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Climatic influences on the evolution and diversity of regional species assemblages

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Abstract

It has long been recognized that climate can influence the diversity and dynamics of communities and regional assemblages. Within this thesis, I ask three questions: 1) which processes are most important in mediating climate-species richness relationships; 2) are predictions of spatial climate-richness models temporally consistent, and 3) is local community structure determined primarily by regional or local processes.

Metabolic theory proposes that climate-richness relationships arise due to the temperature dependence of metabolic rate. I tested the theory's predictions for six taxa in North America. Contrary to the theory's predictions, temperature-richness relationships were curvilinear and their slopes deviated from the predicted value. This suggests that the mechanism proposed by metabolic theory does not underlie climate-richness relationships.

If climate determines species richness, then climate should predict how species richness will change over time. To test this, I compared alternative methods (regression and niche modelling) of forecasting shifts in species richness given global climate change. Models were trained on butterfly richness data from the early 20th century and their predictions were compared to observed changes throughout the 20th century. Overall, regression-based approaches that incorporated spatial autocorrelation outperformed other methods

Broad-scale richness gradients could arise from climatic niche conservatism. I tested this hypothesis for treefrogs (Hylidae) by combining data on species' distributions and phylogeny. I found that while niches were conserved with respect to cold tolerance, species richness was determined by precipitation, not temperature. This suggests that the processes determining regional species composition and richness are controlled by fundamentally different climatic components.

I evaluated the relative importance of regional and local processes and how these were affected by climatic gradients by examining patterns of body size dispersion at local and regional scales for hylid frogs. On average, communities were over-dispersed, but there was no increased signature of competition in the tropics. Dispersion of regional assemblages decreased in cold areas, but this was not due to an elevated tropical rate of body size evolution. Overall, regional processes explained twice as much variance in body size dispersion than did local processes.

This thesis rejected several hypotheses for the link between climate and macroevolutionary patterns. In doing so, it provided new insight to the role of ecological and evolutionary processes along broad-climatic gradients.

Résumé

Il est depuis longtemps reconnu que le climat peut influencer la diversité et les dynamiques des communautés et assemblages régionaux. Dans cette thèse, je pose trois questions: 1) quels sont les plus importants processus pour la médiation des relations climat-richesse en espèces, 2) est-ce que les prédictions des modèles spatiaux de la relation climat-richesse sont consistantes temporellement, et 3) est-ce que la structure communautaire locale est déterminée principalement par des processus régionaux ou locaux.

La théorie métabolique suggère que les relations climat-richesse résultent de la dépendance du taux métabolique sur la température. J'ai éprouvé les prédictions de cette theorie pour six taxa en Amérique du Nord. Contrairement aux prédictions de la theorie, les relations température-richesse sont curvilignes et leurs pentes dévient des valeurs prédites. Ceci suggère que le mécanisme proposé par la théorie métabolique ne produit pas les relations climat-richesse prédites.

Si le climat détermine la richesse en espèces, le climat devrait alors prédire la façon dont la richesse en espèces changera avec le temps. Pour éprouver ceci, j'ai comparé différentes méthodes (régression et modélisation de niches) servant à prédire les changements dans la distribution de richesse en espèces résultant des changements climatiques. Les modèles étaient entraînés avec des données sur la richesse en papillons du début du 20^{ième} siècle et leurs prédictions étaient comparées aux changements observés durant le 20^{ième} siècle. En général, les approches fondées sur la régression et incluant l'autocorrélation spatiale ont surpassé les autres méthodes.

Les gradients de richesse à grandes échelles peuvent survenir en raison du

conservatisme de la niche climatique. J'ai éprouvé cette hypothèse pour les rainettes (les hylidés) en combinant des données sur les distributions d'espèces et leur phylogénie. J'ai découvert que, bien que que les niches soient conservées à l'égard de la tolérance au froid, la richesse en espèces est déterminée par la précipitation et non la température. Ceci suggère que les processus déterminant la composition et la richesse en espèces au niveau régional sont contrôlés par des composantes climatiques fondamentalement différentes.

J'ai évalué l'importance relative des processus régionaux et locaux ainsi que la façon dont ces processus sont influencés par des gradients climatiques en examinant les tendances de dispersion de tailles corporelles à des échelles locales et régionales. En moyenne, les communautés sont sur-dispersées mais il n'y avait pas d'augmentation dans le signal de compétition dans les tropiques. La dispersion des assemblages régionaux diminue dans les régions froides mais ceci n'était pas dû à un taux élevé d'évolution de taille corporelle dans les tropiques. En général, les processus régionaux ont expliqué deux fois plus de variance dans la dispersion de taille corporelles que les processus locaux.

Cette thèse rejette plusieurs hypothèses par rapport au le lien entre le climat et les tendances macroévolutives. De cette façon, elle a permis l'acquisition d'un nouvel aperçu sur le rôle des processus écologiques et évolutifs le long de larges gradients climatiques.

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Introduction

"Once the existence and magnitude of an ecological effect has been accepted it is quite another thing to show that it has consequences at the level we are interested in" - McArdle 1996

The central theme of this thesis is not species diversity, nor is it climate, nor even the relation between the two. Instead, it is something more fundamental: it is an attempt to identify, through the deduction and testing of predictions, those factors and processes that are most important in determining general ecological patterns. This endeavour is based on the philosophical standpoint that much of the tremendous variation in ecological systems can potentially be accounted for by a small number of variables and processes, i.e. much of the variation is tractable (Currie et al. 1999). This position is not ubiquitous in ecology. For example, it is in direct opposition to the 'case study' approach (Shrader-Frechette and McCoy 2000). Shrader-Frechette and McCoy (2000) suggest that ecology is essentially devoid of generalities, in both theory and pattern, and thus general inferences are not useful or even possible. Therefore, searching for the processes driving broad patterns, or testing general theories using specific systems, is fruitless. Instead, Shrader-Frechette and McCoy (2000) argue that ecological questions should be approached on a case-by-case basis through detailed consideration of the unique characteristics and intricacies of individual systems. The 'case study' and 'tractable variation' positions are thus in direct opposition. The former views the tremendous variation among individuals, populations, species, communities and ecosystems as indicative of the absence of generalities. The latter views it as an opportunity to discover them.

To identify the factors and processes that drive natural patterns, I take a macroecological approach. Rather than view nature as an almost infinite set of case studies, or utilize a reductionist, mechanistic approach to ecological generality (e.g. Schoener 2000), macroecology examines ecological systems at broad temporal and spatial scales, with the goal of quantifying general patterns and identifying the processes that underlie them (Brown 1995). This focus on explaining the broad patterns of variation in nature comes at a cost; macroecology ignores many of the interesting biological details and mechanisms that fascinate ecologists who work at narrower scales. However, what is lost in detail is gained in generality.

Strict adherence to a prediction-based evaluation of hypotheses and theories is critical to all ecology (Peters 1991), but to macroecology in particular. The broad spatial and temporal scales that underlie the processes and patterns that are the discipline's focus cannot (practically or morally) be manipulated (Brown 1995, Gaston and Blackburn 1999). Therefore, macroecologists cannot perform controlled and/or randomized manipulative experiments. To evaluate hypotheses, macroecologists must assess predictions using statistical analysis of broad, natural patterns. Thus, the success of a macroecological research program relies on the extent to which hypotheses make numerous and specific predictions of patterns in nature (Currie et al. 1999, McGill 2003, Currie et al. 2004). Only through the strict evaluation of these predictions can macroecology move beyond pattern description and test which underlying processes are most important in generating and maintaining those patterns.

Climate has been implicated in determining patterns of species diversity and other ecological properties since the time of von Humboldt, Wallace, and Darwin (Hawkins 2001). More recently, the importance of climate for the distribution and dynamics of life has also been recognized by Dobzhansky (1950), Hutchinson (1959), and MacArthur (1972); the latter viewed climate as of such importance that he dedicated the opening chapter of his book, *Geographical Ecology* (MacArthur 1972) to a description of global climatic patterns. The importance of climate has, at times, been viewed as so pervasive that theorists have indicated that its effects should be controlled before examining the role of other ecological processes. For example, in *The Theory of Island Biogeography,* MacArthur and Wilson (1967) suggested that island area and isolation interacted as the dominant determinants of species richness within single climatic zones. The implication of this statement is that they expected climatic differences to exert substantial, if not greater, influence on island richness when the study extent spanned broad climatic gradients; an implication that foreshadowed the findings of Kalmar and Currie (2006). Despite this prominent history, there is little current consensus as to how climate influences ecological processes and in turn how these processes govern ecological patterns, such as species richness gradients (e.g. Hawkins et al. 2003, Currie et al. 2004, Evans et al. 2005). The question of which processes mediate the influence of climate on ecological properties, especially diversity, is the primary question addressed by this thesis.

Much of this thesis focuses on what has, historically, been referred to as the latitudinal diversity gradient. The substantial increase in the number of species co-inhabiting a region as one moves from the poles to the tropics is one of the oldest recognized and most general ecological patterns (Hawkins 2001, Hillebrand 2004). Climate has been implicated as critical to the gradient since the earliest writings on the subject by von Humboldt (Hawkins 2001), and more recently by Fischer (1960), Pianka (1966) and MacArthur (1972). Perhaps no other ecological pattern has been so closely linked to climate (e.g. Hawkins et al.

2003). Recently, Hawkins (2004) has argued, convincingly, that the latitudinal diversity gradient is latitudinal only because the most important drivers of broad-scale richness gradients, such as climate, are collinear with latitude. Nevertheless, despite over two centuries of research, the processes that produce and maintain the latitudinal diversity gradient remain controversial (Currie et al. 2004, Ricklefs 2004, Evans et al. 2005, Jablonski et al. 2006, Mittelbach et al. 2007)

Modern study of broad-scale species richness gradients has taken two disparate approaches. One has been based on statistical prediction of species richness patterns and the second on how evolutionary history has produced richness differences between regions. The statistical approach is grounded in the philosophy that the primary goal of ecology should be prediction and that theories should be judged solely on the success of those predictions (Peters 1991). Early studies, such as those by Turner (1987), Currie and Paquin (1987), and Currie (1991) found that a large proportion of the continental variation in species richness can be explained by climate or related variables, a result which has been mirrored in more recent, global studies (e.g. Francis and Currie 2003, Buckley and Jetz 2007). Coefficients of determination for such relationships generally fall in the range of 0.6-0.9 (Hawkins et al. 2003).

Although the strength of the climate-richness correlations suggested that climate has a substantial effect on species richness, these studies were, to some extent, unsatisfying for two reasons. First, it was possible that the correlations were due to the collinearity of climate with some other, unmeasured, variable(s). Second, they did not specify the processes mediating climate and richness. The issue of spurious correlation was expanded upon by Lennon's (2000) suggestion that spatial autocorrelation could account for the observed climate-richness relationships and the development of the mid-domain hypothesis (Colwell et al. 2004). To address these concerns, research into climate-richness correlations incorporated methods to account for spatial autocorrelation in macroecological analyses (e.g. Lichstein et al. 2002, Diniz-Filho et al. 2003), though the issue remains contentious (Beale et al. 2007, Diniz-Filho et al. 2007, Hawkins et al. 2007), and tested and rejected predictions of mid-domain models (Hawkins and Diniz-Filho 2002, Kerr et al. 2006, Currie and Kerr 2008). Numerous studies also attempted to test whether the correlations between richness and climate were spurious by evaluating the ability of climate-based models to predict richness in other biogeographical domains than the one in which they were developed (Francis and Currie 2003, Field et al. 2005). These studies found that climate predicted richness extremely well; however, relatively small differences between regions with similar climatic conditions were still present (Latham and Ricklefs 1993, Qian and Ricklefs 2004, Ricklefs et al. 2004). Several studies also attempted to test the ability of climate-richness models to make temporal predictions by predicting seasonal changes in richness (Hurlbert and Haskell 2002, H-Acevedo and Currie 2003). In general, these models predicted seasonal changes in richness reasonably well, suggesting that at the scale of annual cycles, climate-richness relationships are temporally consistent.

The processes mediating climate-richness relationships have also received substantial attention (e.g. Currie et al. 2004, Evans et al. 2005). Many of the proposed processes are historical in nature and will be dealt with in the succeeding paragraphs. However, several are explicitly ecological. The most prominent of these fall under the heading of energy-richness theory (Wright 1983, Currie 1991, Evans et al. 2005), which actually can encompass a variety of mechanisms. The most-studied of these has been the 'more individuals' hypothesis, which posits that energy increases in warm, wet areas allow for the coexistence of more individuals, which leads to more species. However, the predictions of this hypothesis have been shown to fail (Currie et al. 2004). A more recently proposed mechanism is the temperature dependence of metabolic rate (Allen et al. 2002), which is part of the broad metabolic theory of ecology (Brown et al. 2004).

In direct contrast to the statistical predictive approach to the latitudinal diversity gradient, a second branch of research has stressed the role of evolutionary history in forming the gradient (e.g. Mittelbach et al. 2007). This approach is based on the view that the present cannot be (easily) divorced from the past: "[The] web of existence is strongly influenced by the irreversible and indelible effects of time. Because of this, the potential of the future is hidden within the constraints of the past in biological systems" (Brooks and McLennan 2002). This stance is further strengthened by another logical necessity: the species richness of a region is the sum of past speciation, extinction, and dispersal events (Jablonski et al. 2006, Wiens 2007). Given these constraints, it is not surprising that several authors, including Ricklefs (1987, 2004, 2006), Wiens and Donoghue (2004), and Wiens and Graham (2005) have argued that to increase understanding of broad-scale richness gradients, an historical approach must be embraced.

Numerous evolutionary processes have been proposed to explain broad-scale species richness gradients (reviewed in Mittelbach et al. 2007). Recently the zone-of-origin, or niche conservatism, hypothesis has risen to prominence. This hypothesis suggests that richness gradients arise due to the tropical origin of a particular clade, which then diversifies. Climatic niche conservatism prevents the majority of daughter lineages from escaping the ancestral climatic conditions, leading to an excess of species in the tropics. This hypothesis has the potential to explicitly link climate and present day species richness gradients via an evolutionary process.

One of the goals of this thesis is to attempt to apply the statistical approach to broad-scale ecological patterns to historical and evolutionary hypotheses. The statistical approach has been criticized for ignoring potentially important deviations from its models (e.g. Qian and Ricklefs 2004) and the failure to ground present-day diversity gradients in past patterns of speciation, extinction, and dispersal (Wiens and Donoghue 2004, Jablonski et al. 2006). The evolutionary/historical approach has been criticized for not making explicit predictions that can be tested and potentially falsified (Currie et al. 1999, Currie et al. 2004). This latter criticism arises from two characteristics of the evolutionary approach. The first is that all individuals, populations, species, regions and continents have a history. Therefore, it is not surprising that signatures of history can be found, thus the focus should be on the importance of history, not its existence. The second characteristic of the evolutionary approach is the idea that historical and evolutionary events preclude the discovery of generalities: "[e]volutionary events may be historically unique, or at least so rare as to preclude statistical assessment. Fortunately 'beyond statistical assessment' does not mean 'beyond explanation'" (Brooks and McLennan 2002). This perspective is also part of Shrader-Frechette and McCoy's (2000) case study method, where formal statistical approaches are traded for a less formal case-by-case set of inferences. To unify the statistical and evolutionary approaches it is necessary to deduce explicit predictions from evolutionary hypotheses that can be evaluated, and potentially rejected, using a formal, statistical framework. The goal of such studies is not to evaluate if there is evidence of history, but to identify the evolutionary processes that have been most important in mediating the strong empirical relationship between richness and climate. This method can rescue the statistical approach from becoming a collection of correlations with no processes and the historical approach from becoming a set of unique case-studies with no underlying generalities.

Species richness has, without question, received far more attention than any other ecological property with respect to broad climatic gradients. However, characterizing communities and regions by the distribution of traits they contain, rather than just the number of species, can allow for improved inferences of the ecological and evolutionary processes that determine community and regional dynamics (McGill et al. 2006). For example, the degree of trait similarity among co-occurring species can vary depending on whether community dynamics are dominated by competition or environmental filtering (Kraft et al. 2008, Cornwell and Ackerly 2009).

A trait-based approach allows for the evaluation of hypotheses for the effects of climate on ecological and evolutionary dynamics that cannot be achieved simply by measuring species numbers. For example, a key remaining question is to what extent community structure is determined by regional and local processes. Much research in this field has focussed on the relationship between local and regional richness (Ricklefs 1987, Cornell and Lawton 1992, Harrison and Cornell 2008); recent work has revealed the limitations of this approach (Srivastava 1999, Ricklefs 2006). However, a trait-based approach to community structure has the potential to shed new light on this long-standing question by quantifying variation in trait distributions at regional and local scales.

This thesis is divided into four chapters, each of which addresses a specific question relating to how broad climatic gradients influence ecological and/or evolutionary patterns. The first three chapters focus on species numbers while the last chapter takes a trait-based approach to ecological communities.

Chapter One tests whether the temperature dependence of metabolic rate is the mechanism underlying broad-scale climate species richness gradients. This hypothesis, proposed by Allen et al. (2002), combines the energetic equivalence rule of population energy use (Damuth 1981) and the temperature dependence of ectotherm metabolic rate to predict the shape and slope of the temperature-species richness relationship. I test these predictions for six taxa in North America, north of Mexico: amphibians, reptiles, trees, butterflies, tiger beetles, and blister beetles.

The second chapter combines the question of whether the predictions of climate-richness models can make accurate and precise temporal predictions with the applied question of how ecologists can most reliably predict shifts in species richness under global climate change. This chapter uses climate change in Canada as a (un)natural experiment to directly compare the performance of alternative forecasting methods. It trains a series of models on patterns of Canadian butterfly richness in the early 20th century and compares their predictions, given observed climate change, to richness patterns at the end of the 20th century.

Chapter Three evaluates the relative importance of climatic niche conservatism in determining the species richness gradient of treefrogs (Hylidae) in the continental Americas. This hypothesis suggests that niche conservatism, i.e. the retention of ancestral characters in daughter species, prevents clades that originate in the tropics from colonizing temperate and polar climatic zones (Wiens and Donoghue 2004, Wiens and Graham 2005, Wiens et al. 2006). I combine data on climate, species distributions and phylogenetic relationships, as well as simulation modelling and path analysis, to test the relative importance of niche conservatism for the richness gradient of frogs in the family Hylidae.

The final chapter takes a trait-based approach to the role of climate in influencing ecological systems. It uses the distribution of body sizes in regional assemblages and local communities of hylid frogs to quantify the relative importance of regional and local processes in determining community structure. It develops a method, based on nested-ANOVA, to quantify the variance in body size dispersion explained by processes acting at different scales. It then goes on to test the hypothesis that biotic interactions are stronger in tropical climates (Dobzhansky 1950, Schemske 2002) by examining three predictions: 1) local communities will become increasingly over-dispersed in tropical regions, 2) the relative importance of regional effects on body size dispersion will increase in temperate areas, and 3) trait evolution will be faster in tropical regions.

The goal of this thesis is to attempt to uncover the processes that are most important in determining broad, ecological patterns – especially those that mediate strong correlations between climate and species richness. To achieve this goal, it takes a macroecological approach to ecological patterns and processes. It does not attempt to determine the details of how particular mechanisms work, nor whether particular processes can influence ecological or evolutionary dynamics. By examining patterns at a broad scale, it attempts to identify regular patterns that emerge from the tremendous variation that is inherent in ecological systems and to determine if these regularities are underlain by a single or small set of general processes.

Chapter 1: A test of Metabolic Theory as the mechanism underlying broad-scale species richness gradients

Abstract

Recently, it has been proposed that broad-scale species richness gradients arise from the temperature dependence of individuals' metabolic rates and the energetic equivalence rule of population energy use. I tested two key predictions of this theory using the broad-scale variation in the richness of amphibians, reptiles, trees, tiger beetles, butterflies, and blister beetles. I found that for all taxa, temperature-richness relationships were curvilinear, rather than linear as predicted. Moreover, for five of six taxa, the slope of this relationship was close to the predicted value for only a narrow range of temperatures. Blister beetles displayed the widest temperature range that is consistent with the Metabolic Theory, covering 45% of the study's geographical area. For the remaining taxa, the geographic range in which the slope is consistent with the predicted value amounts to only 10-20 % of North America. For a wide array of taxa in North America, temperature-richness relationships deviate from the pattern predicted by Metabolic Theory. These results demonstrate that the temperature dependence of individuals' metabolic rates is not the sole cause of broad-scale diversity gradients. Even in areas where factors other than temperature have little influence on productivity, the data do not suggest that richness patterns are determined by the temperature dependence of metabolic rate.

Introduction

Broad-scale species richness gradients are among the most prevalent patterns in ecology. The mechanisms responsible for these patterns, however, are still matters of debate (e.g. Currie et al. 2004, Ricklefs 2004). Proposed hypotheses include geometric models, e.g. mid-domain effects (Colwell et al. 2004), historical factors (Latham and Ricklefs 1993, Ricklefs et al. 2004), and climatic explanations (Currie et al. 2004). Evidence consistent with aspects of all these hypotheses has been found, in one form or another. However, rejection of any particular hypothesis is difficult because, while the mechanisms proposed by these hypotheses differ, their primary predictions are not mutually exclusive. Historical and climatic hypothesis predict increasing species richness toward the equator, because of either the tropical origin of a clade, or the correlation between climatic factors and latitude. When distance from domain edge is collinear with climatic factors, mid-domain and climatic hypotheses can also make similar predictions (e.g. Romdal et al. 2005). If this controversy is to be resolved, hypotheses must make additional, unique predictions that can potentially be falsified, rather than simply predicting a richness gradient (Currie et al. 1999).

The strong correlation between energy-based climatic factors, i.e. temperature and potential evapotranspiration (see Hawkins et al. 2003), has led to energetic explanations of the richness-climate relationship (Wright 1983, Currie 1991). Energetic explanations can be divided into two groups: those dependent on ambient energy (i.e. temperature or potential evapotranspiration) and those based upon net primary productivity (Evans et al. 2005). The most prominent energetic explanation has been the energy-richness (or more individuals) hypothesis, which suggests that higher-energy areas can support more individuals, which in turn results in more species (Wright 1983). Tests of the energy-richness hypothesis have shown that species richness does not increase as a simple function of the total number of individuals (Currie et al. 2004, Hurlbert 2004). Numerous other mechanistic links between climate and species richness have been suggested (see Evans et al. 2005), including physiological tolerance (e.g. Kleidon and Mooney 2000) and variation in diversification rates across broad spatial extents (e.g. Cardillo 1999). Neither of these hypotheses has yielded unequivocal results, though rigourous test are rare (Currie et al. 2004). Therefore, though climate has been shown consistently to be the strongest predictor of species richness at broad scales (Hawkins et al. 2003), a mechanistic link from climate to species richness has not yet been identified.

Recently, Allen et al. (2002) proposed that broad-scale diversity patterns result from the temperature dependence of individuals' metabolic rates. This relationship is a prediction of the developing 'Metabolic Theory of Ecology' (Brown et al. 2004). To predict richness gradients, Metabolic Theory connects two previously recognized relationships: the temperature dependence of metabolic rate (e.g. Gillooly et al. 2001), and the energetic-equivalence rule of population energy use (Damuth 1981, Enquist et al. 1998). Assuming that the body temperature of ectotherms is equal to ambient environmental temperature, Metabolic Theory predicts a positive correlation between temperature and species richness by the following mechanism. As body temperature increases, so does metabolic rate, resulting in higher energy use per individual. If population energy use remains approximately constant, then fewer individuals can be supported in a population, i.e. carrying capacity is reduced (Brown et al. 2004). Considering that the total number of individuals in a community remains relatively constant across geographic space, the result is higher species richness in warm areas. Allen et al.'s (2002) hypothesis, however, does not merely predict an increase in richness toward the tropics; it predicts the exact form of the relationship. Specifically, the hypothesis predicts that, for ectothermic taxa, $\ln S = -E/(kT) + C$ where E is the activation energy of metabolism, 0.78 eV, k is Boltzmann's constant, $8.62 \cdot 10^{-5}$ $\mathrm{eV \cdot K^{-1}}$, and T is environmental temperature in kelvins. The intercept term, C, incorporates the effect of mean body size of the study taxon, area, and total community abundance (for details, see Allen et al. 2002). In other words, $\ln(S)$ should vary as a function of $1/(kT)$ (the form more recently used in the Metabolic Theory, Brown et al. 2004) with a slope of $-E$ or -0.78. This relationship is not expected to be equivalent for endotherms as their metabolic rates do not vary with temperature in a manner similar to ectotherms (Allen et al. 2002).

The Metabolic Theory of Ecology is currently a topic of much debate. The lack of consensus is perhaps not surprising considering the theory's potential to explain a broad suite of ecological processes and patterns. Several of the theory's premises have been challenged, including the existence of universal metabolic scaling (Bokma 2004, Kozlowski and Konarzewski 2004), the mechanism underlying metabolic allometry (Darveau et al. 2002), the activation energy of metabolism (Clarke and Fraser 2004), and the energetic-equivalence rule (Russo et al. 2003). The theory's applicability to broad-scale richness gradients has also been questioned (Storch 2003). Many of these comments have been addressed by the authors of Metabolic Theory (e.g. West et al. 2003, Brown et al. 2005). However, hypotheses are not refuted because their premises are untrue; all models represent over-simplifications of the complexities of nature (e.g. Box 1976). Rather, a hypothesis is refuted when observations fail to agree with its predictions. Departures from predicted patterns can then be used as a starting point for the development of new process-based hypotheses.

Metabolic Theory's quantitative predictions of ectotherm species richness allow for particularly rigourous tests of its proposed mechanism. Because both the temperature dependence of metabolic rate and the energetic-equivalence rule potentially apply to a broad spectrum of organisms (Enquist et al. 1998, Gillooly et al. 2001), Metabolic Theory's mechanism, if correct, should drive species richness of ectothermic taxa despite divergent evolutionary histories and/or habitat requirements. In this study, I test whether the slopes of $\ln(S)$ vs. $1/(kT)$ relationships are consistent with Metabolic Theory's predictions in richness gradients in North America, north of Mexico. To test Allen et al.'s (2002) hypothesis, I assessed richness-temperature relationships for six ectothermic taxa, including reptiles, amphibians, trees, and three insect taxa.

