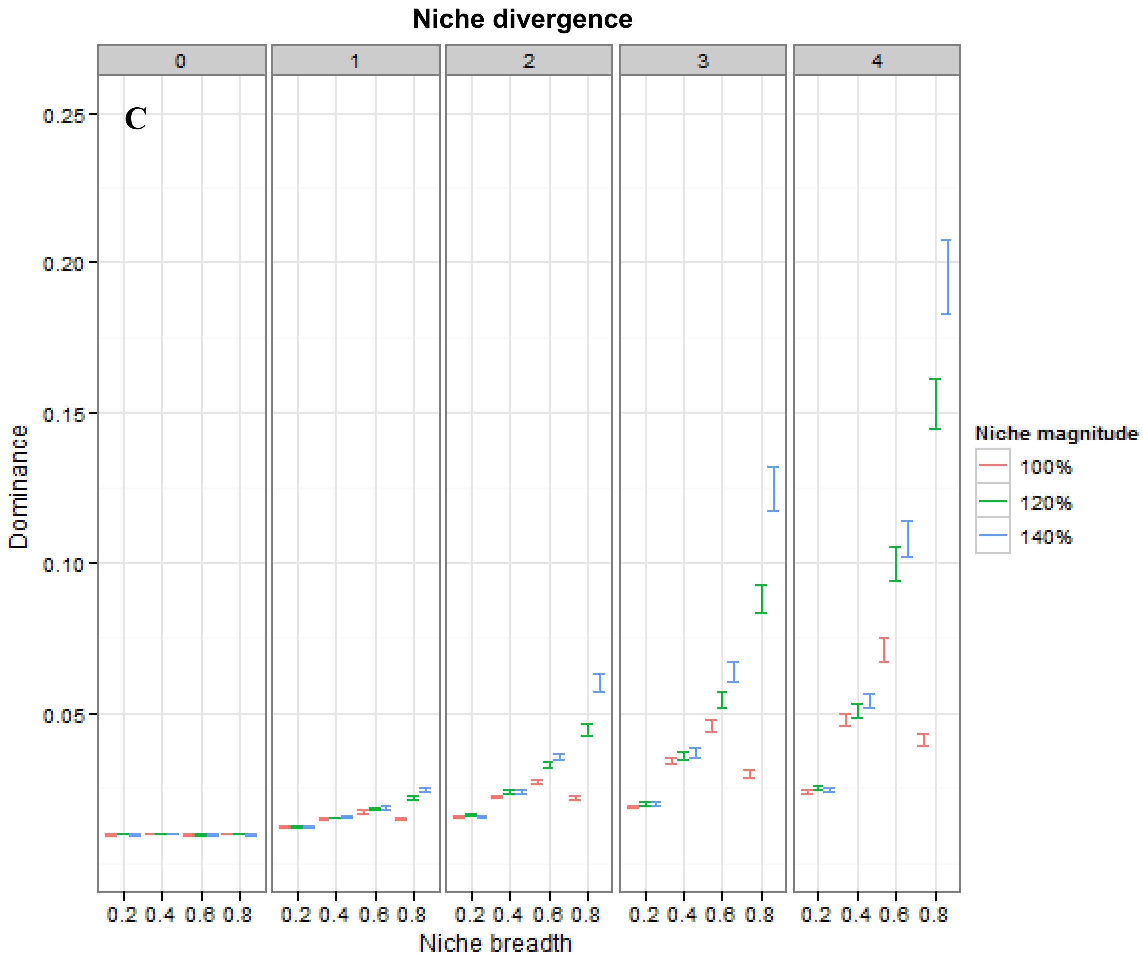
divergence		$P < 0.001$	$P < 0.001$	$P < 0.001$		$P < 0.001$	$P < 0.001$	$P < 0.001$
Breadth x	160	$F = 73.0$	$F = 1953.5$	$F = 5.7$		$F = 138.6$	$F = 230.3$	$F = 26.9$
magnitude x		$P < 0.001$	$P < 0.001$	$P < 0.001$		$P < 0.001$	$P < 0.001$	$P < 0.001$
divergence								

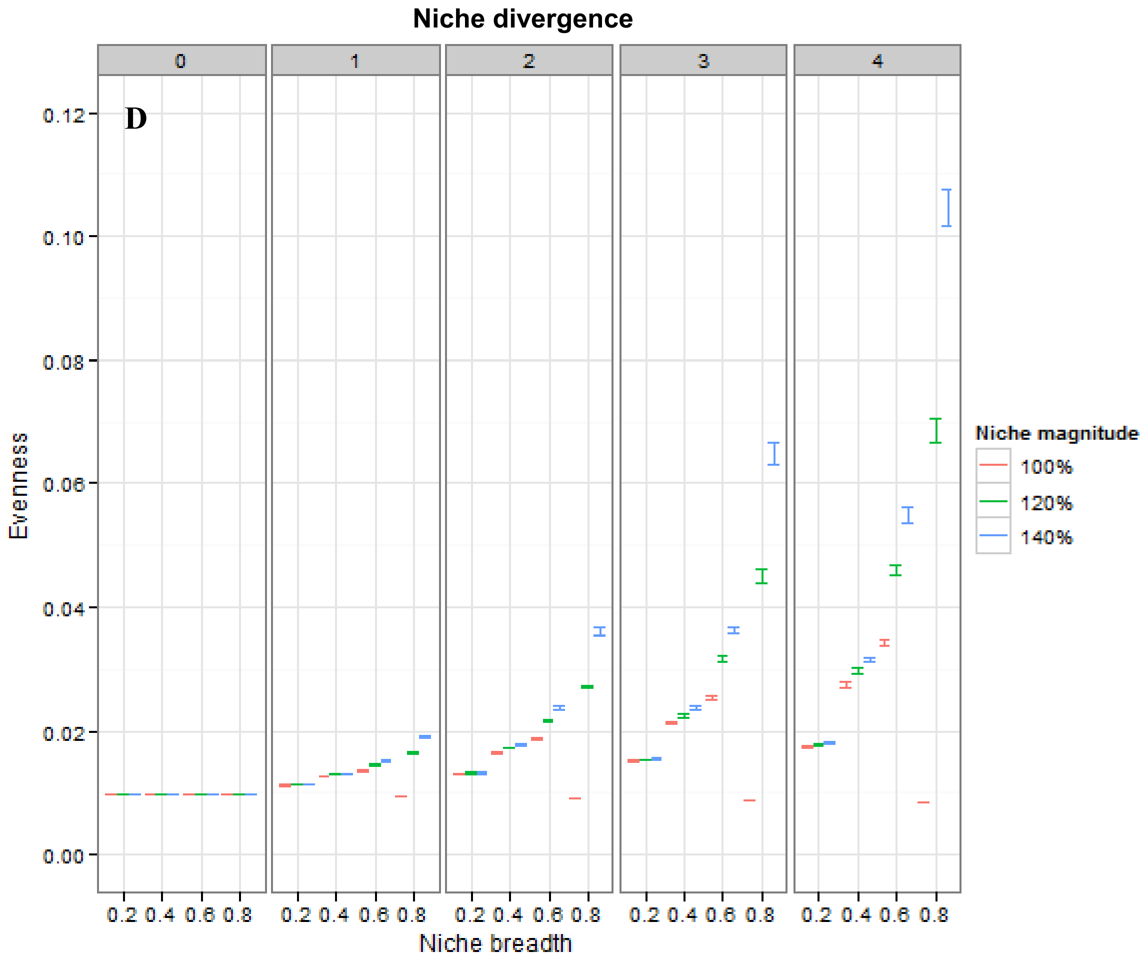


Niche divergence
0
1
2
3
4
A
0.30
0.25
0.20
0.15
0.10
0.05
Total abundance
0.2 0.4 0.6 0.8
Niche breadth
Niche magnitude
100%
120%
140%



Niche divergence
0
1
2
3
4
600
500
400
300
200
100
Sites
B
0.2 0.4 0.6 0.8
Niche breadth
Niche magnitude
100%
120%
140%


Niche divergence
0
1
2
3
4
C
0.25
0.20
0.15
0.10
0.05
Dominance
0.2 0.4 0.6 0.8
Niche breadth
Niche magnitude
100%
120%
140%


Niche divergence
0
1
2
3
4
D
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Evenness
0.2 0.4 0.6 0.8
Niche breadth
Niche magnitude
100%
120%
140%

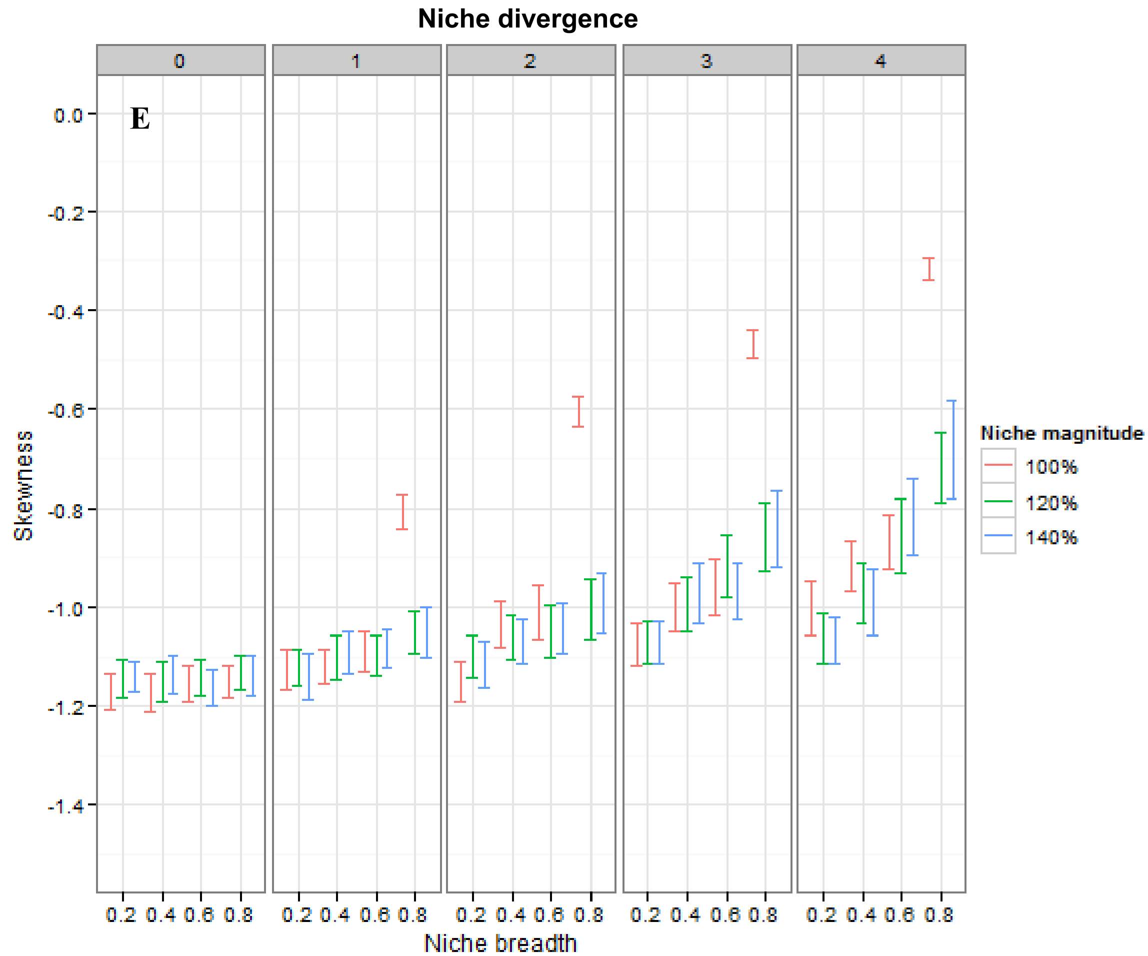


Fig. 3.2. The effects of competition on spatial variation in abundance across three different characterizations of interspecific niche differences. Mean ± 95% confidence intervals of total abundance (a), occupancy (b), dominance (c), evenness (d), and skewness (e) are shown across the three treatments. To ease interpretation, responses to only four of the nine levels of niche breadth and three of the six levels of niche magnitude are shown.

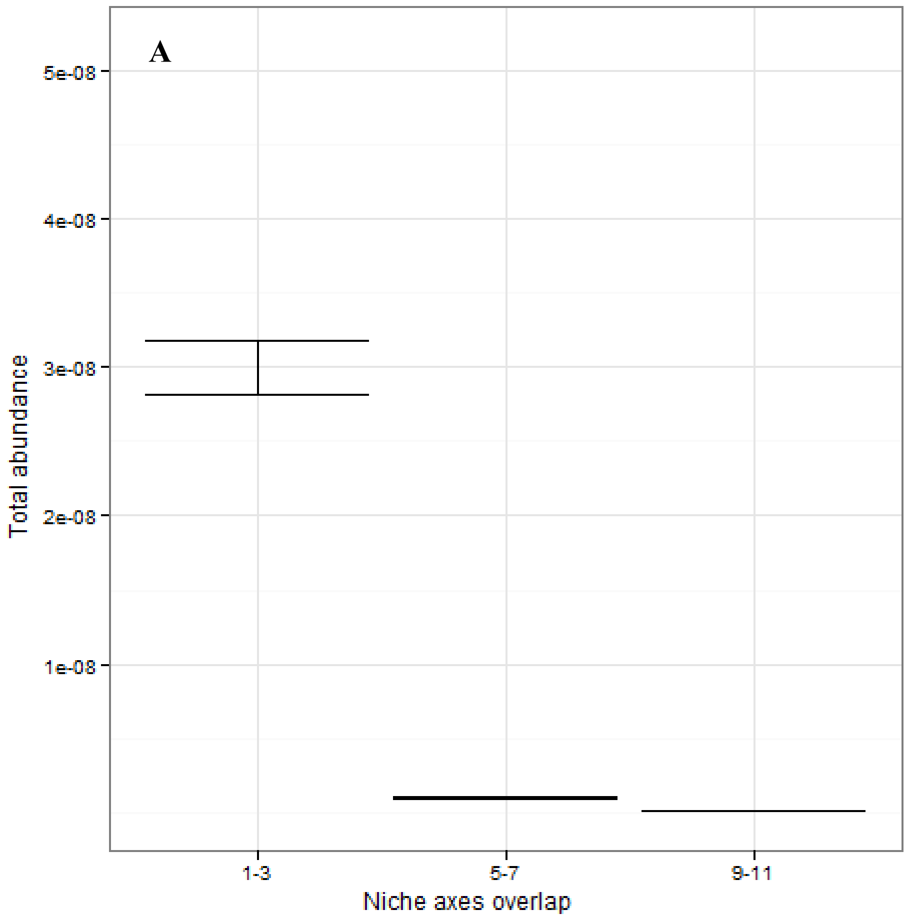
With or without competition, SVA of the focal species' abundance was skewed toward sites of low abundances. Changing the competitor's niche did little to alter skewness values except in the high generality/low magnitude scenario. In this case, skewness significantly shifted toward lower negative values (Fig. 3.2). However, at even higher levels of generality, skewness shifted toward greater negative values (not shown).

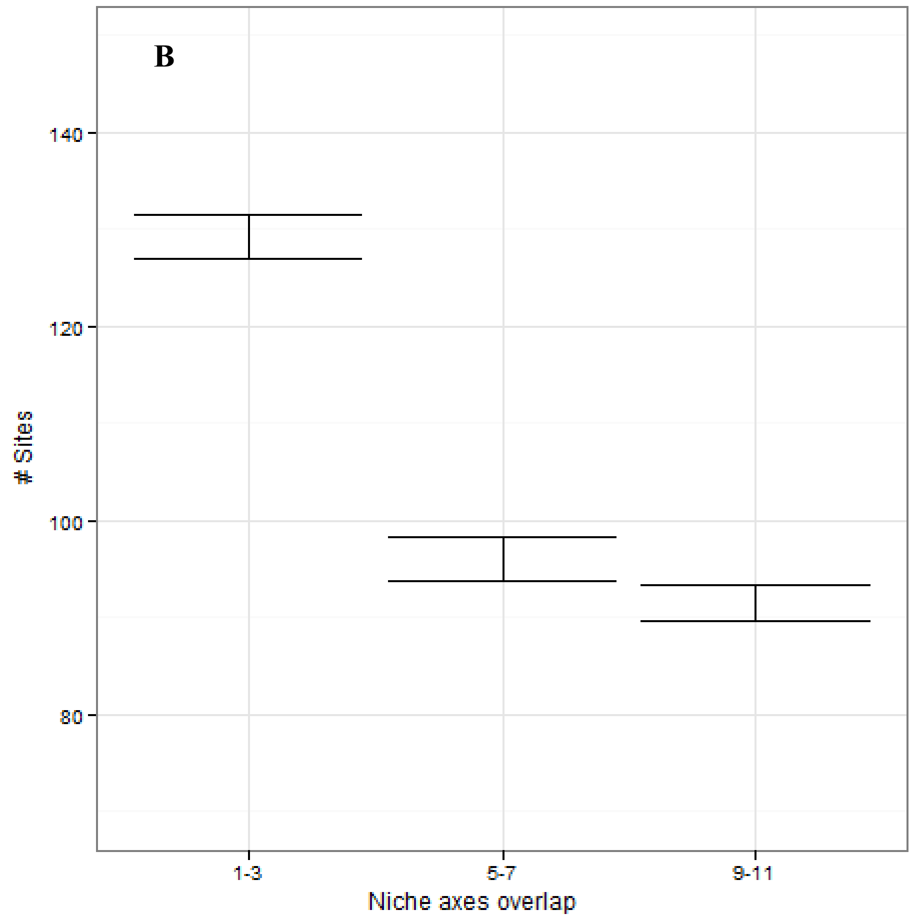
3.4.2. Phylogenetic relatedness

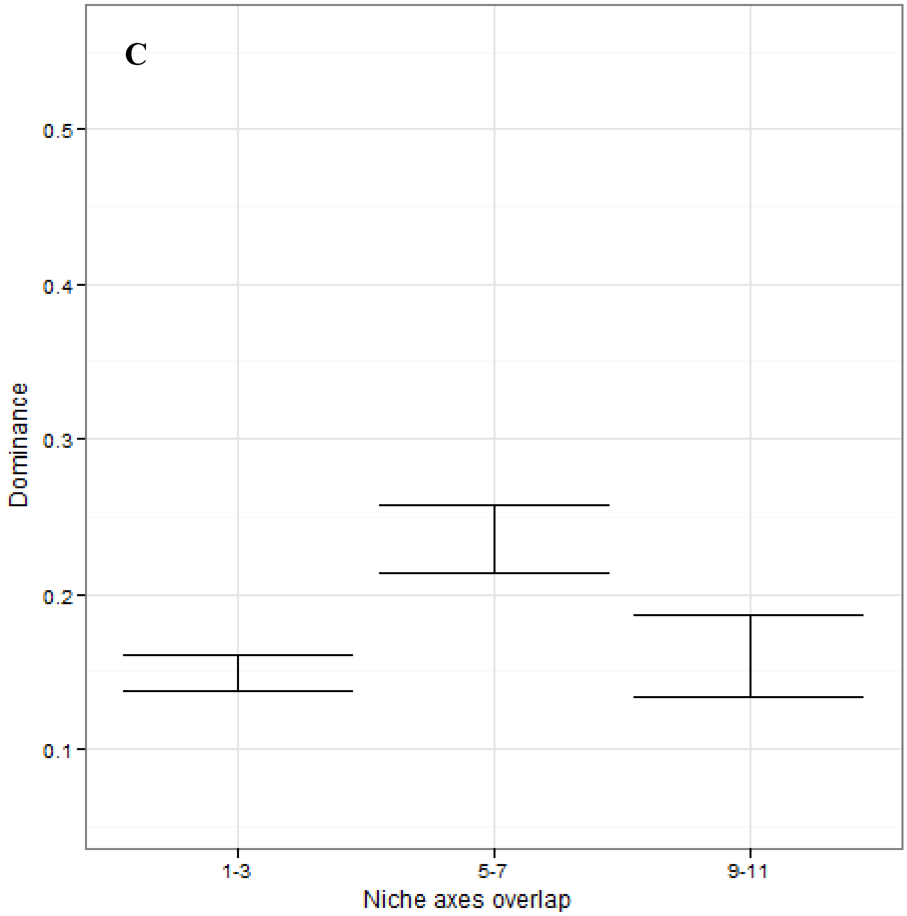
We simulated a multispecies community and varied the number of niche axes upon which the competitors overlapped with the focal species. Since the competitors consist of specialists and generalists, the focal species suffers doubly, first by facing competition over 70% of its niche and second by facing competition from the specialist at its niche optimum. We varied the number of axes upon which the competitors and the focal species competed to simulate varying interspecific phylogenetic relatedness. We found that increasing relatedness reduced the focal species' total abundance, occupancy, and skewness (Table 3.2, Fig. 3.3). However, beyond five - seven niche axes of overlap there was no additional decrease. Dominance peaked at intermediate levels of relatedness and evenness increased linearly with increased relatedness.