Methods

I used the quadrat system of Currie (1991) to examine temperature-species richness relationships. This quadrat system divides North America, north of Mexico, into 336 quadrats. Quadrats spanned 2.5° x 2.5° (latitude x longitude) south of 50° N latitude and 5° x 2.5° (latitude x longitude) north of 50°N. Coastal quadrats were included in the analysis and I included quadrat area in regression analysis to account for their reduced size. Quadrat area was not strongly correlated with either temperature (Pearson's $r < 0.06$) or latitude (Pearson's $r < 0.12$). Allen et al. (2002) used the same quadrat system, and the tree and amphibian data from Currie (1991) in the original development of Metabolic Theory. Our test, therefore, considers the identical spatial resolution and geographical extent as Allen et al. (2002). Mean annual temperature for each quadrat was also obtained from Currie (1991). Species richness per quadrat was acquired for four additional ectothermic groups: reptiles

(Currie 1991), blister beetles (Coleoptera: Meloidae: *Epicauta*, Kerr and Packer 1999), tiger beetles (Coleoptera: Cicindelidae, Kerr and Currie 1999), and butterflies (Lepidoptera: Papilionoidea and Hesperioidea). Butterfly richness data were obtained by scanning and geo-referencing range maps from the Butterflies of North America (Scott 1986). In all cases, species richness data were generated by overlaying relatively coarse range maps. Species are not expected to be found at all locations within their range (Hurlbert and White 2005). However, the resolution of grid cells in my analysis reduces the potential influence of range-filling procedures on measures of species richness. Treating each taxon separately, I found the lowest temperature at which at least one species was present and I excluded quadrats with lower temperatures from the analysis (where the slope of the richness-temperature relationship is clearly zero). To avoid taking the logarithm of zero, I added 0.5 to all species richness values prior to transformation.

Metabolic Theory predicts that the natural logarithm of ectotherm species richness will be a linear function of $1/(kT)$ with a slope of -0.78. Simply performing linear regression to determine if the slope is equal to -0.78 is not an appropriate test of the hypothesis, as it assumes that one of the predictions, linearity, is true. To test this assumption I used two regression models:

$$\ln S = b_0 + b_1 + 1/(kT) + b_2 \ln A \tag{1}$$

$$\ln S = b_0 + 1/(kT) + b_2 (1/kT)^2 + b_3 \ln A \tag{2}$$

where S is species richness, T is mean annual temperature (degrees kelvin), k is Boltzmann's constant, $8.62 \cdot 10^{-5}$ eV·K^{-1}, and A is quadrat area (km^2). I used the natural logarithm of quadrat area, as required by Metabolic Theory (Allen et al. 2002). Equation 2 is a quadratic model, allowing for a curvilinear relationship between species richness and temperature.

To test Allen et al.'s (2002) first prediction, the linearity of the temperature-richness relationship, I used Akaike's Information Criterion (AIC) to choose the model that best fits the data. Although Allen et al. (2002) report that they used Type II regressions, my analyses of the same data yield slope estimates similar to theirs when I use ordinary least squares (OLS). Type II regressions yield much larger differences between predicted and observed slopes (not shown). I feel that OLS is to be preferred on theoretical grounds because the independent variable, mean annual temperature, can be measured with much less error than species richness. For these reasons, and because my use of type I regression is less likely to reject Allen et al.'s (2002) hypothesis, I used OLS. To determine if quadrat area had an effect on model selection, I also compared AIC values after removing the area term from eqs. 1 and 2. The effect of spatial autocorrelation on analyses in geographical ecology is well documented (Dale and Fortin 2002, Lichstein et al. 2002, Tognelli and Kelt 2004, Fortin and Dale 2005). To minimize the possibility that spatial autocorrelation would lead to erroneous model selection, I also computed spatially-corrected AIC values (AIC_S; A.J.F. Diniz-Filho et al., unpublished). AIC_S penalizes models with significant spatial autocorrelation remaining in their residuals (Diniz-Filho et al. unpublished). I did not use conditional autoregressive models (CARs) because CARs can potentially confound model selection when the independent variable is strongly spatially structured (as is the case here), resulting in erroneous conclusions regarding the form of the true relationship.

In the case of quadratic regressions, I tested whether the instantaneous slope of the temperature-species richness relationship differs from -0.78. This procedure allows for the evaluation of the geographical extent over which the predictions of Allen et al. are met. The instantaneous slope of the temperature-species richness relationship, given eq. 2, is found by taking the partial derivative of ln(*S*) with respect to 1/(*kT*):

$$\frac{\partial \ln S}{\partial(1/(kT))}=b_1+2\mathrm{b}_2(1/(kT)) \tag{3}$$

The standard errors of b_1, and b_2 and their covariance can all be estimated from the regression. However, the presence of spatial autocorrelation will result in variance estimates that are artificially small (Dale and Fortin 2002, Fortin and Dale 2005). To account for this, I calculated the geographically effective sample size (n_e), using the formula given by Cressie (1991):

$$n_e=n\frac{1-\rho}{1+\rho} \tag{4}$$

where n is sample size and ρ is the autocorrelation coefficient of model residuals, which was calculated using the program Spatial Analysis in Macroecology (SAM, Rangel et al. 2006). Using n_e, I manually reconstructed the variances of the regression coefficients and their covariance to obtain geographically effective variances ($\mathrm{var_e}$) and covariances ($\mathrm{cov_e}$) These variances can be combined to give the corrected variance of the estimated slope (eq. 3) at a point 1/(*kT*):

$$var_e(2\mathrm{b}_2(1/(kT))+b_1)=var_3(2\mathrm{b}_2(1/(kT)))+var_e(b_1)+2\mathrm{cov}_e(2\mathrm{b}_2(1/(kT)),b_1)$$

$$=(2(1/(kT)))^2 var_3(b_2)+var_e(b_1)+4(1/(kT))cov_e(b_1,b_2) \tag{5}$$

The 95 % confidence interval of eq. 3 is therefore given by:

$$2\mathrm{b}_2(1/(kT))+b_1\pm t_{df_e,\alpha/2}\sqrt{4(1/(kT))^2 var_e(b_2)+var_e(b_1)+4(1/(kT))cov_e(b_1,b_2)} \tag{6}$$

where df_e is the degrees of freedom calculated from n_e. I next calculated the range of temperatures for which the 95% confidence interval of the slope of the temperature-species richness relationship included -0.78, i.e. the range that is consistent with Allen et al.'s (2002) prediction. I also determined the geographical extent of this range.

Results

The temperature-species richness relationship (Figure 1.1) was curvilinear for all taxa, as determined from AIC values (Table 1.1). Since including the quadrat area term in regressions improved model fit, I present AIC values only from models that included this term. In all cases, quadratic terms remained statistically significant after computing corrected variances ($P < 0.01$ in all cases). Using AIC_S rather than AIC did not alter model selection: quadratic models provided a better fit to the data than linear models (Table 1.1). The only difference was that for amphibians, AIC_S indicated a better fit for a quadratic model excluding the area term, indicating that area does not provide additional information to the regression model for this taxon. Nevertheless, because of the well established effect of area on species richness (the species-area relationship), its inclusion in Metabolic Theory (Allen et al. 2002), and to retain consistency among taxa, I performed further analysis on amphibians using the quadratic model including the area term. Quadrat area was only weakly correlated with temperature (Pearson's $r < 0.06$), thus its inclusion, or exclusion, had virtually no effect on subsequent analyses of the temperature-species richness relationship.

Because the relationship between $\ln(S)$ and $1/(kT)$ is non-linear, its instantaneous slope (eq. 3) varied substantially across space, for example the slope for amphibians ranged from -1.71 to +0.07 (Table 1.2). More importantly, for all taxa, with the exception of blister beetles, the 95% confidence interval (eq. 6) included -0.78 over only a narrow range of temperatures (Figure 1.2). Geographically, this accounted for a low percentage of North

America north of Mexico, ranging from 10% for reptiles, to 20% for amphibians (Figure 1.3). Blister beetles showed the widest range of temperatures (Figure 1.2) and geographical area (45% of the study area; Figure 1.3) consistent with the predictions of Metabolic Theory. While the relationship was still curvilinear for this taxon, the confidence interval of the slope estimate is large due to low spatially-corrected degrees of freedom. For most taxa, the area within the range predicted by Metabolic Theory occurred near the centre of the temperature gradient. For blister beetles this range occurred in warm areas, while for butterflies the slope was similar to the predicted value in the coldest areas of North America.

Discussion

A mechanistic link between climate and species richness has not yet been identified, despite the high predictive ability of climate-based empirical models of species richness (e.g. Francis and Currie 2003). The link proposed by Metabolic Theory (Allen et al. 2002) postulates that broad-scale species richness gradients arise due to the temperature dependence of metabolic rate (Gillooly et al. 2001) and the energetic-equivalence rule of population energy use (Damuth 1981, Enquist et al. 1998). Here, I tested this prediction using six ectothermic taxa in North America, north of Mexico.

Using Metabolic Theory, Allen et al. (2002) predicts that, for ectotherms, the natural logarithm of species richness will be a linear function of $1/(kT)$ with a slope of -0.78. For all six ectothermic taxa examined here, including amphibians, reptiles, trees, butterflies, tiger beetles, and blister beetles, the slope of the richness-temperature relationship varied spatially. The temperature-species richness relationships among these taxa were always curvilinear. Moreover, for all but one taxon (blister beetles), even after correcting for spatial autocorrelation, the slope of this relationship was statistically equivalent to -0.78 only over a small proportion of the study area that fell within a narrow temperature range. The curvilinear temperature-species richness relationship and lack of correspondence with the predicted slope both provide strong evidence that the temperature dependency of metabolic rate is not the sole mechanism shaping broad-scale species richness gradients.

Metabolic Theory uses a single environmental variable, temperature, to generate its predictions. Empirical models have shown that, to predict species richness accurately, both water and temperature variables must be considered for most taxa (Currie 1991, Francis and Currie 2003, Hawkins et al. 2003). It is possible that temperature shapes species richness gradients via its effect on metabolic rate, but this effect is distorted by the influence of water variables. It may be that the relationship between metabolic rate and temperature is not stationary across moisture gradients, or that water availability affects richness gradients via a mechanism unrelated to metabolic rates. Allen et al. (2007), for example, suggest that the species richness-temperature relationship should be expected to hold only in areas where productivity is not limited by some factor other than temperature. Under either of these scenarios, if the relationship between temperature and metabolic rate were still a driving factor, I would expect that in areas where water variables are statistically relatively unimportant, i.e. cold or low-energy areas (Hawkins et al. 2003), Metabolic Theory's predictions would be met. For 5 of the 6 taxa I examined, my results are inconsistent with this prediction. In these taxa, the observed slopes were more negative than -0.78 in cold areas, and for all but blister beetles, less negative in warm areas. For butterflies, the temperature range with a slope similar to the predicted value was in the coldest areas of North America, as expected. However, even for butterflies, it is not evident that there is a temperature threshold below which ln(*S*) varies linearly with 1/(*kT*).

The species richness prediction of Metabolic Theory relies on the assumption that, in general, the body temperature of ectotherms closely tracks environmental temperature. It is well established, however, that many ectotherms regulate their body temperature behaviourally to maintain it more closely to optimum levels (Angilletta et al. 2002). It should be noted that the deviation between actual body temperature and environmental temperature may be reduced when examined at broad-scales. Nevertheless, it does provide one potential explanation for the deviation from predictions I have observed here. Trees, however, are unable to regulate their operating temperature behaviourally to the same extent as other groups, though like other organisms they can regulate their freezing point. Thus, if body temperature/environmental temperature discrepancies were distorting the richness-temperature relationship, trees should demonstrate the strongest agreement with predictions. Our results clearly show that tree species richness had a curvilinear relationship with temperature, and that the relationship's slope was close to -0.78 over a range similar to that of other ectothermic taxa. This suggests that Metabolic Theory's failure to explain broad-scale richness gradients in North America does not arise because of behavioural regulation of body temperature.

Allen et al. (2002) suggest that their theory may not apply to taxa whose body size and/or abundance is dependent on temperature (e.g. reptiles), or to groups that are narrowly defined (e.g. pine trees). Our data show that reptiles deviated from the theory's predictions in a manner similar to other groups, such as trees, whose abundance and biomass vary little with latitude (Enquist and Niklas 2001, Allen et al. 2002). Additionally, I tested a variety of taxa which varied from broadly to narrowly defined: the tree data included both angiosperms and gymnosperms, amphibians and reptiles were defined at the class level, butterflies included two superfamilies, tiger beetles were defined at the family level, and blister beetles at the genus level. Departures from the theory's prediction were present, and similar, for all taxa. Indeed, the group that showed the greatest accordance with the theory's predictions (although still deviating from them) was the most narrowly defined group (blister beetles), exactly the opposite of Allen et al.'s (2002) expectation. Results for blister beetles do not generalize to tiger beetles, a larger assemblage of species, which show patterns very much like those observed for trees, vertebrates, and butterflies (i.e. Metabolic Theory's predictions apply across only a small area of North America).

Unlike other mechanisms proposed to explain climate-species richness gradients, Allen et al.'s (2002) hypothesis is remarkable in the precise, quantitative, and testable predictions that it makes. Although the predictions of Metabolic Theory have proven incorrect, it is impressive how close they come. It is possible that other metabolic mechanisms that incorporate effects of water (e.g. Venevsky and Veneskaia 2003) are required to predict species richness gradients more accurately and over a wider geographic range. A critically important contribution of Allen et al.'s (2002) model is the way in which it fails. Why is the richness-temperature relationship non-linear, but overlapping the slope predicted by Metabolic Theory? Can the metabolic model be modified to account for this pattern? For example, it has been suggested that both the ¾ scaling of metabolism (Glazier 2005) and the activation energy of metabolism (Clarke and Fraser 2004) are variable. Systematic variation of these parameters, especially the latter, could result in the patterns observed here, though to be successfully integrated into the theory, the variation in their values would preferably be defined *a priori*. Both the successes and failures of Metabolic

Theory will provide invaluable clues to future efforts to resolve the long-standing controversy over what determines broad-scale variation in species richness.

Tables

Table 1.1. Akaike Information Criterion (AIC) values of linear and quadratic models of the temperature-species richness relationship. Spatially corrected AIC values (AIC_S; A.J.F. Diniz-Filho et al., unpublished) are also presented. All models included ln(quadrat area) as a covariate. ΔAIC is $AIC_{quadratic} - AIC_{linear}$. In all cases, quadratics have lower AIC values than linear models.

	AIC			AIC_s		
Taxon	Linear	Quadratic	ΔAIC	Linear	Quadratic	ΔAIC_s
Amphibians	625	548	-77	374	226	-148
Reptiles	592	456	-96	380	44	-336
Trees	780	716	-64	502	325	-177
Blister beetles	551	517	-34	362	299	-63
Tiger beetles	727	628	-99	486	307	-179
Butterflies	326	290	-36	5	-90	-95

Table 1.2. Range of the instantaneous slope of the temperature-richness relationship for six ectothermic taxa in North America, north of Mexico. Slopes were determined by taking the partial derivative of ln(S) with respect to $1/(kT)$ of the regression:

$\ln S = b_0 + b_1(1/kT) + b_2(1/kT)^2 + b_3 \ln A$, where S is species richness, k is Boltzmann's constant ($8.62 \cdot 10^{-5}$ eV·°K^{-1}), A is quadrat area, and T is mean annual environmental temperature (°K).

Taxon	Minimum slope (95% CI)	Maximum slope (95% CI)
Amphibians	-1.71 (-2.18,-1.24)	0.07 (-0.41,0.55)
Reptiles	-2.91 (-3.35,-2.47)	0.07 (-0.36,0.50)
Trees	-1.58 (-2.03,-1.14)	-0.05 (-0.41,0.51)
Blister beetles	-1.71 (-2.45,-0.98)	-0.01 (-0.80,0.79)
Tiger beetles	-1.93 (-2.47,-1.40)	0.28 (-0.24, 0.79)
Butterflies	-0.84 (-1.14, -0.54)	-0.12 (-0.37, 0.12)

Figures

Figure 1.1. Temperature-species richness relationships for six taxa in North America, north of Mexico. Solid lines are from quadratic regressions. Dashed lines are linear fits. In all cases, Akaike Information Criterion values indicated quadratic models better fit the data. Data are from 336 quadrats measuring 2.5° latitude x 2.5° longitude south of 50°N, and 5° latitude x 2.5° longitude north of 50°N.

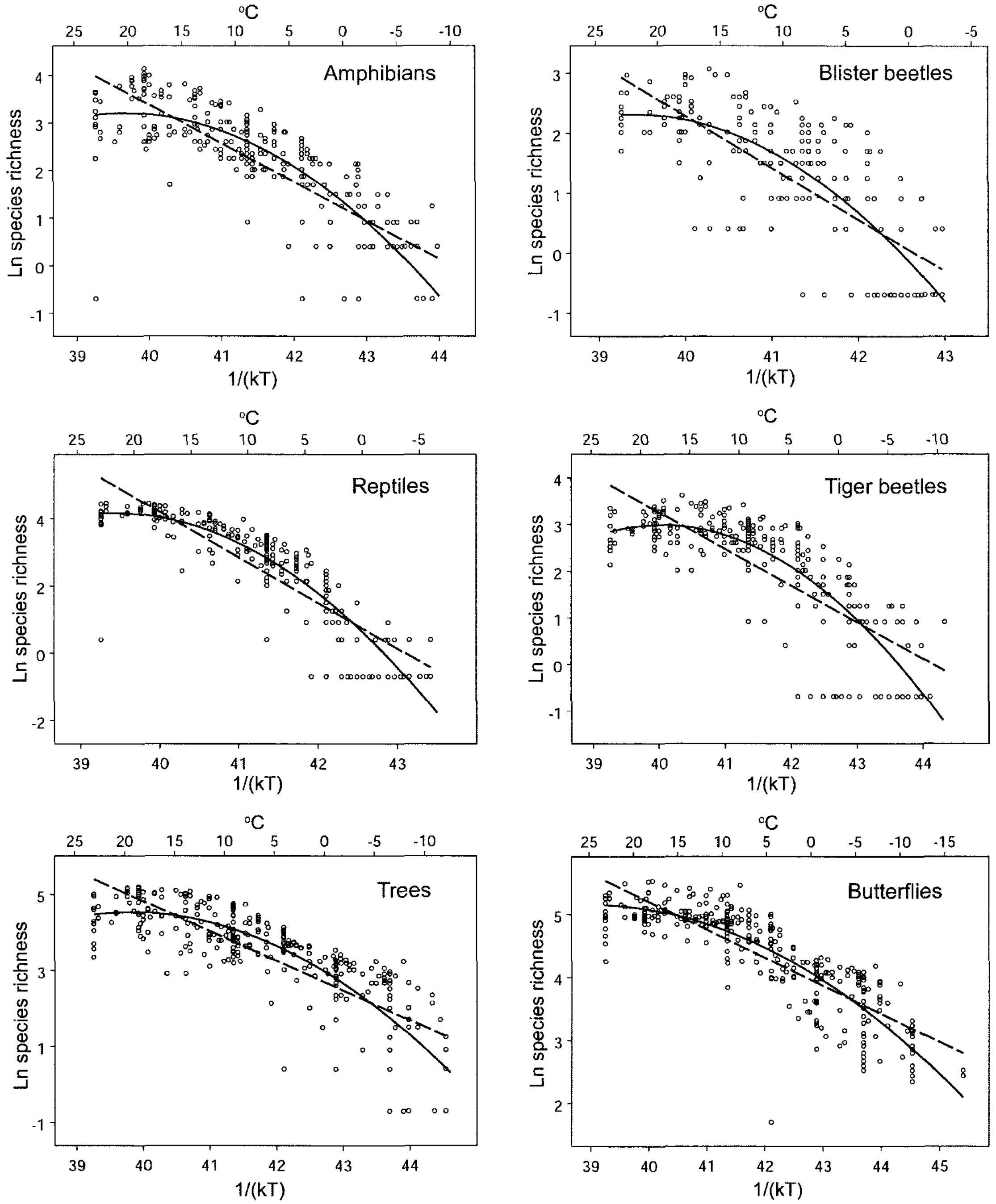
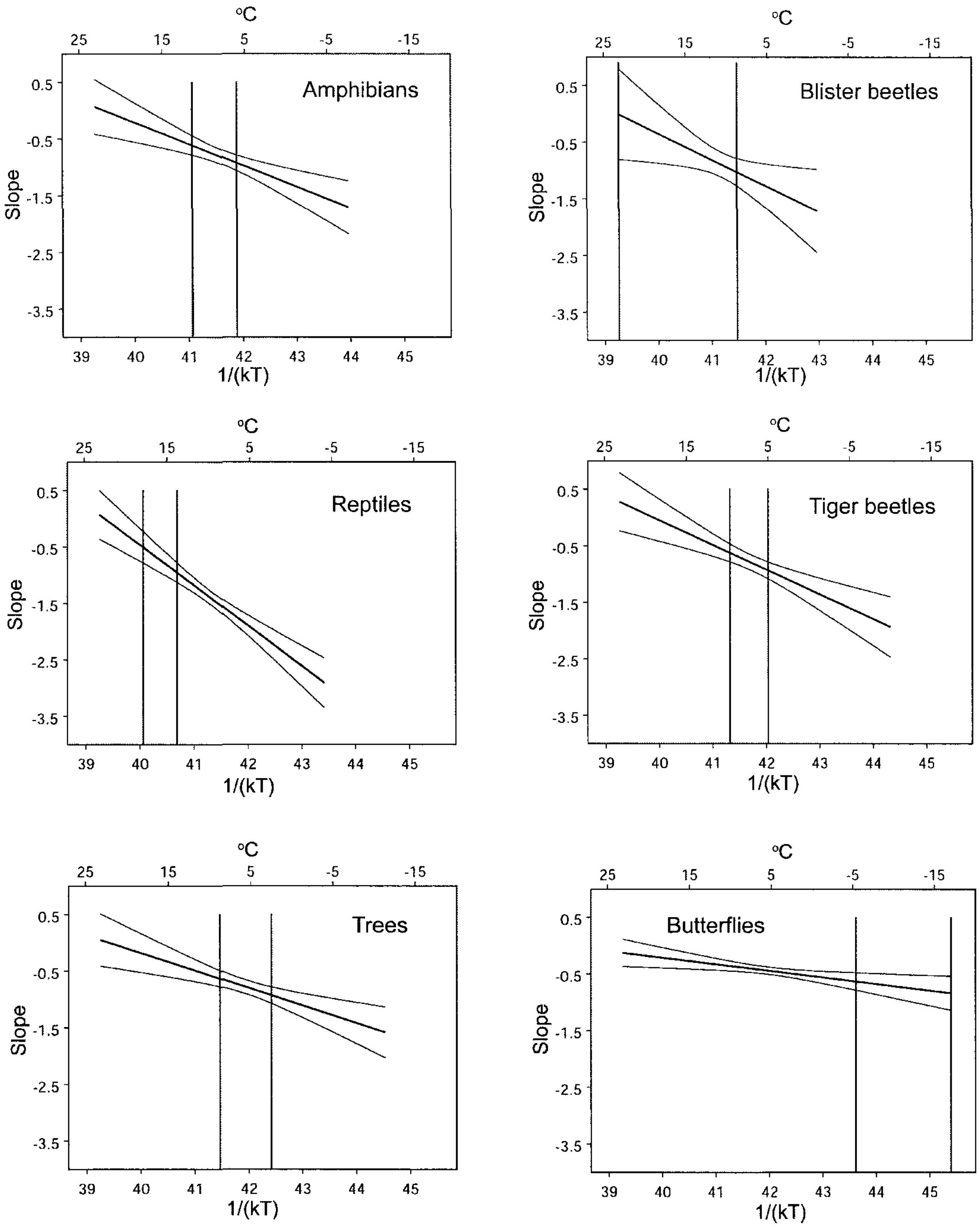

°C
25
20
15
10
5
0
-5
-10
Amphibians
Ln species richness
4
3
2
1
0
-1
39
40
41
42
43
44
1/(kT)
°C
25
20
15
10
5
0
-5
Blister beetles
Ln species richness
3
2
1
0
-1
39
40
41
42
43
1/(kT)
°C
25
20
15
10
5
0
-5
Reptiles
Ln species richness
4
2
0
-2
39
40
41
42
43
1/(kT)
°C
25
20
15
10
5
0
-5
-10
Tiger beetles
Ln species richness
4
3
2
1
0
-1
39
40
41
42
43
44
1/(kT)
°C
25
20
15
10
5
0
-5
-10
Trees
Ln species richness
5
3
1
-1
39
40
41
42
43
44
1/(kT)
°C
25
20
15
10
5
0
-5
-10
-15
Butterflies
Ln species richness
5
4
3
2
39
40
41
42
43
44
45
1/(kT)

Figure 1.2. Instantaneous slopes and 95% confidence intervals of temperature-species richness relationships for six taxa in North America, north of Mexico. 95% confidence intervals were computed using spatially corrected variances. Vertical lines depict the range of temperatures where the 95% confidence interval included -0.78, the value predicted by the metabolic hypothesis for ectotherms. Slopes were calculated by taking the partial derivative with respect to $1/(kT)$ of a quadratic regression, $\ln S = b_0 + b_1(1/kT) + b_2(1/kT)^2$, such that $\frac{\partial \ln S}{\partial(1/(kT))} = b_1 + 2b_2(1/(kT))$ where S is species richness, k is Boltzmann's constant ($8.62 \cdot 10^{-5}$ eV·°K^{-1}), and T is mean annual environmental temperature (°K).


Amphibians
Blister beetles
Reptiles
Tiger beetles
Trees
Butterflies
°C
25
15
5
-5
-15
Slope
0.5
-0.5
-1.5
-2.5
-3.5
1/(kT)
39
40
41
42
43
44
45

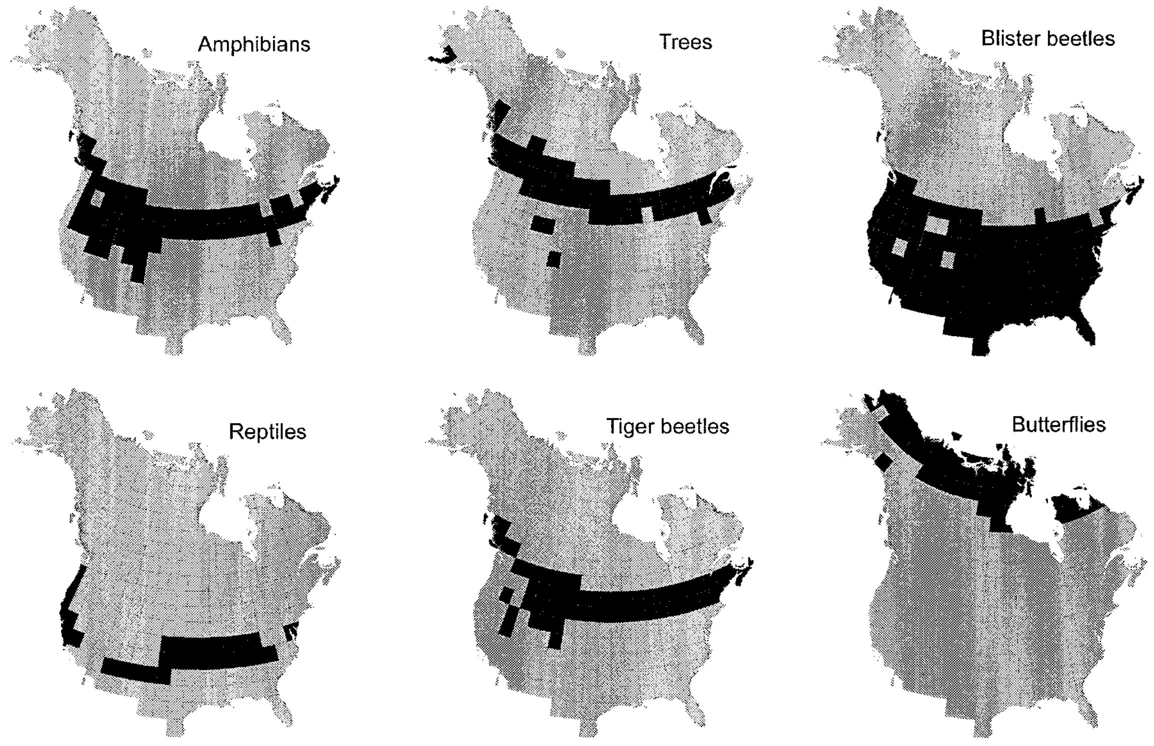


Figure 1.3. Areas of North America, north of Mexico, where the slope of the temperature-richness relationship is consistent with the metabolic hypothesis. Black quadrats are areas where the 95 % confidence interval of the instantaneous slope of the temperature-richness relationship includes -0.78, the value predicted by the metabolic hypothesis. Data are for 336 quadrats measuring 2.5° latitude x 2.5° longitude south of 50°N, and 5° latitude x 2.5° longitude north of 50°N.

Chapter 2: Predicting the future of species diversity: macroecological theory, climate change, and direct tests of alternative forecasting methods.

Abstract

Accurate predictions of future shifts in species diversity in response to global change are critical if useful conservation strategies are to be developed. The most widely used prediction method is to model individual species niches from point observations and project these models forward using future climate scenarios. The resulting changes in individual ranges are then summed to predict diversity changes; multiple models can be combined to produce ensemble forecasts. Predictions based on environment-richness regressions are rarer. However, richness regression models, based on macroecological diversity theory, have a long track record of making reliable spatial predictions of diversity patterns. If these empirical theories capture functional relationships between environment and diversity, then they should make consistent predictions through time as well as space and could complement individual species-based predictions. Here, I use climate change throughout the 20th century to directly test the ability of these different approaches to predict shifts of Canadian butterfly diversity. I found that all approaches performed reasonably well, but the most accurate predictions were made using the single best richness-environment regression model, after accounting for the effects of spatial autocorrelation. These results indicate that spatially trained regression models based on macroecological diversity theory can accurately predict diversity shifts for large assemblages and can generate robust temporal predictions.

Introduction

How will species diversity change in the future? The pervasiveness of anthropogenic climate change impacts on the world's physical and biological systems (Rosenzweig et al. 2008) makes this a critical question for scientists, conservationists, and decision makers. Recent climate and land-use changes have been followed by pronounced biological responses, including phenological changes (Root et al. 2003), range shifts (Parmesan et al. 1999, Root et al. 2003), and increasing diversity of generalist species while more specialized species decline (Menendez et al. 2006, White and Kerr 2006, White and Kerr 2007). These responses are expected to continue, plausibly causing rapid acceleration of extinction rates (Thomas et al. 2004), as climate and land-uses continue to change.

A substantial effort has been made to predict the response of biological systems to global change, particularly with respect to species diversity (e.g. Peterson et al. 2004, Thuiller et al. 2005, McKenney et al. 2007). However, different modelling methods can yield highly divergent predictions, even when spatial assessments of model accuracy appear excellent (Kharouba et al. In Press, Araújo et al. 2005b). Predicting the future is challenging: there is no way to determine which projection is correct and which is not. Given my inability to distinguish reliably between divergent predictions of future states (except by waiting), datasets that combine both historical and more recent data on environmental conditions and species distributions are indispensable for two reasons. First, historically calibrated models, whose performance can be evaluated through time before projecting into the future, are more likely to provide accurate predictions of global change (White and Kerr 2006, Kerr et al. 2007, Nogués-Bravo et al. 2008). Second, such datasets allow for the direct evaluation and comparison of alternative predictive methods (Araújo et al. 2005a).

Spatial models of species' niches can be used to predict where species will shift in response to changing environmental conditions (e.g. McKenney et al. 2007). These models estimate species' niches across geographical space by linking observations of species' presences (and sometimes absences) to environmental or biotic conditions. To translate individual species' niche models into predictions of how species will respond to anticipated environmental change, new environmental data are substituted into the niche models to predict how species' distribution will change. These distributions are then summed to produce predicted species richness.

An alternative approach to predicting diversity shifts could build on established macroecological hypotheses predicting species richness. Macroecologists have devoted decades of study to spatial patterns of diversity (e.g. Fischer 1960, Currie 1991, Hawkins et al. 2003). This research has lead to the development of empirical theory (*sensu* Peters 1991) that predicts the global distribution of species diversity by proposing a direct link between species richness and a small number of climatic (or related) variables; in some cases, heterogeneity in the form of land-cover variety (Kerr et al. 2001) or elevation range (Kerr and Packer 1997), has also been important. Strong environment-richness relationships have been found for nearly all taxa in which they have been investigated, including vertebrates, invertebrates, and multiple plant taxa (Hawkins et al. 2003). Macroecological models reported in such studies not only explain substantial amounts of variation in species richness (R^2 values typically range from 0.6 to 0.9) within their respective study areas, but they can predict patterns in independent geographical regions (Francis and Currie 2003, Field et al. 2005), though in some cases such models may have regional limitations (Whittaker et al.

2007). By applying the coefficients from one of these multiple regression models to future climate scenarios, predictions of future diversity shifts may be possible (e.g. Dormann et al. 2008).

Global change provides pseudo-experimental opportunities to test macroecological hypotheses, which often rely on exclusively spatial data (Kerr et al. 2007). One example is the contemporary climate hypothesis for broad-scale richness gradients. However, a direct relationship between contemporary climate and species richness is only one hypothesis that has been proposed for richness gradients. Alternative hypotheses include evolutionary history (e.g. Ricklefs 2007), and historical climate effects (Svenning and Skov 2007, Araújo et al. 2008). Here, I focus on the contemporary climate hypotheses for two reasons. One, the alternative hypotheses, in their current forms, do not make explicit predictions of richness change over the time scale (<100 years) I consider here. Two, the contemporary climate approach has already been used to predict future diversity shifts (e.g. Dormann et al. 2008). Thus, while my primary goal is to evaluate the capacity of climate-richness regressions to predict observed diversity shifts, my study also provides a temporal test of the contemporary-climate hypothesis. If the observed links between environmental characteristics and species richness are causal, then spatial models based on macroecological theory should accurately predict temporal species richness trends as environment changes (White and Kerr 2006). Hypotheses that fail to predict temporal changes should be rejected, while those making successful temporal predictions may prove valuable in improving decisions intended to ameliorate biological impacts of global change (Kerr et al. 2007).

Relying on a single, spatial model can produce incorrect predictions of future diversity shifts (Araújo et al. 2005b, Dormann et al. 2008). Predictions from these 'single-best' models are more sensitive to the assumptions and particular characteristics of the modelling method selected and differences among methods can degrade the reliability of niche predictions through time (Thuiller 2003, Beaumont et al. 2007). To combat this, some authors have suggested that diversity predictions should be made on the basis of predictions of ensembles of different models (Araújo et al. 2005b, Araújo and New 2007, Dormann et al. 2008). Ensemble forecasting avoids the requirement to select a single, best model from among many approximately equivalent models (Dormann et al. 2008). It also avoids potential errors due to over-fitting and can capture different components of the true basis for species' presences, parts of which may be represented in different models (Araújo and New 2007). For example, ensemble forecasting better predicted individual species ranges of British birds than a single-best model approach (Araújo et al. 2005b). However, it is unknown whether ensemble forecasting produces more reliable predictions than those based on macroecological theory that produces spatio-temporally consistent predictions of species diversity.

This study has two purposes. First, I consider the potential of empirically-derived, macroecological models to predict diversity shifts in response to changing climate and test their performance against more widely used niche models. For the latter, I assess both single-best model and ensemble forecasting approaches. Second, by using historical and recent data on Canadian butterfly richness and climate change from throughout the 20th century, I provide a rare, pseudo-experimental test of whether spatial macroecological models also predict temporal changes in species diversity, as they should if those spatial models are causal, not merely correlative.

Methods

Species Distribution Models

Species distributions were modelled using occurrence records taken from the Canadian National Collection of Butterflies, which contains about 300,000 georeferenced, dated records for 297 Canadian butterfly species (Kharouba et al. In Press, Layberry et al. 1998, Kerr et al. 2001, White and Kerr 2006). Observation points were divided into two time periods: 1900-1930 (historical) and 1960-1990 (recent). Species with fewer than 10 geographically distinct records in either time period were excluded based on modelling accuracy concerns (Hernandez et al. 2006), leaving 139 species for analysis. Data were corrected for increased collection intensity in the recent time period. For each species, a random subset of occurrence points was chosen from the recent time period on which to train and test my models. Thus, for each species, the number of presence points was invariant with respect to time period (for details on additional data corrections, and a list of included species, see Kharouba et al. In Press).

I used seven environmental variables in my distribution models. These included four climate variables, averaged across each time period (historical or recent): mean growing season (April-October) temperature, maximum growing season temperature, minimum annual temperature, and mean annual precipitation (McKenney personal communication, Mekis and Hogg 1999, McKenney et al. 2001). I also included human population density, measured in the 1921 and 1981 censuses (White and Kerr 2006), elevation, and land-cover data delineating generalized physiographic differences in Canadian vegetation and the boundaries of the major agricultural regions in Canada (Beaubien et al. 2000). Climate and human population density data were available for both time periods and elevation, obviously, was constant between the two. Land-cover data (included as a categorical variable) were not available for the historical period so data for the current time period were used to identify major habitat divisions and ecotones within Canada, which have remained relatively consistent during the 20th century (e.g. transition between prairies and aspen woodlands or broadleaf to coniferous forests). Areas where current land-cover data misrepresent natural variability (e.g. southern Ontario) were converted to human land-uses long before the beginning of the earliest time period in this study (e.g. Ramankutty and Foley 1999, Kerr and Cihlar 2003). Change in climate and human population density between the two time periods are shown in Figure 2.1 and rely on data from Mekis and Hogg (1999), McKenney et al. (2001) and McKenney (personal communication). Species distributions were modelled at a resolution of 6.67 km x 6.67 km, which is the effective resolution of the historical climate data available in Canada (McKenney, personal communication) but also sufficiently coarse to ensure georeferencing accuracy among all or nearly all butterfly observations.

Maximum Entropy (Maxent) was used to model species distributions (Phillips et al. 2006), using the default settings. Maxent was developed specifically for use with presence-only occurrence data and consistently performs well relative to other methods (Elith et al. 2006). To build each model, the occurrence records were randomly partitioned into a training (70%) and testing set (30%). This process was repeated to produce 10 model repetitions for each species. Historical and recent distributions were modelled independently.

Historical and Recent Species Richness

Our measures of species richness were limited to the 139 (predominantly common, widespread) species for which I had sufficient data. To determine past and recent species richness, I first converted each species' Maxent suitability map, which ranged from zero indicating low suitability to 100 for high suitability, into a binary range. For each species, in each time period, a decision threshold was defined, above which the species was considered present and below which it was considered absent. The threshold was calculated as the lowest average suitability (across ten repetitions) of a true presence point (Liu et al. 2005, Pearson et al. 2007). Therefore, for each final model, the binary range included all pixels that were predicted to be at least as suitable as those where a species had actually been observed (Pearson et al. 2007). For each time period, species richness was measured by overlaying species' binary ranges on a grid system covering Canada composed of 100km x 100km equal area quadrats. Following conventional macroecological techniques, species were considered present in a quadrat if their range overlapped it. While this can result in some false presences (when ranges barely overlap a quadrat), sampling at a 100km x 100km reduces effects of a single pixel, or small groups of pixels, with unrealistically high levels of climate change that may result from data reconstruction methods (e.g. Figure 2.1). Quadrats with less than 50% land area were excluded to reduce potential area effects leaving 793 quadrats for analysis.

Predicting diversity shifts

I used two main approaches to predict how butterfly species richness would change from the historical to the recent time period. The individual niche model approach considered additive effects of individual species range shifts. The empirical diversity theory approach evaluated species richness as a whole by developing richness-climate regression models. Both methods, and their variants, are described in more detail below. A summary of prediction methods are given in Table 2.1 for quick reference.

The Individual Niche Model Approach

I made individual range-based predictions of species richness in the recent time period by projecting the niche model for each species forward through time by substituting the recent environmental data into the models created for the historical time period. The projected ranges were then overlaid on my quadrat system and summed to produce predicted species richness. For each species, as described above, ten repetitions of the historical models were run using unique test (30%) and training (70%) sets. These produced ten projected ranges for each species. Using these projected ranges, I implemented three alternate forecasting methods: single-best, committee average, and consensus.

I implemented the single-best approach by identifying, for each species, the model repetition with the greatest area under the curve (AUC) of the receiver operating characteristic. AUC is a commonly used measure of niche model accuracy (Fielding and Bell 1997, Elith et al. 2006). However, recent work has highlighted its drawbacks (Lobo et al. 2008). Any statistic used to select the best model has potential disadvantages, including R^2, AIC, BIC, and AUC. I recognize that single-best models could be chosen using alternate methods such as maximizing predictions of true presences (sensitivity). Nevertheless, AUC represents a well known method for distinguishing between models. Future work evaluating alternative 'single-best' statistics by testing their selected models' ability to predict temporal changes is an area of interesting future research. Thresholds for conversion from a continuous cumulative distribution map to a binary range were performed as above, but were based only on the single best repetition for each species. The best projections for all species were then summed, after binary conversion, to predict richness.

Committee averaging and consensus forecasting both incorporate information from all ten repetitions of the projected range for each species. The committee average prediction considered all candidate models equally, while the consensus forecast best captured the common trend among the entire set of predictions. The committee average prediction was calculated by taking the mean projected distribution across all ten repetitions for each species. Following Araújo et al. (2005b), to determine the consensus forecast, I performed a principal component analysis on each species' ten projected distributions. Treating species separately, I then identified the repetition that had the highest loading on the first principal component. As before, after identifying the appropriate projection, continuous maps were converted to binary ranges and summed to predict species richness.

The Empirical Diversity Theory Approach

To predict recent species richness using established macroecological diversity theory, I constructed richness-environment regression models using only the historical data. Regression models potentially included any or all of the environmental variables for which I had both historical and recent data. All of these variables (or extremely similar ones) have been examined as predictors of diversity in the macroecological literature. Mean climatic and human population density values were extracted for each quadrat. Land-cover and elevation were converted to measures of heterogeneity by sampling the number of land-cover types (Kerr et al. 2001) and the elevation range per quadrat (Kerr and Packer 1997). Additionally, I also considered quadratic terms and all first order interactions, resulting in 35 possible independent variables (for a similar approach, see Dormann et al. 2008).

To potentially be included in the candidate model set for ensemble forecasting, regression models had to meet several criteria. First, since macroecological theory indicates that relatively simple models can predict diversity (e.g. Francis and Currie 2003, Buckley and Jetz 2007), I limited the maximum number of variables in a model to five plus an intercept (for a similar decision, see Dormann et al. 2008). Second, due to high collinearity, mean growing season temperature and maximum growing season temperature were forbidden from occurring in the same regression model (Table 2.2). Lastly, if models included quadratic or interaction terms, the matching linear terms had to be included.

One method of identifying the candidate model set is to consider all models that are indistinguishable with respect to their Bayesian information criteria (BIC, Hoeting et al. 1999). For my dataset, BIC did not identify a useful set of candidate models. The model with the lowest BIC always had a substantially (>10) lower BIC than all other models, limiting my set to one. However, these lower BIC values often corresponded to changes in adjusted R^2 of less than 0.01; a difference that I considered biologically insignificant. The large differences in BIC also meant that Bayesian Model Averaging (Hoeting et al. 1999) was not appropriate.

I determined my set of candidate models based on adjusted R^2. R^2 has long been the benchmark for model selection in macroecology. To identify the candidate set, I used the leaps function (Lumley and Miller 2007) in R 2.6.0 (R Development Core Team 2007) to find, at most, the best 10000 regression models of each possible size. This process was repeated once with maximum growing season temperature included in the set of predictors, and once with mean growing season temperature included. The two sets of models were then combined. Redundant models, and those that did not meet the other criteria described above were then culled. All remaining models with adjusted R^2 values within 0.05 of the best model were included in the candidate set. While this criterion is arbitrary, it identifies a justifiable set of relatively simple models that explain nearly equivalent amounts of variation in geographical patterns of species richness.

The model with the highest adjusted R^2 was chosen as the single-best model using ordinary least squares regression (OLS). However, it is well known that spatial autocorrelation in model residuals can bias OLS regression (Lennon 2000, Kühn 2007). Thus, I also fitted a conditional autoregressive model (best-CAR) that included the same variables as the best-OLS model. For the CAR, the spatial weights matrix was an inverse function of distance between quadrat centres ($w_{ij} = d_{ij}^{-\alpha}$). Three weighting schemes were considered: α=1.0, α=1.5, and α=2.0. In all schemes, distances greater than the distance at which Moran's I was non-significant in OLS residuals were given weights of zero (Lichstein et al. 2002). The weighting scheme that resulted in the lowest level of autocorrelation in resulting model residuals was retained. The CAR was calculated using the spdep package (Bivand et al. 2007) in R 2.6.0 (R Development Core Team 2007)

The committee average and consensus forecasts were determined analogously to the procedure used for the individual approach. The committee average was the mean predicted richness across all candidate models. The consensus model was identified by its loading on the first principal component of a PCA on all candidate predictions.

I considered one final predictive model, based on established empirical macroecological theory. This minimum macroecological model included only three variables (plus intercept): mean growing season temperature, mean annual precipitation and their interaction. Similar models have been shown to predict species richness globally (Francis and Currie 2003, Buckley and Jetz 2007) and among continents, suggesting that these variables influence species richness and are not merely collinear with other unidentified variables.

Evaluating predictive methods

I directly selected among approaches by comparing their predictions of richness in the recent time period to the actual pattern by regressing observed recent richness (dependent variable) against predicted recent richness (independent variable), following Piñeiro et al. (2008). I considered four criteria for evaluation. 1) Accuracy; evaluated by determining if the slope and intercept of observed-predicted regression were close to one and zero, respectively. 2) Precision; judged by the correlation (Pearson's r) between observed and predicted richness. 3) Linearity; determined by including a quadratic term in the regression of observed versus predicted richness values; the P-value of this term was used as a continuous index. 4) Prediction consistency; determined by evaluating the homoscedasticity of observed-predicted residuals by regressing the square of the residuals against the predicted values. Finally, predictive methods were ranked based on each of these criteria and the ranks summed across all criteria to produce an integrated measure of performance. Lower rank-sums indicated stronger overall performance. I also compared ranks using a Kruskal-Wallis test.

Results

Species richness patterns

In both periods, species richness generally increased from north to south (Figure 2.2), consistent with other studies of butterflies in Canada (Kerr 2001, Kerr et al. 2001, White and Kerr 2006). Generally, species richness increased throughout the 20th century in more northerly areas and decreased at lower latitudes (Figure 2.2).

Niche and regression models

The mean AUC values across all species (based on the mean of 10 repetitions for each species) in the historical and recent time periods were 0.94 and 0.92 respectively. The mean of the maximum AUC values observed among model runs (i.e. that were used for single-best prediction) across all species from the historical time period was 0.97.

The best regression model (highest adjusted R^2) was:

$$S = 1018.0 - 0.82(Tmaxgr) + 0.15(Tmaxgr)^2 + 4.33(Tmin) - 0.67(Erange) - 0.011(Erange)^2$$

where S is species richness, *Tmaxgr* is maximum growing season temperature, *Tmin* is minimum yearly temperature, and *Erange* is elevation range. This model explained 91% of the geographical variation in historical species richness. The best-CAR was:

$$S = 722.0 - 0.61(Tmaxgr) + 0.11(Tmaxgr)^2 + 3.74(Tmin) - 0.49(Erange) - 0.0090(Erange)^2$$

Our model selection procedure identified a set of 165 models with adjusted R^2 values within 0.05 of the best OLS model. The set of candidate models did not include the minimum macroecological model (adjusted $R^2 = 0.82$).

Comparing Prediction Methods

Accuracy and Precision

All approaches predicted recent species richness relatively accurately; intercepts and slopes of the observed vs. predicted richness regressions ranged from -0.9 to 4.3 and 0.9 to 1.0 respectively (Table 2.3). The single best and consensus niche model predictions had accurate predictions in areas with low richness (intercepts not significantly different from zero, $P > 0.05$), but displayed a tendency to over-predict richness in highly diverse areas (slopes significantly less than unity, $P < 0.001$, Figure 2.3). With the exception of the best-CAR, the remaining approaches had a tendency to under-predict richness in species poor areas (intercepts greater than zero) but their predictive accuracy improved as richness increased (Figure 2.3). However, the best-CAR clearly outperformed all other approaches with slope and intercept values that were remarkably close to one and zero, respectively (intercept ± s.e. = 0.22 ± 0.64, $H_0 = 0$, $P > 0.7$; slope ± s.e. = 1.007 ± 0.0087, $H_0 = 1$, $P > 0.2$).

All approaches' predictions estimated recent species richness precisely (Table 2.3). Niche model predictions were more precise than regression predictions, though the improvement over the best-CAR approach was marginal. The minimum macroecological model had the lowest correlation, though it was still high ($r = 0.91$). This is not surprising since it was not included in the candidate set of models due to its lower R^2 value in the historical period.

Linearity and Homoscedasticity

The best-CAR and minimum macroecological model were the only approaches without a statistically significant quadratic term in the observed vs. predicted regression, though the single-best niche model prediction had a quadratic term at the edge of statistical significance ($P \approx 0.04$). Curvilinearity indicates that predictive accuracy is conditional on the diversity of the area in which the predictions are made, i.e. the slope of the observed vs. predicted regression moves away from one in more (or less) diverse areas.

None of the observed vs. predicted regressions had homoscedastic residuals (Table 2.3). The individual niche model approaches outperformed the empirical diversity theory approaches, including the best-CAR (though best-CAR performed relatively well with a residuals^2 vs. predicted richness slope of 0.98). The niche model committee-averaged prediction had the slope closest to zero (0.18; Table 2.3). All approaches had larger residuals in highly diverse areas, indicating that predictions become more variable as richness increased.

Overall Performance

The best-CAR approach performed well in every evaluation criterion (Table 2.3) and ranked best overall. The individual niche model approach with the best overall score was the single-best, though it scored poorly with respect to slope; the committee average had a slope much closer to unity. The approach with the worst overall performance was the minimum macroecological model. A Kruskal-Wallis test identified differences among approaches that were of borderline statistical significance (Kruskal-Wallis $X^2 = 13.8$, df = 7, $P = 0.054$), despite very limited statistical power to detect differences.

Discussion

Species responses to recent global change have already been documented (Kharouba et al. In Press, Root et al. 2003). The need for reliable predictions of biological responses to global change is likely to become more acute. Different approaches to building such predictions are possible (Table 2.1). Here, I compared the ability of these approaches to predict shifts in species richness through time. I found that the most reliable predictions were made by a relatively simple regression model, after incorporating spatial autocorrelation. This approach, based on established macroecological diversity theory, outperformed the more common method of summing projected changes of individual species ranges.

If empirical macroecological theories of diversity represent actual functional relationships between environment and species richness, then they should successfully predict changes through time as well as space (H-Acevedo and Currie 2003, Kerr et al. 2007). Thus, global climate and land-use changes comprise a pseudo-experimental opportunity to test these hypotheses (Kerr et al. 2007). Macroecologists have long suggested that relatively simple environmental-richness relationships underlie broad-scale diversity gradients (Currie 1991, Hawkins et al. 2003). The temporal consistency of the best-CAR model's predictions is consistent with this explanation. However, as I have not explicitly tested temporal predictions of other macroecological hypotheses for richness gradients (e.g. historical climate or evolutionary history), I cannot reject these alternatives in favour of the contemporary climate hypothesis. Nevertheless, my results suggest that, at least for Canadian butterflies, diversity shifts can be reliably predicted using a relatively simple model based on links between climate, heterogeneity and species diversity. Further work using different taxa in different geographical domains will determine the generality of this result.

Our niche and regression models are both correlative approaches to modelling diversity shifts. An alternative approach, not examined here, is to generate *a priori*, process-based or mechanistic models predicting each species' distribution, and to aggregate these models to predict diversity shifts. Such mechanistic models are rare but have considerable promise to improve predictions of individual species' distributions and sometimes abundance (e.g. Buckley 2007). Their application to predicting range shifts for large assemblages will require further development of their generality and scope. All models, from the simplest correlation to most elaborate mechanistic model, must overcome the problem that future climates and land uses may lack current analogues, requiring extrapolation beyond current conditions (Williams et al. 2007). Nevertheless, despite changes in land-use and climate combinations throughout the 20th century, the empirical approach I have used successfully predicted diversity shifts within that period, implying that these models capture the critical relations governing where species can be detected. Whether this approach will remain reliable as climate changes continue and novel combinations become more extreme is uncertain.

The best-CAR regression model generated more reliable predictions than its OLS analogue. The effect of spatial autocorrelation (the non-independence of geographically proximate data points) on regression analysis of geographical ecological data has received prolonged attention in recent years (e.g. Dormann 2007a). Recently, debate on this topic has focused on whether ignoring spatial autocorrelation biases coefficient estimates from OLS regression (Beale et al. 2007, Dormann 2007b, Hawkins et al. 2007, Kühn 2007). Our dataset provides a novel perspective on this debate. By incorporating a temporal component, I directly compared the predictive ability of coefficient estimates from OLS and conditional autoregression. The best-CAR's coefficients predicted recent species richness much better than OLS estimates, suggesting that accounting for spatial autocorrelation in regression analysis more closely captures true biological relationships between environment and species richness than standard OLS regression analysis.

It is important to note that although predictions based on individual niche model projections were inferior to those of the best-CAR, they performed well, and outperformed the OLS based approaches. This result suggests that individual niche modelling approaches offer an improved mode of prediction over models based on OLS regression. Since species richness is, ultimately, the sum of individual species' presences and absences, why did the individual niche model approach not, at the very least, make predictions equivalent to the best-CAR's? One potential reason is that no niche model can be truly comprehensive, i.e. include all niche characteristics (Araújo and New 2007, Dormann 2007b). Similarly, no realistic regression model can be truly comprehensive (or there would be no residual variation). However, by including an influence of neighbouring quadrats (i.e. spatial effects) on species richness, the best-CAR provides an estimate of the relations between measured environmental variables and richness that are conditioned on the potential relations between richness and unmeasured, spatially structured variables. Although my best-CAR predictions of recent richness used only the coefficients of the measured environmental variables, these coefficients differed from the OLS estimates, due to the incorporation of spatial effects. Our niche models did not include analogous spatial effects. Therefore, the projections are based solely on the measured variables, without considering influences of unmeasured, but spatially structured variables. Potentially useful inclusion of spatial effects in distribution models has been demonstrated in North American birds (Bahn and McGill 2007, Allouche et al. 2008). Spatial effects could be modelled concomitantly with environmental variables in Maxent by including distance from the nearest presence point (Allouche et al. 2008) or by using spatial eigenvectors as predictors (suggested by C. Dormann). However, Maxent currently does not have the capacity to generate projections based solely on the subset of environmental relations as I have done for my Best-CAR prediction. Such a procedure would allow for Maxent projections to be conditioned on unmeasured, spatially structured variables.