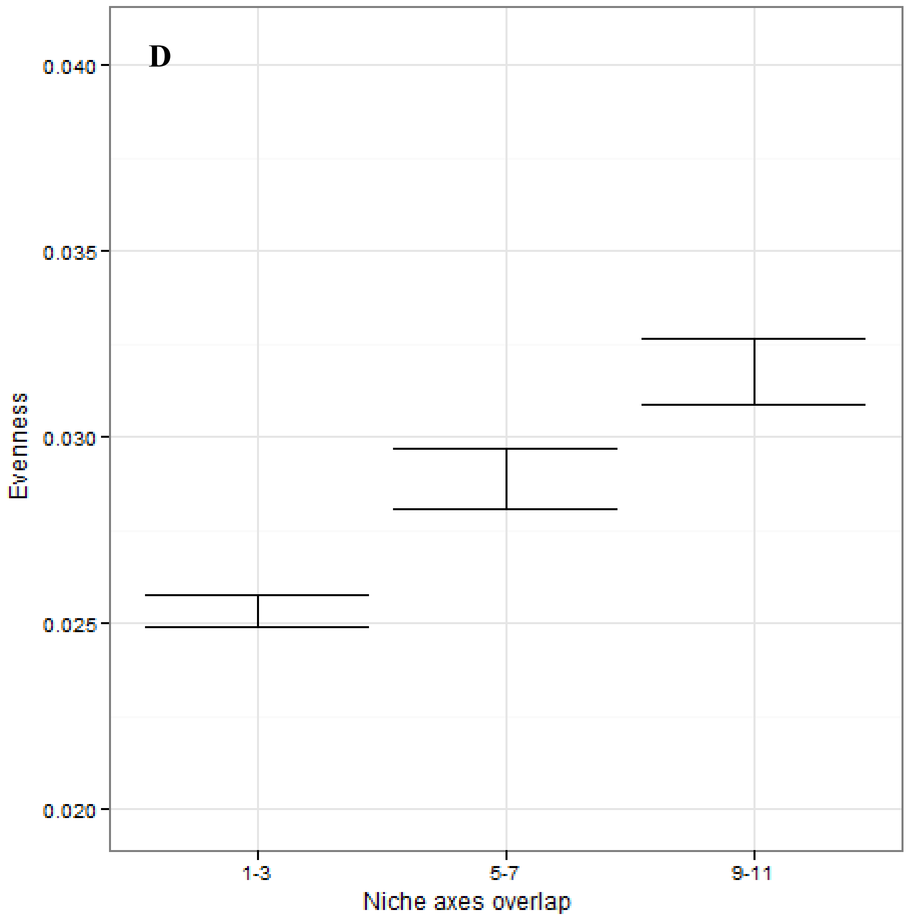
Table 3.2. MANOVA and ANOVA results for the five measures of spatial variation in abundance across three levels of phylogenetic relatedness between the focal species and three competitor species. Residual degrees of freedom = 207.

Factor	df	All	Occupancy	Total abundance	Dominance	Evenness	Skewness
Phylogenetic	8	$F = 46.7$	$F = 369.1$	$F = 1007.2$	$F = 19.7$	$F = 77.6$	$F = 8.5$
Relatedness		$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$


A
5e-08
4e-08
3e-08
2e-08
1e-08
Total abundance
1-3
5-7
9-11
Niche axes overlap


B
140
120
100
80
Sites
1-3
5-7
9-11
Niche axes overlap


C
0.5
0.4
0.3
0.2
0.1
Dominance
1-3
5-7
9-11
Niche axes overlap


D
0.040
0.035
0.030
0.025
0.020
Evenness
1-3
5-7
9-11
Niche axes overlap

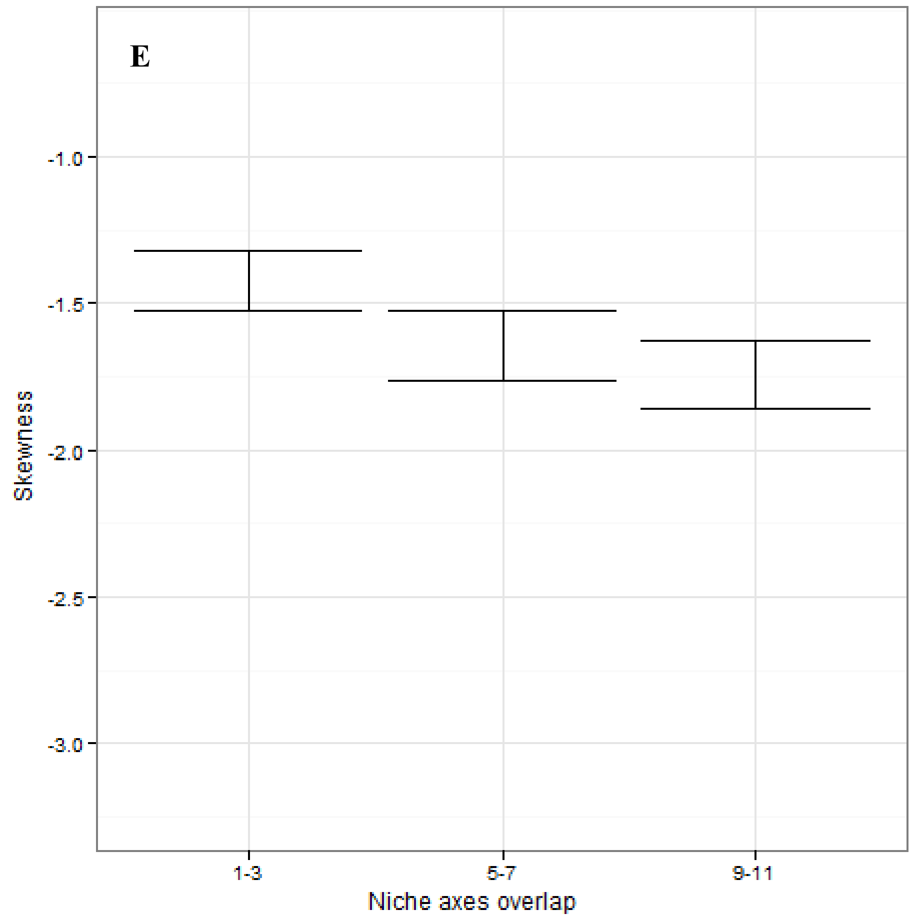


Fig. 3.3. The effects of competition on spatial variation in abundance across three different levels of phylogenetic relatedness. Mean ± 95% confidence intervals of total abundance (a), occupancy (b), dominance (c), evenness (d), and skewness (e) are shown across the three treatment levels. Phylogenetic relatedness describes the number of niche axes (out of a total of 11) upon which the focal species and its competitors competed. For three competitors, the number of niche axes was chosen randomly from the number of niche axes indicated on the x-axis.

3.5. Discussion

Ecologists for a long time have emphasized understanding variation in species diversity among communities. Often the approach has been to connect niche differences among species – observed locally - to the possibility of their coexistence (e.g. Chesson 2000). Niche differences, therefore, explain how resources are partitioned among multiple species at one location. However fundamental niches and niche differences arise from large scale processes such as speciation and adaptation. The consequences of niche differences should thus be manifested at similar scales. The results of our simulation experiments support this hypothesis. We have shown that differences in the ways in which species' fundamental niches relate to each other contribute to variation in how abundance is distributed over a species range. Consequently, there is a niche-based explanation for interspecific differences in spatial variation in abundance (SVA).

Critically, however, the mechanism that connects large scale process to large scale pattern occurs locally. Niche differences set the outcome of interspecific competition at each site within the species range from which the large scale pattern – spatial variation in abundance – emerges. Our study thus emphasizes the importance of framing local interactions in terms of the geographic distributions of the component species (Ricklefs 2004, 2008).

3.5.1. Abundance-occupancy-spatial variation relationships

Niche differences affected SVA because they determined the number of sites within a range at which a species was competitively excluded. As the competitor's niche breadth increased, it excluded the focal species at an increasing number of sites, driving down occupancy and overall abundance. However, with lower occupancy came a different pattern of abundance: the distribution of abundances became more evenly spread among sites and, at the same time, the most abundant site had a higher proportion of overall abundance. It is well known that occupancy and abundance are positively correlated (Brown 1984; Gaston et al. 2000). Implicit in the relationship is that the aggregation (i.e. spatial pattern) of individuals across a range mediates the form of the relationship: the clumping of individuals necessarily dictates whether total abundance is apportioned over more or fewer sites (Hartley 1998; Holt et al. 2002). Our study supports the assertion that occupancy, abundance, and spatial variation in abundance are all linked. Moreover, we have shown that niche differences among species may be the ultimate cause of interspecific differences in aggregative behaviour and, therefore, a proximate cause of the interspecific abundance-occupancy relationship.

Regardless of whether abundance was apportioned more or less evenly among sites, there was a consistent overrepresentation of sites of low abundance relative to a lognormal distribution of abundances. Moreover, this negative skew of abundances changed very little as we modeled different types of niche differences between the focal species and its competitor. Consequently, skewness is unlikely to characterize the aggregative behaviour that generates the interspecific abundance-occupancy relationship. As long as both abundance and occupancy declined, the proportion of abundant and rare sites stayed relatively the same. Only when niche differences caused a drop in abundance but no change in occupancy did skewness of the realized distribution of abundances noticeably differ from the fundamental distribution. Under this situation an entirely different dynamic was observed: evenness and dominance fell to very low values and decreased with a further increase in the competitor's niche breadth while skewness fell from low to high negative values. Consequently, the effects of niche differences on SVA are entirely different when competition causes both abundance and occupancy to change in concert versus when occupancy is held constant.

The importance of the abundance-occupancy relationship emphasizes exclusion as the dominant competitive mechanism modifying SVA. Both generalists and specialists lead to competitive exclusion but the former did so over a greater portion of the focal species' range and hence had a greater effect on evenness and dominance. The trade-off of being a generalist competitor is that it reduces the abundance of the focal species to a lesser degree than does the specialist competitor at sites where the fundamental niches overlap. This consequence of the trade-off only occurred for extreme generalists because competitive asymmetry was so minimal that the focal species was never excluded at any sites. When we increased competitive asymmetry by changing niche magnitude, the trade-off disappeared because there was always some competitive exclusion. The results of our model are therefore consistent with predictions from classical coexistence models: the smaller the fitness differences among competitors, the more likely the species coexist (Chesson 2000). Our study extends this relationship from communities to the scale of species ranges. Moreover, we could define the point at which fitness differences prevented coexistence in terms of niche overlap. For the way we modeled competition, this point occurred when the competitor species overlapped on approximately 80% of one of the focal species niche axes. If we had modeled a weaker effect of competition, this point would have occurred at a lower value of niche axis overlap.

3.5.2. Phylogenetic relatedness

Niche differences among species can be manifested in two ways: the degree of overlap along a particular niche axis and the number of niche factors upon which two species have any overlap. As described above, the first type of niche difference affected SVA. However, the latter type of niche differences also modified SVA: the more axes upon which the competitor and focal species competed, the stronger the deviation of the realized from the fundamental pattern of abundance. Almost paradoxically, the number of niche axes two species share is an oft-ignored aspect of niche differences. Most studies of niches, whether theoretical or empirical, measure overlap on a single resource, a convention rooted in MacArthur and Levins' (1967) interpretation of Lotka-Volterra competition coefficients (Leibold 1995). Similarly, phylogenetic relatedness among species is vaguely defined as ecological or phenotypic similarity (Losos 2008) which, in practice, is measured as niche overlap on one niche factor or gradient (e.g. Cavender-Bares et al. 2004; Kraft et al. 2008). Yet relatedness describes similarity in the fundamental niches of competing species (Webb et al. 2002; Wiens & Graham 2005), which should ideally correspond to all of the niche's "n-dimensions" (*sensu* Hutchinson 1957). If overlap occurs in n-dimensions then it is likely that there will be no overlap on most of these dimensions. We have shown that the number of dimensions of overlap and the degree of overlap when there is overlap are two separate but interacting processes acting on SVA. Whether they interact to affect community patterns (e.g. community assembly) has not yet been explored.

We further tested the "number of dimensions" aspect of species relatedness by building a multispecies community and varying the number of niche axes upon which the focal species overlaps with its competitors. The model is analogous to comparing species from clades with high and low niche conservatism (*sensu* Wiens & Graham 2005). All measures of SVA changed with relatedness but in different ways. For example, evenness increased but dominance peaked at intermediate levels of relatedness. For skewness, total abundance, and occupancy we found evidence of a threshold effect: the measures changed between low and intermediate levels of relatedness but did not change any further when relatedness was increased to high levels. It has been suggested that niche conservatism is higher in the tropics than in temperate regions (Wiens & Donoghue 2004). Based on our results, we could hypothesize that, all else being equal, tropical species should exhibit different patterns of abundance than temperate species.

3.5.3. Negatively skewed spatial variation in abundance

All our patterns of abundance were negatively skewed indicating more sites of low abundance than would be expected by a lognormal distribution. Negative skew also characterizes most species abundance distributions (e.g. Nee et al. 1991; Gregory 1994). Such skew has been attributed to neutral dynamics (i.e. independent of niche differences [Hubbell 2001]) and also to a sampling artifact

(McGill 2003), though this does not necessarily rule out niche-based explanations. The niche hierarchy model, for example, leads to negatively skewed distributions that vary in evenness depending on the branching pattern of phylogenetic trees (Nee et al. 1991; Sugihara et al. 2003). Moreover, Sugihara et al. (2003) suggested that evenness should decrease when species compete on fewer niche axes, which is consistent with our results. In our model, negative skew is an outcome of inclusive niches: with competitive exclusion species only persisted in the sites at the margins of their fundamental niches. The niche hierarchy model does not specify whether niches are divided in an inclusive manner. However, implicit in the model is that niches are continuously subdivided, which would leave both generalists and specialists in the overall assemblage (Sugihara 1980). Thus in both our model and the niche hierarchy model, the coexistence of specialists and generalists, the degree of relatedness between the two, and the number of axes upon which the species overlap generate and mediate the degree of evenness in abundance distributions.

It is not surprising that similar types of niche differences alter both SVA and SADs. McGill (2010) suggests that the former is a consistent "assertion" among models that generate the latter. Specifically, the clumping of individuals at different scales is one of three properties that, in combination, sufficiently explain large scale patterns. Within this framework, SVA is an intermediate step connecting interspecific niche differences to SADs (see also McGill and Collins 2003). Our results on phylogenetic relatedness suggest that macroevolutionary processes that generate niche difference in the first place manifest themselves as macroecological patterns. The "unified theory of unified theories" approach of

McGill (2010) underscores the importance of studying the causes and consequences of SVA.

3.5.4. Model limitations and future directions

Like with any model, we have made some simplifying assumptions to reduce complexity and test specific hypotheses. Here, we outline three key elements missing from our model that would enhance its ability to make quantitative predictions. First, we created a species range by drawing sites at random from within the focal species' fundamental niche. In reality, spatial autocorrelation in the values of each niche factor will create environmental gradients or patchiness in the distribution of sites of varying quality (Brown 1984; Brown et al. 1995). Nearly two decades after Brown et al. (1995) highlighted this fact, ecologists still do not have a good handle on how abundance changes over large scale environmental gradients (Ricklefs 2008). Second, the different niche factors themselves may be correlated. For example, temperature and precipitation may covary in space but have independent influences on abundance. Third, we did not explicitly model dispersal, which is a critical element influencing the relationship between fundamental and realized niches (Pulliam 2000).

Despite excluding these important influences on abundance, we accomplished our goal of explicitly examining the effect of interspecific niche differences on spatial variation in abundance. We highlight that just as niche differences affect patterns of coexistence and abundance at community scales they also lead to patterns of abundance at the scale of species ranges. Moreover, species from different clades or from different regions potentially may have different patterns of abundance because of differences in phylogenetic relatedness and subsequent niche differences. The power of our approach is that we began only with (evolutionarily derived) interspecific differences in species traits and from this a large scale pattern emerged. Our approach is thus complimentary to models rooted in population dynamics that likewise begin only by considering sites where the intrinsic population growth is greater than one and from this model the abundance and occupancy of entire species ranges (Holt et al. 1997; Pulliam 2000).

3.6. Acknowledgements

We are indebted to Etienne Low-Decarie for help with some of the R coding. Julie Messier and Peter White provided comments on an earlier version of the manuscript. Richard Feldman was supported by a NSERC PGS-D doctoral scholarship and McGill University.

3.7. References

Abramsky, Z., Rosenzweig, M.L., Pinshow, B., Brown, J.S., Kotler, B. & Mitchell, W.A. (1990). Habitat selection: an experimental field test with two gerbil species. *Ecology*, 71, 2358-2369.

Adler, P.B., Ellner, S.P. & Levine, J.M. (2010). Coexistence of perennial plants: an embarrassment of niches. *Ecol. Lett.,* 13, 1020-1029.

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

Brewer, A.M. & Gaston, K.J. (2002). The geographical range structure of the holly leaf-miner. I. Population density. *J. Anim. Ecol.*, 71, 99-111.

Brown, J.H. (1971). Mechanisms of competitive exclusion between two species of chipmunks. *Ecology*, 52, 305-311.

Brown, J.H. (1984). On the relationship between abundance and distribution of species. *Am. Nat.*, 124, 255-279.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995). Spatial variation in abundance. *Ecology,* 76, 2028-2043.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996). The geographic range: size, shape, boundaries, and internal structure. *Annu. Rev. Ecol. Syst.,* 27, 597-623.

Cadena, C.D. & Loiselle, B.A. (2007). Limits to elevational □istributions in two species of emberizine finches : disentangling the role of interspecific competition, autoecology, and geographic variation in the environment. *Ecography*, 30, 491-504.

Case, T.J. & Taper, M.L (2000). Interspecific competition, environmental gradients, gene flow, and the coevolution of species borders. *Am. Nat.*, 155, 583-605.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A & Bazzaz, F.A. (2004). Phylogenetic overdispersion in Floridian oak communities. *Am. Nat.*, 163, 823-843.

Chase, J.M. (1996). Differential competitive interactions and the included niche: an experimental analysis with grasshoppers. *Oikos*, 76, 103-112.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343-366.

Colwell, R.K. & Fuentes, E.R (1975). Experimental studies of the niche. *Annu. Rev. Ecol. Syst.*, 6, 281-310.

Connell, J.H. (1961). Influence of interspecific competition and other factors on distribution of the barnacle *Chthamalus stellatus*. *Ecology*, 42, 710-723.

Fretwell, S.D. & Lucas, H.L. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Bioth.,* 19**,** 16-36.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M. & Lawton, J.H. (2000). Abundance-occupancy relationships. *J. Appl. Ecol.*, 37, 39-59.

Gill, J.A., Sutherland, W.J. & Norris, K. (2001). Depletion models can predict shorebird distribution at different spatial scales. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, 268, 369-376.

Gonzalez, A., Lawton, J.H., Gilbert, F.S., Blackburn, T.M. & Evans-Freke, I. (1998). Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science*, 281, 2045-2047.

Gregory, R.D. (1994). Species abundance patterns of British birds. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, 257, 299-301.

Greiner La Peyre, M.K., Grace, J.B., Hahn, E. & Mendelssohn, I.A. (2001). The importance of competition in regulating plant species abundance along a salinity gradient. *Ecology*, 82, 62-69.

Hartley, S. (1998). A positive relationship between local abundance and regional occupancy is almost inevitable (but not all positive relationships are the same). *J. Anim. Ecol.*, 67, 992-994.

Holt, A.R., Gaston, K.J. & He, F. (2002). Occupancy-abundance relationships and spatial distribution: a review. *Basic and Appl. Ecol.*, 3, 1-13.

Holt, R.D., Lawton, J.H., Gaston, K.J. & Blackburn, T.M. (1997). On the relationship between range size and local abundance: back to basics. *Oikos*, 78, 183-190.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography.* Princeton University Press, Princeton, NJ.

Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, 22, 415-427.

Jarema, S.I., Samson, J., McGill, B.J. & Humphries, M.M. (2009). Variation in abundance across a species' range predicts climate change responses in the range interior will exceed those at the edge: a case study with North American beaver. *Glob. Change Biol.*, 15, 508-522.

Kerr, J.T., Kharouba, H.M. & Currie, D.J. (2007). The macroecological contribution to global change solutions. *Science*, 316, 1581-1584.

Kingsolver, J.G. (2009). The well-temperatured biologist. *Am. Nat.*, 174, 755-768.

Kneitel, J.M. & Chase, J.M. (2007). Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecol. Lett.*, 7, 69-80.

Kraft, N.J.B., Valencia, R. & Ackerly, D.D. (2008). Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, 322, 580-582.

Leibold, M.A. (1995). The niche concept revisited: mechanistic models and community context. *Ecology*, 76, 1371-1382.

Losos, J.B. (2008). Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.*, 11, 995-1007.

Lovette, I.J. & Hochachka, W. (2006). Simultaneous effects of phylogenetic niche conservatism and competition on avian community structure. *Ecology*, 87, S14-S28.

MacArthur, R.H. (1972). *Geographical Ecology: Patterns in the Distribution of Species.* Harper & Row, New York.

MacArthur, R.H. & Levins, R. (1967). The limiting similarity, convergence and divergence of coexisting species. *Am. Nat.,* 101, 377-385.

McGeoch, M.A. & Price, P.W. (2004). Spatial abundance structures in an assemblage of gall-forming sawflies. *J. Anim. Ecol.*, 73, 506-516.

McGill, B.J. (2003). Does Mother Nature really prefer rare species or are log-left-skewed SADs a sampling artifact? *Ecol. Lett.*, 6, 766-773.

McGill, B.J. (2010). Towards a unification of unified theories of biodiversity. *Ecol. Lett.*, 13, 627-642.

McGill, B.J. (2011). Species abundance distributions. In: *Biological Diversity: Frontiers in Measurement and Assessment.* (eds. Magurran, A.E & McGill, B.J.). Oxford University Press, Oxford, pp. 105-122.

McGill, B.J. & Collins, C. (2003). A unified theory for macroecology based on spatial patterns of abundance. *Evol. Ecol. Res.*, 5, 469-492.

McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Kassa Benecha, H. *et al.* (2007). Species abundance distributions : moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.*, 10, 995-1015.

McGill, B.J., Maurer, B.A. & Weiser, M.D. (2006). Empirical evaluation of the neutral theory. *Ecology*, 87, 1411-1423.

McNaughton, S.J. & Wolf, L.L. (1970). Dominance and the niche in ecological systems. *Science*, 167, 131-139.

Mehlman, D.W. (1997). Change in avian abundance across the geographic range in response to environmental change. *Ecol. Appl.*, 7, 614-624.

Murphy, H.T., VanDerWal, J. & Lovett-Doust, J. (2006). Distribution of abundance across the range in eastern North American trees. *Glob. Ecol. Biogeogr.*, 15, 63-71.

Murphy, H.T., VanDerWal, J. & Lovett-Doust, J. (2010). Signatures of range expansion and erosion in eastern North American trees. *Ecol. Lett.*, 13, 1233-1244.

Nee, S., Harvey, P.H. & May, R.M. (1991). Lifting the veil on abundance patterns. *Proc. R. Soc. Lond. Ser. B Biol. Sci.*, 243, 161-163.

Pulliam, H.R. (2000). On the relationship between niche and distribution. *Ecol. Lett.*, 3, 349-361.

R Development Core Team. (2009). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Ricklefs, R.E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecol. Lett.*, 7, 1-15.

Ricklefs, R.E. (2008). Disintegration of the ecological community. *Am. Nat.*, 172, 741-750.

Rosenzweig, M.L. (1991). Habitat selection and population interactions: the search for mechanism. *Am. Nat.*, 137, S5-S28.

Sagarin, R.D. & Gaines, S.D. (2002). The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecol. Lett.*, 5, 137-147.

Samis, K.E. & Eckert, C.G. (2007). Testing the abundant center model using range-wide demographic surveys of two coastal dune plants. *Ecology*, 88, 1747-1758.

Sugihara, G. (1980). Minimal community structure: an explanation of species abundance patterns. *Am. Nat.*, 116, 770-787.

Sugihara, G., Bersier, L-F, Southwood, T.R, Pimm, S.L. & May, R.M. (2003). Predicted correspondence between species abundances and dendrograms of niche similarities. *Proc. R. Soc. Lond.. Biol. Sci.*, 100, 5246-5251.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.*, 33, 475-505.

Wiens, J.J. & Donoghue, M.J. (2004). Historical biogeography, ecology, and species richness. *Trends Ecol. Evol.*, 19, 639-644.

Wiens, J.J. & Graham, C.H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.*, 36, 519-539.

Wisheu, I.C. (1998). How organisms partition habitats: different types of community organization can produce identical patterns. *Oikos*, 83, 246-258.

Wisheu, I.C. & Keddy, P.A. (1992). Competition and centrifugal organization of plant communities: theory and tests. *J. Veg. Sci.*, 3, 147-156.

3.8. Linking statement between Chapters 3 and 4

In the previous chapter, I used hypothetical species and environmental gradients in a simulation model to test generally how interspecific niche differences affect spatial variation in abundance. In the following chapter, I test the theory using a specific study system. The species correspond to Black-chinned and Broad-tailed hummingbirds, the environmental gradients correspond to food density and elevation, and interspecific niche differences correspond to differences in interference and exploitation competitive ability.

CHAPTER 4:

Mechanisms of variation in hummingbird abundance along environmental gradients

4.1. Abstract

Across an organism's range, abundance varies in part based on underlying environmental gradients. One hypothesis explaining this relationship is that the environment dictates whether an interference or exploitation strategy is most efficient for acquiring resources. Due to an interference-exploitation trade-off among organisms, the superior exploitation competitor should decline in abundance as it faces increasing interference competition along gradients that reduce interference costs. We test whether this hypothesis explains abundance differences between breeding black-chinned and broad-tailed hummingbirds and between male and female black-chinned hummingbirds in western Colorado, USA. We created an interference-exploitation gradient by manipulating food density and elevation and observing the effects on foraging activity and chasing frequency. While we observed differences in interspecific abundances consistent with the trade-off hypothesis, we found little support for interspecific interference competition being the mechanism causing abundance differences. Instead, the patterns we observed are better explained by a model that includes a third foraging strategy – the distraction sneaker. With sneakers present in the system, the asymmetries between exploitation and interference abilities are reduced and the importance of interference competition is minimized. We suggest that the sneaker model performs better than the trade-off model because of differences in male and female breeding behavior.

4.2. Introduction

Organisms compete for resources through interference and exploitation (Maurer 1984). In many communities, species that are inferior in one form of competition are superior in the other (e.g. Brown 1971; Feinsinger 1976). Theoretically, this interference-exploitation trade-off allows for species coexistence (Vance 1984; Amarasekare 2002) and leads to systematic changes in the distribution and abundance of species along resource availability gradients (Case and Gilpin 1974).

Empirically, the predictions of the model have been well supported by examining patterns in the distribution of hummingbirds. Along gradients of food (i.e. nectar) density, a hummingbird's energetic gain is determined by a trade-off between its ability to defend clumped flowers and its ability to exploit sparse flowers. When nectar flowers are clumped, usually one species dominates through resource defense (Pimm et al. 1985). As flowers become more dispersed, territory area increases (Kodric-Brown and Brown 1978; Hixon et al. 1983) and less time can be devoted to defense (Tiebout 1992). The competitive release allows other less aggressive species to achieve high abundance (Feinsinger 1976). At the same time, less aggressive species are comparatively more efficient at hovering, can forage on sparse flowers without costs exceeding foraging gains, and gain a competitive advantage by being the superior exploitation competitor (Carpenter et al. 1993).

The same type of trait-influenced trade-off that occurs on food density gradients occurs along elevation gradients. At high elevation, air density is low, limiting the ability of birds to produce enough power for the types of flight important in competitive interactions (Altshuler and Dudley 2003). However, these limitations are not equal among species. The less aggressive species has better flight performance at high elevation and dominates resource patches against the more aggressive species (Altshuler 2006). Such a trade-off translates to species turnover along elevation gradients based on tolerance to reduced air density (e.g. Feinsinger et al. 1979). A given species is excluded at low elevation by interference competition. As elevation increases, the species invades the community because it is a relatively better interference competitor than high elevation species. At even higher elevations, the species is no longer the community's best interference competitor and is outcompeted until, at even higher elevations, it is excluded because reduced air density raises foraging costs in excess of foraging gains. Despite the fact that a similar trade-off mechanism mediates hummingbird distribution on nectar density and elevation gradients, the two environmental gradients have always been studied in isolation.

The patterns of distributional changes along resource density and elevation gradients occur not just among species but within species as well (Carpenter et al. 1993; Altshuler and Dudley 2003). For North American hummingbirds, male wings differ in size and shape in a manner suggesting more efficient interference competition (Stiles et al. 2005). Moreover, males are more limited in their ability to hover than females in reduced air density (Chai and Dudley 1999), suggesting that females are more tolerant of high elevation environments. While mating necessitates coarse-grained coexistence between males and females, the trade-offs responsible for interspecific differences in abundance may similarly lead to gender-based spatial segregation at finer grains (e.g. Pitelka 1951; Stiles 1982).

The trade-off model has only ever been substantiated by looking at patterns in the distribution of organisms. However, the model predicts that abundance should change as well: the abundance of the superior exploitation competitor should decline as resource density increases because resource defense by the more aggressive species increases in frequency and efficacy (Case and Gilpin 1974). It is our goal with this paper to test whether hummingbird abundance changes along interacting food density and elevation gradients in a manner consistent with the interference-exploitation framework. We explicitly test the hypothesis that how a species responds to changes in elevation depends on nectar density.

To test our hypothesis, we use a two species natural system: black-chinned (*Archilochus alexandri*) and broad-tailed (*Selasphorus platycercus*) hummingbirds in an area of range overlap in southwest Colorado, USA. We experimentally manipulate the defendability of nectar resources by altering the spacing between two hummingbird feeders and do so along multiple elevation gradients. Despite the fact that black-chinneds and broad-taileds are the only two breeding hummingbirds over a large portion of the western USA and despite the number of studies conducted on each separately or in combination with other species (e.g. Ewald 1985; Pimm et al. 1985; Altshuler 2006), there have been no studies of competition between black-chinneds or broad-taileds.

4.3. Methods

4.3.1. Study sites and species

Black-chinned and broad-tailed hummingbird species ranges overlap primarily in the mountains and foothills of western New Mexico and western Colorado (fig. 4.1). It is in the latter where we conducted our experiment. For both species, variation in mass is greater between sexes than between species (Calder and Calder 1992; Baltosser and Russell 2000).

We conducted our experiment in four independent locations (fig. 4.1) with each location comprised of four sites corresponding to four different elevations (table 4.1). The majority of sites were Piñon-Juniper (*Pinus edulis-Juniperus osteosperma*) woodland or Oak-Cottonwood (*Quercus gambelii-Populus angustifolia*) riparian sites. Some of the higher elevation sites were mixed with Ponderosa Pine (*Pinus ponderosa*) forest. All sites were at least 4 km apart in an attempt to represent independent hummingbird populations. All our sites were in the Uncompahgre and San Juan National Forests far from any human habitation that might have hummingbird feeders. We began the study on May 19, 2009 and ended the study on July 21, 2009.

Table 4.1: Study locations and sites at which we carried out our experiments.

Location	Site	Latitude	Longitude	Elevation (m)	Nectar production (kJ)	Start date
San Juan National Forest – West	1	37.59	-108.60	2014	107.32	05/19/2009
	2	37.62	-108.64	2013	0.00	
	3	37.66	-108.72	2176	590.99	
	4	37.69	-108.68	2346	35336.80	
San Juan National Forest - East	1	37.46	-108.52	2200	1360.80	07/08/2009
	2	37.51	-108.47	2326	0.00	
	3	37.55	-108.47	2212	9823.16	
	4	37.52	-108.52	2140	936.79	
Uncompahgre National Forest - South	1	38.14	-108.34	2082	0.00	06/05/2009
	2	38.02	-108.11	2274	153.93	
	3	38.05	-108.14	2130	1149.71	
	4	38.12	-108.20	2047	1322.61	
Uncompahgre National Forest - North	1	38.27	-108.45	1904	0.00	06/20/2009
	2	38.27	-108.38	1855	458.91	
	3	38.26	-108.33	2062	0.00	
	4	38.26	-108.28	2273	290.96	

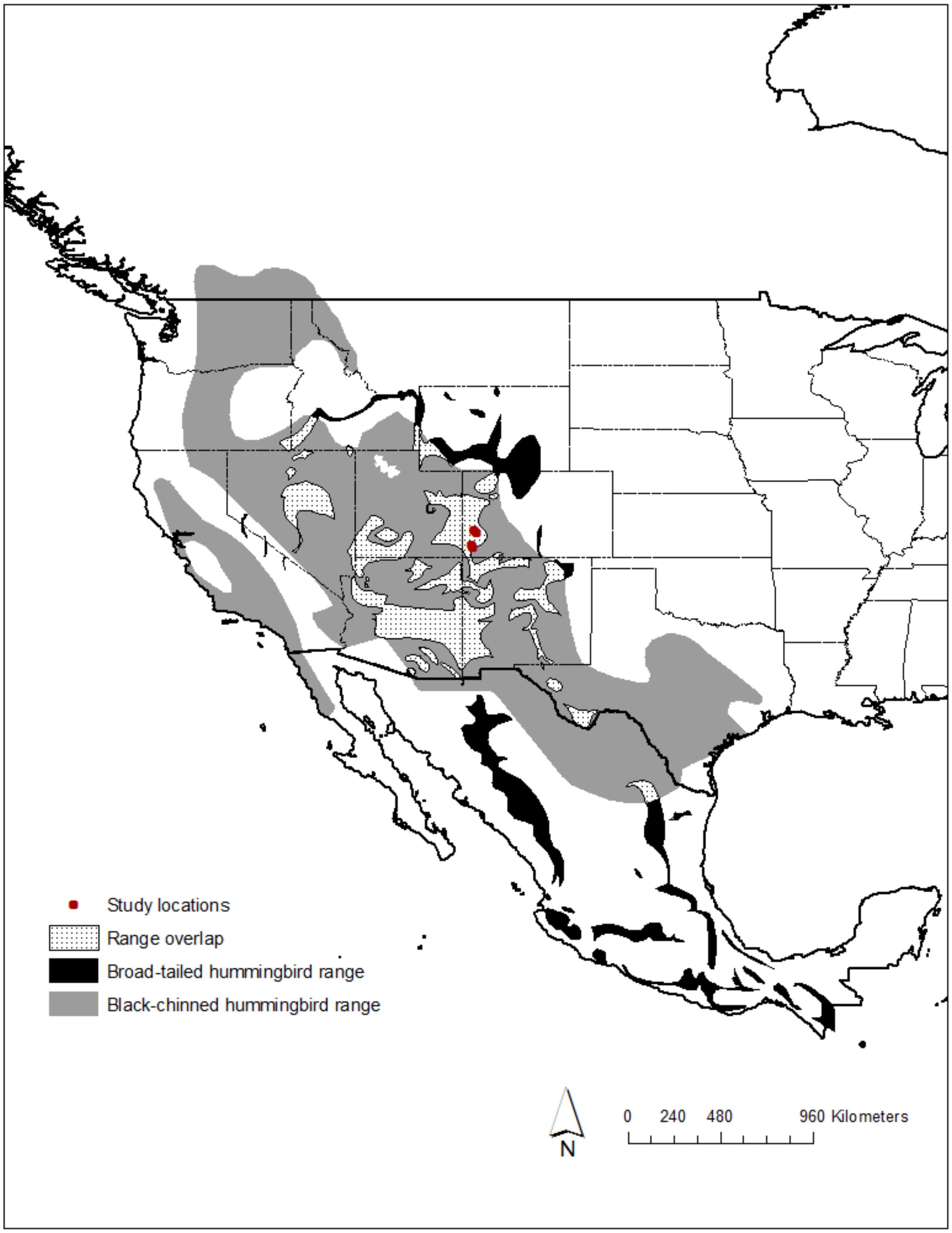


Figure 4.1: The breeding distributions of black-chinned and broad-tailed hummingbirds (from Ridgely et al. 2005) and our study locations in the Uncompahgre and San Juan National Forests.

4.3.2. Field methods

At each site, we established two perchless hummingbird feeders (Perky Pet model #211) separated by 12m. Both feeders were filled with 235ml of 26% (w/w) sucrose solution (288.1 g/L sucrose). We maintained this level of food availability over four days to allow birds to become habituated to and establish territories around the feeders. The feeders were suspended from a wooden pole, 3.0m from the ground.

After the fourth day, the volume of the sugar solution was reduced to 30ml. The feeders were moved into one of three spacing treatments: 3m between feeders, 6m between feeders, or left at 12m between feeders. We visited the feeders later that day (15h00 – 17h00) and refilled the feeders with 30ml of fresh sugar solution. We refilled the feeders again the following day once in the morning (5h30 – 7h30) and once in the afternoon (15h00 – 17h00). On the second day after the feeders were rearranged, we refilled the feeders with fresh sugar solution and then videorecorded hummingbird activity (see below). After recording, we refilled the feeders with 235ml of sugar solution and placed them 12m apart and waited two full days, periodically refilling the feeders. On the third day, we rearranged the feeders into another treatment configuration, waited a day, and recorded activity on the treatment set-up. We repeated the cycle until all three feeder spacing treatments were recorded on each site. The assignment of treatment sequence to each site was done randomly. The order of site visit on a particular morning was also conducted randomly.

Each videorecording lasted one hour. One video camera (Sony Handycam DCR-SR45) was placed 1.0-1.5 m from the feeder and focused on the feeding ports. Another video camera was placed 4.0-6.0 m away and recorded activity surrounding the feeder. This set-up occurred at both feeders for a total of four cameras capturing hummingbird activity. Recordings began between 5h30 and 11h00.

Hummingbird activity at feeders is known to be affected by nectar availability in the surrounding landscape (Inouye et al. 1991; McCaffrey and Wethington 2009). To account for this effect we measured nectar production from flowers in a 250 m x 250 m plot surrounding the feeders at each site. We walked four 250 m transects spaced 50 m apart and counted all flowers from a list of hummingbird pollinated flowers. We converted the number of flowers to nectar production by using literature values of nectar production for each genus that we found. More details can be found in Chapter 2. We included landscape-scale nectar production in all our models of hummingbird activity and competition though interpreting its effect is beyond the scope of this study. By including it in our models, however, the effect estimates of our other parameters are all interpreted for the same level of landscape-scale nectar production.

4.3.3. Data analysis

We recorded three different types of feeder activity: foraging, chasing, and simultaneous foraging. Each type of activity became the dependent variable we related to the independent variables of: feeder spacing treatment (a categorical variable because the actual distance was not important), elevation, and nectar production in the surrounding landscape. We constructed separate models for female black-chinneds, male black-chinneds, and female broad-taileds. We recorded very few instances of male broad-taileds foraging. While we occasionally observed juveniles, we did not include them in any of our analyses.

All our models used a binomial distribution of the independent variable. Consequently, our results are probabilities of success: the probability of foraging, being chased during a foraging bout, or foraging at the same time another individual is foraging at the adjacent feeder.

For foraging, we measured the proportion of the 60 min. videorecording period in which the species/sex of interest was observed foraging. Measuring foraging activity as a proportion indicates the degree to which resources are being co-opted by one sex/species at the expense of another. Activity measured in this way has been used as an estimate of relative competitor pressure ("activity density") when individual identification is not possible (Pimm et al. 1985; Sandlin 2000). Since we are interested in the relative dominance of one sex/species over another, we use the probability of foraging as an indicator of relative abundance.

We used chasing as an indicator of interference competition. We measured chasing as the proportion of foraging bouts in each 60 min. observation period that ended in a chase. We also included instances where a bird approached the feeder but was chased before being able to feed. Since most of these chases were viewed only by the camera at a distance from the feeder, we were unable to identify the species/sex of the chaser.