Given these differences in the best-CAR and niche models, the failure of the niche model approaches to out-predict the best-CAR approach suggests that my niche models lacked some relevant niche characteristic(s); possible exclusions could be either an abiotic variable, or the effects of biotic interactions (Araújo and Luoto 2007, Dormann 2007b). Empirical diversity theory approaches that used OLS regression performed less well than the individual niche modelling approaches, suggesting that unmeasured variables introduce more bias into these regression models than individual niche models. The ease with which spatial effects can be included in regression models, thereby correcting this bias (at least in my study system), is another advantage of this approach. Nevertheless, the high accuracy of the niche modelling approach's predictions suggest that they successfully identified the dominant factors determining species distributions and niche characteristics that I failed to include likely played only minor roles.

The niche modelling approach to predicting how species diversity will change has two potential advantages over regression modelling. First, the empirical diversity theory approach I have used is limited to predictions of species numbers, though Ferrier's generalized dissimilarity modelling (Ferrier 2002, Ferrier et al. 2004) and related approaches (Hortal and Lobo 2006) can incorporate measures of species turnover among regions or sites. The individual niche modelling approach can predict both species richness and composition, a major advantage if there are species (such as those listed as 'at risk') whose distributions are of particular interest. Second, approaches using regression may be limited to predictions of widespread, generalist species richness, as I have used here. Geographical patterns of the diversity of widespread species are better predicted by climate than geographically restricted species (Jetz and Rahbek 2002). Therefore, the success of the empirical diversity theory approach will be determined primarily by the similarity of widespread species responses to climate change; these changes may not necessarily be representative of changes in geographically rare species' ranges. I could not explicitly evaluate empirical diversity theory or the niche modelling approach's ability to predict shifts in the diversity of geographically rare species as I only had sufficient data to model ranges of widespread, relatively common species. However, when sufficient data are available, niche models often perform better on species with small ranges (McPherson and Jetz 2007), though this could result, at least in part, from using AUC as a measure of model performance (Lobo et al. 2008). Nevertheless, niche modelling predictions may prove more effective than regression based predictions for assemblages of geographically rare species or for complete assemblages where range-restricted species have sufficient geographic overlap to non-randomly affect the overall richness gradient, though the latter case may occur only rarely.

Committee averaging produced both accurate and precise predictions of richness, but overall it performed less well than the single-best approach. This result is expected if the single-best model accurately captures the functional links between environment and species richness. When this is the case, the incorporation of other models will bias the final projection away from the best model's predictions. However, when a model with strong theoretical and empirical support is unavailable or a single best model cannot be easily identified (e.g. Dormann et al. 2008) committee averaging can be used to reliably predict diversity.

The minimum macroecological model was not as effective as other methods, but it performed reasonably well considering it was the only model whose variables I defined *a priori*. Instead, its variables – mean growing season temperature, mean annual precipitation, and their interaction – were chosen based on an established hypothesis linking global diversity gradients to climate (Francis and Currie 2003). The model's predictions were likely hindered by two factors. First, it excluded effects of habitat heterogeneity, which are known to affect butterfly species richness in Canada (Kerr 2001, Kerr et al. 2001) and, second, precipitation effects are most prominent in sub-tropical and tropical areas (Hawkins et al. 2003) well south of Canada. Despite these limitations, the minimum macroecological model's predictions were still sufficiently accurate and precise to be useful in a conservation context if other, system-specific, regression models were unavailable.

Our results are unlikely to be biased by the necessary level of estimation involved in reconstructing historical and recent diversity patterns. Small errors in estimated ranges, especially at their margins, are unlikely to have substantial influence on my results due to my method of sampling richness at a relatively coarse grain (100km x 100km). Although I constructed distribution models and generated predictions using the same environmental data, this approach is not tautological, since each species range was modelled independently. Thus, all species could potentially have responded to the relevant environmental variables in a manner that produced patterns of richness that were not highly correlated with climate. Thus, areas of high richness reflect underlying commonalities in species' niche requirements.

Empirical diversity theory, based on decades of macroecological research into spatial diversity gradients, produces reliable and remarkably accurate predictions of diversity shifts as environmental conditions change. Moreover, this approach, when incorporating spatial autocorrelation, outperformed the more common aspatial method of summing projected range shifts of individual species. This result highlights: 1) the usefulness of using global change to test ecological theory; 2) the importance of incorporating spatial information in lieu of complete information on environmental influences; and 3) how ecologists can exploit past global change to produce the most reliable predictions possible of future biological responses to continually changing climate and land-use regimes.

Tables

Table 2.1. Summary of predictive approaches compared in this study.

	Approach	Description
Empirical diversity theory approaches	Best-OLS	Fits a series richness-environment regression to historical data; The best of these is the one with the highest R^2. These coefficients are then used to predict richness in recent time period.
	Best-CAR	Fits a richness-environment regression to historical data using the same environmental variables as the Best-OLS. Conditional autoregression is used to estimate coefficients to account for the influence of spatial autocorrelation
	Committee Average	Fits a large number of richness-environment regressions to historical data. Identifies a candidate set of models with adjusted-R^2 values within 0.05 of the best model. The committee average is the mean prediction across all models in the candidate set
	Consensus Forecast	A principal components analysis is performed on the predictions of all models in the candidate set (defined above). The model with the highest loading on PC1 is identified and its predictions are considered to represent the consensus among all candidate models
Individual niche model approaches	Committee Average	For each species, ten repetitions of the historical Maxent niche model were projected forward. The mean of these projections was converted to a binary range for each species and the ranges summed to produce richness predictions
	Single-Best	For each species, the historical Maxent model repetition with the highest area under the curve (AUC) was projected forward and converted to a binary range. Ranges were then summed across all species
	Consensus Forecast	For each species, a principal components analysis was run on the 10 Maxent model projections and the repetition with the highest loading on PC1 was converted to a binary range. Richness was calculated as described above.

Table 2.2. Correlation matrix of variables used in regression analysis from the historical time period. Tmaxgr is maximum growing season temperature, Tavggr is mean growing season temperature, Tmin is minimum yearly temperature, Pcpyr is mean annual precipitation, Popn is human population densisty, Erange is elevation range and Vgtvar is the number of land-cover classes.

	Tmaxgr	**Tavggr**	**Tmin**	**Pcpyr**	**Popn**	**Erange**
Tmaxgr						
Tavggr	0.991					
Tmin	0.953	0.930				
Pcpyr	0.581	0.543	0.732			
Popn	0.570	0.570	0.556	0.361		
Erange	-0.190	-0.117	-0.105	0.131	-0.109	
Vgtvar	0.531	0.554	0.523	0.429	0.010	0.271

Table 2.3. Comparison of multiple approaches of predicting diversity shifts. Slopes and intercepts are from observed-predicted richness regressions, Pearson's r is the correlation between observed and predicted richness, P-value quadratic is the P-value of a predicted^2 term in observed-richness regressions. Trend in residuals is the slope of the residuals^2-predicted regression, where residuals are from the linear observed-predicted richness linear regression. Bracketed terms are performance rankings relative to the other approaches.

	Approach	**Slope†**	**Intercept‡**	**Pearson's r**	**P-value quadratic‡**	**Trend in residuals‡**	**Rank sums**
Empirical diversity theory approaches	Best-OLS	0.96*** (4)	4.29*** (5)	0.96*** (5)	$<10^{-8}$ (6)	1.14*** (5)	**25**
	Best-CAR	1.01 (1)	0.23 (1)	0.97*** (4)	0.74 (1)	0.99*** (4)	**11**
	Committee Average	0.97* (3)	3.22*** (4)	0.95*** (7)	0.08 (3)	1.39*** (6)	**23**
	Consensus Forecast	0.95*** (5)	4.66*** (6)	0.95*** (6)	$<10^{-10}$ (7)	1.49*** (7)	**31**
	Min. Macro. Model	0.92*** (7)	5.34*** (8)	0.91*** (8)	0.12 (2)	1.60*** (8)	**33**
Individual niche model approaches	Committee Average	0.98* (2)	4.95*** (7)	0.99*** (3)	$<10^{-29}$ (8)	0.19*** (1)	**21**
	Single-Best	0.93*** (6)	–0.56 (2)	0.99*** (1)	0.04 (4)	0.44*** (3)	**16**
	Consensus Forecast	0.92*** (8)	–0.86 (3)	0.99*** (2)	$<10^{-7}$ (5)	0.44*** (2)	**20**

†$H_0 = 1.0$, ‡$H_0 = 0.0$

*p<0.05, **p<0.01,***p<0.001

Figures

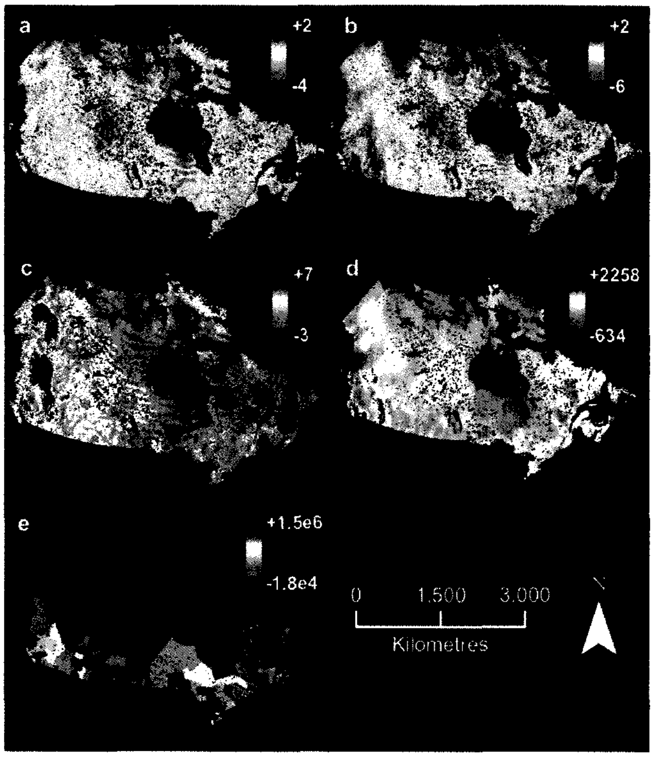


Figure 2.1. Climate and human population change in Canada from the historical (1900-1930) to recent (1960-1990) time periods. Difference maps were created by subtracting historical from recent conditions. Maps are for mean growing season temperature (a), maximum growing season temperature (b), minimum yearly temperature (c), mean annual precipitation (d), and human population density (e). Data are from a variety of sources: Mekis and Hogg (1999), McKenney et al. (2001), McKenney (personal communication), and White and Kerr (2006).

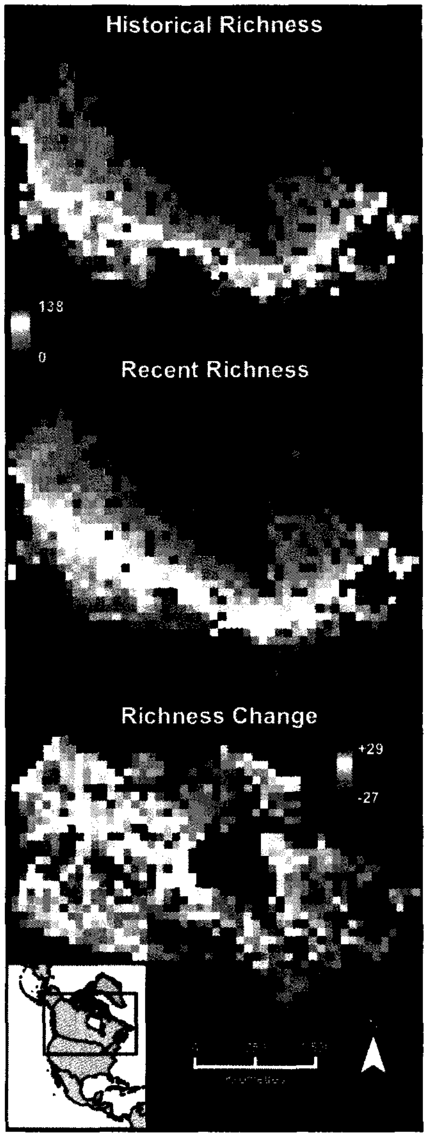
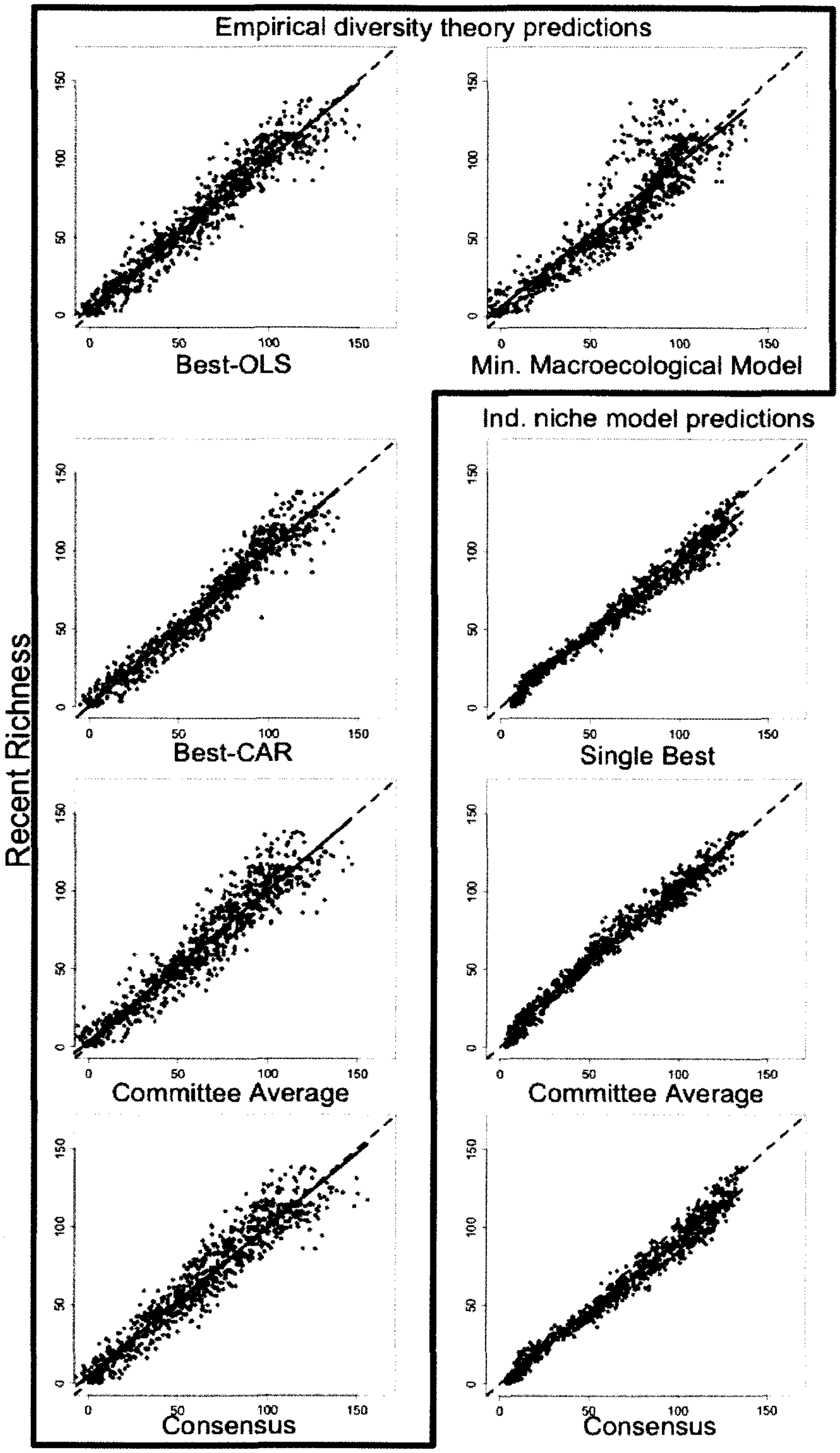


Figure 2.2. Patterns and change in butterfly species richness throughout Canada during the 20th century for the 139 species used in our analysis. In the historical (1900-1930) and recent time periods (1960-1990), reds represent high diversity and blues low diversity. For richness change, reds indicate increases in diversity, blues indicate decreases. Richness was measured in 100km x 100km quadrats.

Figure 2.3. Observed vs. predicted richness in the recent time period for various predictive approaches. Predictions are on the x-axis. See Table 2.1 for methods description. Models were trained on data on butterfly species richness in the early 20th century (1900-1930) and predictions of richness in the late 1900s (1960-1990) were generated based on observed environmental changes. Observed richness is the observed richness in the late 20th century. The red-line is the OLS regression line and the black line is the 1:1 line representing perfect agreement between expectations and observations. OLS is ordinary-least-squares and CAR is conditional autoregression.


Empirical diversity theory predictions
Best-OLS
Min. Macroecological Model
Ind. niche model predictions
Best-CAR
Single Best
Committee Average
Committee Average
Consensus
Consensus
Recent Richness
0
50
100
150

Chapter 3: Evolutionary constraints on regional faunas: whom, but not how many

Abstract

The latitudinal diversity gradient has been hypothesized to reflect past evolutionary dynamics driven by climatic niche conservation during cladogenesis, i.e. the tropical conservatism hypothesis. Here I show that the species diversity of treefrogs (Hylidae) across the western hemisphere is actually independent of evolutionary niche dynamics. I evaluated three key predictions of the tropical conservatism hypothesis that relate to the relationships between climate, species richness and the phylogenetic structure of regional treefrog faunas across the continental Americas. Species composition was dependent on the inability of some lineages to evolve cold tolerance, but the actual number of species in a region was strongly predicted by precipitation, not temperature. Moreover, phylogenetic structure was independent of precipitation. Thus, species in low richness areas were no more closely related than species in highly diverse regions. These results provide no support for the tropical conservatism hypothesis. Instead, they show that regional species composition and richness are constrained by different climatic components, demonstrating that global biodiversity gradients can be independent of niche stasis during cladogenesis.

Introduction

Climate plays a key role in the distribution of global biodiversity and in the evolution of individual species' niches during cladogenesis (Hawkins et al. 2003, Smith et al. 2005, Wiens et al. 2006). The well-known latitudinal diversity gradient is a global phenomenon (Orme et al. 2005, Grenyer et al. 2006, Buckley and Jetz 2007) that is nearly ubiquitous across all major taxonomic groups in terrestrial environments (Hillebrand 2004). This increase in species richness from the poles to the tropics is highly collinear with climate, producing some of the strongest correlations in any ecological field ($r = 0.6$ to 0.9, Hawkins et al. 2003). Phylogenetic correlations of climatic tolerances are similarly high, demonstrating that even across diverse clades, niches can be strongly conserved (Smith et al. 2005, Wiens et al. 2006). It is generally thought that the latter produces the former: the latitudinal diversity gradient is a result of niche dynamics during cladogenesis, specifically the conservation of climatic niche components (the tropical conservatism hypothesis, Hawkins et al. 2005, Hawkins et al. 2006, Ricklefs 2006, Wiens et al. 2006).

Climatic niche conservatism is central to the idea that evolutionary niche dynamics create the latitudinal diversity gradient. Simply put, niche conservatism is the maintenance of ancestral niche characteristics in daughter species (Wiens and Graham 2005). Niche characteristics could encompass any number of abiotic or biotic interactions. The tropical conservatism hypothesis relies most clearly on Hutchinson's concept of the fundamental niche (Wiens and Graham 2005). In this context, climatic niche components define a species' abiotic tolerances and, consequently, its fundamental niche. At regional scales, these limits are the most extreme value of a given climatic component experienced by a species

(Wiens and Graham 2005).

As an explanation of low temperate diversity, the tropical conservatism hypothesis integrates the phylogenetic correlation of species climatic tolerances with the observation that many clades originated in the tropics (Ricklefs 2006). After such a clade arises, the hypothesis suggests that during subsequent cladogenesis, niche conservatism maintains climatic barriers to dispersal and range expansion that result in a build-up of species close to the area of origin. Rarely, an evolutionary event produces a species that is able to survive and reproduce in novel climatic conditions (Wiens and Donoghue 2004, Wiens and Graham 2005, Ricklefs 2006), for example by evolving the ability to tolerate freezing. This derived lineage can then continue to diversify, with descendent species eventually invading even more challenging environments. Under such a process, relatively few clades will escape the tropics, resulting in decreasing species richness from the tropics to the poles: the latitudinal diversity gradient.

Evolutionary-based hypotheses have considerable potential to explain the substantial increase in species diversity from polar to tropical regions; however, they are often hindered by the difficulty in generating testable predictions from their proposed processes. To be rigourously tested, evolutionary hypotheses must explicitly predict links between evolutionary patterns and species richness across broad spatial extents. Despite its prominence in recent literature (Wiens and Donoghue 2004, Hawkins et al. 2005, Wiens and Graham 2005, Hawkins et al. 2006, Ricklefs 2006, Wiens et al. 2006), studies of niche conservatism and diversity gradients have not tested such predictions. Most research to date has focused primarily on establishing whether any evidence consistent with phylogenetically conserved niches can be identified (Hawkins et al. 2006; Wiens et al. 2006). Such investigations have revealed some intriguing patterns (Currie et al. 2004): Hawkins et al. (2006) showed increased evolutionary derivedness toward polar regions for birds, while Wiens et al. (2006) and Smith et al. (2005) both found phylogenetic evidence of climatic niche conservatism in hylid frogs. However, these studies have left the critical prediction untested: if climatic niche conservatism during cladogenesis determines global diversity gradients, then regional diversity must be directly linked to the phylogenetic signature of niche conservatism.

Here, I examine data on both treefrog (Hylidae) species richness and phylogeny (Faivovitch et al. 2005) to provide a novel test of the link between climatic niche conservatism and the latitudinal diversity gradient in the western hemisphere. To spatially quantify the phylogenetic signature of niche conservatism, I utilize two recently developed fauna-wide metrics of phylogenetic structure (Kerr and Currie 1999, Helmus et al. 2007a). Mean root distance (MRD) measures the evolutionary derivedness of species (Kerr and Currie 1999, Hawkins et al. 2005, Hawkins et al. 2006); it is the average number of nodes separating the species in a region from the root of their phylogenetic tree. Phylogenetic species variability (PSV, Helmus et al. 2007a) is a measure of faunal relatedness, or phylogenetic clustering (Webb 2000). PSV is calculated from the number of nodes between the tips and root of the tree that are shared by all pair-wise combinations of species in a fauna. It ranges from zero for highly clustered faunas to one for non-clustered faunas (Helmus et al. 2007a).

Simple scenarios of niche conservatism during cladogenesis along an environmental gradient predict specific relations among environment, richness, MRD, and PSV (Figure 1.1). A simple simulation model indicates that these predicted relationships also apply to less idealized scenarios that incorporate additional effects of extinction (Appendix 1). Three explicit relationships are predicted. First, geographical variation in MRD and PSV should be predicted by climate; since the warm, wet tropics represent the clade's ancestral climatic conditions (Wiens et al. 2006), niche conservatism should cause phylogenetic clustering to be greater and MRD higher in areas of lower temperature and/or precipitation (or related variables, Figure 3.1, Appendix 1, Stevens 2006, Kraft et al. 2007). Second, richness should correlate positively with PSV and negatively with MRD (Figure 3.1, Appendix 1). Third, after accounting for the effect of evolutionary structure, little or no residual correlation between climate and richness should remain. Treefrogs are an ideal model taxon on which to test these predictions: they are diverse (492 species were used in my analysis), originated in the tropics, and display no latitudinal trends in absolute diversification rates that could obscure the effects of niche conservatism (Wiens et al. 2006). The latter point is important as latitudinal variation in absolute diversification rate (diversification events in a region per unit time, as compared to diversification events per species per unit time) could confound measures of root distance and phylogenetic clustering.

Our analysis revealed that the latitudinal diversity gradient is independent of niche conservatism during cladogenesis. Faunal phylogenetic structure (PSV and MRD) was strongly related to minimum annual temperature, indicating the evolutionary conservation of cold tolerance. However, species richness was best predicted by precipitation, not temperature, and was independent of phylogenetic structure, a direct contradiction of tropical conservatism's predictions. These results demonstrate the strong role of climate in determining regional faunal structure, but they provide no support for clear evolutionary control of regional diversity gradients via niche conservatism. Instead, for the diverse treefrogs, the latitudinal diversity gradient is dominated by a strong relationship with precipitation.

Materials and Methods

Indices of phylogenetic structure

I examined two measures of phylogenetic structure that are indices of niche conservatism: mean root distance (MRD), which is a measure of average evolutionary derivedness (Kerr and Currie 1999, Hawkins et al. 2005, Hawkins et al. 2006), and phylogenetic species variability (PSV), which is a measure of phylogenetic clustering (Helmus et al. 2007a). MRD is easily calculated by tallying the number of nodes separating each species in a fauna from the root of the phylogenetic tree, and then taking the mean over all species in any given assemblage. PSV ranges from zero to one, where the latter indicates that species in a region are unrelated (all species are from disparate parts of the tree), and values of zero indicate perfect relatedness. PSV is calculated from a matrix, **V**, whose diagonal elements give the evolutionary divergence of each species from the root to the tips of the tree, and the off-diagonal elements represent the degree of shared evolutionary history among species. **V** can thus be thought of as a variance-covariance matrix of neutral trait values, where elements on the diagonal represent variance in the neutral trait, and off-diagonal elements covariance in trait values among species Though Helmus et al. (2007a) formulated their metric in the context of a neutral trait, they note that no actual information on trait values is necessary to compute or interpret the index.

Helmus *et al.* (2007a) present the following equation (their eq. 1), for the expected variance in trait values among species in an assemblage, for a tree with contemporaneous tips:

$$E\{(X_i-\bar{x})^2\}=\frac{\sigma^2}{n^2}(ntr(\boldsymbol{C})-\Sigma\,\boldsymbol{C}) \tag{1}$$

where, σ^2 is the average rate of evolutionary divergence for all species, **C** is the matrix **V** scaled to have ones on the diagonal (i.e. a correlation matrix), tr(C) is the trace of C, ΣC is the sum of all elements in C, and *n* is the number of species. Eq. 1 can then be converted to PSV by standardizing by the maximum possible variance among species, which occurs when the underlying phylogeny is a star (equation 2 in Helmus et al. 2007a):

$$PSV=\frac{ntr(\boldsymbol{C})-\Sigma\,\boldsymbol{C}}{n(n-1)} \tag{2}$$

In a tree lacking branch lengths, tips are not contemporaneous; instead species are separated from the root of the tree by differing numbers of nodes and thus the matrix **V** cannot be scaled to a correlation matrix with ones on the diagonal. Fortunately, equation 2 can be easily modified to account for these differences, by replacing **C** with **V** in the numerator of eq. 2, and replacing the *n* term in the denominator (which in eq 2 represents tr(**C**) because **C** is a correlation matrix) with tr(**V**). Replacing tr(**C**) with tr(**V**) accounts for the differences in root distance among species:

$$PSV=\frac{ntr(\boldsymbol{V})-\Sigma\,\boldsymbol{V}}{tr(\boldsymbol{V})(n-1)} \tag{3}$$

Eq. 3 gives identical results as eq. 2 when the tree is ultrametric. Note that MRD can also be easily calculated from the matrix **V**, where *MRD* = tr(**V**)/*n*.