We measured simultaneous foraging in order to test whether feeder spacing affected the probability that a territorial bird abandoned defense of one of the feeders. Such a result would obscure any pattern because if each feeder were defended separately then the foraging and defense costs would be much lower than if both feeders were defended. We measured this potential as the proportion of foraging bouts in which two birds simultaneously foraged from each feeder. We measured this separately as two female black-chinneds simultaneously foraging or as a female black-chinned simultaneously foraging with a male black-chinned. We did not record enough instances of female black-chinneds and broad-taileds simultaneously foraging to warrant statistical analysis.

Our experimental design was hierarchical in nature. We had four locations each comprised of four different sites and within each site we had three treatments for a total of 48 experimental units. Feeder spacing varied within sites while elevation and nectar production varied between sites. Foraging activity, chasing activity, and simultaneous foraging can vary both between and within sites. In fact, we explicitly hypothesized that differences in activity would vary between sites and that this variation would be due to differences in elevation. We first tested the importance of location-level variation by constructing an intercept-only model with site nested in location as a random effect. If there was variation at the location level, we kept this nested term as a random effect in further modeling. If variance at the location level was zero or near zero, we only included site as a random effect.

We constructed a hierarchical linear mixed model in order to test the relationship between our dependent and independent variables. We carried out analysis using package lme4 (Bates and Maechler 2009) in R (R development core team 2009). We first constructed a full model with cross-scale interactions between feeder spacing treatment and elevation and feeder spacing treatment and nectar production. We compared models with and without random effects to test for site-level variation in the independent variable. We compared the models using AICc. It is currently being debated whether models of different random effects can be effectively compared because of uncertainty in how many parameters to assign the random effects (Bolker et al. 2008). The package AICcmodavg (Mazerolle 2010) in R assigns one parameter to each random effect. However, in all cases, the differences in AICc between models with and without random effects were large enough such that if more parameters were assigned to random effects, the model selection result would not change.

Once the correct random effects structure was chosen we systematically dropped fixed effects variables and chose the best model by AICc. For the variables in the selected model, we report parameter estimates and 95% confidence intervals averaged over all the models in which that variable appears (Burnham and Anderson 2002). Prior to all analyses, we examined the fit of the full model by visually inspecting the relationship between fitted values and residuals and dropped outliers when they occurred. We also standardized the elevation and nectar production variables by centering their mean and dividing by their standard deviation.

4.4. Results

For all species and sexes and for foraging, chasing, and simultaneous foraging probabilities, the best model was the full model, containing both feeder spacing x elevation and feeder spacing x landscape-scale nectar production interaction terms (tables A4.1-A4.3).

The model intercept is the probability of foraging or being chased at the 3 m feeder spacing and at average elevation and landscape-scale nectar production. Examining the intercepts indicates that female broad-taileds were rarer and more likely to be chased than either female or male black-chinneds (tables A4.2-A4.3). When we could identify the species and sex of the bird that chased broad-taileds, it was almost always a female black-chinned. Only twice did we observe a broad-tailed being chased by a male black-chinned and we never observed it being chased by another broad-tailed. On the other hand, broad-taileds were the chaser for 5.54% of identified female black-chinned chases.

Male black-chinneds foraged less often than females but were chased only slightly more frequently. For male black-chinneds, 77.8% of the time we could identify the chaser, it was a female black-chinned. Conversely, only 14.0% of the time a female was chased by a male. The remainder of the time, females chased each other.

4.4.1. Interspecific and intraspecific trade-offs

Under a trade-off model, a change in broad-tailed abundance along an elevation gradient should coincide with the opposite change in black-chinned abundance and the probability it is chased. We observed such a pattern but only for female black-chinned abundance (fig. 4.2). The probability of being chased declined as broad-tailed abundance increased only for the 6m feeder spacing treatment. However, there was such high variability in the frequency with which broad-taileds were chased that we do not attempt to draw inferences from this pattern.

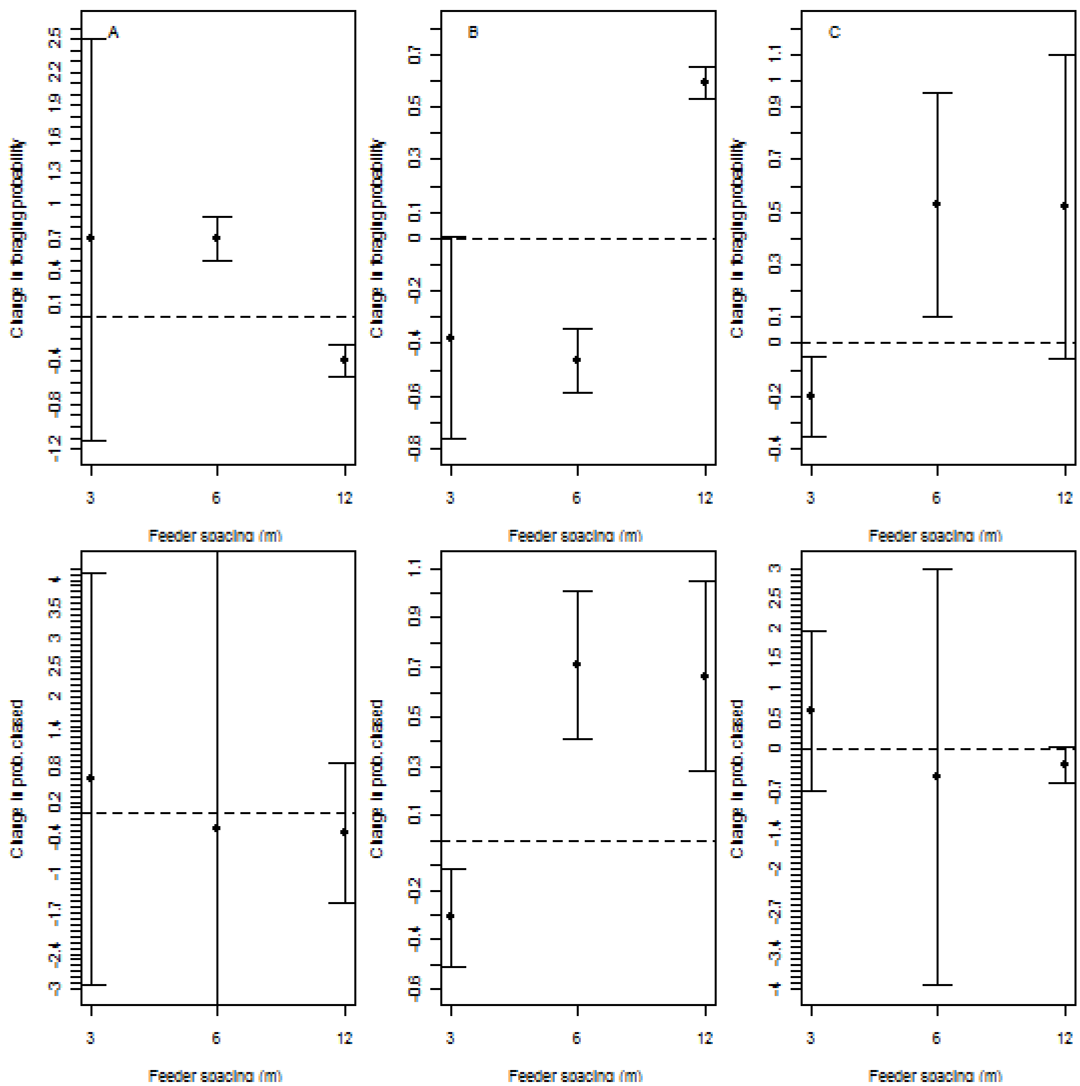


Figure 4.2: The change in the probability of observing a female broad-tailed (A), female black-chinned (B), and a male black-chinned (C) hummingbird foraging (top) or being chased (bottom) for each one standard deviation increase in elevation (~140m) for each of three feeder spacing treatments. Error bars represent 95% confidence intervals of the parameter estimates.

The trade-off model was also insufficient to explain differences in abundance patterns for male and female black-chinneds. While the direction of male abundance change was inversely related to the probability of being chased, there was high uncertainty in the measurements of the latter (fig. 4.2). There was much more confidence in the connection between male black-chinned abundance and the probability a female was chased. As females were increasingly busy chasing themselves, male abundance increased (fig. 4.2).

As expected, the costs imposed by higher elevations lead to a lower probability of observing a female black-chinned foraging but only at the 3m and 6m feeder spacing treatments (fig. 4.2). An increase in abundance at 12m could occur if the wide feeder spacing and high elevation encourages territory holders to defend only one feeder instead of two. We did not observe this to be the case: the degree to which two female black-chinneds foraged at both feeders simultaneously changed with elevation equally regardless of feeder spacing (fig. 4.3). While we observed a higher probability of males simultaneously feeding, the measure occurred with high uncertainty.

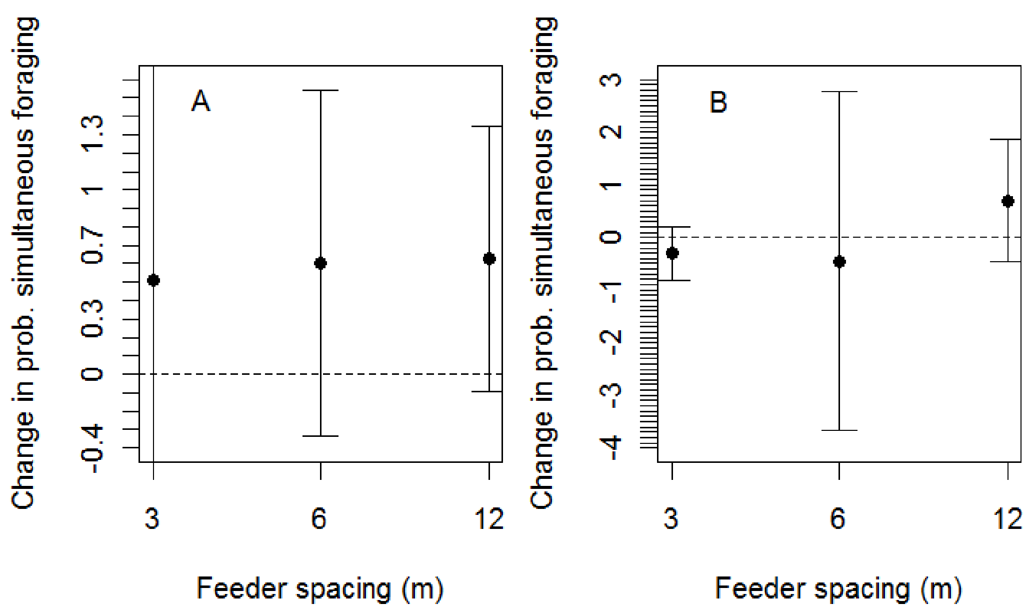


Figure 4.3: The change in the probability of observing two female black-chinned hummingbirds (A) and a female and male black-chinned hummingbird (B) simultaneously forage at both feeders for each one standard deviation increase in elevation (~140m) for each of three feeder spacing treatments. Error bars represent 95% confidence intervals of the parameter estimates.

4.4.2. Geographic variation

There is little evidence for geographic variation in the probability of foraging for black-chinned hummingbirds at scales greater than the site level (table A4.1). For the probability of being chased, on the other hand, more variation occurred among locations (table A4.2), which is a collection of sites clustered in space and time. The average probability of being chased was generally above average for the locations observed later in the summer (table A4.4). We suspect that at this time some of the unidentified chasers included juveniles, which tended to engage in chases more frequently than adults (R. E. Feldman, personal observation).

For broad-taileds, on the other hand, the probability of foraging but not the probability of being chased varied more among locations than sites (tables A4.1-A4.3). However, there was no spatial or temporal trend in the magnitude by which foraging probability at each differed from the overall mean probability (table A4.4). It is possible that this variation was due to factors we did not measure. Comparing variance among models with and without elevation and landscape-scale nectar production indicates how much of the between location or between site variation is explained by those variables. For chasing probabilities, our measured variables explained < 15% of total variation (tables A4.2-A4.3), indicating that other unmeasured factors may vary at those scales and have an influence on hummingbird activity.

4.5. Discussion

The changes we observed in the abundances of female black-chinned and broad-tailed hummingbirds are consistent with the interference-exploitation trade-off. However the mechanism is not consistent with the trade-off (*sensu* Case and Gilpin 1974); changes in abundance were not related to changes in interspecific interference competition. This inconsistency arises because our system consists of three not two resource acquisition strategies: interference competitors, exploitation competitors, and distraction sneakers (*sensu* Dubois et al. 2004). With sneakers present, the abundances of foragers can change without corresponding changes in the level of aggression, a theoretical prediction (Dubois et al. 2004), we now support with empirical results.

4.5.1. The importance of sneakers

The differences in aggression we observed among female black-chinned and broad-tailed hummingbirds suggests that each uses a different foraging strategy to acquire food resources. Female black-chinneds were always the most aggressive of the species/sex groups, accounting for the highest proportion of inter- and intraspecific chases. Female broad-taileds, on the other hand, are less aggressive. They accounted for only 5% of interspecific encounters. They also tended to increase in abundance with increasing elevation, which corresponds to increasing interference defense costs (Altshuler and Dudley 2003).

Intraspecifically, the two black-chinned sexes were split along a different axis; changes in male black-chinned abundances along elevation gradients were not related to changes in female abundance. Instead, their abundance paralleled changes in the probability a female black-chinned was chased, which consisted mostly of females chasing themselves. This is the hallmark of the distraction sneaker; individuals that take advantage of a territory holder's engagement in another activity to forage without harassment (Wilson 1975; Dubois et al. 2004). Such behaviour in hummingbirds has been observed before (e.g. Powers and McKee 1994, Bachi 2008) and is sometimes called aggressive neglect (*sensu* Hutchinson and MacArthur 1959; Brown 1971).

Our three strategy system corresponds to that of a model testing how sneakers affect levels of aggression in foraging groups (Dubois et al. 2004). The model, which labels aggressive and non-aggressive individuals "hawks" and "doves," predicts the competitive dynamics we observed. The model shows that any fitness gains made via more efficient and effective interference competition are offset by losses to increasing numbers of sneakers. Consequently instead of there being a decline in interspecific aggression as elevation increases, there is little or no change because there are also fewer sneakers ensuring that a payoff to aggression is maintained. At the same time, there is no benefit for non-aggressive female black-chinneds to adopt a sneaker or non-aggressive strategy so overall abundance decreases. Likewise, sneaker male black-chinneds benefit from an increase in the frequency and duration with which female black-chinneds engage same sex competitors. However, male abundance is not related to female abundance because the latter depends on how many individuals switch to the sneaker strategy. In summary, the model predicts the two key outcomes that are not consistent with the strict interference-exploitation trade-off model (*sensu* Case and Gilpin 1974).

By supporting the predictions of the hawk-dove-sneaker model, we show that its assumptions may be valid not just at the individual level at which the model was developed but at the group level as well. In fact, for hummingbirds, foraging strategies may be more variable between than within species and sexes because traits related to foraging and competition vary more between than within species and sexes (e.g. body size and flight performance [Altshuler and Dudley 2003; Stiles et al. 2005]). Hence individuals may be constrained in the strategy they can adopt relative to the other species/sex. It will be interesting to formally include such groups in the hawk-dove-sneaker model and test whether the outcomes even more precisely predict the patterns we observed.

The key problem in applying any theoretical foraging model, be it the interspecific-exploitation model (Case and Gilpin 1974) or the hawk-dove-sneaker model (Dubois et al. 2004), is that they predict responses to one environmental variable at a time. In our study, we found that the changes in abundance and competition that occurred along a gradient of increasing elevation varied depending on food density. We suggest that we observed a significant interaction between elevation and feeder spacing because there may be substantial flexibility in hummingbird behaviour. Such complexity may be difficult to capture in theoretical models yet substantially influence empirical patterns. For example, in both the hawk-dove-sneaker model and in field studies of hummingbirds, levels of aggression are an outcome of the number of intruders (Ewald and Carpenter 1978; Ewald and Bransfield 1987), which depends on nectar availability at multiple spatial scales (Carpenter 1987). Hummingbirds have been observed to both decrease (Ewald and Carpenter 1978; Ewald 1985) and increase (Powers and McKee 1994) their use of chases as food availability declines depending on the identity of the intruders, the rate of intrusion, and the degree to which food availability meets energetic requirements. As well, territory defenders may respond to intrusion by altering territory size (Norton et al. 1982) or type of aggressive behavior (e.g. switching from chases to threat vocalizations [Ewald and Carpenter 1978; Camfield 2003]).

4.5.2. The non-aggressive male

Our results suggest that female black-chinneds are the more aggressive sex and males forage only when they can avoid competitive encounters. This contrasts with what has been observed for other species (e.g. Kodric-Brown and Brown 1978; Carpenter et al. 1993). In these studies, an interference-exploitation trade-off was clearly demonstrated. Males were more aggressive and excluded females from the richest foraging patches. Females, on the other hand, suffered little energetically because they were more efficient exploiters. In these observations, the environment dictated the level of male aggression, which dictated where and when females could forage (see also Stiles et al. 2005).

Our results do not fit this pattern because our study took place during the breeding season, when hummingbird behavior and resource requirements differ from the late summer period of the other studies. In the non-breeding season, birds must fatten quickly in advance of migration (Carpenter et al. 1983), which then places emphasis on the defense of rich nectar patches (Gass et al. 1976). In the breeding season, on the other hand, males may forego defending the richest foraging patches and instead establish territories around resources that help procure mates such as access to perch sites (Armstrong 1987). Territories may also be based on the availability of arthropod prey (Stiles 1995; Powers et al. 2010) or the presence of insects that compete for nectar (Brown et al. 1981; Gill et al. 1982). Since males do not have a role in raising young, they are freer than females to roam to track spatial and temporal variation in resource availability.

Males may have the capacity to be more aggressive than females because flight traits related to interference competition may be beneficial in male-male competition and courtship displays (Stiles et al. 2005). However, males may focus their energy toward these activities and not to the defense of rich food patches (see also Powers and McKee 1994). Male-male competition may further weaken male body condition making them even more vulnerable to competitive interactions with females. Therefore given that the defense of food patches yields little benefit but imposes a cost on reproduction, males may adopt a sneaker foraging strategy.

4.5.3. A place for trade-offs

Sneakers effectively narrow competitive asymmetries. When the environment favors interference, the costs of defense may be low but the presence of sneakers reduces the amount of the defended resource. When the environment favors exploitation, the costs of defense may be high but the presence of sneakers increases the amount of defended resource. We believe that sneaker male black-chinned hummingbirds had such a strong effect in our system because natural levels of nectar availability in our study region have selected for two similarly efficient exploitation species. During the breeding season and across the region where black-chinneds and broad-taileds overlap, flowers are sparsely distributed (see Chapter 2). Flower scarcity may select for only the most efficient exploiters, which may be why black-chinneds and broad-taileds are the only two breeding hummingbirds in the region (*sensu* Feinsinger et al. 1985). The flipside is that both species are the less aggressive species when competing with others in locations where or time periods when flowers are more clumped. It may be in these places in space and time where the interspecific differences in interference and exploitation abilities influence large-scale distribution patterns. For example, the trade-off between broad-tailed and rufous hummingbirds (*Selasphorus rufus*) that occurs in late summer (Kodric-Brown and Brown 1978; Altshuler 2006) might bias broad-tailed abundance toward higher elevations even during the breeding season. For black-chinneds, being prevented from foraging in blue-throated hummingbird (*Lampornis clemenciae*) territories where they co-occur in southeastern Arizona (Pimm et al. 1985; Powers and McKee 1994) means interspecific competition could be responsible for the black-chinned's southern range limit. Similarly, the more aggressive Anna's hummingbird (*Calypte anna*) has been shown to limit black-chinneds to lower quality territories (Ewald and Bransfield 1987). With Anna's hummingbirds being primarily a coastal Pacific species, such competition may place a western limit to the black-chinned range.

Range limits may be more obviously associated with interference-exploitation trade-offs because such a trade-off is a specific characterization of the competitive ability-environmental tolerance trade-off, which has shown to influence large-scale distribution patterns (Loehle 1998; Normand et al. 2009). Our study shows that what happens within a species range, i.e. spatial variation in abundance, instead reflects the complex ways in which underlying environmental gradients influence the costs and benefits of resource defense. Therefore we suggest that that behavioral models, which typically make predictions at small scales, also may be able to contribute to our understanding of large-scale spatial patterns (see also Gill et al. 2001).