Phylogeny

I used the phylogeny of Faivovitch *et al.* (2005) to evaluate faunal phylogenetic structure. This phylogeny includes the majority of Hylidae genera in the Americas and is resolved to the genus and species group level. Eleven of the 492 species in my analysis were not included in Faivovitch et al.'s lists; I placed these species in the phylogeny on the basis of their generic name and assigned them randomly to a species group within their genus. The Faivovitch et al. phylogeny is based on both morphological and molecular characteristics and has been broadly corroborated by Wiens et al. (2005). The phylogeny lacks branch lengths; therefore, I considered all branches to have a length of one. Nodes that involved branches to lineages not present in the study area were left in the phylogeny as these still represent potentially important branching events. Because the Faivovitch et al. phylogeny is resolved only to the generic and species group level, and my phylogenetic-structure measures required all species to be included in the phylogeny (Webb et al. 2002), I included species by grafting them onto the tips of the phylogeny as polytomies with branch lengths of zero. While not optimal, the grafting of polytomies is a common practice in studies of community phylogenetic structure (Webb 2000, Hawkins et al. 2005, Hawkins et al. 2006, Stevens 2006). Our method creates a tree in which species within species groups retain closer linkages to each other than to species in other groups, a reasonable approximation. Unfortunately, phylogenies that are well-resolved at the species level for all species in a clade are rare, and they are non-existent for widespread, diverse taxa that can be used to test broad-scale hypotheses. To limit biases generated by this uncertainty, I also performed my analysis using a phylogenetic tree in which the branch lengths within each polytomy were set to the average number of nodes separating a species from the root in randomly resolved trees of a given diversity (Webb 2000). In the resulting tree, two species that arise from a small polytomy are, on average, more closely related than two species arising from a large polytomy, a reasonable approximation.

Species richness and environmental data

I obtained, from Natureserve (www.natureserve.org), range maps for all hylid species in the continental Americas represented in the Faivovitch et al. (2005) phylogeny. Natureserve did not have ranges for the genus *Dendropsophus*, therefore I excluded this genus from my analysis. To sample richness, I overlaid these maps on a grid of 100 km x 100 km equal area quadrats covering the continental Americas. To reduce potential effects of small land areas of coastal quadrats, I removed all quadrats that contained less than 50% land. The species richness of a quadrat was considered to be the number of individual ranges that overlap the quadrat. Since my goal was to analyse patterns in faunal relatedness, I also removed all quadrats that contained less than two species, since a fauna that contains only a single species is, by definition, perfectly related. This left me with 2244 equal area quadrats.

Environmental data were sampled for the same 2244 quadrats. Climatic measures were obtained from Worldclim (www.worldclim.org) at 30 second resolution. For each quadrat I sampled the mean annual temperature, mean minimum temperature (the average minimum temperature of the coldest month), mean annual precipitation, and mean minimum precipitation. I also obtained mean net primary production from the MODIS satellite (www.disc.sci.gsfc.nasa.gov/MODIS/), and I considered two measures of heterogeneity: the number of land-cover classes per quadrat, generated from Global Mosaic SPOT VGT 2000 data (http://www-tem.jrc.it//Processed_Satellite_Data_Sets/glc2000 vegetationmosaic.htm), and the range in elevation within a quadrat, which was also obtained from Worldclim.

Regression and path analysis

To guide my path analysis, and to ensure that I were including the strongest environmental predictors of species richness, PSV, and MRD, I first performed a series of regressions. I examined univariate relationships between my three response variables and each of the environmental predictors. I next tested whether these relationships were better described by a curvilinear model by including a quadratic term in each regression. Testing for curvilinearity was especially important since path analysis requires linear relationships between variables (Shipley 2000, Grace 2006). Lastly, I tested models that included temperature and precipitation (the strongest univariate predictors of all response variables) and an interaction term between the two (a model that is commonly considered in macroecological analysis; the interaction term is also highly collinear with actual evapotranspiration). For all analyses, mean minimum precipitation, mean annual precipitation, and net primary productivity were log transformed to improve normality. Species richness and MRD were square-root and log transformed, respectively, to maximize normality in regression residuals. It was not necessary to transform PSV. As my goal was simply to identify predictors for my path analysis, I did not yet consider potential effects of spatial autocorrelation or null models of phylogenetic structure.

Our regression analysis identified mean minimum temperature (MINT) and mean annual precipitation (MAP) as the strongest predictors of richness, PSV, and MRD (Table 3.1). To test whether richness was primarily affected by climate via evolutionary processes, I constructed a path model that included direct effects of MINT and MAP, as well as indirect effects via PSV and MRD. I analysed my model using the sem library (Fox 2007) in R v. 2.6.0 (R Development Core Team 2007). All variables were first standardized to a mean of zero and a variance of one to allow for the comparison of path coefficients connecting variables with different initial units.

Spatial patterns in MRD and PSV can arise simply as a result of sampling effects due to differences in species richness between regions; therefore it is necessary to compare results to a null model (Webb 2000, Hawkins et al. 2005, Hawkins et al. 2006, Stevens 2006, Helmus et al. 2007a). A variety of null models have been used in ecological analysis, therefore it is important to utilize a model that provides an appropriate null hypothesis. Our hypotheses about the processes that produce spatial patterns of richness made predictions about where co-occurring species would occur on the phylogenetic tree, which were quantified using PSV and MRD. I therefore generated a null distribution in which species were randomly shuffled on the tips of the phylogeny. Our primary interest was not in the statistical significance of MRD and PSV for individual faunas, but rather the gradients of MRD and PSV along climatic gradients (for further justification, see Stevens 2006). Therefore, for each of 999 randomly shuffled phylogenies, I computed MRD and PSV for all 2244 quadrats. I next recalculated my path model 999 times to generate null distributions of path coefficients for paths that involved either MRD or PSV for comparison to the actual coefficients. Because I had specific expectations as to the direction of these effects, I considered one-tailed tests with $\alpha = 0.05$. Spatial autocorrelation remained in the residuals of my path analysis. To account for this, I adjusted the degrees of freedom and re-performed statistical tests of path coefficients to ensure that my analysis were not prone to inflated Type

I error rates (Fortin and Dale 2005). Geographically effective degrees of freedom were calculated using the observed spatial autocorrelation in model residuals, following the procedure described in detail by Dale and Fortin (2002). This procedure left 432 degrees of freedom to evaluate paths linking climate and PSV, 321 for MRD, and 299 for paths leading to species richness. This approach has been used successfully in other studies that have used path analysis to examine richness gradients (Harrison and Grace 2007).

Our analysis could be confounded by the effects of widespread species if they also have high root distances (e.g. Prinzing et al. 2004). Since widespread species occur in more quadrats than narrow-ranged species, then if they are consistently highly evolutionarily-derived, they will disproportionately increase the MRD of multiple regions. I tested for this effect by computing the correlation between the number of quadrats occupied by a species (i.e. range size) and root distance for all species.

Results

Species richness, PSV, and MRD all displayed substantial geographic variation (Figure 3.2). Of a wider set of environmental variables, including net primary productivity and two measures of environmental heterogeneity, the hemispheric variation in MRD and PSV was most strongly related to minimum temperature ($r^2 > 0.45$ in both cases) and to a lesser extent, to mean annual precipitation (Table 3.1; Figure 3.3). Spatial variation in species richness was strongly related to both precipitation (r^2=0.57) and minimum temperature (r^2=0.51).

Our path analysis clearly shows that geographical patterns of faunal phylogenetic structure show a strong direct relationship with minimum temperature (Figure 3.4). Also, the sign of the path coefficients leading to PSV matched my predictions. The coefficient leading from minimum temperature to MRD also matched my prediction; though adjusting branch lengths to account for differing polytomy sizes suggests that this result may not be robust to phylogenetic uncertainty (Appendix 2). Paths leading to PSV remained consistent after applying this correction. These results held even after I adjusted the degrees of freedom of statistical tests to account for spatial autocorrelation and randomly shuffled species on the phylogeny's tips to account for constraints of overall tree structure (Figure 3.4). These results are not confounded by an effect of widespread species as range size was not correlated with species' root distances (Pearson's $r = 0.02$, $P > 0.33$).

Species richness was effectively independent of faunal phylogenetic structure (Figure 3.4). Richness was only weakly related to PSV and MRD; these constituted only 14% of the total effect of all factors on richness (Figure 3.4). Instead, species richness was strongly and directly related to precipitation with a path coefficient of 0.48, comprising 51% of the total effect on richness. However, precipitation had no role in determining either PSV or MRD (Figure 3.4), revealing an almost complete climatic decoupling of species richness and niche dynamics during cladogenesis. Minimum temperature did have a smaller direct effect on species richness, but this was also independent of phylogenetic structure of the assemblages present in any given location (Figure 3.4). These conclusions were unaffected by applying the polytomy branch length correction (Appendix 2).

Discussion

The tropical conservatism hypothesis posits that evolutionary niche dynamics, coupled with the tropical origin of many clades, produce the latitudinal diversity gradient

(Wiens and Donoghue 2004, Wiens and Graham 2005, Ricklefs 2006, Wiens et al. 2006). If climate affected phylogenetic structure, which in turn determined richness, then richness should be most strongly related to phylogenetic structure, and only indirectly related to climate. Our analysis reveals that minimum temperature predicts faunal phylogenetic structure very well, indicating that cold tolerance (or lack thereof) is phylogenetically conserved. This result is consistent with the first prediction of the tropical conservatism hypothesis and with purely phylogenetic analysis of niche correlations in temperate hylids (Smith et al. 2005). However, the correlation between phylogenetic structure and climate represents only the first half of the evolutionary conservatism hypothesis; the second half is the correlations between species diversity and phylogenetic structure. Here, the tropical conservatism hypothesis fails. Contrary to the hypothesis's predictions, the hemispherical diversity gradient in hylid frogs is independent of niche conservatism's effects on faunal phylogenetic structure. Instead, richness is best predicted by precipitation.

I suggest that the constraints that evolutionary niche dynamics place on regional faunal structure determine the species composition in a region, but not the number of species that persist there. Previous work on hylid frogs revealed a strong phylogenetic signature of niche conservatism: Smith et al. (2005) found strong phylogenetic correlation of minimum temperature tolerance in temperate hylids, while Wiens et al. (2006) found that temperature seasonality predicted northern range limits of six tropical hylid species. Our analyses of entire hylid assemblages across the Americas are consistent with these findings but clarify niche conservatism's role in determining ecological patterns along environmental gradients. Our findings indicate that phylogenetically constrained niche components, such as cold tolerance, relate to broad patterns of species co-occurrence. An extension of this finding is that phylogenetic information can increase my ability to predict which species will occur where (Peterson et al. 1999). However, niche conservatism during cladogenesis does not constrain the species diversity of a region: species inhabiting low richness areas are no more likely to be closely related than those in species rich regions. While evolutionary history has left an indelible imprint on regional species composition, its influence over the latitudinal diversity gradient, at least for hylid frogs, is minimal.

Although my study focused solely on hylid frogs, several consistencies suggest that my results may apply more broadly, though further tests are necessary to test this conjecture. First, global variation in the species richness of amphibians as a whole is strongly related to precipitation (Buckley and Jetz 2007), a somewhat intuitive relationship given this class's obvious water requirements. For amphibians there is evidence that absolute diversification rates are higher in tropical regions, though the hylids are an exception (Wiens 2007); explicit tests of whether variation in absolute diversification rate can account for the amphibian climate-richness relationship are still lacking. The strong relationship between precipitation and species richness is also shared by a wide variety of other taxa in warm regions, including both ectotherms and endotherms, vertebrates and invertebrates, and plants (Hawkins et al. 2003). I do not know if evolutionary niche dynamics in these other groups are more strongly related to temperature than to precipitation, as in hylids, since phylogenies of broad clades over hemispheric extents are not generally available. As these phylogenies are generated, they will allow for the generality of my findings to be tested in additional clades and geographical domains.

It is still unknown what mechanism(s) produce(s) the broad-scale correlation between richness and precipitation. The lack of correlation between precipitation and phylogenetic structure indicates it is not a result of niche constraints with respect to precipitation regimes. It is also unlikely to be due to systematic variation in absolute diversification rates as hylid absolute diversification rate does not vary with latitude (Wiens et al. 2006). Our analysis also eliminates a response to primary productivity or habitat heterogeneity as potential dominant explanations since both predicted less variation in diversity than precipitation. One remaining possible explanation is suitable habitat area: regions with high precipitation may contain large amounts of habitat that is sufficient for hylid persistence, or have increased coincidence of pre- and post-metamorphic habitats in wetter regions, both of which can predict richness at local-scales (Becker et al. 2007, Werner et al. 2007). Tests of this possibility at a global scale are still lacking. Alternatively, perhaps the population densities at which species can persist vary inversely with precipitation, leading to increased richness when the total number of individuals in a region is constant. Finally, I also cannot exclude the possibility that some complex set of evolutionary and ecological factors combine to produce the precipitation-richness correlation.

Phylogenetic information can contribute substantially to our understanding of the processes structuring ecological communities (Webb et al. 2002). Tests of evolutionary explanations for the latitudinal diversity gradient have been historically rare due to the difficulty of deducing quantitative predictions that can be explicitly linked to the macroecological pattern (Currie et al. 2004). However, I have shown that incorporating faunal phylogenetic metrics into macroecological analyses allows for rigourous tests of evolutionary hypotheses. Such tests require substantial information on species distributions and phylogenetic relationships (Webb et al. 2002). Unfortunately, well resolved species level phylogenies do not exist for any diverse, broadly distributed clade. Therefore, it is necessary to make assumptions with respect to final tree structure, especially with respect to intra-generic relationships. Our analysis appears to be relatively robust to these assumptions; correcting branch lengths to account for differing polytomy size had no effect on my conclusions. Despite these corrections, I cannot completely eliminate potential effects of phylogenetic uncertainty, especially the influence of poorly supported or incorrectly resolved nodes. However, changes in tree topology would have to be very substantial to destroy the correlation I observed with temperature and to yield one with precipitation instead. Such a major reorganization seems unlikely. It is more likely that phylogenetic uncertainty introduced noise into observed relationships. Nevertheless, the development of well resolved trees for diverse clades will undoubtedly allow for increasingly precise evaluation of faunal phylogenetic patterns and the processes that generate them.

To be considered strong, tests of evolutionary hypotheses for the latitudinal diversity gradient must not only evaluate explicit predictions, but must quantify evolutionary and diversity patterns at comparable spatial resolutions. Past studies of niche conservatism have relied on taxonomically coarse paleo-data that count orders instead of species (Martin et al. 2007), or have been limited to binary comparisons at coarse geographic resolution, comparing the tropics to extra-tropics (Jablonski et al. 2006). Studies of contemporary patterns have suffered from similar limitations, focusing on tropical or temperate areas in isolation (Kerr and Currie 1999, Smith et al. 2005, Wiens et al. 2006), or phylogenies with only family-level resolution (Hawkins et al. 2005, Hawkins et al. 2006). Our study is not free from these limitations, as I used generalized range maps and a species group-level, not a species-level, phylogeny; however, my study does have the advantage of having examined the entire hemispherical gradient with a large number of degrees of freedom. Additionally, my measures of phylogenetic structure allowed me to quantify the effects of niche conservatism at the same spatial scale at which the latitudinal diversity gradient is strongly apparent. It remains to be determined whether my findings not only apply to other taxonomic groups, but also at other spatial scales, especially with respect to local communities where species interactions are expected to play a greater role than in the 100 km x 100 km regions that have been my focus.

In conclusion, my study is not consistent with the hypothesis that niche conservatism from a tropical ancestor has produced the latitudinal diversity gradient in hylid frogs. This hypothesis postulates links between environment, niche dynamics, cladogenesis and diversity. Our tests showed that several of these links were missing. Instead, I found that species diversity and faunal phylogenetic structure are related to different climatic niche axes. Therefore, evidence of phylogenetic conservatism should not be taken as evidence that niche conservatism necessarily controls the latitudinal diversity gradient. For hylid frogs, the evolutionary constraints on regional faunas are limited to which species co-inhabit a region, but do not influence the number of species that persist there: whom, but not how many.

Tables

Table 3.1. Model fit parameters for regressions of species richness, phylogenetic species variability (PSV) and mean root distance (MRD) on environmental variables. MAT is mean annual temperature, MINT is mean minimum temperature, MAP is mean annual precipitation, MINP is mean minimum precipitation, NPP in net primary productivity, VGT is land-cover (vegetation) variety, ELEV is elevation range, ns indicates $P > 0.05$.

	Species Richness (square root)		PSV		MRD (log10)	
Variables in regression	R^2	AIC	R^2	AIC	R^2	AIC
MAT	0.468	6354.8	0.411	-2730.1	0.428	-6897.1
MINT	0.516	6141.0	0.468	-2960.7	0.477	-7095.8
log10(MAP)	0.570	5875.8	0.285	-2296.5	0.228	-6224.3
log10(MINP)	0.119	7484.1	0.004	-1552.6	MINP ns	MINP ns
log10(NPP)	0.359	6769.9	0.152	-1912.2	0.155	-6020.6
VGT	0.003	7761.4	0.028	-1607.9	0.025	-5700.8
ELEV	0.044	7668.6	0.004	-1553.1	0.006	-5656.6
MAT; MAT^2	0.480	6303.6	0.442	-2852.5	all ns	all ns
MINT; $MINT^2$	0.533	6062.3	0.489	-3048.6	0.477	-7096.1
MAP; MAP^2	MAP ns	MAP ns	all ns	all ns	MAP ns	MAP ns
NPP; NPP^2	all ns	all ns	NPP ns	NPP ns	NPP ns	NPP ns
VGT; VGT^2	0.045	7666.9	0.081	-1731.8	0.056	-5769.4
ELEV; $ELEV^2$	0.048	7659.5	0.027	-1603.2	0.035	-5719.8
MAT; MAP	0.647	5437.3	0.442	-2849.1	0.437	-6930.0
MAT; MAP; MAT*MAP	0.651	5413.0	MAT ns	MAT ns	MAT ns	MAT ns
MINT; MAP	0.650	5412.8	0.478	-3000.2	MAP ns	MAP ns
MINT; MAP; MINT*MAP	MAP;MAP*MINT ns	MAP;MAP*MINT ns	MINT;MAP ns	MINT;MAP ns	MINT ns	MINT ns

Figures

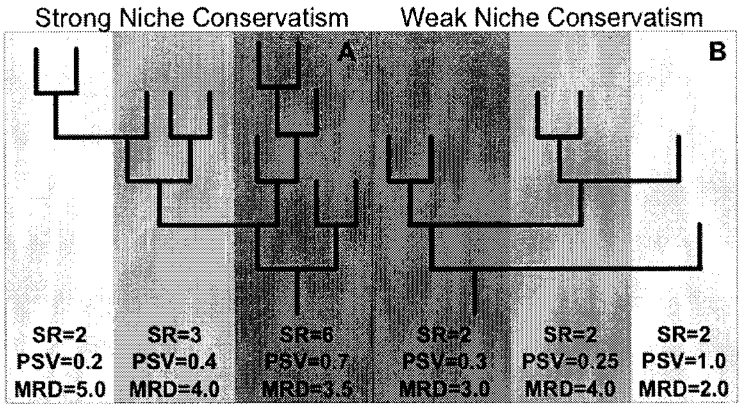


Figure 3.1. Idealized scenarios of cladogenesis along an environmental gradient when niche conservatism is strong or weak. When niche conservatism is strong (A), phylogenetic species variability (PSV) decreases and mean root distance (MRD) increases along the environmental gradient as species richness decreases. No pattern in MRD or PSV is expected when niche conservatism is weak (B). See also Ricklefs (2006).

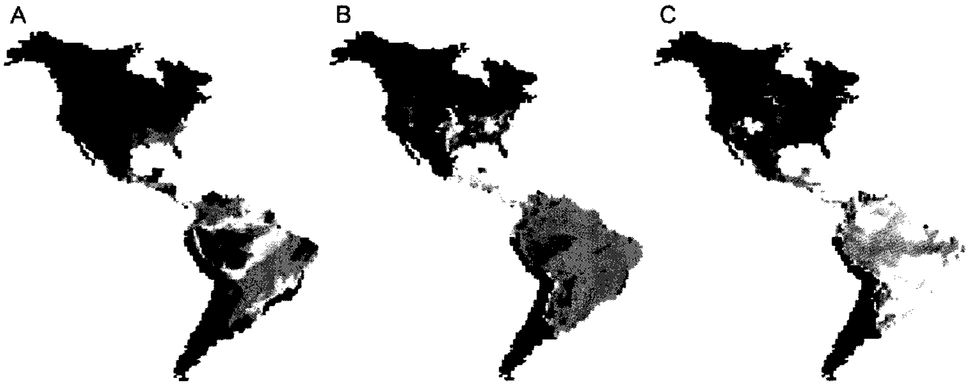


Figure 3.2. Spatial variation in species richness (A), mean root distance (B), and phylogenetic species variability (C). Black areas are those with less than two species in which PSV cannot be calculated. Hot (reds) and cold (blues) colours indicate high and low values respectively. Colour values are not comparable between maps.

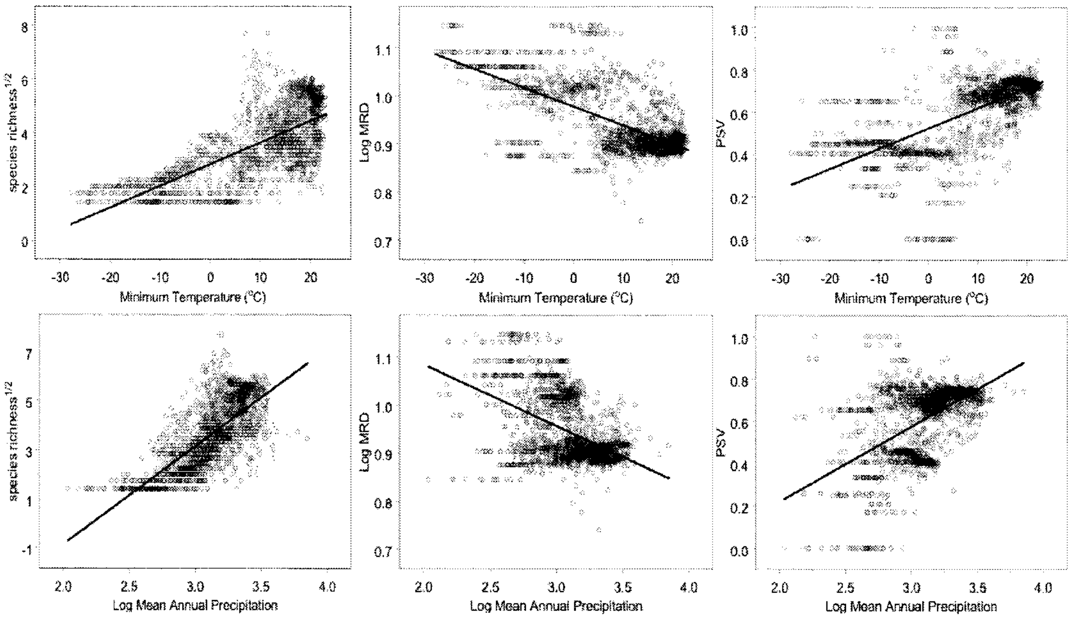


Figure 3.3. Relationships between species richness, mean root distance (MRD), and phylogenetic species variability (PSV) and minimum temperature and mean annual precipitation in the western hemisphere.

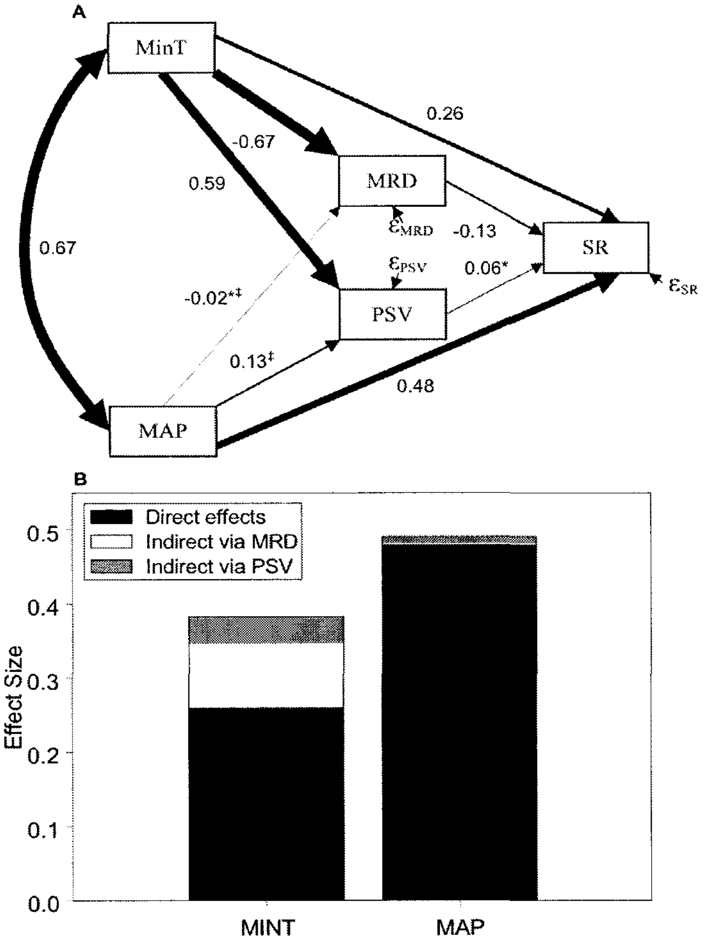


Figure 3.4. Direct and indirect effects of climate on species richness (SR). PSV is phylogenetic species variability, MRD is mean root distance, MINT is minimum temperature, MAP is mean annual precipitation, and ε is unexplained variation. (A) Values are standardized path coefficients; line width is proportional to the strength of the effect. * and ‡ indicate coefficients that were not statistically significant (α=0.05) after accounting for spatial autocorrelation or randomizing species on the phylogeny's tips, respectively; all other paths had $P < 0.05$. (B) The total effects of mean annual precipitation and minimum temperature on species richness.

Chapter 4: The relative importance of regional and local processes for community structure and trait evolution along a tropical-temperate gradient

Abstract

Communities can be structured by local and regional processes, but their relative importance is unknown. Furthermore, it has been suggested that at high latitudes regional climatic filters dominate, while in tropical climates, local competition is more important. To quantify the importance and variation of regional and local processes in structuring communities, I examined patterns of body size dispersion (BSD) in 61 treefrog (Hylidae) communities nested within 14 regional assemblages in the continental Americas. Overall, regional processes explained twice the variation in BSD than did local processes, but there was no strong increase in the importance of regional processes in cold areas. Hylid communities were generally slightly over-dispersed, suggesting they are competitively structured; however, there was no evidence for increased in over-dispersion in tropical areas. Regional BSD significantly decreased in cold areas, but there was no evidence of an elevated rate of body size evolution; the regional BSD gradient could be explained by a single-rate model of Brownian motion, suggesting that it arises primarily from the underlying geographic pattern of diversification in this clade.

Introduction

Ecological communities are nested within regional assemblages of species which are in turn nested within continental (and global) species pools. The structure of these communities is potentially subject to processes acting at both regional and local scales (Ricklefs 1987, Huston 1999, Willis and Whittaker 2002, Harrison and Cornell 2008). Regional processes shape the composition of regional species assemblages which in turn provide a pool of species which can potentially occur in a given local community (Cornell and Lawton 1992, Mittelbach et al. 2007). Regional processes include long-term evolutionary dynamics, large-scale dispersal between regions, and environmental (e.g. climatic) filters that prevent particular species from surviving within a region (Ricklefs 1987, Willis and Whittaker 2002). Local processes limit the membership of communities to a subset of the regional species pool. These processes include local scale habitat and environmental filtering (Kraft et al. 2008), biotic interactions (e.g. competition, Willis and Whittaker, Huston 1999), and ecological drift (Hubbell 2001). Local processes determine which species from the regional assemblage co-exist in individual communities.

A key unresolved question for ecologists is to what extent regional and local processes structure communities. Much of the research into local vs. regional processes has focussed on species numbers and determining whether regional richness influences local species richness (Ricklefs 1987, Cornell and Lawton 1992, Ricklefs 2006, Harrison and Cornell 2008). Such studies do not address questions of what determines species composition, or which processes structure the regional assemblage and how this may influence local communities. Also, although they detect a regional influence on local communities, they do not quantify the importance of these effects relative to those processes that are occurring at local scales.

The relative importance of regional and local processes are expected to change along broad climatic gradients. Building on the writings of Wallace and Darwin (Mittelbach et al. 2007), Dobzhansky (1950), Fischer (1960) and MacArthur (1972) all suggested that in high latitude environments, community structure will be determined by the requirement to survive and reproduce in 'harsh' climatic conditions; in more 'benign' environments, biotic interactions such as competition will determine community structure. This 'biotic interactions' hypothesis predicts that competition should be stronger in the tropics, and also that the relative importance of regional processes should increase in temperate climates.

It is becoming increasingly recognized that trait-based, rather than species-based, approaches to ecology can provide improved insight into the structuring of communities (McGill et al. 2006). Different processes are predicted to produce different patterns in the trait distributions of assemblages and communities. Abiotic conditions can act as environmental filters, limiting membership in the assemblage or community to those species with particular trait values, resulting in communities or assemblages with clustered distributions of trait values (Weiher et al. 1998, Kraft et al. 2008, Cornwell and Ackerly 2009). Alternately, competition among similar species can lead to competitive exclusion and trait distributions that are over-dispersed (Weiher et al. 1998, Kraft et al. 2008). This approach mirrors recent advancements in measures of phylogenetic community structure (Webb 2000, Webb et al. 2002). However, the phylogenetic approach relies on the oft-violated assumption that the relevant traits phylogenetically are conserved (or show phylogenetic signal, Losos 2008); the trait-based approach avoids this assumption.

Regional climatic conditions are suggested to act as environmental filters, limiting the composition of regional species assemblages to those species that can persist given the region's climatic regime (Algar et al. 2009). Given the large areas of most regions, competition is not likely to occur at the regional scale (Webb et al. 2002). Therefore, I predict regional assemblages to be clustered relative to the continental species pool, as clustering has been shown to increase with increasing spatial scale (Cavender-Bares et al. 2006, Swenson et al. 2007). If, as predicted by the 'biotic interactions' hypothesis, climatic filters become more important in harsh climates, then regional trait clustering should increase (i.e. trait dispersion should decrease) in cold and\or dry conditions.

Local communities can be structured by competition, or fine-scale environmental filtering (Weiher et al. 1998, Webb 2000, Kraft et al. 2008). If competition structures these communities, then I predict communities' trait distributions to be over-dispersed, relative to the regional species pool; fine-scale environmental filtering predicts clustered local communities. Comparing local communities to the regional species pool isolates the effects of processes acting at local scales from those occurring regionally (e.g. Stevens et al. 2006, Heard and Cox 2007). If local processes have only weak effects on community structure, then the trait distribution within local communities should not differ from the regional pool. If competition increases in importance toward the tropics, then communities should be increasingly over-dispersed in tropical regions.

The 'biotic interactions' hypothesis also predicts a gradient in the rate of trait evolution, with elevated rates in tropical areas (Mittelbach et al. 2007). This gradient could arise from two separate mechanisms. The first is a regional process: if climate acts as a regional filter, limiting the distribution of traits within the assemblage, then rates of trait divergence should be lower when regional filters are strong, i.e. in temperate areas. The second mechanism is 'bottom-up' rather than 'top-down'. Strong competition is predicted to lead to divergent natural selection amongst similar species, which in turn leads to trait divergence (Schluter 2000). This pattern, often linked to adaptive radiations, has been shown to occur in numerous taxa (Schluter 2000), including treefrogs (Moen and Wiens 2009), which are the subject of this study. Moen and Wiens (2009) found that *Osteopilus* (Hylidae) assemblages on Caribbean islands have evolved a wider range of body sizes, and have an elevated rate of evolution than comparable continental assemblages, probably as a result of strong competition between species.

In studies of trait community structure, it is critical to identify traits that are relevant to the processes under study (Kraft et al. 2008), and that vary between species and can be measured on continuous scales (McGill et al. 2006). I focus on patterns of body size dispersion (BSD) within local communities and regional assemblages of treefrogs in the family Hylidae. Across many taxa, body size is highly correlated with a broad suite of other physiological, morphological, and ecological traits (Peters 1983). At continental scales, recent work on hylids has shown that continental assemblages in temperate areas display less body size divergence (there is a lack of large species) than tropical assemblages (Moen and Wiens 2009), suggesting a potential link between body size and climate. At local scales, body size dispersion as an indicator of competition has a long (and somewhat chequered) history (e.g. Hutchinson 1959, Simberloff and Boecklen 1981, Dayan and Simberloff 2005). However, Moen and Wiens (2009) examined the relationship between prey size and type and body size in the hylid genus *Osteopilus*. They found that species generally overlapped in prey type, and that prey size was correlated with body size, suggesting that similarly sized species will compete more strongly for food resources than dissimilarly sized species. While these data are for a single, small genus of island endemic treefrogs, it suggests that competition for food can plausibly prevent the co-occurrence of similarly-sized hylid species. Therefore, body size has the potential to reflect both regional and local processes structuring communities.

Here, I examine variation in the relative importance of regional and local processes in structuring communities along a tropical-temperate gradient. I test four predictions: 1) regional body size dispersion will decrease in cold and/or dry climatic conditions; 2) body size dispersion will increase in tropical regions where regions are less clustered, relative to the regional species pool; 3) regional filters will account for more variation in body size dispersion in temperate regions compared to tropical ones; 4) rates of body size divergence will be higher in tropical regions than in temperate regions.

Methods

I compiled information on local community composition for 61 local communities from the published literature (Figure 4.1). These communities were nested within 14 World Wildlife Fund ecoregions (Figure 4.1, Olson et al. 2001). Details on these communities are given in Appendix 3. To be included in my study, papers had to provide the following information: adult species composition of individual ponds or stream segments (and surrounding habitat), latitude and longitude, elevation, and survey area. For water bodies for which only volume was reported, I converted this to surface area assuming a depth of 0.89 m^2 (the mean depth of other water bodies in the analysis). If elevation was provided in the original study, I used the given value. Otherwise, elevation was determined from a global digital elevation model (Worldclim; http://www.worldclim.org). Since the precision of geo-coordinates varied between the studies, the accuracy of my elevation estimates also varied unavoidably.

I considered regional assemblages to be all hylid species whose ranges overlapped the relevant WWF ecoregion. I used the Natureserve (http://www.natureserve.org) range maps for the 492 species compiled by Algar et al. (2009). As Natureserve did not include range maps for the genus *Dendropsophus*, I geo-referenced range maps provided online at http://www.amphibiaweb.org using ArcGIS 9.0 (ESRI 2004). Overall, my analysis included 580 species. For each ecoregion, in addition to species composition, I also obtained mean elevation, elevation range, and mean climatic data from Worldclim (http://worldclim.org). I considered four climatic variables: mean annual temperature, minimum annual temperature, mean annual precipitation, and minimum monthl ly precipitation. I also obtained mean actual evapotranspiration (AET) for each ecoregion from Tateishi and Ahn (1996). Macroecological analyses often use equal area quadrats (e.g. Hurlbert and Jetz 2007) to control for species-area effects. Although ecoregions differ in area (which I account for in subsequent analyses), they are less arbitrary than uniformly-sized quadrats and, at the very least, approximate legitimate ecological units.

Following Moen and Wiens (2009), I quantified body size as the maximum snout-vent length (SVL) for a species, regardless of sex. For the majority of South and Middle American species I used the body sizes given by Moen and Wiens (2009). Body sizes not included in Moen and Wiens' list were obtained from taxonomic references, field guides, and original species descriptions (Appendix 4)

To examine the rate of body size evolution, I used the phylogeny of Faivovitch et al.

(2005), which is resolved to the species group or genus level. The Faivovitch et al. phylogeny does not include branch lengths. To account for this I used two different branch length transformations. For the first I simply set all branch lengths equal to one. For the second I obtained four fossil dates from Wiens et al. (2005), including a root age of 55 million years. I then used the bladj function in Phylocom (Webb et al. 2008) to transform branch lengths. This transformation minimizes the variance among branch lengths given the constraints imposed by the supplied node ages (e.g. Swenson et al. 2006). Our results were nearly identical for both branch length transformations.

I quantified body size dispersion (BSD) in local communities and regional assemblages by calculating the mean distance, in trait space, between all pairs of species. Since I were dealing with a single trait, body size, this distance is the mean body size difference between pairs of species. Other measures of trait dispersion, most notably the range, have been used in other studies to quantify dispersion (e.g. Kraft et al. 2008, Moen and Wiens 2009). In my data, body size range and difference are highly correlated in both local communities (Pearson's $r = 0.85$, df=59, $p<10^{-15}$) and regional assemblages (Pearson's $r = 0.96$, df=12, $p<10^{-7}$). I focus on mean body size difference rather than range in subsequent analyses.

To determine if the BSD of regional assemblages decreased in 'harsh' climates, I compared a series of regression models that fit regional BSD to the temperature and precipitation variables and AET. I also examined a possible effect of elevation range (as a measure of heterogeneity). I transformed regional BSD (log(BSD + 0.5)) to retain consistency with local BSD for later analyses (see below). I considered linear and quadratic relationships as well as a model that included temperature, precipitation and their interaction

– a commonly used model in macroecology (e.g. Francis and Currie 2003). I used OLS regression because no detectable spatial autocorrelation remained in the residuals from the best fitting models (Moran's I = 0.09, P = 0.46). I evaluated whether differences in species richness among regions affected the observed relationship between regional BSD and environment by generating 1000 sets of null regional assemblages with species richnesses identical to the observed values by randomly drawing species, without replacement, from the continental species pool. I also generated 1000 sets of null regional assemblages by randomly shuffling body sizes among species. This latter approach accounts for differences in occurrence number (i.e. range size) among species. I used these null regional assemblages to generate expected distributions of the regression slope of the best-fitting model against which to compare the observed slope. I evaluated the significance of the relationship using a one-tailed test since I expected BSD to decrease with decreasing minimum temperature (the strongest predictor of regional BSD). This expectation is based on two previous observations. First, Moen and Wiens (2009) found that the range in hylid body sizes was reduced in temperate North America due to an absence of large species; Secondly, hylid body size shows a significant phylogenetic signal (Blomberg's K=0.66, P<0.001 using fossil calibrated branch lengths) and Algar et al. (2009) found that phylogenetic clustering of regional hylid assemblages increased with decreasing temperature.

To determine if local BSD increased in regions where regional filtering was weak, as predicted by the 'biotic interactions' hypothesis, I regressed local BSD on regional BSD. However, since my 61 local communities were located within 14 ecoregions, many local communities shared the same ecoregion. Local communities within an ecoregion should not be treated as independent data points since they share regional influences, as well as spatial proximity. The non-independence of spatially proximate data points (spatial autocorrelation) can bias coefficient estimates from ordinary least squares (OLS) regression and raise Type I error rates (Lennon 2000, Hawkins et al. 2007, but cf Beale et al. 2007, Diniz-Filho et al. 2007, Dormann 2007a). Therefore, I used a conditional autoregressive model (CAR, Lichstein et al. 2002) to evaluate the relationship between local and regional BSD. For the CAR, neighbours were defined as local communities within the same ecoregion. Also, for my regressions, local BSD was transformed (log (BSD+0.5)) to improve normality and account for BSDs that may equal zero (after transformation, Kolmogorov-Smirnov D = 0.14, P = 0.15). Log transformation of regional BSD did not improve its normality, however, I performed the transformation to retain comparability with local BSD. Generally, log transforming regional BSD increased the P-values of my subsequent statistical tests when compared to using raw regional BSD values.

To determine how local BSD would be expected to increase as a function of regional BSD in the absence of any regional-to-local filtering, I determined null expectations for the slope and intercept of the local-regional BSD relationship by generating a set of null local communities. Each of these null local communities was created by drawing, without replacement, from the relevant regional assemblage. The number of null local communities drawn from each region matched the number of communities sampled in each region; the species richness of null communities also matched the sampled communities. BSD was then calculated for each null community and null local BSD was conditionally autoregressed on regional BSD using the same connectivity matrix as above. This process was repeated 1000 times. The slope and intercept from the real data were then compared to the distributions of null values to determine if they differed significantly from the random expectation.

It is possible that survey area of local communities, or their position along local environmental gradients could influence the local-regional BSD relationship. Several studies have shown that clustering (trait or phylogenetic) of local communities can vary regularly along local gradients (Weiher et al. 1998, Bryant et al. 2008, Cornwell and Ackerly 2009), and with survey area (Swenson et al. 2007). To check for these effects I separately regressed local BSD on local area and relative elevation (local community elevation – mean regional elevation). Neither of these variables had significant effects ($P > 0.15$ in both cases) on local BSD. Ecoregion area also did not influence local BSD ($P > 0.10$). Therefore, I did not consider these variables further.

To test whether the observed gradient in regional BSD arose from an elevated rate of trait evolution in tropical areas, I used the sim.char function in the Geiger package (Harmon et al. 2008) for R 2.8.1 (R Development Core Team 2008) to simulate Brownian motion evolution of body size along my phylogeny. The Brownian motion model was parameterized using the phylogenetic mean (calculated using the R function Phylogmean; Luke Harmon, personal communication) as the ancestral state and the maximum likelihood estimate of the divergence rate parameter determined using the fitContinuous function in Geiger (Harmon et al. 2008). Using my simulated body sizes, I recalculated the BSD of my regional assemblages and recalculated the slope of the regional BSD-minimum temperature relationship. I repeated these simulations 1000 times to generate the distribution of slopes expected based on a single rate of body size evolution.

To quantify the proportion of the variance in BSD explained by local versus regional-scale processes, I developed a novel approach that modifies the traditional nested-ANOVA (Sokal and Rohlf 1995). The basic structure of my data allows the BSD of a local community to be partitioned into regional, local, and unexplained (community specific) effects. More formally, the BSD of local community *j* nested within region *i* can be expressed as a linear model:

$$L_{ij}=C+(R_i-C)+(\bar{L}_i-R_i)+(L_{ij}-\bar{L}_i) \tag{1}$$

where L_{ij} is the BSD of local community *j* in region *i*, *C* is the BSD of the continental species pool, R_i is the BSD of regional assemblage *i*, and $\bar{L}_i$ is the mean BSD of the n_i local communities in region i, calculated as:

$$\bar{L}_i=\frac{1}{n_i}\sum_{j=1}^{n} L_{ij}$$

The linear model in equation 1 can be expressed as the deviation of a local community's BSD from the BSD of the continental species pool:

$$(L_{ij}-C)=(R_i-C)+(\bar{L}_i-R_i)+(L_{ij}-\bar{L}_i) \tag{2}$$

The first term on the right side of the equation represents the regional effect on BSD. The second term represents the average local effect, and the third term represents the differences among local communities within a region. I determined the total variance, and the variance attributable to each of these effects by squaring both sides of equation 2 and summing across all local communities in *m* regions, assuming that the number of local communities (*n*) is invariant across regions:

$$\sum_{i=1}^{m}\sum_{j=1}^{n}(L_{ij}-C)^2=n\sum_{i=1}^{m}(R_i-C)^2+n\sum_{i=1}^{m}(\bar{L}_i-R_i)^2+2n\sum_{i=1}^{m}(R_i-C)(\bar{L}_i-R_i)+\sum_{i=1}^{m}\sum_{j=1}^{n}(L_{ij}-\bar{L}_i)^2$$

(3)

This equation differs from the standard nested ANOVA equation because of the existence of the covariance-like term on the right side of the equation. In a nested ANOVA, it would equal zero (Sokal and Rohlf 1995). However, in my formulation, the regional and continental BSD are not the mean of the samples at the next lower hierarchical level. Therefore, this term does not necessarily sum to zero, though empirically it could take this value. This covariance-like term will be positive if both regional and local effects push BSD in the same direction, i.e. if regions are clustered with respect to the continental species pool and local communities are clustered with respect to the regional assemblage. It will be negative if regional and local effects oppose each other (e.g. Helmus et al. 2007b). When these opposing effects are present, then the realized total sums of squares, expressed by the left side of equation 3, will be reduced. A more meaningful measure of the total sums of squares, which is not confounded by a negative interaction between local and region effect, is the absolute total sums of squares:

$$TSS=\left|n\sum_{i=1}^{m}(R_i-C)^2\right|+\left|n\sum_{i=1}^{m}(\bar{L}_i-R_i)^2\right|+\left|2\mathrm{n}\sum_{i=1}^{m}(R_i-C)(\bar{L}_i-R_i)\right|+\left|\sum_{i=1}^{m}\sum_{j=1}^{n}(L_{ij}-\bar{L}_i)^2\right|$$

Using this formulation, I then partitioned the variance in BSD explained by the regional effect, the average local effect, the regional-local interaction, and the residual variance among localities with a region (Table 4.1). To evaluate whether the relative importance of regional versus local effects varied with the environment, I calculated the relative regional effect (*RRE*) for each region:

$$RRE_i=\frac{(R_i-C)^2}{(R_i-C)^2(\bar{L}_i-R_i)^2}$$

I then regressed *RRE* against minimum temperature (the strongest predictor of regional BSD, see Results section).

The formulation presented above requires that multiple local communities have been sampled within each region, and that the design be balanced, i.e. an equivalent number of local communities per region across all regions. Our data meet neither of these assumptions. I considered a minimum of three local communities per ecoregion as minimally sufficient; four regions that failed to meet this criterion were excluded from the variance partitioning analysis. The number of local communities in retained regions ranged from three to thirteen. To achieve a balanced design, I randomly sampled three communities from each region. To quantify the variability on my results associated with this sampling procedure, I repeated it and the subsequent analyses 1000 times.

Results

Regional BSD was lower in cold, temperate, areas than in tropical regions. The strongest predictor of this gradient was minimum annual temperature (Figure 4.2; Table 4.2). Minimum temperature explained the vast majority of the variance in regional BSD (adjusted $R^2 = 0.79$). Including a quadratic term in this model increased the adjusted-R^2 to 0.85, and the quadratic term was significant ($P = 0.04$). However the AICc difference between the models (quadratic AICc – linear AICc) was only -2.18, indicating that the linear term did not substantially improve the overall fit of the model (Burnham and Anderson 2002). Therefore, I considered the linear model to provide an adequate representation of the regional BSD-minimum temperature relationship. I note also that the precise form of this relationship is not critical to the interpretation of my findings. Regional BSD was not related to ecoregion area ($P = 0.34$), nor did including area in a multiple regression with minimum temperature improve the AICc value. The slope of the regional BSD-minimum temperature relationship was significantly greater than expected by chance based on both the random draw (observed slope = 0.012; mean null slope = 0.0013; P = 0.005) and body size randomization (mean null slope = 0.0012; P = 0.04). Moreover, the observed regression line actually crossed the null expectation (Figure 4.2), indicating that in cold areas, regional assemblages are clustered with respect to body size and in warm areas they are over-dispersed.

Body sizes in local communities were slightly over-dispersed relative to the regional assemblages. Local BSD increased with increasing regional BSD, as expected (Figure 4.2). However, the intercept of the local BSD on regional BSD was in the upper tail of the null distribution and was marginally statistically significant at α=0.05 (observed intercept=0.27; mean null intercept = -0.39; two-sided P-value = 0.06). Furthermore, at no point did the observed regression line cross the expected line, indicating that, on average, local communities were slightly over-dispersed (with respect to body size) regardless of the composition of the regional assemblage. The slope of the local BSD vs. regional BSD regression did not differ statistically from the slope based on the null expectation (Figure 4.2; observed slope = 0.85; mean null slope = 1.22; two-sided P-value = 0.16). The slope and intercept values were calculated using conditional autoregression; after fitting this model, no significant spatial autocorrelation remained in the residuals (Moran's I = -0.054, P = 0.72).

To determine if the regional BSD – temperature relationship arose from temperature-based differences in the rate at which body size evolves, I simulated Brownian motion evolution of body size along the hylid phylogeny using the maximum likelihood estimate of the divergence rate parameter based on the real distribution of body sizes on the phylogeny. Then, I recalculated the regional BSD-temperature regression using the simulated data. Brownian motion evolution produced slope values that were quite variable. Slopes ranged from -1.93 to 1.06 when age constrained branch lengths were used and between -0.83 and

0.61 when all branch lengths equalled one. The observed (real) slope was close to the mean slope based on Brownian motion (BM) with a single rate across the entire phylogeny using age-constrained branch lengths (Figure 4.2; observed slope = 0.012; BM-slope = 0.005; one-sided P-value = 0.16). This result did not change when BM simulations were performed after setting all branch lengths equal to one (BM-slope =0.003; one-sided P-value = 0.10).

On average, regional effects explained substantially more variation in BSD among local communities than did average local effects (45% versus 21%; Table 4.1; based on the absolute total sums of squares). The importance of regional filters, measured as relative region effect (*RRE*), did not increase significantly in colder regions (Figure 4.3; P = 0.35); however my sample size was small (n = 9). The interaction between local and regional effects was negative and accounted for 24% of the total variance (Table 4.1). The negative interaction arises because local communities were generally over-dispersed with respect to the regional assemblage, while regional communities in all but the warmest regions were clustered with respect to the continental species pool (Figure 4.2). The negative interaction reduces the realized total variance, measured as the departure of local BSD from the mean BSD of the continental species pool. On average, 48% of the total variance was masked by this negative interaction. Overall, regional and average local effects explained an average of 90% of the variance in local BSD. 95% confidence intervals of the above estimates, based on random subsampling of available local communities, were always small on the order of tenths of a percentage point.

Discussion

I evaluated the role of regional and local processes in structuring communities along a tropical-temperate gradient. In particular, I examined whether the relative importance of regional environmental filtering and local competition varied with climate. To do so, I tested three predictions based on the 'biotic interactions' hypothesis (Dobzhansky 1950, Fischer 1960, MacArthur 1969, MacArthur 1972, Schemske 2002). The predictions were: 1) body sizes within local communities will become increasingly over-dispersed along a temperate to tropical gradient, relative to their regional species pool, 2) regional filters will explain increased variance in the body size dispersion (BSD) of local communities in temperate regions, 3) body size evolution will be faster in tropical regions. For hylid frogs in the continental Americas, my results were inconsistent with all of these predictions.

In general, regardless of position on the temperate-tropical gradient, I found that local communities were slightly over-dispersed relative to the composition of their respective regional assemblages. While patterns of trait or phylogenetic over-dispersion are by no means ubiquitous across taxa or habitats (Kembel and Hubbell 2006, Bryant et al. 2008, Cornwell and Ackerly 2009), numerous studies have found patterns of over-dispersion in a variety of taxa including oaks (Cavender-Bares et al. 2004), tropical trees (Kembel and Hubbell 2006), birds (Lovette and Hochachka 2006), plants (Bryant et al. 2008, Cornwell and Ackerly 2009), and mammals (Cooper et al. 2008). Over-dispersion of local communities is consistent with the predicted pattern when competition prevents the co-existence of similar species (Webb 2000, Webb et al. 2002). However, patterns of phylogenetic over-dispersion can arise under other processes when traits are evolutionarily labile (Kraft et al. 2007). By examining dispersion in an ecologically relevant trait (body size), rather than using phylogenetic similarity as a proxy, I avoid this potential confounding factor. However, I cannot rule out other possibilities such as predation pressure or reproductive character displacement (Moen and Wiens 2009), in producing patterns of over-dispersion.

I found no evidence of increased over-dispersion in tropical communities relative to temperate ones. In fact, the weak, non-statistically significant patterns was for communities to be more over-dispersed in temperate regions, suggesting that if there is variation in the strength of competition (which is unlikely), then it may be slightly stronger in colder, temperate communities. However, it is important to note that this pattern is conditioned on the trait structure of the regional species assemblage. Ignoring regional effects, local BSD did increase in tropical regions, indicating that variation in the trait dispersion of local communities is primarily due to regional processes. A similar pattern has been observed in bats, where phenetic diversity in local communities increased with decreasing latitude, but the pattern disappeared when local phenetic diversity was conditioned on the regional assemblage (Stevens et al. 2006).

MacArthur (1969) suggested that, in the tropics, strong competition leads to a finer division of resources among species (see also Dobzhansky 1950). This could lead to a lack of increased over-dispersion in tropical communities, if species with more similar body sizes can coexist in these areas. However, if this process was occurring, I would expect that the absolute BSD (i.e. not the relative difference from the regional BSD) of local communities in the tropics to be less than in temperate areas. This is not the case; body size differences are greater in the tropics when the regional assemblage is not considered. Although it is possible that tropical species divide resources more finely along niche axes that are not correlated with body size, I found no evidence of finer niche division, with respect to body size, in tropical communities.

A second potential explanation for the lack of increased relative over-dispersion in tropical communities is that in tropical regions, a history of strong competition has lead to increased evolutionary divergence in body size. Thus, the over-dispersion of regional assemblages in tropical areas could indicate the 'ghost of competition past' and result in local community BSDs that do not differ much from the regional assemblage. This is an appealing explanation, since it has the capacity to explain both the lack of an increased competitive signal in tropical communities and the gradient in regional assemblages. However, my complete analysis rejects this hypothesis, at least given the current available phylogenetic information. If, as suggested by the ecological theory of adaptive radiation (Schluter 2000), strong competition has lead to divergent natural selection for niche (i.e. body size) divergence, then I would expect to see an increased rate of body size evolution in tropical regions, a pattern that has been observed in the Caribbean hylid genus, *Osteopilus* (Moen and Wiens 2009). However, I found no evidence that the gradient in regional BSD has arisen because of an increased rate of body size divergence in continental tropical areas; the gradient can be explained by a simple single-rate model of Brownian motion evolution. Overall, I have no evidence that a history of disproportionately strong competition in the continental tropics has led to increased body size divergence in the regional assemblage.