4.6. Acknowledgements

R.E.F. was supported by an NSERC PGS-D scholarship. We thank the Dolores Public Lands Office and the Uncompahgre National Forest-Norwood Office for allowing us access to their land. F. Dubois, L-A. Giraldeau, D. Powers, and S. M. Wethington provided fruitful discussion about hummingbirds, energetics, and competition.

4.7. References

Altshuler, D. L. 2006. Flight performance and competitive displacement of hummingbirds across elevational gradients. American Naturalist 167:216-229.

Altshuler, D. L., and R. Dudley. 2003. Kinematics of hovering hummingbird flight along simulated and natural elevation gradients. Journal of Experimental Biology 206:3139-3147.

Amarasekare, P. 2002. Interference competition and species coexistence. Proceedings of the Royal Society B: Biological Sciences 269:2541-2550.

Armstrong, D. P. 1987. Economics of breeding territoriality in male calliope hummingbirds. Auk 104:242 – 253.

Bachi, A. 2008. Applying community ecology to manipulate and conserve hummingbird diversity in urban habitats. PhD thesis. Univ. Arizona. 196 pp.

Baltosser, W. H., and S. M. Russell. 2000. Black-chinned hummingbird (*Archilochus alexandri*). *in* A. Poole, ed. The birds of North America Online. No. 495. Cornell Lab of Ornithology, Ithaca, NY.

Bates, D., and M. Maechler. 2009. lme4: linear mixed-effects models using S4 classes. R package versions 0.999375-31. http://CRAN.R-project.org/package=lme4

Bolker, B. M., M. E. Brooks. C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J-S. S. White. 2008. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127-135.

Brown, J. H. 1971. Mechanisms of competitive exclusion between two species of chipmunks. Ecology 52:305-311.

Brown, J. H., A. Kodric-Brown, T. G. Whitham, and H. W. Bond. 1981. Competition between hummingbirds and insects for the nectar of two species of shrubs. Southwestern Naturalist 26:133-145.

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

Calder, W. A., and L. L. Calder. 1992. Broad-tailed hummingbird (*Selasphorus platycercus*). *in* A. Poole, ed. The birds of North America Online. No. 16. Cornell Lab of Ornithology, Ithaca, NY

Camfield, A. F. 2003. Quality of food source affects female visitation and display rates of male broad-tailed hummingbirds. Condor 105:603-606.

Carpenter, F. L. 1987. Food abundance and territoriality: to defend or not to defend? American Zoologist 27:387-399.

Carpenter, F. L., D. C. Paton, and M. A. Hixon. 1983. Weight gain and adjustment of feeding territory size in migrant hummingbirds. Proceedings of the National Academy of Sciences of the USA 80:7259-7263.

Carpenter, F. L., M. A. Hixon, E. J. Temeles, R. W. Russell, and D. C. Paton. 1993. Exploitative compensation by subordinate age-sex classes of migrant rufous hummingbirds. Behavioral Ecology and Sociobiology 33:305-312.

Case, T. J. and M. E. Gilpin. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences USA 71:3073-3077.

Chai, P., and R. Dudley. 1999. Maximum flight performance of hummingbirds: capacities, constraints and trade-offs. American Naturalist 153:398-411.

Dubois, F., L-A. Giraldeau, I. M. Hamilton, J. W. A. Grant, and L. Lefebvre. 2004. Distraction sneakers decrease the expected level of aggression within groups: a game-theoretic model. American Naturalist 164:E32-E45.

Ewald, P. W. 1985. Influence of asymmetries of resource quality and age on aggression and dominance in black-chinned hummingbirds. Animal Behaviour 33:705-719.

Ewald, P. W., and F. L. Carpenter. 1978. Territorial responses to energy manipulations in the Anna hummingbird. Oecologia 31:277-292.

Ewald, P. W., and R. J. Bransfield. 1987. Territory quality and territorial behavior in two sympatric species of hummingbirds. Behavioral Ecology and Sociobiology 20:285-293.

Feinsinger, P. 1976. Organization of a tropical guild of nectarivorous birds. Ecological Monographs 46:257-291.

Feinsinger, P., R. K. Colwell, J. Terborgh, and S. B. Chaplin. 1979. Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. American Naturalist 113:481-497.

Feinsinger, P., Swarm, L.A. & Wolfe, J.A. (1985) Nectar-feeding birds on Trinidad and Tobago: comparison of diverse and depauperate guilds. *Ecological Monographs*, **55**, 1-28.

Gass, C. L., G. Angehr, and J. Centa. 1976. Regulation of food supply by feeding territoriality in the rufous hummingbird. Canadian Journal of Zoology 54:2046-2054.

Gill, F. B., A. L. Mack, and R. T. Ray. Competition between hermit hummingbirds *Phaethorninae* and insects for nectar in a Costa Rican rain forest. Ibis 124:44-49.

Hixon, M. A., F. L. Carpenter, and D. C. Paton. 1983. Territory area, flower density, and time budgeting in hummingbirds: an experimental and theoretical analysis. American Naturalist 122:366-391.

Hutchinson, G. E. and R. H. MacArthur. 1959. Appendix on the theoretical significance of aggressive neglect in interspecific competition. American Naturalist 93:133-134.

Inouye, D. W., W. A. Calder, and N. M. Waser. 1991. The effect of floral abundance on feeder censuses of hummingbird populations. Condor 93:279-285.

Kodric-Brown, A., and J. H. Brown. 1978. Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. Ecology 59:285-296.

Loehle, C. 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. Journal of Biogeography 25: 735-742.

Maurer, B. A. 1984. Interference and exploitation in bird communities. Wilson Bulletin 96:380-395.

Mazerolle M. J. 2010. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package versions 1.11. http://cran.r-project.org/package=AICcmodavg

McCaffrey, R. E., and S. M. Wethington. 2008. How the presence of feeders affects the use of local floral resources by hummingbirds: a case study from southern Arizona. Condor 110:786-791.

Normand, S., U. A. Treier, C. Randin, P. Vittoz, A. Guisan, and J-C. Svenning. 2009. Importance of abiotic stress as a range determinant for European plants: insights from species responses to climatic gradients. Global Ecology and Biogeography 18:437-449.

Norton, M. E., P. Arcese, and P. W. Ewald. 1982. Effect of intrusion pressure on territory size in Black-chinned Hummingbirds (*Archilochus alexandri*). Auk 99:761-764.

Pimm, S. L., M. L. Rosenzweig, and W. Mitchell. 1985. Competition and food selection: field tests of a theory. Ecology 66:798-807.

Pitelka, F. A. 1951. Ecologic overlap and interspecific strife in breeding populations of Anna and Allen hummingbirds. Ecology 32:641-661.

Powers, D. R., and T. McKee, 1994. The effect of food availability on time and energy expenditures of territorial and non-territorial hummingbirds. Condor 96:1064-1075.

Powers, D. R., J. A. Van Hook, E. A. Sandlin, and T. J. McWhorter. 2010. Arthropod foraging by a southeastern Arizona hummingbird guild. Wilson Journal of Ornithology 122:494-502.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Ridgely, R. S., T. F. Allnutt, T. Brooks, D. K. McNicol, D. W. Mehlman, B. E. Young, and J. R. Zook. 2005. Digital Distribution Maps of the Birds of the Western Hemisphere, version 2.1. NatureServe, Arlington, VA.

Sandlin, E. A. 2000. Foraging information affects the nature of competitive interactions. Oikos 91:18-28.

Stiles, F. G. 1982. Aggressive and courtship displays of the male Anna's hummingbird. Condor 84:208-225.

Stiles, F. G. 1995. Behavioral, ecological, and morphological correlates of foraging for arthropods by the hummingbirds of a tropical forest. Condor 97:853-878.

Stiles, F. G., D. L. Altshuler, and R. Dudley. 2005. Wing morphology and flight behavior of some North American hummingbird species. Auk 122:872-886.

Tiebout, H. M. 1992. Comparative energetics of divergent foraging modes: a doubly labeled water experiment on hummingbird competition. Animal Behaviour 44:895-906.

Vance, R. R. 1984. Interference competition and the coexistence of two competitors on a single limiting resource. Ecology 65:1349-1357.

Wilson, E. O. 1975. Sociobiology: the new synthesis. Harvard University Press, Cambridge, Mass.

4.8. Appendix 1. Model selection results

Table A4.1. Model selection results relating the probability of foraging to three interacting environmental gradients. Parameter estimates have been converted from LogOdds to probabilities with the direction of change also indicated. Since elevation and nectar production were standardized by their mean and standard deviation, the indicated change in probability is for a one standard deviation increase in elevation (~140m) and nectar production (~33kJ). The final column indicates how much of the site-level random variation could be accounted for by elevation and nectar production.

	Variance partitioning		Fixed effects in best model			Model weight	Var. Exp. Par. (%)
	Scale	Variance (%)	Parameter	Estimate	95% Confidence Interval		
♀ black-chinned humming bird	Location	0.00	Intercept	0.057	0.010	1.00	23.04
	Site	100	Elevation	-0.378	0.385		
			Feeder spacing (6m)	0.505	0.990		
			Feeder spacing (12m)	0.705	0.032		
			Nectar production	-0.350	0.287		
			Elevation*Feeder spacing (6m)	-0.463	0.121		
			Elevation*Feeder spacing (12m)	0.591	0.0627		
			Nectar production*Feeder spacing (6m)	0.537	0.140		
			Nectar production*Feeder spacing (12m)	0.611	0.0532		
♂ black-chinned	Location	0.00	Intercept	0.00653	0.00122	0.97	53.75
	Site	100	Elevation	-0.202	0.150		

humming bird			Feeder spacing (6m)	0.582	0.172		
			Feeder spacing (12m)	0.591	0.157		
			Nectar production	-0.348	0.565		
			Elevation*Feeder spacing (6m)	0.531	0.425		
			Elevation*Feeder spacing (12m)	0.522	0.578		
			Nectar production*Feeder spacing (6m)	-0.418	0.125		
			Nectar production*Feeder spacing (12m)	-0.313	0.0390		
♂ broad-tailed humming bird	Location	49.99	Intercept	0.0000275	0.0000152	1.00	48.50
	Site	50.01	Elevation	0.689	1.81		
			Feeder spacing (6m)	-0.307	0.0667		
			Feeder spacing (12m)	0.552	0.311		
			Nectar production	0.880	1.03		
			Elevation*Feeder spacing (6m)	0.700	0.194		
			Elevation*Feeder spacing (12m)	-0.408	0.149		
			Nectar production*Feeder spacing (6m)	0.539	0.744		
			Nectar production*Feeder spacing (12m)	0.629	0.186		

Table A4.2. Model selection results relating the probability of being chased to three interacting environmental gradients. Parameter estimates have been converted from LogOdds to probabilities with the direction of change also indicated. Since elevation and nectar production were standardized by their mean and standard deviation, the indicated change in probability is for a one standard deviation increase in elevation (~140m) and nectar production (~33kJ). The final column indicates how much of the site-level random variation could be accounted for by elevation and nectar production.

	Variance partitioning		Fixed effects in best model			Model weight	Var. Exp. Par. (%)
	Scale	Variance (%)	Parameter	Estimate	95% Confidence Interval		
♁ black-chinned humming bird	Location	87.8	Intercept	0.143	0.130	1.00	11.46
	Site	12.2	Elevation	-0.312	0.201		
			Feeder spacing (6m)	-0.354	0.243		
			Feeder spacing (12m)	-0.387	0.280		
			Nectar production	0.655	0.521		
			Elevation*Feeder spacing (6m)	0.709	0.297		
			Elevation*Feeder spacing (12m)	0.664	0.383		
			Nectar production*Feeder spacing (6m)	-0.168	0.0432		
			Nectar production*Feeder spacing (12m)	-0.359	0.255		
♂ black-chinned humming bird	Location	52.95	Intercept	0.158	0.0930	0.78	12.55
	Site	47.05	Elevation	0.613	1.33		
			Feeder spacing (6m)	-0.478	4.58		
			Feeder spacing (12m)	-0.413	1.13		
			Nectar production	-0.277	0.237		
			Elevation*Feeder spacing (6m)	-0.465	3.45		
			Elevation*Feeder spacing (12m)	-0.273	0.295		
			Nectar production*Feeder spacing (6m)	0.659	0.861		
			Nectar production*Feeder spacing (12m)	0.659	0.901		
♁ broad-tailed humming bird	Location	21.12	Intercept	0.332	0.669	0.22	2.10
	Site	78.88	Elevation	0.582	3.52		
			Feeder spacing (6m)	-0.488	3736.79		
			Feeder spacing (12m)	-0.490	18.0		
			Nectar production	-0.413	3.01		

	Elevation*Feeder spacing (6m)	-0.246	22.3
	Elevation*Feeder spacing (12m)	-0.336	1.19
	Nectar production*Feeder spacing (6m)	-0.00240	0.754
	Nectar production*Feeder spacing (12m)	0.540	10.6

Table A4.3. Model selection results relating the probability of simultaneous foraging to three interacting environmental gradients. Parameter estimates have been converted from LogOdds to probabilities with the direction of change also indicated. Since elevation and nectar production were standardized by their mean and standard deviation, the indicated change in probability is for a one standard deviation increase in elevation (~140m) and nectar production (~33kJ). The final column indicates how much of the site-level random variation could be accounted for by elevation and nectar production. ♀ - ♀ indicates two female black-chinned hummingbirds simultaneously foraging. ♀ - ♂ indicates a female and male black-chinned hummingbird simultaneously foraging.

	Variance partitioning		Fixed effects in best model			Model weight	Var. Exp. Par. (%)
	Scale	Variance (%)	Parameter	Estimate	95% Confidence Interval		
♀ – ♀	Location	0.00	Intercept	0.0279	0.00540	0.42	18.18
	Site	100	Elevation	0.507	10.6		
			Feeder spacing (6m)	-0.470	3.22		
			Feeder spacing (12m)	0.715	0.518		
			Nectar production	-0.380	0.532		

			Elevation*Feeder spacing (6m)	0.606	0.939		
			Elevation*Feeder spacing (12m)	0.629	0.722		
			Nectar production*Feeder spacing (6m)	0.555	1.93		
			Nectar production*Feeder spacing (12m)	0.577	1.13		
♀ – ♂	Location	0.00	Intercept	0.0293	0.0128	0.49	57.32
	Site	100	Elevation	-0.304	0.509		
			Feeder spacing (6m)	0.507	28.5		
			Feeder spacing (12m)	0.832	0.826		
			Nectar production	-0.325	0.384		
			Elevation*Feeder spacing (6m)	-0.450	3.221		
			Elevation*Feeder spacing (12m)	0.698	1.16		
			Nectar production*Feeder spacing (6m)	0.589	1.80		
			Nectar production*Feeder spacing (12m)	0.555	2.77		

4.9. Appendix 2. Large scale geographic variation

Table A4.4. The difference in the overall average probability of foraging or being chased and the average probability at each study location. Only those cases where a large portion of the variation in the data occurred at the location level.

Location	Start date	Prob. chased - ♀ black-chinned	Prob. chased - ♂ black-chinned	Prob. foraging - ♀ broad-tailed
San Juan National Forest – West	05/19/2009	0.678	-0.554	0.919
Uncompahgre National Forest – South	06/05/2009	-0.920	-0.672	0.996
Uncompahgre National Forest – North	06/20/2009	0.724	0.636	-0.861
San Juan National Forest – East	07/08/2009	0.737	0.630	0.673

4.10. Linking statement between Chapters 4 and 5

All previous chapters tested hypotheses connecting spatial variation in the environment to spatial variation in abundance. In the following chapter I use the environment-abundance relationship to predict the response of birds to climate change. Moreover, I explore the practical ramifications of using abundance data: how one can build and use environment-abundance models when abundance data collected at large spatial scales contains noise due to biases and data deficiencies in survey methodologies.

CHAPTER 5:

Distribution models help in combining data from divergent sources: a case study on birds in Québec under climate change

5.1. Abstract

Aim: Species distribution models are currently the most common way of predicting species responses to climate change. These models are almost always based on species' occurrence data even though models of abundance can better predict extinction risk. However, the greater ecological information delivered by abundance data brings with it more noise due to biases and data deficiencies in particular survey methodologies. We tested the hypothesis that species distribution models, when applied to abundance data, can reduce noise allowing different data sources to be combined.

Location: Eastern United States and Canada with an emphasis on Québec, Canada

Methods: We predicted current and future bird abundances using two datasets: the continent-wide North American Breeding Bird Survey and a checklist dataset for Québec, Canada. We used an ensemble forecasting technique to predict abundances from each dataset separately across a study grid of 20 km x 20 km resolution.

Results: The raw abundances from each dataset were not correlated across space suggesting that the data was excessively noisy. We found that predicted abundances from the two different data sources were significantly better correlated than raw abundances. Variation in latitude among species' ranges explained variation in correlation coefficients for raw abundances but not for predicted abundances.

Main conclusions: The species distribution models were able to capture consistent bird-climate relationships from uncorrelated and noisy data sources. A species' geographical position was not related to model performance. However,

geographical position reflected Breeding Bird Survey coverage and influenced the degree of divergence among the two data sources. This study is the first to confront the problem of how to model abundance data from multiple sources and is the first to show that distribution models are robust to noise in abundance data caused by sampling methodology.

5.2. Introduction

The recognition that anthropogenically driven climate change is an ongoing phenomenon with wide-ranging social and environmental consequences has dominated discussion in scientific and non-scientific communities across the world. One of the major outcomes of this discussion is an awareness that society needs to anticipate changes in our social and ecological systems so that individuals and institutions can prepare and adapt to future climates. Biologists have responded to this need mainly by predicting where species are going to occur in the future, thereby indicating which species may be most threatened with extinction or local extirpation (e.g. Thomas *et al.* 2004, Araújo *et al.* 2006), which regions may see above-average declines in biodiversity (e.g. Pompe *et al.* 2008, Lawler *et al.* 2009), and whether existing reserve networks are sufficient for protecting future biodiversity projections (e.g. Coetzee *et al.* 2009, Hole *et al.* 2009).

The most common approach used to predict species responses to climate change has been to build Species Distribution Models (SDMs). Also known as climate envelope or ecological niche models, SDMs statistically relate species' locations to the climate at those locations. The estimated parameters from these models allow predictions to be made under novel climate scenarios (see Elith & Leathwick 2009 for a review). Despite some shortcomings with this approach (Davis *et al.* 1998, Berteaux *et al.* 2006, Bahn & McGill 2007), SDMs are often the best tool when lacking detailed data on how a species responds mechanistically to environmental variation (Pearson & Dawson 2003) and sometimes perform as well as more mechanistic models (Kearney *et al.* 2010). In addition, important factors such as land-use change, dispersal capacity, and biotic interactions are now being included in SDMs (Preston *et al.* 2008, Engler *et al.* 2009, Nobis *et al.* 2009).

As the name implies, SDMs mainly consider species distributions, i.e. where a species is and is not located. Mostly this is an artifact of available data, which consists of georeferenced species occurrences and sometimes absences. However, presence-absence distributions fail to account for much of the ecological story when it comes to describing species ranges and how they might respond to climate change (Hengeveld 1990, Mehlman 1997). How much and where abundance changes with climate change is a more direct and proximate measure of extinction risk than changes in distribution (O'Grady *et al.* 2004, Shoo *et al.* 2005) and better indicates the capacity for range expansion (Iverson *et al.* 2004). Studies of past climate change have shown that climate predicts overall abundance (Shoo *et al.* 2005, Forcey *et al.* 2007, Albright *et al.* 2010, 2011) and where in a species range abundance changes (Mehlman 1997).