The regional BSD-minimum temperature relationship could result from two alternate possibilities. First, minimum temperature could act as a direct environmental filter, preventing the persistence of species with particular body sizes in cold regions. This process, acting through evolutionary time, would slow the rate of body size evolution in cold areas. Second, in temperate regions, there may have been insufficient time for body sizes to diverge (Moen and Wiens 2009). Since hylids originated in the warm, wet tropics (Wiens et al.

2006), assemblages in cold, high latitude regions are younger (Wiens et al. 2006, Moen and Wiens 2009); they are also more clustered phylogenetically (Algar et al. 2009). Therefore, the decrease in regional BSD in colder areas may be due to the past geographic patterns of diversification in the hylid clade, which may be driven by the evolution of cold tolerance (Smith et al. 2005, Algar et al. 2009). Although I cannot differentiate conclusively between these two alternatives, given the available phylogenetic information, the data are consistent with Moen and Wiens' (2009) time hypothesis: I found no evidence for a reduced rate of body size evolution in cold areas. However, climate still could act as a direct contemporary, rather than evolutionary, environmental filter by preventing species with disparate body sizes from dispersing into cold regions.

The biotic interactions hypothesis predicts that regional filters should increase in importance relative to local filters as one moves away from the tropics. I found no significant gradient in the relative importance of regional filters, although my sample size was small. However, in cold regions, regional and local processes acted in opposition, with regional filters reducing BSD and local filters increasing it. This resulted in hidden variance, where the opposing effects cancel each other out and reduce the apparent structure in local communities. This phenomenon has been identified in other systems as well: Helmus (2007b) found that among lakes, environmental conditions favoured the co-occurrence of phylogenetically similar species, but within lakes, phylogenetic repulsion, likely due to competition between similar species, resulted in over-dispersed communities.

Overall, regional processes explained substantially more variance in community BSD than did local processes. This suggests that the trait structure of local communities may be more attributable to large scale climate-driven evolutionary and biogeographic processes than local community dynamics. This does not mean that local scale dynamics are non-existent – local processes still explained >20% of the variance in local BSD – but rather that, when compared along a broad, continental gradient, they are less important than regional factors. Furthermore, regional and average local effects explained the vast majority of variance (approximately 90%) in local community BSD, suggesting that differences among communities due to within-region environmental gradients (e.g. Bryant et al. 2008, Cornwell and Ackerly 2009) are of little import for hylid community structure. However, since my data were determined by availability in the literature and were not collected specifically to sample across within-region environmental gradients, it is possible that they were not suitable to detect the effects of within-region environmental variation.

Our analysis assumes a 'top down' model of community assembly, where regional processes determine the pool of species that can potentially occur within local communities and the subset of species that do co-occur is determined by local processes (e.g. Harrison and Cornell 2008). However, some authors have suggested that local dynamics can control the regional species pool and that regional assemblages are simply collections of local communities (Huston 1999). Our analysis of the rate of body size evolution are not consistent with the 'bottom up' control model. If local processes, such as competition, determined the evolution of the regional pool, I would have expected to see elevated rates of body size divergence, driven by strong competition, in regions with high BSD. Instead, I found that the rate of body size evolution did not vary with climate. Also, local BSD (relative to the regional pool) varied little along the same gradient, but substantial variation was observed at the regional level. These results are consistent with the 'top down' model. Interestingly, this result for mainland regions differs from the findings of Moen and Wiens

(2009) who found evidence for bottom-up, competition driven body size divergence in hylids on Caribbean islands, suggesting that there is a fundamental difference in the ways mainland and island assemblages are structured.

Our analysis combined data on regional assemblage and local community compositions, body size, and phylogeny along a tropical-temperate gradient. The requirements for such a wide array of data covering a broad geographical extent for a group as diverse as the hylids renders generalization inevitable. In particular, several points should be kept in mind. The first is that my analysis relied on the published literature and thus there were relatively few local communities sampled per region. Increased, and standardized, sampling of local communities would be represent a substantial improvement and could allow for the incorporation of metacommunity dynamics (Leibold et al. 2004). Secondly, my analysis focused on a single trait, body size. Although body size is correlated with a suite of other traits in a variety of taxa (Peters 1983), information on more traits would improve future analyses, especially since other studies have found that, even in the same communities, traits can differ in how they are distributed (e.g. Weiher et al. 1998, Cornwell and Ackerly 2009). Furthermore, due to data availability, my body size data was confined to the maximum body size of each species regardless of sex (see also Moen and Wiens 2009); this measure cannot account for either intraspecific variation or sexual size dimorphism. Lastly, I used the phylogeny of Faivovitch et al. (2005), which is resolved only to the species group or genus level and which does not include branch lengths. Although I attempted to account for this by estimating branch lengths based on the small number of fossil dates available, it is possible that a true species-level phylogeny with real branch lengths would have allowed me to detect variation in the rate of body size evolution. However, my analysis seems relatively robust to the specific branch lengths used as I found identical results when all branch lengths were set to one.

Overall, my results suggest that while local processes are hardly trivial, community structure is predominantly determined by regional processes. Furthermore, variation in community structure along broad climatic gradients is predominantly due to regional processes. In particular, I found no increased signature of competition in tropical areas, either in contemporary body size distributions, or in their past rates of evolution. Further development of molecular-based, species level phylogenies for diverse clades and in increased focus on trait-based ecology will, undoubtedly, shed further light on how the dynamics of communities vary across scales and environmental gradients.

Tables

Table 4.1. Mean variance in body size dispersion of local communities explained by regional and local effects and their interaction. Means were based on 1000 random draws of size *n* local communities from each region (*n*=3). Proportions were based on the sum on the absolute sums of squares (a*bsTSS*). R_i is the BSD of regional assemblage i, *C* is the BSD of the continental species pool, $\bar{L}_i$ is the mean BSD of the *n* local communities in region *i* and *m* is the number of regions. *TSS* is the absolute sums of squares.

Effect	Formula (TSS^{-1})	Prop. Var. Explained (95% CI)
Region	$n\sum_{i=1}^{m}(R_i-C)^2$	0.453 (0.450, 0.455)
Local	$n\sum_{i=1}^{m}(\bar{L}_i-R_i)^2$	0.207 (0.205, 0.209)
Region x Local	$2n\sum_{i=1}^{m}(R_i-C)(\bar{L}_i-R_i)$	-0.244 (-0.246, -0.241)

Table 4.2. Model fit parameters for regressions of the logarithm of regional body size dispersion on environmental variables. MAT is mean annual temperature, MINT is mean minimum temperature, MAP is mean annual precipitation, MINP is mean minimum precipitation, mAET is mean actual evapotranspiration, ELEV is elevation range, ns indicates $P > 0.05$.

Variables in regression	adj-R^2	AIC	AICc
MAP	0.51	-14	-13
MINP	ns	ns	ns
MAT	0.69	-20	-19
MINT	0.79	-26	-25
mAET	0.65	-19	-17
ELEV	0.34	-10	-9
MAP; MAP^2	ns	ns	ns
MINP; MINP^2	ns	ns	ns
MAT; MAT^2	ns	ns	ns
MINT;MINT^2	0.84	-29	-27
mAET; mAET^2	ns	ns	ns
ELEV; ELEV^2	ns	ns	ns
MINT;MAP; MINT*MAP	ns	ns	ns

Figures

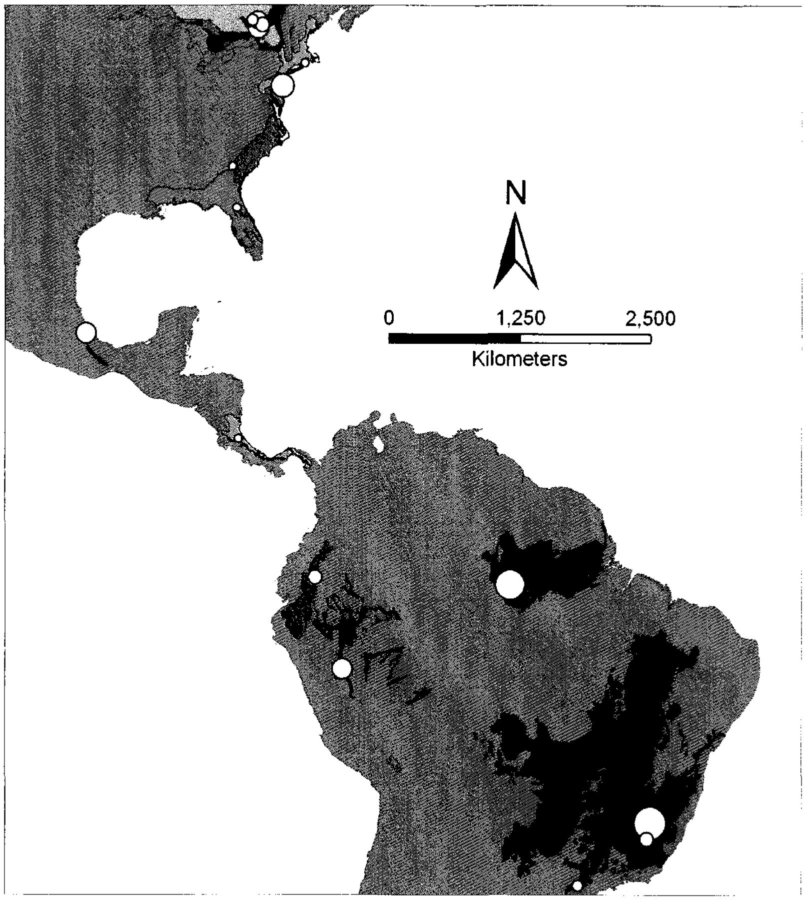
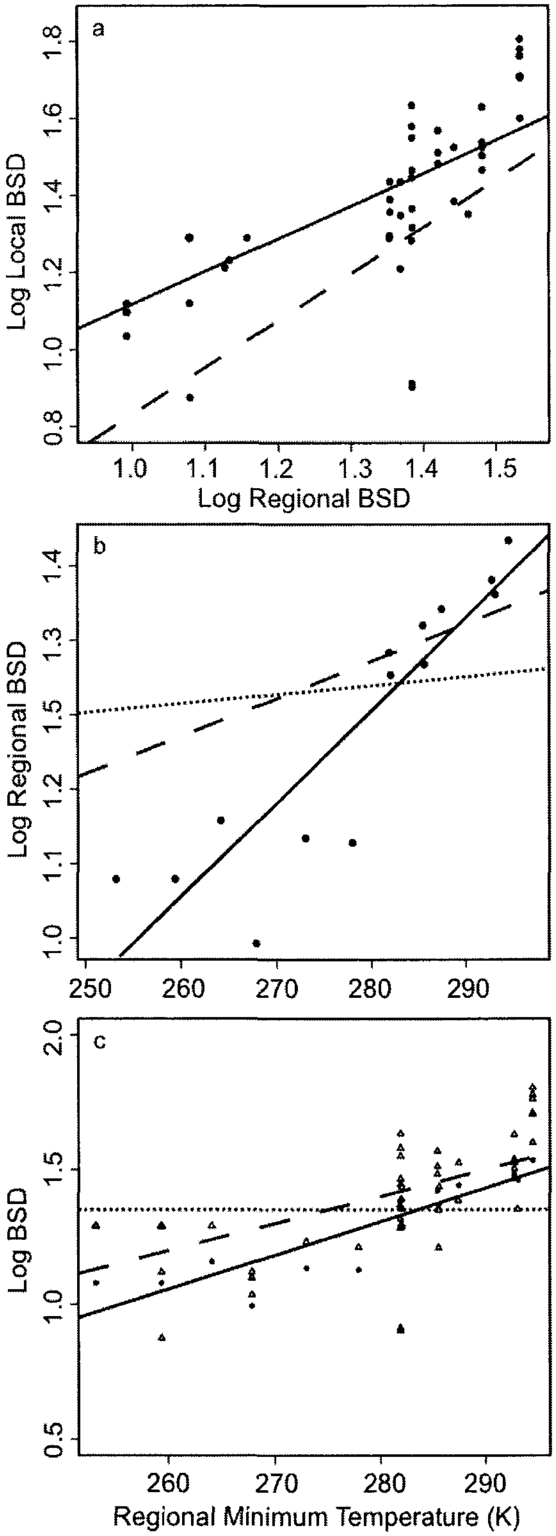


Figure 4.1. Location of 61 local communities collected from the literature. Communities are distributed within 14 ecoregions (in colour). Local communities are shown by the white circles. Circle size is proportional to the number of local communities sampled at a location (or at geographically indistinguishable coordinates, given the map's scale).

Figure 4.2. The relationship between local and regional body size dispersion (BSD), minimum temperature and the BSD of the continental species pool. (a) The relationship between local BSD and regional BSD. The dashed line is the mean slope and intercept of the null expectation based on random community draws. The intercepts are almost significantly different at $\alpha=0.05$ ($P=0.06$), the slopes are not. (b) The relationship between regional BSD and minimum temperature. The dotted line is the mean expectation based on randomization of body sizes in the continental species pool. The dashed line is the mean expected relationship based on Brownian motion body size evolution along the hylid phylogeny. The observed slope differs significantly from the randomization slope ($\alpha=0.05$), but not the Brownian motion slope. (c) The relationship between local BSD (open triangles, dashed line), regional BSD (filled circles, solid line), and the BSD of the continental species pool (dotted line).


a
Log Local BSD
0.8
1.0
1.2
1.4
1.6
1.8
1.0
1.1
1.2
1.3
1.4
1.5
Log Regional BSD
b
Log Regional BSD
1.0
1.1
1.2
1.5
1.3
1.4
250
260
270
280
290
c
Log BSD
0.5
1.0
1.5
2.0
260
270
280
290
Regional Minimum Temperature (K)

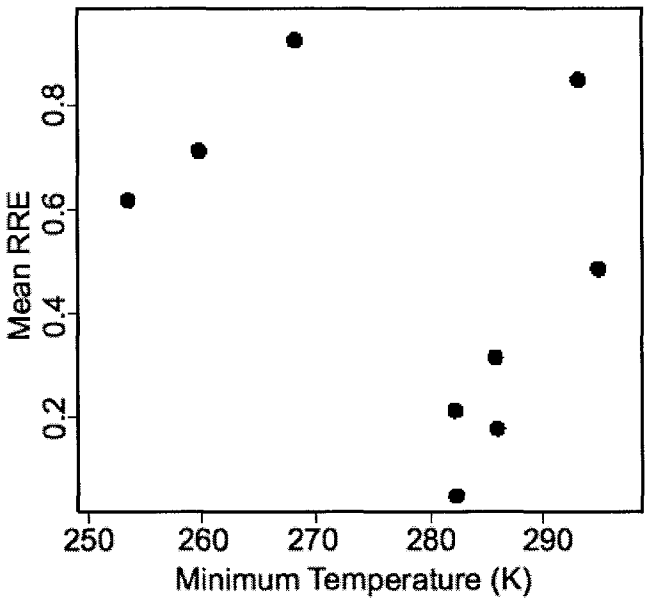


Figure 4.3. The relative importance of regional filters along the minimum temperature gradient. *RRE* is the relative region effect: $RRE_i = (R_i - C)^2 / (R_i - C)^2 (\bar{L}_i - R_i)^2$. The relationship is not statistically significant ($\alpha = 0.05$).

Conclusions

This thesis set out to attempt to identify those processes that are most important in determining ecological patterns and dynamics along broad climatic gradients. The question of whether a particular process or effect is important at a particular scale differs greatly from other types of question asked by science, such as does this effect exist, or how does this mechanism operate (McArdle 1996). The question of importance must be approached by analysis of ecological systems *in situ*. The deduction and evaluation of predictions, especially multiple predictions from single hypotheses, is critical to the success of this approach. For example, a hypothesis that predicts only that species richness will increase from the poles to the tropics is not a useful hypothesis, since it predicts a pattern that we already know to exist, a pattern that is also predicted by numerous other hypotheses (e.g. Willig et al. 2003, Currie et al. 2004, Evans et al. 2005, Mittelbach et al. 2007). Progress can be made only by the strict assessment of predictions and the rejection of hypotheses whose predictions fail (Peters 1991, Currie et al. 1999).

Identifying the processes that are most important in determining broad-scale ecological patterns relies on the assumption that they will leave behind a statistically detectable signal in present-day patterns, whether they be in phylogenetic, trait, or species distribution data. This approach relies heavily on correlation and thus, practitioners must be wary that 'correlation does not mean causation'. However, as stated by Shipley (1999): "correlation does not imply causation but causation implies correlation". Therefore, if a predicted correlation is not observed, then the proposed causes, or processes, can be rejected as important in generating and/or maintaining the pattern. It is this approach that I have attempted to implement throughout this thesis.

This thesis has focused on the effects of climate on broad-scale gradients of regional species richness and the relative importance of biotic interactions and environmental filtering at local and regional scales. Specifically it asked three questions: 1) which processes are most important in mediating climate-species richness relationships; 2) are predictions of spatial climate-richness models temporally consistent and which type of forecasting makes the most reliable predictions, and 3) what is the relative importance of local and regional processes for community structure and does this vary along climatic gradients.

Chapter One tested whether the temperature dependence of metabolic rate and the energetic equivalence rule are responsible for species richness gradients of ectothermic taxa (Allen et al. 2002). In general, my results were inconsistent with the metabolic theory's predictions, allowing me to reject the proposed mechanism as the process underlying the climate-richness relationship for this diverse array of taxa.

Chapter Two asked which type of species richness forecasting made the best predictions of richness shifts under recent climate change. In doing so, I also asked whether spatially-trained climate-richness regression models could make consistent temporal predictions, as predicted if climate does influence species richness (H-Acevedo and Currie 2003, Kerr et al. 2007). I found that individual niche models and regression-based approaches made relatively accurate predictions of changes in butterfly richness throughout the 20th century. However, single-best model regression that accounted for spatial autocorrelation outperformed all other tested methods. These results suggest that there is a causative relationship between climate and species richness and that using spatial regression methods to estimate coefficients more accurately captures the functional relationship.

Chapter Three attempted to unify the evolutionary and statistical predictive approaches to broad-scale diversity gradients by testing predictions of the niche conservatism hypothesis (Wiens and Donoghue 2004, Wiens and Graham 2005, Wiens et al. 2006) for hylid frogs in the continental Americas. I tested predictions based on the relationship between climate, richness and the phylogenetic structure of regional faunas. I found that while niche conservatism, likely with respect to cold tolerance, is important for the composition of regional assemblages, richness is independent of its effects. Richness was best predicted by precipitation, not temperature. These results demonstrate the importance of testing explicit predictions of evolutionary hypotheses and reject the niche conservatism hypothesis as the dominant process producing hylid richness gradients.

Chapter Four examined the relative importance of local and regional processes for community structure and whether biotic interactions, specifically competition, had greater effects on tropical communities than in temperate areas (Dobzhansky 1950). Contrary to the hypothesis' predictions, I found that local communities were over-dispersed relative to regional pools, but that the magnitude of this effect did not increase toward the tropics. Overall, regional filters were of greater importance than local filters, but there was no strong trend toward greater importance in colder regions, although the sample size was small. Additionally, I found no evidence that the strong relationship between regional body size dispersion and minimum temperature was due to differences in the rate of body size divergence. This suggests that regional assemblages in cold areas may be clustered with respect to body size due to the underlying geographical phylogenetic patterns and their body sizes have not had sufficient time to diverge substantially (Moen and Wiens 2009).

Overall, this thesis has rejected several high profile hypotheses for the effects of broad-scale climatic gradients on species richness and community dynamics. In many cases, the ideas I have tested can be traced back to the origins of biogeography and ecology. They have persisted in the literature for so long largely because their predictions have either not been deduced or subjected to rigourous tests (Currie et al. 2004). The deduction and testing of such prediction has been one of the primary goals of this thesis.

Although I have rejected several hypothesis, I have failed to identify a model whose predictions did not fail. However, science advances by refutation and falsification, not by confirmation (Popper 1963, Peters 1991, Currie et al. 1999). Often it is the way in which models fail that is more informative than their successes. The rejection of the hypotheses tested here has shed new light on the role of geographic patterns of diversification and niche dynamics on the composition of regional communities, the role of regional and local filters on the trait structure of communities, and how to predict the effects of future climate change.

Throughout this thesis, I have focused on the relative importance of different processes in determining broad patterns in nature. Rather than view the tremendous variation that is present among ecological systems as a series of disconnected, historically contingent, unique case studies, I have tried to identify generalities in this variation. In doing so I have attempted a synthesis of evolutionary/historical and statistical/predictive approaches to broad-scale ecology by searching for and testing generalities in the way diversification, niche shifts, and trait evolution occurs along environmental gradients. If, as argued by Cooper (2003), ecology is the 'science of the struggle for existence', then I have attempted to determine the most formidable opponent, and how they are defeated.

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Appendix 1: Simulation model of diversification along an environmental gradient

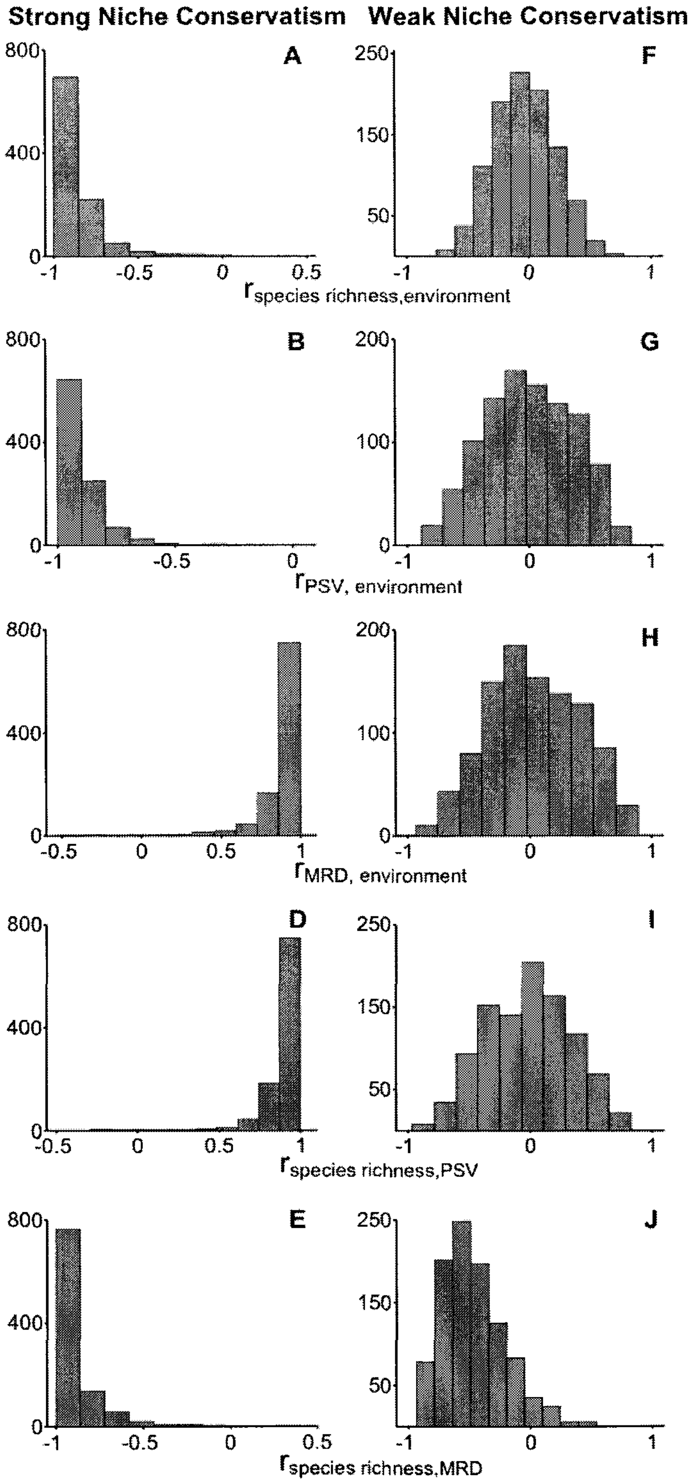
Appendix 1.1: Model structure and results

The goal of my simulation model was not to evaluate all possible scenarios in which evolutionary dynamics can produce diversity gradients, but rather to determine if the relationships predicted by the verbal and visual model still apply to less-idealized scenarios that include the fundamental aspects of the hypothesis. I used a one-dimensional environmental gradient to model the rise of diversity gradients under niche conservatism. The environment was divided into 10 discrete bins (with corresponding hypothetical environmental conditions from one to ten) and species inhabited a single bin, i.e. set of environmental conditions. For each simulation, the model was seeded with the ancestral species inhabiting the first environmental bin (environment = 1; mimicking a tropical origin). During each time step, for each occupied bin, a species present at the beginning of the time step was randomly chosen to diversify. This approach that maintains equal absolute diversification rates along the gradient, a requirement of the tropical conservatism hypothesis. For each diversification event, one daughter species remained in the focal bin, while the other's environment was determined by the probability of a niche shift occurring, pr_shift. If a shift occurred, the magnitude (number of bins) was randomly chosen from a normal distribution with $\mu = 0$, and σ = stdev_shift. Shifts could occur in either environmental direction with equal probability. When stdev_shift was small, large shifts were unlikely. As stdev_shift increased, the probability of small and large shifts became increasing similar. Also, after each diversification event, an extinction event could occur at a low probability (0.1 for all simulations). Species survived a minimum of one time step before becoming available for extinction. This process continued until a preset global richness value was attained (global richness was 200 for all my simulations). Species richness, MRD, and PSV were then calculated for each bin and relevant correlations determined. I evaluated scenarios in which niche conservatism was strong (pr_shift = 0.05, stdev_shift = 1) or weak (pr_shift = 0.9 and stdev_shift = 10). For each parameter set, I ran 1000 simulations.

Our simulation results showed that when a clade originates at one end of the gradient (mimicking a tropical origin) and niche conservatism was strong (probability and magnitude of niche shifts were both small), richness and PSV declined away from the zone of origin (negative correlations with environment), while MRD increased. Also, when niches were strongly conserved, richness was highly correlated with MRD and PSV (Figure A1.1a-e). When niche conservatism was weak (probability and magnitude of niche shifts were large), these patterns did not emerge. Instead, the diversity gradient disappeared and richness and environment were not correlated with PSV. Similarly, the correlation between MRD and environment was close to zero. The richness-MRD correlation remained but was reduced from its previous level (Figure A1.1f-j).

Appendix 1.2: Simulation model figures

Figure A1.1. Simulation results showing the correlations between environment, richness and phylogenetic structure during diversification along an environmental gradient when niche conservatism is strong or weak. PSV is phylogenetic species variability and MRD is mean rood distance. Histograms are Pearson's r values for 1000 simulations for each scenario. In all cases, a clade originated at one end of an environmental gradient (mimicking a tropical origin.