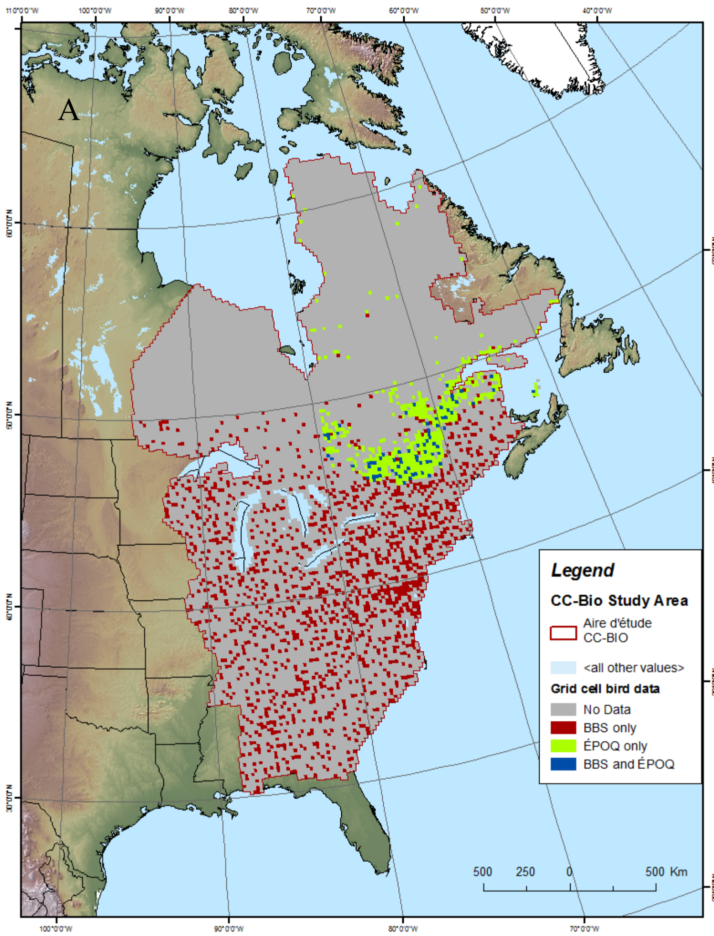
One of the challenges in using abundance data is that it is inherently noisy. Every abundance survey comes with its own data deficiencies such as being biased toward roads (Hanowski and Niemi 1995), using observers of varying skill levels (Sauer *et al.* 1994), or imperfectly detecting some species (Norvell *et al.* 2003). Such deficiencies can obscure the true relationship between abundance and climate (Royle *et al.* 2007). SDMs have been shown to be robust to data deficiencies common in presence-absence models, such as the lack of species absence records (Elith *et al.* 2006), low sample size (Wisz *et al.* 2008), or being geographically restricted (Peterson *et al.* 2007, Giovanelli *et al.* 2010). In this study our goal is to test whether SDMs are also robust to the data deficiencies typically arising in abundance data.

One way to minimize deficiencies in species abundance data is to combine data from different sources. If survey methodologies differ then the problems in one dataset may be compensated for by the other. If SDMs are robust to noise then even if the raw data from multiple datasets do not match, the predicted abundances will be similar (Kadmon *et al.* 2004). The combined output may be more accurate than when predicting from one dataset alone. In this study we test whether SDMs minimize noise by modeling current and future abundances of breeding birds in Québec, Canada using two independent datasets. We first test for the potential for survey deficiencies by correlating *raw* abundances from each dataset. Weak correlations indicate that each dataset captures different information on species abundances despite sampling the same location. Second, we test whether SDMs reduce noise by correlating the *predicted* abundances from each dataset. An improvement in the correlation coefficients over the raw data indicates that SDMs extract the same abundance-climate relationship despite the initial data deficiencies. Third, we test whether the latitude where species are most abundant explains variation in how well both datasets are correlated. If so, geographical bias of the two surveys may be a key data deficiency that is resolved by SDMs. Fourth, we combine datasets and predict shifts in peak abundance and compare this to the shifts predicted when each dataset is modeled separately.

5.3. Methods

5.3.1. Study area

The geographical extent of our study is a 12252 cell study grid covering Québec, Ontario, and all states east of the 100th meridian excluding Florida (Fig. 5.1). Québec itself comprises 4108 grid cells. Each grid cell is 20 km x 20 km. This study is part of a larger project detailing the effects of past and future climate change on biodiversity in Québec, Canada (CC-Bio: http://cc-bio.uqar.ca/; [Berteaux *et al.* 2010]).


A
Legend
CC-Bio Study Area
Aire d'étude CC-BIO
<all other values>
Grid cell bird data
No Data
BBS only
ÉPOQ only
BBS and ÉPOQ
500 250 0 500 Km

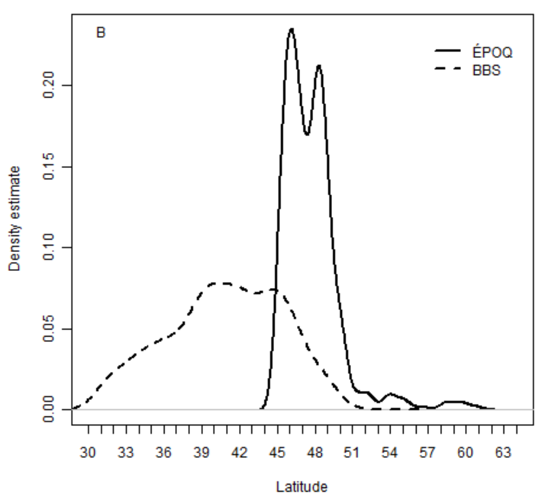

B
ÉPOQ
BBS
Density estimate
0.00
0.05
0.10
0.15
0.20
30 33 36 39 42 45 48 51 54 57 60 63
Latitude

Fig. 5.1. The CC-Bio study grid showing the grid cells with only BBS routes, only ÉPOQ checklists, and data from both surveys (a). Kernel density estimates show the distribution of BBS routes and ÉPOQ checklists with respect to latitude (b).

5.3.2. Bird data

The North American Breeding Bird Survey (BBS) consists of more than 3500 40 km roadside routes in the continental United States, southern Canada, and northern Mexico. Observers record all birds seen and heard for 3 min. on each of the 50 stops along a route; abundance of each species is summed across all stops. Each route is run once per year in late May or early June with the date and observer as consistent as possible among years. The BBS has been used extensively in the ecological literature for measuring and understanding changes in bird abundances (e.g. Curnutt *et al.* 1996, Mehlman 1997, Bahn *et al.* 2006).

We reduced each linear BBS route to its centroid and joined it to the study grid using ArcGIS 9.3.1 (ESRI 1999-2009). For grid cells containing BBS routes, we calculated the abundance of each species by averaging across each route and each survey year, for the years 1971 – 2000 (to match our climate data). We did not measure abundance in grid cells for which there was less than five years of survey data. In total there are 1969 BBS routes in 1655 grid cells (i.e. there are some grid cells with more than one BBS route). In Québec there are 85 BBS routes each corresponding to a unique grid cell. We excluded species with sparse coverage (< 2% of the study grid, 35 grid cells). After doing so we had a dataset consisting of 155 species.

L'Étude des populations d'oiseaux du Québec (ÉPOQ) is a checklist database of bird sightings limited to the Province of Québec, Canada. Initiated in 1966, ÉPOQ collects data submitted by recreational birders. Unlike BBS, ÉPOQ is non-systematic with the checklists varying by length of observation period, time of observation period, and method of observation. We minimized some of the differences between BBS and ÉPOQ by only including checklists with an observation period greater than 60 min. and checklists conducted between May 15 and July 31, roughly corresponding to the breeding season in Québec. We similarly matched ÉPOQ checklists to the study grid and eliminated cells with low sample size (< 5 checklists) and species with sparse coverage (< 2% of the Québec grid, 10 grid cells). This left 516 cells with bird data, corresponding to 126 species.

5.3.3. Climate data

Current climate data is an average of measurements for the years 1961 – 1990. Data was downloaded from the US Forest Service, Rocky Mountain Research Station website (http://forest.moscowfsl.wsu.edu/climate). In this dataset, temperature and precipitation surfaces were interpolated from weather station data using Anusplin thin-plate spline (Rehfeldt 2006). The resolution of the downloaded data was 0.0083 decimal degrees (~1 km), which was subsequently averaged for each 20 km x 20 km grid cell in the study area.

Future climate scenarios were created for 2041 – 2070 (hereafter 2050) and 2071 – 2100 (hereafter 2080). We used climate predictions from the Canadian Regional Climate Model (CRCM version 4.2.0) run ADJ (Music and Caya 2007).

Monthly predictions were made using the “delta” or “change field” method (IPCC 2001). All climate data consisted of monthly average, maximum, and minimum temperatures and monthly total precipitation. From these we derived the climate variables we used in our modeling routines (Table 5.1).

Table 5.1. Climate variables used in distribution models.

Climate variable	Explanation
Average annual temperature	Calculated from monthly averages
Total annual precipitation	-
Temperature seasonality	Coefficient of variation of monthly mean temperatures
Precipitation seasonality	Coefficient of variation of monthly total precipitation
Temperature range	Average range between warmest monthly maximum temperature and coldest monthly minimum temperature
Annual potential evapotranspiration (PET)	Calculated according to Thornwaite (1948)
PET seasonality	Coefficient of variation of monthly PET
Growing season growing degree days	Days with average temperature > 5°C and for dates between the last freeze in the spring and the first freeze in the fall (Rehfeldt, 2006)

5.3.4. Species distribution modeling

In order to relate climate variables to bird abundances, we used the S'AMP package (Casajus, personal communication) in R, version 2.10.1 (R core development team, 2009). S'AMP takes its inspiration from BIOMOD (Thuiller *et al.* 2009) but explicitly models abundance instead of presence-absence. Like BIOMOD, S'AMP is an ensemble forecasting package that averages predictions made using several statistical techniques (boosted regression trees, generalized additive models, generalized linear models, multivariate adaptive regression splines, random forests, regression tree analysis). Model performance was assessed by splitting the data, into training (70% of the initial dataset) and test (30% of the initial dataset) datasets and then calculating the correlation of determination (R^2) of the predictions from the former and observed in the latter. We only used species with $R^2 > 0.30$. Predicted abundance in each grid cell was calculated as a weighted average of the predictions from each individual model (Araújo *et al.* 2005, Marmion *et al.* 2009). Prior to all analyses, we square root transformed the abundance data (Bahn & McGill 2007). We predicted abundances for the entire study grid and also we predicted abundances only for Québec. For the latter we only used the BBS routes in Québec to make predictions. We used the same ÉPOQ data for both grids.

5.3.5. Bird dataset comparison

We tested whether each dataset captured the same information on bird abundances by correlating abundances in the grid cells containing both BBS and ÉPOQ data (objective 1). We then tested whether the modeling procedure resolved any differences in the input data by modeling each dataset separately and then correlating the predictions for each of the time periods (current, 2050, 2080) (objective 2).

One of the major differences among the datasets concerns their position on the continent (Fig. 5.1). Species with a southern distribution may be poorly captured by ÉPOQ and species with a northern distribution may be poorly captured by BBS. We hypothesize that such a bias accounts for interspecific differences in the correlation between ÉPOQ and BBS data. We tested this hypothesis by first finding the latitude where each species has its highest BBS abundance. Then we regressed latitude onto the correlation coefficient (objective 3). We used a quadratic latitude term because we expected mid-latitude species to be best captured by both datasets. We compared quadratic, power, linear, and intercept-only models by ranking them by their AIC value and selected the model with the lowest AIC.

5.3.6. Measuring abundance shifts

We were interested in the degree to which combining datasets lead to different predictions in abundance than when predictions were made from each dataset separately (objective 4). Specifically, we compared the distance and direction by which the grid cell with the highest abundance shifted between the current climate and the 2050 climate. Initially, we located the grid cell with the highest abundance as predicted by BBS and ÉPOQ separately for the two time periods. (If we found more than one grid cell, we chose the most northern one.) For each species, we expressed abundance as a proportion of the species' maximum abundance. We then combined the two datasets by averaging the abundances from each dataset and located the grid cell with the highest averaged abundance in both time periods. We only compared species that had their predicted abundances correlated with $r > 0.70$. We also only made the comparison for the full study grid.

We quantitatively compared the Euclidean distance by which abundance shifted among the individual and combined datasets with a generalized linear mixed model. We used dataset as a categorical predictor and species as a random effect. We considered the distance of the abundance shift to be significantly different among datasets when the predictions from each dataset had non overlapping 95% confidence intervals.

5.4. Results

BBS routes and ÉPOQ checklists overlapped for 29 species across 59 grid cells. This input data was poorly correlated meaning a species abundant in a particular cell as indicated by the BBS was not necessarily abundant according to the ÉPOQ and vice versa (Table 5.2). The maximum correlation coefficient was only 0.575 (Red-winged Blackbird [*Agelaius phoeniceus*]) and for six species the correlation coefficient was negative (Fig. 5.2).

After building models on each dataset separately, the predicted abundances were generally better correlated (Table 5.2). For the entire study grid, ten species had a correlation coefficient > 0.70 (fig. 5.2A). On average, the correlation between the two datasets was significantly higher for the predictions than for the input data (Table 5.2).

Table 5.2. Results of correlating abundances from BBS and ÉPOQ datasets for 29 species. Correlations were based on observed and predicted abundances at two different geographical extents and during three periods under current and future climate. The difference between correlations coefficients based on observed and predicted abundances was tested with a paired t-test. We also fit regressions to the correlation coefficients with latitude and polynomial derivatives as explanatory variables and identified the best model by the lowest AIC.

Grid	Time period	Correlation coefficient (mean ± sd)	Compare to input (paired t-test d.f. = 28)	Relationship with latitude Model (AIC)	R2 of best fitting model
	Input	0.244 ± 0.284	-	Latitude^2 (-97.54)	0.642
				Latitude (-97.43)	
				Latitude + Latitude^2 (-96.22)	
				Intercept-only (-70.76)	
Full	Current	0.536 ± 0.303	T = -4.621	Latitude (-65.72)	0.095
			p < 0.001	Latitude^2 (-65.70)	
				Intercept-only (-64.93)	
				Latitude + Latitude^2 (-64.10)	
	2050	0.498 ± 0.353	T = -3.160	Intercept-only (-56.51)	-
			p = 0.004	Latitude (-54.52)	
				Latitude^2 (-54.52)	

				Latitude + Latitude^2 (-52.66)	
	2080	0.537 ± 0.331	T = -3.646	Intercept-only (-59.96)	-
			p = 0.001	Latitude (-58.00)	
				Latitude^2 (-58.00)	
				Latitude + Latitude^2 (-56.10)	
Québec	Current	0.184 ± 0.456	T = 0.660	Intercept-only (-42.59)	-
			p = 0.514	Latitude (-41.43)	
				Latitude^2 (-41.42)	
				Latitude + Latitude^2 (-39.61)	
	2050	0.429 ± 0.372	T = -2.310	Intercept-only (-53.66)	-
			p = 0.029	Latitude^2 (-52.73)	
				Latitude (-52.72)	
				Latitude + Latitude^2 (-50.88)	
	2080	0.657 ± 0.275	T = -6.854	Latitude^2 (-71.11)	0.080
			p < 0.001	Latitude (-71.09)	
				Intercept-only (-70.78)	
				Latitude + Latitude^2 (-69.36)	

For the Québec grid, the predictions for five species had correlations > 0.70 (fig. 5.2B). However overall the correlations remained weak and not significantly different from the input data (Table 5.2). Interestingly, the predictions were better correlated when predicted onto future climates and improved the farther in time the predictions were made (Table 5.2).

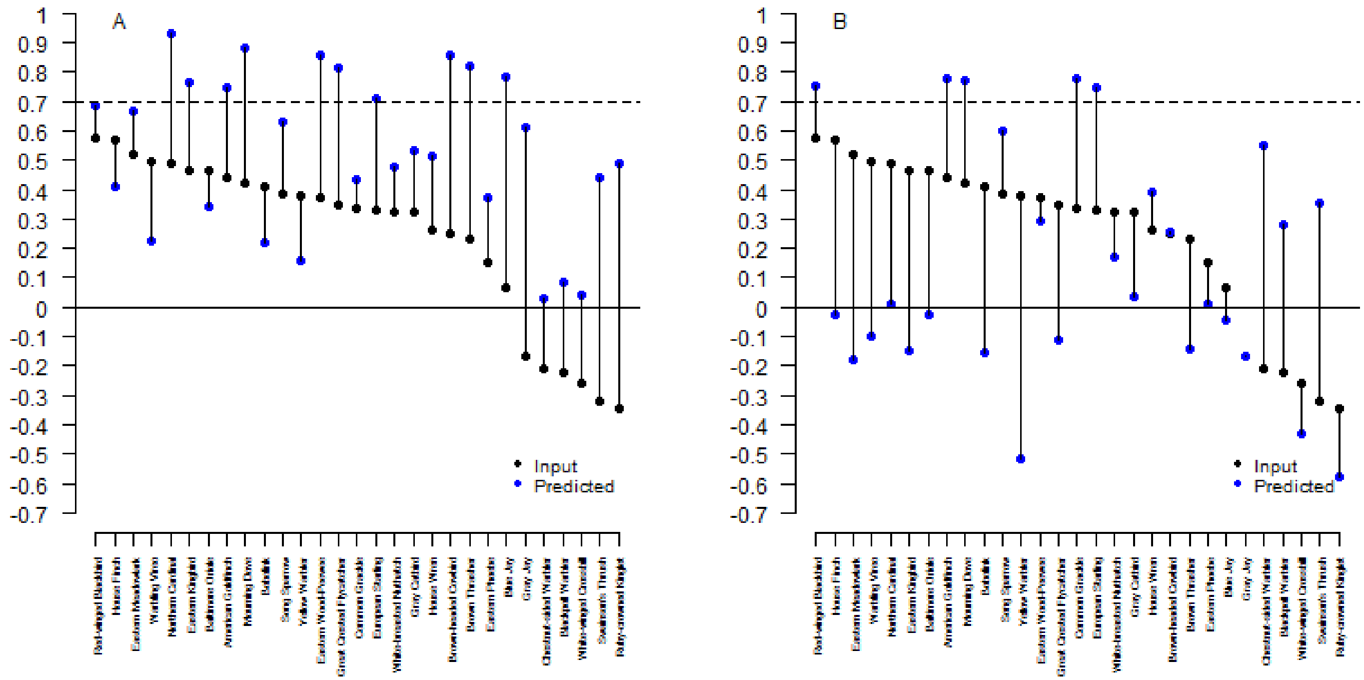


Fig 5.2. The correlation coefficients between BBS route and ÉPOQ checklist data for 29 species across the 85 grid cells containing data of both types and for the predicted abundances stemming from separate distribution models of each dataset. BBS data were taken from and predicted for the 12252 cell study grid (a) and taken from and predicted for the 4108 grid cells that comprise Québec (b).

Our hypothesis that the datasets were better correlated for those species that were most abundant at mid-latitudes was only partially supported. While we did find a relationship between latitude and correlation coefficient for the input data, the best fitting model was a power-law as opposed to quadratic or linear (Table 5.2). We found that it was the species that were more abundant at more southern latitudes that were best correlated (Fig. 5.3). The distribution was split into two groups, with species distributed < 46.5°N weakly positively correlated and species distributed > 47.5°N all negatively correlated. This latitude corresponds to where BBS route coverage declines (Fig. 5.1B). For predicted abundances, the strength of correlation was either weakly linearly or not related to latitude (Table 5.2).

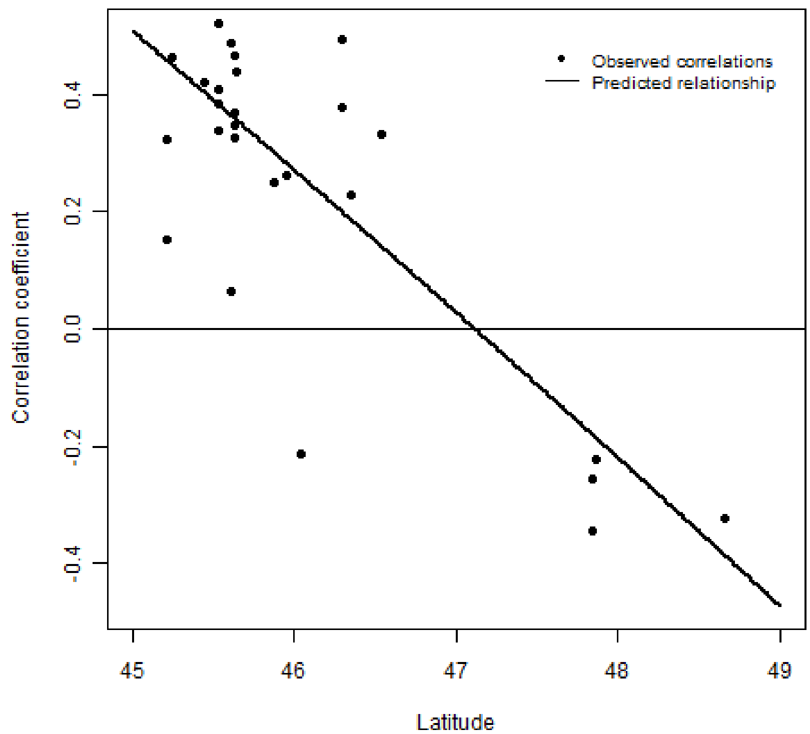


Fig. 5.3. The predicted relationship between the latitude at which a species has its highest abundance and the correlation coefficient among BBS and ÉPOQ data. Note: one species (Gray Jay [*Perisoreus Canadensis*]) was eliminated as an outlier.

The distance and direction by which predicted abundances shifted between the current time period and 2050 varied across species and datasets (Table A5.1). For some species, the grid cell with the highest abundance shifted in a southerly direction and for others it did not shift at all. On average, BBS predicted the largest shifts and ÉPOQ the smallest (predicted shifts [mean ± 95% confidence interval], BBS: 748.9 ± 323.2 km, ÉPOQ: 424.1 ± 540.2 km, Combined: 547.6 ± 1125.4 km). Since the confidence intervals overlap, the distances were not significantly different among the three datasets. This is in part due to high among species variability in terms of which dataset predicted the greatest shifts (residual variance: 205222, variance among species: 45513 ≈22% of total variance).

5.5. Discussion

Despite their limitations, species distribution models remain the most frequently used tool to predict species responses to climate change. Recent work has been directed at improving model performance and reducing prediction uncertainty (e.g. Araújo *et al.* 2005, Peterson *et al.* 2008). However, no matter how well a model performs, it is only as good as the data it is fed. Studies that have tested how variation in the quality of species data affects model performance use one dataset and subsample from within it (Araújo *et al.* 2005, Dormann *et al.* 2008, Giovanelli *et al.* 2010, Grenouillet *et al.* 2010). One study used two different survey methods to estimate population trends yet made no mention of how comparable the data was nor how it was combined (Juillard *et al.* 2003). Ours is the first study to compare two completely different species datasets that differ in methodology but overlap in coverage.

Variations in how species data are collected are especially problematic when modeling abundances; the subtle distinction between an area of a few or many individuals will affect accurately quantifying the abundance-environment relationship. One of the ways in which to minimize the effect of data deficiencies is to combine data from multiple sources hoping that deficiencies in one survey average out with the deficiencies in another. We found, however, that this may not be necessary, at least for some species. Despite having uncorrelated raw survey data, predicted abundances were well correlated. Moreover, combining datasets made similar predictions in the shift of abundance hotspots compared to not combining the data. Essentially, the species distribution models extracted the same abundance-climate relationship for each dataset. This suggests that the lack of correlation between the datasets was caused by noise rather than severe, systematic biases in the datasets with respect to a broad range of climatic conditions (Kadmon *et al.* 2003). Our result is consistent with Kadmon *et al.* (2004) who showed that roadside bias in plant survey data did not lead to inaccurate predictions of species distributions.

The input data was especially poorly correlated for species that had their highest abundances at higher latitudes. These are species for which the majority of the BBS routes occur away from that part of its range where it is most abundant. Since abundance is inversely related to spatial and temporal variability (Taylor 1961, Curnutt *et al.* 1996), surveys sampling less abundant populations are sampling more variable populations. Given that each grid cell is 20 km x 20 km and contains abundances averaged over 40 years, population variability may enhance any finer-scale spatial and temporal differences in where and when the two surveys obtain their samples. For example, if the BBS samples two consecutive years but one of these years the species is abundant and the other it is rare and the ÉPOQ misses the first of these years, then the average abundance of the two will be different. The importance of BBS sample size was further demonstrated in that when only using BBS routes in Québec, the correlations of the predictions remained weak.

Regardless of the grid used, latitude did not explain variation in the correlations among predictions. This is surprising given that model performance is generally enhanced when data is sampled from the edge of species ranges (Segurado & Araújo 2004, Luoto *et al.* 2005). Perhaps reduced BBS coverage overwhelms the effect of geographical position (see also Dormann *et al.* 2008). There are also many other factors that may have accounted for variation in correlation coefficients that we did not measure such as range size and the degree of ecological specialization (Seguardo & Araújo 2004, Schwartz *et al.* 2006).

The fact that the predictions were so much better correlated for the entire grid than for Québec suggests that extrapolating ÉPOQ data outside of Québec was less of a problem than reducing BBS sample size by restricting its coverage to Québec. The degree to which models developed in one region can be transferred to another is variable among species but can be weak (Randin *et al.* 2006). However, other than constituting a wider climatic region, the grid outside of Québec does not necessarily constitute a separate region *per se* (*sensu* Randin *et al.* 2006). Hence extrapolating outside of Québec is no different than extrapolating into future climates and any hesitations about the former remain for the latter.

Despite an expected northward shift in species distributions and range limits, we found that the location where abundance is highest did not necessarily shift north and, in some cases, shifted south. This suggests that the movement of abundance within a range may be decoupled from the movement of the range itself. While we can speculate that abundance and distribution arise from different ecological processes (e.g. compare abundance change along geographic gradients [Saether *et al.* 2008] to range limits along geographic gradients [Root 1988]), there is little theory and few empirical examples from which to develop hypotheses of how local abundance might change in future climates.

To support our assertion that the climate change literature is overwhelmingly biased toward models of presence-absence/distribution, we conducted a literature review of studies that explicitly model species' responses to climate change using species distribution models. Using Web of Science and conducting two searches (niche-based model OR species distribution model ecological niche model; climate change AND abundance) we found only seven of a total of 107 papers used abundance or abundance-like data (Iverson & Prasad. 1998, Iverson *et al.* 2004, 2008a, 2008b; Matthews *et al.* 2004, Schwartz *et al.* 2006, Rodenhouse *et al.* 2008). All seven were from the same research group, using the same survey data, and predicting into the same study area. However, these studies did show that for some species total abundance declined even though overall range size did not change (Iverson & Prasad. 1998, Rodenhouse *et al.* 2008). Such an assessment could not have been made with presence-absence data. Hence, models that account for changes in abundance offer a more comprehensive view of the effects of climate change (see also Shoo *et al.* 2005). We hope that the increasing availability of abundance data collected at large spatial and temporal extents encourages climate-envelope modelers to shift their focus toward abundance. We also hope this encourages the development and assessment of tools that can combine information from across multiple datasets in order to make the best predictions possible.

5.6. Acknowledgements

No study of bird abundance would be possible without the effort of the thousands of birders that contribute to survey and checklist datasets and for this we are in gratitude. We thank Sergio Estrada Villegas, John Donoghue II, Julie Messier, and Peter White for comments on an earlier version of the manuscript. The CC-Bio project is administered at Université du Québec à Rimouski and is financially supported by (alphabetical order) Ducks Unlimited Canada, the Government of Canada, the Ministère des Ressources naturelles et de la Faune du Québec, the Ouranos Consortium on Regional Climatology and Adaptation to Climate Change, and the Natural Sciences and Engineering Research Council of Canada (Strategic Project Grant STPGP 350816–07).

5.7. References

Albright, T.P., Pidgeon, A.M., Rittenhouse, C.D., Clayton, M.K., Flather, C.H., Culbert, P.D., Wardlow, B.D. & Radeloff, V.C. (2010) Effects of drought on avian community structure. *Global Change Biology*, **16**, 2158-2170.

Albright, T.P., Pidgeon, A.M., Rittenhouse, C.D., Clayton, M.K., Flather, C.H., Culbert, P.D. & Radeloff, V.C. (2010) Heat waves measured with MODIS land surface temperature data predict changes in avian community structure. *Remote Sensing of Environment*, **115**, 245 – 254.

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

Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, **33**, 1712 – 1728.

Bahn, V. & McGill, B.J. (2007) Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography*, **16**, 733 – 742.

Bahn, V., O'Connor, R.J. & Krohn, W.B. (2006 Importance of spatial autocorrelation in modeling bird distributions at a continental scale. *Ecography*, **29**, 835 – 844.

Berteaux, D., Humphries, M., Krebs, C.J. *et al.* (2006) Constraints to projecting the effects of climate change on mammals. *Climate Research*, **32**, 151 – 158.

Berteaux, D., DeBlois, S., Angers, J. *et al.* (2010) The CC-Bio project: studying the effects of climate change on Quebec biodiversity. *Diversity*, **2**, 1181 – 1204.

Coetzee, B.W.T., Robertson, M.P., Erasmus, B.F.N., van Rensburg, B.J. & Thuiller, W. (2009) Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. *Global Ecology and Biogeography*, **18**, 701 – 710.

Curnutt, J.L., Pimm, S.L. & Maurer, B.A. (1996) Population variability of sparrows in space and time. *Oikos*, **76**, 131 – 144.

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

Dormann, C.F., Purschke, O., García Márquez, J.R., Lautenbach, S. & Schröeder, B. (2008) Components of uncertainty in species distribution analysis: a case study of the Great Grey Shrike. *Ecology*, **89**, 3371 – 3386.

Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129-151.

Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology and Systematics*, **40**, 677 – 697.

Engler, R., Randin, C.F., Vittoz, P., Czáka, T., Beniston, M., Zimmermann, N.E. & Guisan, A. (2009) Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography*, **32**, 34 – 45.

ESRI. (1999-2009) ArcMap 9.3.1. ESRI Inc. Redlands, CA.

Forcey, G.M., Linz, G.M., Thogmartin, W.E. & Bleier, W.J. (2007) Influence of land use and climate on wetland breeding birds in the Prairie Pothole region of Canada. *Canadian Journal of Zoology*, **85**, 421 – 436.

Giovanelli, J.G.R., Ferreira de Siqueira, M., Haddad, C.F.B. & Alexandrino, J. (2010) Modeling a spatially restricted distribution in the Neotropics: how the size of the calibration area affects the performance of five presence-only methods. *Ecological Modelling*, **221**, 215 – 224.

Grenouillet, G., Buisson, L., Casajus, N. & Lek, S. (2010) Ensemble modeling of species distribution: the effects of geographical and environmental ranges. *Ecography*, **33**, 1 – 9.

Hengeveld, R. 1990. Dynamic biogeography. Cambridge University Press, Cambridge, UK.

Hole, D.G., Willis, S.G., Pain, D.J., Fishpool, L.D., Butchart, S.H.M., Collingham, Y.C., Rahbek, C. & Huntley, B. (2009) Projected impacts of climate change on a continent-wide protected area network. *Ecology Letters*, **12**, 420 – 431.

IPCC. (2001) Impacts, adaptation, and vulnerability. *Contribution of working group II to the third assessment of the Intergovernmental Panel on Climate Change* (ed. by J. McCarthy, O.F. Canziani, N.A. Leary, D.J. Dokken, and K.S. White). Cambridge University Press, Cambridge, UK and New York, USA.

Iverson, L.R. & Prasad, A.M. (1998). Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecological Monographs*, **68**, 465 – 485.

Iverson, L.R., Schwartz, M.W. & Prasad, A.M. (2004) Potential colonization of newly available tree-species habitat under climate change: an analysis for five eastern US species. *Landscape Ecology*, **19**, 787 – 799.

Iverson, L.R., Prasad, A.M. & Matthews, S.N. (2008a) Modeling potential climate change impacts on the trees of the northeastern United States. *Mitigation and Adaptation Strategies for Global Change*, **13**, 487 – 516.

Iverson, L.R., Prasad, A.M., Matthews, S.N. & Peters, M. (2008b) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management*, **254**, 390 – 406.

Julliard, R., Jiguet, F. & Couvet, D. (2003) Common birds facing global changes: what makes a species at risk? *Global Change Biology*, **10**, 148-154.

Kadmon, R., Farber, O. & Danin, A. (2003) A systematic analysis of factors affecting the performance of climatic envelope models. *Ecological Applications*, **13**, 853 – 867.

Kadmon, R., Farber, O. & Danin, A. (2004) Effects of roadside bias on the accuracy of predictive maps produced by bioclimatic models. *Ecological Applications*, **14**, 401 – 413.

Kearney, M.R., Wintle, B.A. & Porter, W.P. (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, **3**, 203 – 213.

Lawler, J.J., Shafer, S.L., White, D., Kareiva, P., Maurer, E.P., Blaustein, A.R. & Bartlein, P.J. (2009) Projected climate-induced faunal changes in the Western Hemisphere. *Ecology*, **90**, 588 – 597.

Luoto, M., Pöyry, J., Heikkinen, R.K. & Saarinen, K. (2005) Uncertainty of bioclimate envelope models based on the geographical distribution of species. *Global Ecology and Biogeography*, **14**, 575 – 584.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modeling. *Diversity and Distributions*, **15**, 59 – 69.

Matthews, S.N., O'Connor, R.J., Iverson, L.R. & Prasad, A.M. (2004) Atlas of climate change effects in 150 bird species of the eastern United States. *Gen. Tech. Rep. NE-318.* Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station, 340 p.

Mehlman, D.W. (1997) Change in avian abundance across the geographic range in response to environmental change. *Ecological Applications*, **7**, 614-624.

Music, B. & Caya, D. (2007) Evaluation of the Hydrological cycle over the Mississippi River basin as simulated by the Canadian Regional Climate Model (CRCM). *Journal of Hydrometeorology*, **8**, 969 – 988.

Nobis, M.P., Jaeger, J.A.G. & Zimmermann, N.E. (2009). Neophyte species richness at the landscape scale under urban sprawl and climate warming. *Diversity and Distributions*, **15**, 928 – 939.

Norvell, R.E., Howe, F.P. & Parrish, J.R. (2003) A seven-year comparison of relative-abundance and distance-sampling methods. *Auk*, **120**, 1013-1028.

O'Grady, J.J., Reed, D.H., Brook, B.W. & Frankham, R. (2004). What are the best correlates of predicted extinction risk? *Biological Conservation*, **118**, 513 – 520.

Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361 – 371.

Peterson, A.T., Papes, M. & Eaton, M. (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography*, **30**, 550-560.

Peterson, A.T., Papes, M. & Soberón, J. (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling*, **213**, 63 – 72.

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

Preston, K.L., Rotenberry, J.T., Redak, R.A. & Allen, M.F. (2008) Habitat shifts of endangered species under altered climate conditions: importance of biotic interactions. *Global Change Biology*, **14**, 2501 – 2515.

R Development Core Team. (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, **33**, 1689 – 1703.

Rehfeldt, G.E. (2006) A spline model of climate for the Western United States. *Gen. Tech. Rep. RMRS-165*. For Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, 21 p.

Rodenhouse, N.L., Matthews, S.N., McFarland, K.P., Lambert, J.D., Iverson, L.R., Prasad, A.M., Sillett, T.S. & Holmes, R.T. (2008). Potential effects of climate change on birds of the Northeast. *Mitigation and Adaptation Strategies for Global Change*, **13**, 517 – 540.

Root, T. 1988. Energy constraints on avian distributions and abundances. *Ecology*, **69**, 330-339.

Royle, J.A., Kéry, M., Gautier, R. & Schmid, H. (2007). Hierarchical spatial models of abundance and occurrence from imperfect survey data. *Ecological Monographs*, **77**, 465-481.

Saether, B-E., Lillegard, M., Grotan, V., Drever, M.C., Engen, S., Nudds, T.D. & Podruzny, K.M. (2008) Geographical gradients in the population dynamics of North American prairie ducks. *Journal of Animal Ecology*, **77**, 869-882.

Sauer, J.R., Peterjohn, B.G. & Link, W.A. (1994) Observer differences in the North American Breeding Bird Survey. *Auk*, **111**, 50-62.

Schwartz, M.W., Iverson, L.R., Prasad, A.M., Matthews, S.N. & O'Connor, R.J. (2006) Predicting extinctions as a result of climate change. *Ecology*, **87**, 1611 - 1615.

Segurado, P. & Araújo, M.B. (2004) An evaluation of methods for modeling species distributions. *Journal of Biogeography*, **31**, 1555 – 1568.

Shoo, L.P., Williams, S.E. & Hero, J-M. (2005) Climate warming and the rainforest birds of the Australian Wet Tropics: using abundance data as a sensitive predictor of change in total population size. *Biological Conservation*, **125**, 335 - 343.

Taylor, L.R. 1961. Aggregation, variance and the mean. *Nature*, **189**, 732 – 735.

Thomas, C.D., Cameron, A., Green, R.E. *et al.* 2004. Extinction risk from climate change. *Nature*, **427**, 145 – 148.

Thornwaite, C.W. 1948. An approach towards a rational classification of climate. *Geographical Review*, **38**, 55 – 94.

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009). BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography*, **32**, 369 – 373.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A. & NCEAS Predicting Species Distributions Working Group. (2008) Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, **14**, 763-773.

5.8. Appendix

Table A5.1: Expected shift in distance and direction of the grid cell with the highest predicted abundance between the current time period and 2050. The predictions were made from BBS and ÉPOQ datasets separately. We also combined the datasets by averaging the predictions from each dataset across all grid cells.

Species	Dataset		
	BBS	ÉPOQ	Combined
Red-winged Blackbird	402.04 km	0.00 km	370.83 km
Agelaius phoeniceus	332.62°	NA	335.57°
Northern Cardinal	457.23 km	0.00 km	520.55 km
Cardinalis cardinalis	331.52°	NA	85.39°
House Finch	1657.58 km	0.00 km	1588.30 km
Carpodacus mexicanus	290.15°	NA	286.85°
Swainson’s Thrush	0.00 km	345.55 km	0.00 km

Catharus ustulatus	NA	316.29°	NA
Eastern Wood-peewee	573.55 km	83.91 km	573.55 km
Contopus virens	259.93°	38.61°	259.93°
Blue Jay	507.05 km	430.18 km	548.86 km
Cyanocitta cristata	97.85°	219.86°	104.08°
Chestnut-sided Warbler	1236.06 km	430.18 km	2043.01 km
Dendroica pensylvanica	79.06°	219.86°	187.34°
Yellow Warbler	1576.79 km	717.87 km	2069.93 km
Dendroica petechia	68.82°	88.28°	220.53°
Blackpoll Warbler	0.00 km	0.00 km	0.00 km
Dendroica striata	NA	NA	NA
Bobolink	701.70 km	924.84 km	2121.98 km
Dolichonyx oryzivorus	66.69°	48.76°	211.86°
Gray Catbird	1104.39 km	717.87 km	1104.39 km
Dumetella carolinensis	252.64°	88.28°	252.64°
Baltimore Oriole	1003.97 km	0.00 km	2279.42 km
Icterus galbula	60.35°	NA	233.06°
White-winged Crossbill	0.00 km	2867.99 km	3170.49 km
Loxia leucoptera	NA	93.54°	69.49°
Song Sparrow	61.41 km	611.27 km	1136.99 km
Melospiza melodia	273.83°	350.69°	70.39°
Brown-headed Cowbird	292.39 km	165.43 km	981.68 km

Molothrus ater	313.51°	33.56°	171.37°
Great Crested	634.68 km	717.87 km	33.16 km
Flycatcher	227.39°	88.28°	131.47°
Myriarchus crinitus			
Gray Jay	1588.55 km	96.01 km	43.25 km
Perisoreus Canadensis	102.90°	18.36°	300.15°
Common Grackle	777.37 km	786.56 km	2050.33 km
Quiscalus quiscula	50.61°	243.03°	77.01°
Ruby-crowned Kinglet	0.00 km	0.00 km	1371.35 km
Regulus calendula	NA	NA	151.95°
Eastern Phoebe	1040.31km	430.18 km	839.13 km
Sayornis phoebe	240.04°	219.86°	187.99°
White-breasted	1602.52 km	86.55 km	139.54 km
Nuthatch	304.62°	239.62°	99.80°
Sitta carolinensis			
American Goldfinch	1008.53 km	1983.86 km	1177.60 km
Spinus tristus	284.17°	77.98°	288.43°
Eastern Meadowlark	622.59 km	430.18 km	373.69 km
Sturnella magna	127.91°	219.86°	115.81°
European Starling	1144.22 km	0.00 km	1151.82 km
Sturnus vulgaris	69.36°	NA	68.35°
Brown Thrasher	241.30 km	430.18 km	120.89 km
Toxostoma rufum	204.66°	219.86°	154.21°

House Wren	1157.43 km	733.55 km	864.82 km
Troglodytes aedon	75.99°	273.85°	314.03°
Eastern Kingbird	1723.50 km	430.18 km	267.06 km
Tyrannus tyrannus	204.94°	219.86°	143.93°
Warbling Vireo	1027.85 km	0.00 km	1598.28 km
Vireo gilvus	298.25°	NA	194.71°
Mourning Dove	906.97 km	0.00 km	101.31 km
Zenaida macroura	294.59°	NA	149.03°
Mean ± 95% confidence interval	794.83 ± 207.06 km 196.50 ± 39.11°	462.77 ± 239.43 km 165.92 ± 38.66°	987.66 ± 320.64 km 180.20 ± 31.19°

5.9. Linking statement between Chapters 5 and 6

In the following chapter I discuss how the main results from across the entire thesis contribute to a general theory of abundance at large spatial scales. I discuss the limitations in applying my results to theory, the aspects in need of further study, and alternative and complementary approaches to understanding spatial variation in abundance. The synthesis reasserts that having a theory of abundance at large spatial scales is crucial to broader ecological theory and to conservation.