Strong Niche Conservatism
Weak Niche Conservatism
A
F
800
400
0
250
150
50
-1
-0.5
0
0.5
1
$r_{\text{species richness,environment}}$
B
G
200
100
$r_{\text{PSV, environment}}$
H
$r_{\text{MRD, environment}}$
D
I
$r_{\text{species richness,PSV}}$
E
J
$r_{\text{species richness,MRD}}$

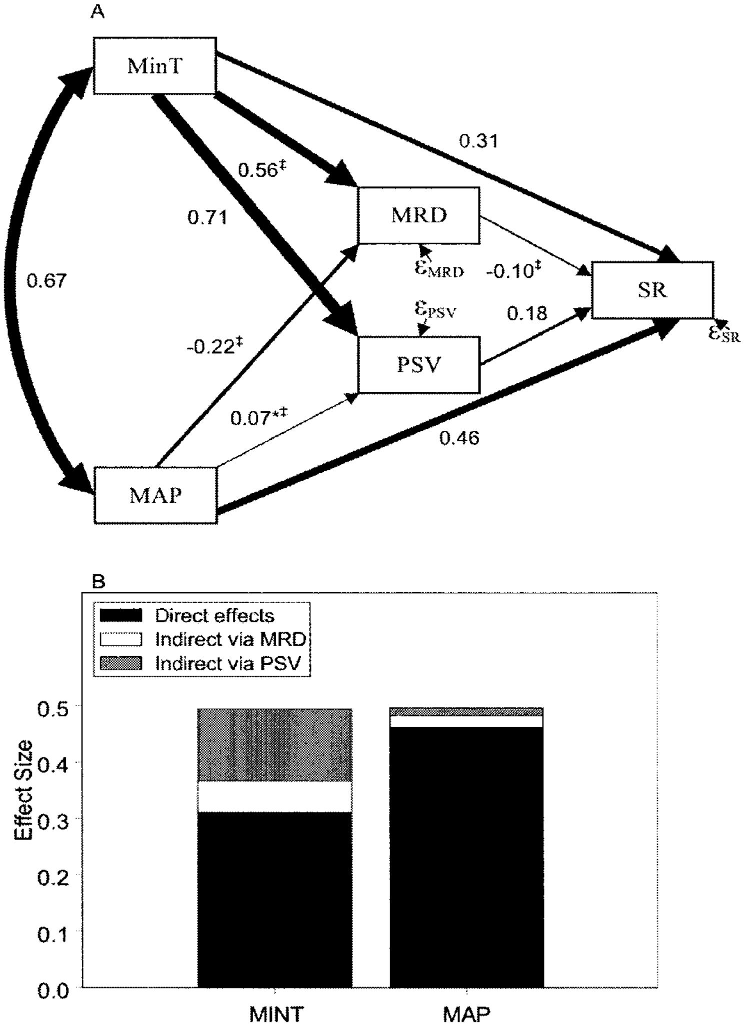
Appendix 2: Path analysis using alternate polytomy branch lengths

Appendix 2.1: Path analysis results

After recalculating PSV and MRD using the alternate polytomy branch lengths, we re-performed our path analysis. Generally, path coefficients were similar to those in our main analysis, except for the effect of minimum temperature on MRD (Figure A2.1). After correcting branch lengths for differing polytomy diversity, the effect of temperature on MRD did not differ from the value expected when species are randomly shuffled on the phylogeny. Alternately, PSV increased slightly in importance. These changes do not alter our primary conclusion since direct effects of precipitation still primarily determined species richness while contributions from PSV and MRD were weak (Fig. A2.1). However, the differing result with respect to temperature and MRD suggests that PSV is a more robust index of the effects of niche conservatism.

Appendix 2.2: Path analysis figures

Figure A2.1. Direct and indirect effects of climate on species richness (SR) after applying the polytomy branch length correction. PSV is phylogenetic species variability, MRD is mean root distance, MINT is minimum temperature, MAP is mean annual precipitation, and ε is unexplained variation. (A) Values are standardized path coefficients, line width is proportional to the strength of the effect. * and ‡ indicate that coefficients that were not statistically significant ($\alpha=0.05$) after accounting for spatial autocorrelation or randomizing species on the phylogeny's tips, respectively. (B) The total effects of mean annual precipitation and minimum temperature on species richness.


A
MinT
MRD
PSV
SR
MAP
0.31
0.56‡
0.71
0.67
-0.10‡
0.18
-0.22‡
0.07*‡
0.46
εMRD
εPSV
εSR
B
Direct effects
Indirect via MRD
Indirect via PSV
Effect Size
0.0
0.1
0.2
0.3
0.4
0.5
MINT
MAP

Appendix 3: Chapter 4 local community data

Appendix 3.1: Local community data table

Table A3.1. Summary statistics for 61 Hylidae communities collected from the literature. Elevation data is based on a digital elevation model. Sources are given in Appendix 3.2.

ID	Ref.	Latitude (dd)	Longitude (dd)	Area (m^2)	Elevation (m)	Richness	Ecoregion
20062	1	-8.383	-74.933	1000	260	11	Iquitos varze
20059	1	-8.383	-74.933	400	260	10	Iquitos varze
20058	1	-8.383	-74.933	100	260	4	Iquitos varze
20061	1	-8.383	-74.933	50	260	4	Iquitos varze
20060	1	-8.383	-74.933	300	260	11	Iquitos varze
20052	2	39.747	-74.721	1600	22	2	Atlantic coastal pine barrens
20054	2	39.686	-74.740	400	18	2	Atlantic coastal pine barrens
20055	2	39.721	-74.769	2400	24	4	Atlantic coastal pine barrens
20001	2	39.798	-74.614	1200	28	2	Atlantic coastal pine barrens
20053	2	39.761	-74.800	2400	30	3	Atlantic coastal pine barrens
20047	3	-24.046	-49.221	4500	631	7	Cerrado
20046	3	-24.048	-49.221	9	657	5	Cerrado
20002	4	29.683	-82.000	1600	46	5	Southeastern conifer and broadleaf forests
20004	5	10.433	-83.983	2199	55	11	Isthmian-Atlantic moist forests
20072	6	45.104	-75.588	1162	89	2	Eastern Great Lakes lowland forests
20065	6	45.063	-74.875	157	85	2	Eastern Great Lakes lowland forests
20066	6	45.490	-75.229	856	83	2	Eastern Great Lakes lowland forests
20071	6	45.409	-76.259	451	97	2	Eastern Great Lakes lowland forests
20070	6	45.522	-75.814	788	167	2	Eastern forest-boreal

							transition
20069	6	45.151	-75.440	2566	75	2	Eastern Great Lakes lowland forests
20068	6	45.546	-75.834	5504	192	2	Eastern forest-boreal transition
20064	6	45.360	-75.481	617	81	2	Eastern Great Lakes lowland forests
20067	6	45.332	-76.370	1359	200	2	Eastern forest-boreal transition
20077	7	44.836	-75.391	438	79	3	Eastern Great Lakes lowland forests
20073	7	44.828	-75.425	89	81	2	Eastern Great Lakes lowland forests
20078	7	44.814	-75.464	3381	86	2	Eastern Great Lakes lowland forests
20079	7	44.812	-75.444	821	83	2	Eastern Great Lakes lowland forests
20074	7	44.992	-75.064	3600	89	2	Eastern Great Lakes lowland forests
20075	7	44.929	-75.199	927	81	2	Eastern Great Lakes lowland forests
20076	7	44.800	-75.488	161	87	2	Eastern Great Lakes lowland forests
20007	8	-18.750	-43.539	15	1155	2	Campos Rupestres montane savanna
20015	8	-18.733	-43.542	108	1152	2	Campos Rupestres montane savanna
20014	8	-18.742	-43.554	244	1137	2	Campos Rupestres montane savanna
20017	8	-18.750	-43.550	8	1136	2	Campos Rupestres montane savanna
20016	8	-18.738	-43.533	31	1197	3	Campos Rupestres montane savanna
20009	8	-18.704	-43.567	206	1067	5	Campos Rupestres montane savanna
20008	8	-18.744	-43.542	214	1136	5	Campos Rupestres montane savanna
20013	8	-18.704	-43.565	68	1055	4	Campos Rupestres montane savanna
20010	8	-18.708	-43.592	44	1160	4	Campos Rupestres montane savanna
20006	9	-18.710	-43.592	388	1200	3	Campos Rupestres montane savanna
20018	10	33.217	-81.750	100000	55	7	Middle Atlantic coastal forests

20022	11	-19.891	-43.490	503	1248	11	Bahia interior forests
20021	11	-19.895	-43.489	2705	1266	9	Bahia interior forests
20020	11	-19.891	-43.507	85	1290	8	Bahia interior forests
20063	12	41.367	-71.583	1625	16	2	Northeastern coastal forests
20025	13	-0.933	-77.600	7850	450	3	Eastern Cordillera real montane forests
20023	13	-0.933	-77.600	7850	891	7	Eastern Cordillera real montane forests
20026	13	-0.933	-77.600	7850	450	2	Eastern Cordillera real montane forests
20031	14	19.450	-96.983	16	1180	3	Oaxacan montane forests
20030	14	19.550	-96.983	17	1560	2	Oaxacan montane forests
20029	14	19.467	-97.033	55	1570	4	Oaxacan montane forests
20027	14	19.517	-97.000	72	1510	4	Oaxacan montane forests
20028	14	19.583	-96.950	62	1550	3	Oaxacan montane forests
20041	15	-1.500	-60.000	600	40	5	Uatuma-Trombetas moist forests
20045	15	-1.500	-60.000	400	40	3	Uatuma-Trombetas moist forests
20044	15	-1.500	-60.000	8	40	3	Uatuma-Trombetas moist forests
20043	15	-1.500	-60.000	100	40	4	Uatuma-Trombetas moist forests
20033	15	-1.500	-60.000	150	40	3	Uatuma-Trombetas moist forests
20035	15	-1.500	-60.000	250	40	5	Uatuma-Trombetas moist forests
20038	15	-1.500	-60.000	600	40	5	Uatuma-Trombetas moist forests
20039	15	-1.500	-60.000	22500	40	4	Uatuma-Trombetas moist forests

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Appendix 3.3: Species occurrence in local hylid communities

20001
Hyla andersonii
Pseudacris crucifer

20002
Acris gryllus
Hyla chrysoscelis
Hyla femoralis
Hyla squirella
Pseudacris ocularis

20004
Agalychnis callidryas
Agalychnis saltator
Dendropsophus ebraccatus
Dendropsophus phlebodes
Hypsiboas rufitelus
Scinax boulengeri
Scinax elaeochroa
Smilisca baudinii
Smilisca puma
Smilisca sordida
Tlalocohyla loquax

20006
Bokermannohyla alvarengai
Bokermannohyla saxicola
Scinax duartei

20007
Bokermannohyla alvarengai
Hypsiboas cipoensis

20008
Bokermannohyla nanuzae
Bokermannohyla saxicola
Hypsiboas albopunctata
Hypsiboas cipoensis
Phasmahyla jandaia

20009
Bokermannohyla saxicola
Hypsiboas albopunctata
Hypsiboas cipoensis
Hypsiboas lundii
Scinax machadoi

20010
Bokermannohyla alvarengai
Bokermannohyla saxicola
Hypsiboas cipoensis
Scinax duartei

20013
Bokermannohyla saxicola
Hypsiboas albopunctata
Hypsiboas cipoensis
Scinax duartei

20014
Bokermannohyla alvarengai
Bokermannohyla saxicola

20015
Bokermannohyla saxicola
Hypsiboas cipoensis

20016
Hypsiboas cipoensis
Scinax duartei
Scinax machadoi

20017
Hypsiboas albopunctata
Hypsiboas cipoensis

20018
Acris gryllus
Hyla chrysoscelis
Hyla cinerea
Hyla gratiosa
Hyla squirella
Pseudacris crucifer
Pseudacris ornata

20020
Bokermannohyla gr circumdata
Dendrosophus minutus
Hypsiboas albopunctata
Hypsiboas polytaenius
Scinax curicica
Scinax luizotavioi
Scinax perereca
Scinax squalirostris

20021
Dendropsophus elegans
Dendrosophus minutus
Dendrosophus seniculus
Hypsiboas albopunctata

20022
Dendropsophus elegans
Dendrosophus minutus
Dendrosophus seniculus
Hypsiboas albopunctata

20023
Dendropsophus parviceps
Dendropsophus sarayacuensis
Hyla calcarata
Osteocephalus cf elkejungingerae

Scinax cf fuscovarius
Scinax curicica
Scinax eurydice
Scinax perereca
Scinax squalirostris

Hypsiboas faber
Hypsiboas polytaenius
Phyllomedusa burmeisteri
Scinax curicica
Scinax eurydice
Scinax perereca
Scinax squalirostris

Osteocephalus taurinus
Phyllomedusa tomopterna
Phyllomedusa vaillanti

20025
Osteocephalus buckleyi
Osteocephalus taurinus
Phyllomedusa tomopterna

20026
Dendropsophus parviceps
Phyllomedusa tomopterna

20027
Charadrahyla taeniopus
Ecnomiohyla miotympanum
Plectrohyla arborescandens
Tlalocohyla picta

20028
Charadrahyla taeniopus
Ecnomiohyla miotympanum
Megatostomatohyla mixomaculata

20029
Ecnomiohyla miotympanum
Megatostomatohyla mixomaculata
Plectrohyla arborescandens
Smilisca baudinii

20030
Charadrahyla taeniopus
Ecnomiohyla miotympanum

20031
Ecnomiohyla miotympanum
Scinax staufferi
Tlalocohyla picta

20033
Dendrosophus minutus
Phyllomedusa tarsius
Phyllomedusa tomopterna

20035
Dendropsophus brevifons
Dendrosophus minutus
Osteocephalus taurinus
Phyllomedusa tarsius
Phyllomedusa tomopterna

20038
Dendropsophus brevifons
Dendrosophus minutus
Osteocephalus taurinus
Phyllomedusa bicolor
Phyllomedusa tomopterna

20039
Dendrosophus minutus
Phyllomedusa bicolor
Phyllomedusa tarsius
Phyllomedusa tomopterna

20041
Dendropsophus brevifons
Dendrosophus minutus
Osteocephalus taurinus
Phyllomedusa tarsius
Phyllomedusa tomopterna

20043
Osteocephalus taurinus
Phyllomedusa bicolor
Phyllomedusa tarsius
Phyllomedusa tomopterna

20044
Phyllomedusa bicolor
Phyllomedusa tarsius
Phyllomedusa tomopterna

20045
Phyllomedusa bicolor
Phyllomedusa tarsius
Phyllomedusa tomopterna

20046
Aplastodiscus albosignatus
Bokermannohyla circumdata
Hypsiboas bischoffi
Scinax berthae
Scinax perereca

20047
Hypsiboas albopunctata
Hypsiboas bischoffi
Hypsiboas faber
Hypsiboas prasinus
Scinax perereca
Scinax squalirostris
Sphaenorhynchus surdus

20052
Hyla andersonii
Pseudacris crucifer

20053
Hyla andersonii

20054
Hyla andersonii

20055
Hyla andersonii

Hyla versicolor
Pseudacris crucifer

Pseudacris crucifer

Hyla versicolor
Pseudacris crucifer
Pseudacris triseriata

20058
Dendropsophus brevifons
Dendropsophus parviceps
Hypsiboas cinerascens
Phyllomedusa vaillanti

20059
Dendropsophus brevifons
Dendropsophus parviceps
Dendropsophus rhodopepla
Dendropsophus riveroi
Dendropsophus rossalleni
Dendropsophus sarayacuensis
Hypsiboas cinerascens
Phyllomedusa tarsius
Phyllomedusa tomopterna
Phyllomedusa vaillanti

20060
Dendropsophus brevifons
Dendropsophus leucophyllata
Dendropsophus marmorata
Dendropsophus parviceps
Dendropsophus rhodopepla
Dendropsophus riveroi
Dendropsophus sarayacuensis
Hypsiboas cinerascens
Hypsiboas fasciatusa
Osteocephalus taurinus
Phyllomedusa vaillanti

20061
Dendropsophus parviceps
Osteocephalus leprieurii
Osteocephalus taurinus
Phyllomedusa vaillanti

20062
Dendropsophus brevifons
Dendropsophus parviceps
Dendropsophus rhodopepla
Dendropsophus riveroi
Dendropsophus sarayacuensis
Hypsiboas cinerascens
Hypsiboas fasciatusa
Osteocephalus leprieurii
Phyllomedusa tarsius
Phyllomedusa tomopterna
Phyllomedusa vaillanti

20063
Hyla versicolor
Pseudacris crucifer

20064
Hyla versicolor
Pseudacris crucifer

20065
Hyla versicolor
Pseudacris crucifer

20066
Hyla versicolor
Pseudacris crucifer

20067
Hyla versicolor
Pseudacris crucifer

20068
Hyla versicolor
Pseudacris crucifer

20069
Hyla versicolor
Pseudacris crucifer

20070
Hyla versicolor
Pseudacris crucifer

20071
Hyla versicolor
Pseudacris crucifer

20072
Hyla versicolor
Pseudacris crucifer

20070
Hyla versicolor
Pseudacris crucifer

20071
Hyla versicolor
Pseudacris crucifer

20072
Hyla versicolor
Pseudacris crucifer

20073
Hyla versicolor
Pseudacris crucifer

20074
Hyla versicolor
Pseudacris crucifer

20075
Pseudacris crucifer
Pseudacris triseriata

20076

20077

20078

Hyla versicolor
Pseudacris crucifer

Hyla versicolor
Pseudacris crucifer
Pseudacris triseriata

Hyla versicolor
Pseudacris crucifer

20079
Hyla versicolor
Pseudacris crucifer

Appendix 4: Hylid body size data

Appendix 4.1: Hylid body sizes

Table A4.1. Maximum body size (snout-vent length; SVL), regardless of sex, of Hylidae species not included in Moen and Wiens (Evolution 63: 195).

Species Name	**SVL (mm)**	**Reference**
Acris crepitans	35	Conant and Collins 1998
Acris gryllus	32	Conant and Collins 1998
Agalychnis annae	84.2	Duellman 2001
Agalychnis callidryas	77.2	Duellman 2001
Agalychnis moreletii	82.9	Duellman 2001
Agalychnis saltator	66	Savage 2002
Anotheca spinosa	80	Savage 2002
Bromeliohyla bromeliacia	32.7	Duellman 2001
Bromeliohyla dendroscarta	34.6	Duellman 2001
Charadrahyla altipotens	75.3	Duellman 2001
Charadrahyla chaneque	79.3	Duellman 2001
Charadrahyla nephila	81	Duellman 2001
Charadrahyla taeniopus	70	Duellman 2001
Charadrahyla trux	81	Duellman 2001
Dendropsophus garagoensis	30.8	Kaplan 1991
Dendropsophus minimus	14	Ahl 1933
Dendropsophus robertmertensi	28.1	Duellman 2001
Dendropsophus sartori	28.6	Duellman 2001
Duellmanohyla chamulae	31.8	Duellman 2001
Duellmanohyla ignicolor	33.1	Duellman 2001
Duellmanohyla lythrodes	36	Savage 2002
Duellmanohyla rufioculis	40	Savage 2002
Duellmanohyla salvavida	34.3	Duellman 2001
Duellmanohyla schmidtorum	38.3	Duellman 2001
Duellmanohyla soralia	37.7	Duellman 2001
Duellmanohyla uranochroa	40	Savage 2002
Ecnomiohyla echinata	60.2	Duellman 2001
Ecnomiohyla fimbrimembra	86	Duellman 2001
Ecnomiohyla miliaria	110	Savage 2002
Ecnomiohyla minera	83.1	Duellman 2001

Ecnomiohyla miotympanum	51	Duellman 2001
Ecnomiohyla salvaje	86	Duellman 2001
Ecnomiohyla thysanota	95.7	Duellman 2001
Ecnomiohyla valancifer	82	Duellman 2001
Exerodonta abdivita	27.5	Duellman 2001
Exerodonta bivocata	28.5	Duellman 2001
Exerodonta catracha	32.1	Duellman 2001
Exerodonta chimalapa	26.6	Duellman 2001
Exerodonta juanitae	39.8	Duellman 2001
Exerodonta melanomma	31.5	Duellman 2001
Exerodonta perkinsi	37.5	Duellman 2001
Exerodonta pinorum	34.6	Duellman 2001
Exerodonta smaragdina	28	Duellman 2001
Exerodonta sumichrasti	33	Duellman 2001
Exerodonta xera	27.9	Duellman 2001
Hyla andersonii	44	Conant and Collins 1998
Hyla arboricola	37.5	Taylor 1941
Hyla arenicolor	57.1	Duellman 2001
Hyla avivoca	44	Conant and Collins 1998
Hyla bocourti	37.7	Duellman 2001
Hyla chrysoscelis	51	Conant and Collins 1998
Hyla cinerea	57	Conant and Collins 1998
Hyla euphorbiacea	40.6	Duellman 2001
Hyla eximia	36.2	Duellman 2001
Hyla femoralis	38	Conant and Collins 1998
Hyla gratiosa	67	Conant and Collins 1998
Hyla plicata	47.4	Duellman 2001
Hyla squirella	41	Conant and Collins 1998
Hyla versicolor	51	Conant and Collins 1998
Hyla walkeri	37.8	Duellman 2001
Hyla wrightorum	40.5	Duellman 2001
Hylomantis lemur	53	Savage 2002
Hyloscirtus colymba	43.3	Duellman 2001
Hypsiboas picturatus	59	Boulenger 1899
Hypsiboas rufitelus	65	Savage 2002
Hypsiboas semilineatus	57.1	Spix 1824
Isthmohyla calypsa	41	Savage 2002
Isthmohyla debilis	32	Savage 2002
Isthmohyla graceae	41.4	Duellman 2001
Isthmohyla infucata	45.6	Duellman 2001
Isthmohyla insolita	38	Duellman 2001
Isthmohyla lancasteri	41.1	Duellman 2001
Isthmohyla picadoi	35.2	Duellman 2001
Isthmohyla pictipes	45.1	Duellman 2001
Isthmohyla pseudopuma	52	Savage 2002

Isthmohyla rivularis	37	Savage 2002
Isthmohyla tica	42	Savage 2002
Isthmohyla xanthosticta	29.3	Duellman 2001
Isthmohyla zeteki	27	Savage 2002
Megastomatohyla mixe	33.9	Duellman 2001
Megastomatohyla mixomaculata	36.6	Duellman 2001
Megastomatohyla nubicola	37.3	Duellman 2001
Megastomatohyla pellita	31.6	Duellman 2001
Pachymedusa dacnicolor	103.6	Duellman 2001
Phyllomedusa ayeaye	43	Lutz 1966
Plectrohyla acanthodes	63.2	Duellman 2001
Plectrohyla ameibothalame	43.1	Canseco-Marquez et al. 2002
Plectrohyla arborescandens	51.6	Duellman 2001
Plectrohyla avia	90.4	Duellman 2001
Plectrohyla bistincta	67.6	Duellman 2001
Plectrohyla calthula	61.3	Duellman 2001
Plectrohyla calvicollina	37.6	Duellman 2001
Plectrohyla celata	51.1	Duellman 2001
Plectrohyla cembra	37	Duellman 2001
Plectrohyla charadricola	50.9	Duellman 2001
Plectrohyla chryses	42.2	Duellman 2001
Plectrohyla chrysopleura	62.4	Duellman 2001
Plectrohyla crassa	53.7	Duellman 2001
Plectrohyla cyanomma	64.5	Duellman 2001
Plectrohyla cyclada	49.9	Duellman 2001
Plectrohyla dasypus	48.3	Duellman 2001
Plectrohyla exquisita	80.7	Duellman 2001
Plectrohyla glandulosa	49.7	Duellman 2001
Plectrohyla guatemalensis	59.1	Duellman 2001
Plectrohyla hargwegi	76.7	Duellman 2001
Plectrohyla hazelae	38.6	Duellman 2001
Plectrohyla ixil	46.5	Duellman 2001
Plectrohyla labedactyla	44.7	Duellman 2001
Plectrohyla lacertosa	48.1	Duellman 2001
Plectrohyla matudai	49	Duellman 2001
Plectrohyla mykter	52.3	Duellman 2001
Plectrohyla pachyderma	55.7	Duellman 2001
Plectrohyla pentheter	56.4	Duellman 2001
Plectrohyla pokomchi	55.2	Duellman 2001
Plectrohyla psarosema	37.3	Duellman 2001
Plectrohyla psiloderma	49	Duellman 2001
Plectrohyla pycnochila	60.5	Duellman 2001
Plectrohyla quecchi	46.7	Duellman 2001
Plectrohyla robertsorum	50.8	Duellman 2001

Plectrohyla sabrina	41.7	Duellman 2001
Plectrohyla sagorum	51.9	Duellman 2001
Plectrohyla siopela	52.5	Duellman 2001
Plectrohyla tecunumani	60.7	Duellman 2001
Plectrohyla teuchestes	76.1	Duellman 2001
Plectrohyla thorectes	37.3	Duellman 2001
Pseudacris brachyphona	32	Conant and Collins 1998
Pseudacris brimleyi	32	Conant and Collins 1998
Pseudacris cadaverina	45	Duellman 2001
Pseudacris clarkii	32	Conant and Collins 1998
Pseudacris crucifer	32	Conant and Collins 1998
Pseudacris feriarum	35	Conant and Collins 1998
Pseudacris nigrita	32	Conant and Collins 1998
Pseudacris ocularis	16	Conant and Collins 1998
Pseudacris ornata	32	Conant and Collins 1998
Pseudacris regilla	51	Stebbins 1966
Pseudacris streckeri	41	Conant and Collins 1998
Pseudacris triseriata	39	Conant and Collins 1998
Ptychohyla acrochorda	57.5	Duellman 2001
Ptychohyla dendrophasma	84.1	Duellman 2001
Ptychohyla erythromma	26.2	Duellman 2001
Ptychohyla euthysanota	43.3	Duellman 2001
Ptychohyla hypomykter	44.6	Duellman 2001
Ptychohyla legleri	39	Savage 2002
Ptychohyla leonhardschultzei	43.4	Duellman 2001
Ptychohyla macrotympanum	44.8	Duellman 2001
Ptychohyla panchoi	37.3	Duellman 2001
Ptychohyla salvadorensis	35.9	Duellman 2001
Ptychohyla sanctaecrucis	50.7	Duellman 2001
Ptychohyla spinipollex	44.6	Duellman 2001
Ptychohyla zophodes	43.6	Duellman 2001
Scinax boulengeri	58.5	Rivera 1961
Scinax cardosoi	29.1	Carvalho e Silva and Peixoto 1991
Scinax kautskyi	28.6	Carvalho e Silva and Peixoto 1991
Scinax staufferi	32	Savage 2002
Smilisca baudinii	90	Savage 2002
Smilisca cyanosticta	70	Duellman 2001
Smilisca dentata	62.1	Duellman 2001
Smilisca fodiens	63.7	Duellman 2001
Smilisca phaeota	78	Savage 2002
Smilisca puma	46	Duellman 2001
Smilisca sila	62	Savage 2002
Smilisca sordida	64	Savage 2002
Tlalocohyla loquax	47	Savage 2002
Tlalocohyla picta	22.1	Duellman 2001

Tlalocohyla smithii	30.8	Duellman 2001
Triprion petasatus	74.2	Duellman 2001
Triprion spatulatus	101	Duellman 2001

Appendix 4.2: References for Appendix 4.1

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