CHAPTER 6:

General discussion

6.1. Niche-based theory: correlation

Current theory of spatial variation in abundance relates abundance to underlying environmental variation (Brown 1984; Brown et al. 1995). In other words, spatial structure in abundance is generated by spatial structure in the environment. Is such a simple relationship sufficient for a theory of abundance? If so, then theory should focus on explaining spatial structure in the environment, from which abundance patterns will necessarily emerge (Borregaard & Rahbek 2010). I found that spatial variation in the abundance of two species could be explained by spatial variation in one niche factor. In my particular case, the abundances of Black-chinned and Broad-tailed Hummingbirds at a spatial grain of a 40 km roadside transect and a spatial extent of $\approx 4.0 \times 10^5$ km^2 could be explained by underlying variation in nectar production, which corresponds to the energy available to foraging individuals.

The scale at which I conducted the study did not match exactly the scale of the pattern for which a theory should be developed, i.e. grain corresponding to a population and extent corresponding to an entire species range. My spatial grain was likely too coarse and thus averaged variation in abundance and nectar production across multiple populations. It is unclear whether such “scaling-up” would affect observed patterns. As well, my study area missed some of the range edges of both species. If edge populations are generally less abundant than elsewhere in the range (Curnutt et al. 1996; Williams et al. 2003), then I may not have sampled from across the full range of abundances. On the other hand, I captured areas of occupancy transition for both species along elevation gradients.

Abundance declines with respect to gradients within the geographic range may be no different than declines with respect to latitude (*sensu* Bahn et al. 2006).

Despite the scale limitations in our study, the result still supports a niche-based approach to understanding spatial variation in abundance. However, there are three additional caveats that must be taken into account when attempting to build a theory from this study. First, nectar production was only a significant predictor of abundance at sites where the birds were already present. Variation in nectar production could not discriminate between occupied and unoccupied sites. Thus a niche factor such as available energy may only partially define a species' niche; it can describe the distribution of abundances but not the limits of that distribution. There may be a different variable or process that determines occupancy. For example, it may not matter how much food there is at a site if there are no opportunities for nesting. Second, there was not a one-to-one relationship between available energy and abundance and the relationship occurred with a one year time lag. Consequently there may be important processes, such as competition or dispersal, that mediate the degree to which abundance is matched to the underlying environment. Third, I did not compare the effect of energy from food with other potential niche factors. Consequently, if theory is simply about describing spatial variation in the environment, I cannot yet say how many or which aspects of the environment need to be studied. More importantly, for a theory to apply generally, the number and identity of niche factors would need to be the same across species and systems. If not, then a theory must be able to predict these properties based on more general aspects of a species' ecology (e.g. body size).

6.2. Niche-based theory: mechanism

Building a theory from correlation-type studies does not address the mechanism that relates abundance to the environment. A general mechanism can side-step the issue of having to uncover every aspect of a species' niche. For example, an environmental tolerance-competitive ability trade-off may describe the same direct and indirect effects of environment on abundance for a species that responds to temperature as a species that responds to elevation. In my fourth chapter, I drew inspiration from McGill et al. (2006a) and attempted to uncover a mechanism based on how species traits affect performance along environmental gradients. I found that the mechanism was not straightforward because of the complicated and uncertain ways in which species traits map onto performance and how performance maps onto abundance. (Performance here means the ability for an organism to obtain resources that contribute to individual or population maintenance or growth [McGill et al. 2006a]). In my experimental system, I found that individual behaviour mediated the relationship between traits and abundance. The simple deterministic chain of events – that traits influence whether a particular hummingbird species or sex is an interference or exploitation competitor, which determines relative abundance based on environmental context – was not well supported. Instead, my results support a game-theoretic approach where performance maps onto abundance based on other individuals as much as on the environment. Of course the environment also affects other individuals, hence the complicated path by which traits affect abundance.

Based on what is known about traits related to foraging and competition, male Black-chinneds should have been the most aggressive of the three species and sex groups in my system (Carpenter et al. 1993; Stiles et al. 2005). In my study, however, female Black-chinneds were the most aggressive; male behaviour suggested they foraged with a “sneaker” strategy (Dubois et al. 2004). Consequently, traits related to aggression were being expressed based on a different environmental context then the one I measured; elevation and food density were insufficient in understanding how species traits translate to performance and abundance. (Indeed, I found high levels of between site random variation in abundance and competition that could not be attributed to elevation or food density). I hypothesized that elevation and food density were key gradients driving spatial variation in abundance based on previous studies (e.g. Feinsinger et al. 1979; Carpenter et al. 1993; Altshuler 2006). However, all these studies were conducted during the non-breeding season whereas I conducted my study during the breeding season. Therefore, my results highlight that the environmental gradients upon which traits translate to abundance vary in time as well as space.

The trait and trade-off approach maps environment onto abundance via performance and fitness (McGill et al. 2006a). An alternative approach is to map environment onto abundance via demography and population dynamics. Necessarily, demographic parameters are influenced by fitness; the latter explicitly describes long term population growth via survival and reproduction. However, generality in how demographics and dynamics vary in space - independent of any measures of fitness - may be able to be used to indirectly to infer spatial variation in abundance.

Studies have shown that spatial structure in the variation of demographics and dynamics across geographic ranges exists and can arise from underlying spatial environmental variation (Williams et al. 2003; Saether et al. 2008). In some cases, demographic rates consistently vary between the range core and periphery suggesting that abundance varies in a similar way (Curnutt et al. 1996; Williams et al. 2003; Saether et al. 2008), which is a pattern that does apply generally across species (Sagarin & Gaines 2002). Hence the utility in using demographics as a link between environment and abundance depends on explaining this mismatch.

Translating spatial variation in demography to spatial variation in abundance is complicated by the fact that: i) different demographic components independently vary over space and exhibit different spatial structure (Brewer & Gaston 2003; Purves 2009); ii) the relative contribution of different demographic components to abundance varies over space (Saether et al. 2008; Purves 2009); iii) at equilibrium, density-dependence acts in concert with environment (i.e. density-independent) factors to affect abundance (Maurer & Brown 1989; Purves 2009); iv) the relative effect of density-dependent and density-independent controls on demographic rates may themselves vary in space (Williams et al. 2003); v) the contribution of temporal stochasticity in demographic rates to population dynamics varies over space (Saether et al. 2008).

6.3. Spatial variation in abundance: neutral approaches

The results of my thesis suggest that a theory of abundance should take into account spatial structure in the environment and the mechanism that turns such structure into abundance, both directly and indirectly (via interspecific interactions). However it is possible for spatial structure in abundance to arise independently from or in addition to spatial structure in the underlying environment. This non-niche based spatial structure arises from dispersal acting on populations that vary in abundance. To date, Ives & Klopfer (1997) are the only ones to generate variation in abundance completely independently of spatial environment variation. In their model, variation arises because of stochastic variation in demographic parameters. Dispersal smoothes the stochastic differences among populations at different sites therefore creating spatial autocorrelation (i.e. the peak-and-tail pattern) among sites in a species range.

Two other studies highlight how dispersal creates spatial structure in the abundance of an organism at the scale of species ranges. However, in both, initial spatial variation in abundance is generated by spatial structure in the environment. Consequently, these studies are best thought of as showing how spatial structure due to dispersal complements spatial structure due to the environment. In Pulliam (2000), high dispersal rates contribute to a source-sink dynamic, allowing individuals to persist in “unsuitable” habitat. Therefore, predicting the pattern of abundance purely from the underlying environment would underestimate abundances in “unsuitable” habitat. In Bahn et al. (2006), dispersal maintains initial disparities in abundance between core and range edge populations. The latter are metapopulations with a high level of isolation where dispersal leads to higher mortality than it does at the core. The edge-core pattern of abundance occurs in the absence of environmental gradients, except for a gradient in isolation. As with Pulliam (2000), predicting abundances from spatial environmental variation alone might not capture the additional effect of metapopulation structure.

Importantly, both models highlight that dispersal can act locally but contribute to patterns that manifest themselves across the species range. On the other hand, it has been shown that dispersal can act at spatial extents as large as the islands of Iceland and Great Britain: populations over time expanded out of high quality sites into low quality sites across each island in a density-dependent manner (Gill et al. 2001; Gunnarson et al. 2005). This type of population regulation – known as the buffer effect (Brown 1969) – was demonstrated for a migratory shorebird, for which distance among sites was unrelated to the probability a site was colonized (Gunnarson et al. 2005). Hence it is unknown whether such a mechanism could work for sessile or movement limited species.

The question whether underlying environmental variation is necessary to generate spatial variation in abundance mimics the recent debate over the relative influence of neutral and niche based dynamics in shaping local patterns of coexistence and macroecological patterns such as the species abundance distribution (Chave 2004; McGill et al. 2006b). Essentially, if underlying environmental variation is not necessary to generate spatial variation in abundance then the niche, the very idea that a species responds differently to different types of environments, does not have any influence on dynamics. Instead, as Ives & Klopfer (1997) show, spatial variation in abundance is sufficiently described by temporal stochasticity and dispersal (limitation), which is consistent with neutral theory (Bell 2001; Hubbell 2001). Likely, spatial variation in abundance is an outcome of both temporal stochasticity and deterministic spatial and temporal environmental variability (Saether et al. 2008).

It is not surprising that the neutral/niche dichotomy applies equally well to spatial variation in abundance as it does to other community level and macroecological patterns because the patterns are all connected. In fact, McGill (2010) suggests that the spatial clumping of individuals is an “assertion” of the niche and neutral “unified” models that predict community level and macroecological patterns. If spatial clumping includes the aggregation of populations into a peak and tail pattern across the species range then explaining spatial variation is the proximate mechanism from which the other patterns emerge. Consequently, the fundamental difference between neutral and niche models – ecological equivalence of species – must be explained in terms of the patterns of spatial variation in abundance they produce. In this regard, intraspecific equivalence is as necessary as interspecific equivalence: individuals of a species must respond similarly to the environment at all places in its range despite any underlying heterogeneity. As with interspecific equivalence, this premise may be difficult to support on either theoretical or empirical grounds (Gilbert & Lechowicz 2004; Leibold & McPeek 2006). After all, if individuals respond similarly across environments then natural selection could not operate. However, if clumping at different scales arises from different processes then it is possible that intraspecific differences and niche dynamics generate clumping at small scales. At larger scales, the average site level response is equivalent, which would then allow neutral dynamics to drive clumping at large scales (Chave 2004; Holyoak & Loreau 2006). Therefore, reconciling niche and neutral perspectives requires explicitly defining the scale-dependent processes that generate different patterns of clumping (i.e. spatial variation in abundance) at different scales.

6.4. Spatial variation in abundance: conservation implications

One of the longstanding aims of conservation ecology has been to maintain biodiversity across scales, which ultimately depends on preventing species extinctions. At some temporal scale, species extinction is the simultaneous extinction of all local populations. Thus, extinction is a process with a spatial extent equal to a species range and a spatial grain equal to a population.

Spatial variation in abundance characterizes extinction risk at both spatial scales because it captures information on the abundance of populations, the spatial relationship among populations, and the number of populations across a range (i.e. occupancy [Hurlbert & White 2005]). All three properties interact to link local and large scale dynamics. Local population abundance is negatively correlated with extinction risk (Pimm et al. 1988). Since occupancy is correlated with local abundance (Gaston et al. 2000), species with small population sizes occupy fewer sites at large scales (Borregaard & Rahbek 2010) and thus there are fewer sites that have to go extinct for the entire species to go extinct. Both abundance and occupancy work in concert to quantify the potential for similar local scale dynamics (i.e. population decline) to happen everywhere across a species range.

Importantly, however, local population decline and extinction is also an outcome of isolation (Pimm et al. 1988; Hanski 1991). The spatial autocorrelation among populations characterized by patterns of spatial variation in abundance makes explicit the neighbourhood or metapopulation context of each population. Thus, the feedbacks that occur between abundance and occupancy (e.g. Borregaard & Rahbek 2010) are mediated by the spatial pattern of populations.

The influence of spatial pattern can be seen in the context of climate change, which alters the environment at global and local scales (Parmesan 2006). Isolation and limited dispersal have been shown to limit the potential for range edge populations to expand into novel environments that become available due to climate change (Iverson et al. 2004; Bahn et al. 2006; Anderson et al. 2009). Similarly, predicting species local abundances in novel environments can be predicted better from the abundances of nearby species than by environmental variables (Bahn & McGill 2007). Spatial variation in abundance further describes how populations may shift with climate change, regardless of whether range edges also move (Iverson et al. 2008; Jarema et al. 2009; Murphy et al. 2010).

The challenge in using spatial variation in abundance as a tool predicting extinction risk is to make the pattern spatially implicit. In this way a general relationship can be established without having to model what is happening to each local population, including describing all demographic and dispersal parameters. Linking simple metrics of spatial variation in abundance, such as evenness and skewness, to the probability of range expansion or contraction is a necessary step. Hopefully such generality then improves the precision of models that predict future losses and gains in biodiversity at the local level. Despite the importance of large scale processes and context, it is locally where human communities and individuals tackle the environmental problems that directly affect their health and livelihoods and where the personal appreciation of biodiversity is created.

6.5. References

Altshuler, D.L. (2006). Flight performance and competitive displacement of hummingbirds across elevational gradients. *American Naturalist*, 167, 216-229.

Anderson, B.J., Akçakaya, H.R., Araújo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W. & Brook, B.W. (2009). Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B,* 276, 1415-1420.

Bahn, V. & McGill, B.J. (2007). Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography*, 16, 733–742.

Bahn, V., O'Connor, R.J. & Krohn, W.B. (2006). Effect of dispersal at range edges on the structure of species ranges. *Oikos*, 115, 89-96.

Bell, G. (2001). Ecology – neutral macroecology. *Science*, 293, 2413-2418.

Borregaard, M.K. & Rahbek, C. (2010). Causality of the relationship between geographic distribution and species abundance. *Quarterly Review of Biology*, 85, 4-25.

Brewer, A.M. & Gaston, K.J. (2003). The geographical range structure of the holly leaf-miner. II. Demographic rates. *Journal of Animal Ecology*, 72, 82-93.

Brown, J.H. (1984). On the relationship between abundance and distribution of species. *American Naturalist*, 124, 255-279.

Brown, J.H., Mehlman, D.W. & Stevens, G.C. (1995). Spatial variation in abundance. *Ecology,* 76, 2028-2043.

Brown, J.L. (1969). The buffer effect and productivity in tit populations. *American Naturalist,* 103, 347-354.

Carpenter, F.L., Hixon, M.A., Temeles, E.J., Russell, R.W. & Paton, D.C. (1993). Exploitative compensation by subordinate age-sex classes of migrant Rufous Hummingbirds. *Behavioral Ecology and Sociobiology,* 33, 305-312.

Chave, J. (2004). Neutral theory and community ecology. *Ecology Letters*, 7, 241-253.

Curnutt, J.L., Pimm, S.L. & Maurer, B.A. (1996). Population variability of sparrows in space and time. *Oikos*, 76, 131–144.

Dubois, F., Giraldeau, L-A, Hamilton, I.M., Grant, J.W.A & Lefebvre, L. (2004). Distraction sneakers decrease the expected level of aggression within groups: a game-theoretic model. *American Naturalist*, 164, E32-E45.

Feinsinger, P., Colwell, R.K., Terborgh, J. & Chaplin, S.B. (1979). Elevation and the morphology, flight energetics, and foraging ecology of tropical hummingbirds. *American Naturalist*, 113, 481-497.

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

Gilbert, B. & Lechowicz, M.J. (2004). Neutrality, niches, and dispersal in a temperate forest understory. *Proceedings of the National Academy of Sciences USA*, 101, 7651-7656.

Gill, J.A., Norris, K., Potts, P.M., Gunnarsson, T.G., Atkinson, P.W. & Sutherland, W.J. (2001). The buffer effect and large-scale population regulation in migratory birds. *Nature*, 412, 436-438.

Gunnarsson, T.G., Gill, J.A., Petersen, A., Appleton, G.F. & Sutherland, W.J. (2005). A double buffer effect in a migratory shorebird population. *Journal of Animal Ecology,* 74, 965-971.

Hanski, I. (1991). Single-species metapopulation dynamics: concepts, models and observations. *Biological Journal of the Linnean Society*, 42, 17-38.

Holyoak, M. & Loreau, M. (2006). Reconciling empirical ecology with neutral community models. *Ecology*, 87, 1370-1377.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography.* Princeton University Press, Princeton, NJ.

Hurlbert, A.H. & White, E.P. (2005). Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. *Ecology Letters*, 8, 319-327.

Iverson, L.R., Schwartz, M.W. & Prasad, A.M. (2004). Potential colonization of newly available tree-species habitat under climate change: an analysis for five eastern US species. *Landscape Ecology*, 19, 787–799.

Iverson, L.R., Prasad, A.M., Matthews, S.N. & Peters, M. (2008) Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management*, 254, 390–406.

Ives, A.R. & Klopfer, E.D. (1997). Spatial variation in abundance created by stochastic temporal variation. *Ecology*, 78, 1907-1913.

Jarema, S.I., Samson, J., McGill, B.J. & Humphries, M.M. (2009). Variation in abundance across a species' range predicts climate change responses in the range interior will exceed those at the edge: a case study with North American beaver. *Global Change Biology*, 15, 508-522.

Leibold, M.A. & McPeek, M.A. (2006). Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, 87, 1399-1410.

Maurer, B.A. & Brown, J.H. (1989). Distributional consequences of spatial variation in local demographic processes. *Annales Zoologici Fennici*, 26, 121-131.

McGill, B.J. (2010). Towards a unification of unified theories of biodiversity. *Ecology Letters*, 13, 627-642.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006a). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, 21, 178-185.

McGill, B.J., Maurer, B.A. & Weiser, M.D. (2006b). Empirical evaluation of the neutral theory. *Ecology*, 87, 1411-1423.

Murphy, H.T., VanDerWal, J. & Lovett-Doust, J. (2010). Signatures of range expansion and erosion in eastern North American trees. *Ecology Letters*, 13, 1233-1244.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637-669.

Pimm, S.L., Jones, H.L. & Diamond, J. (1988). On the risk of extinction. *American Naturalist*, 132, 757-785.

Pulliam, H.R. (2000). On the relationship between niche and distribution. *Ecology Letters*, 3, 349-361.

Purves, D.W. (2009). The demography of range boundaries versus range cores in eastern US tree species. *Proceedings of the Royal Society B*, 276, 1477-1484.

Saether, B-E., Lillegard, M., Grotan, V., Drever, M.C., Engen, S., Nudds, T.D. & Podruzny, K.M. (2008). Geographical gradients in the population dynamics of North American prairie ducks. *Journal of Animal Ecology*, 77, 869-882.

Sagarin, R.D. & Gaines, S.D. (2002). The 'abundant centre' distribution: to what extent is it a biogeographical rule? *Ecology Letters.*, 5, 137-147.

Stiles, F.G., Altshuler, D.L. & Dudley, R. (2005). Wing morphology and flight behavior of some North American hummingbird species. *Auk,* 122, 872-886.

Williams, C.K., Ives, A.R. & Applegate, R.D. (2003). Population dynamics across geographical ranges: time-series analysis of three small game species. *Ecology*, 84, 2654-2667.