

SPECIAL FEATURE

Latitudinal Gradients¹

In 1772, J. R. Forster sailed with Captain Cook in search of the great southern continent hypothesized by geographers to be necessary to “balance” the world. During the three-year trip they ranged from below the Antarctic Circle to the southern tropics, and Forster sampled the flora throughout the Pacific. On his return, he published his account of the voyage in which he noted that different islands support a variable number of species, which he attributed primarily to climate (tropical islands support more species than Antarctic islands), and secondarily to island “circumference” (large islands support more species than small ones). Thus, we have what is probably the first documented geographical pattern in ecology, as well as an explanation for it that differs from some modern explanations only by lacking an evolutionary component. Of course, we now refer to the first part of the pattern as the “latitudinal diversity gradient,” and the second as a “species–area relationship.”

The study of geographic patterns faces two fundamental challenges. First, ecological data across very large scales are not easy to generate. For example, to understand diversity gradients, we need global estimates of species richness for particular taxonomic groups. Given our poor state of knowledge about the diversity of most taxa, we are mostly restricted to the study of a handful of groups or, alternatively, to the geographic regions where we have reasonable databases of species distributions. If this were not problem enough, to explain gradients we also need a wide range of quantitative explanatory variables. Historically, the dominant explanatory variable included in geographical analyses was latitude, simply because it was the only variable that could be measured (hence the term “latitudinal gradients”). Although better than nothing, a problem with latitude and other purely geographical variables is that they can only describe a pattern; they cannot explain it. Thus, the literature is replete with possible explanations based on what workers believed to underlie correlations between space and ecology.

This leads to the second fundamental challenge in geographical ecology. When faced with a collection of correlations, how do we test hypotheses when it is essentially impossible to conduct controlled experiments? Nearly all studies of broadscale patterns must use statistical techniques to tease apart complex patterns of covariation among suites of variables. Given the challenges geographical ecologists face—financial, methodological, and epistemological—progress is perhaps slow. Nonetheless, recent major advances have been made. This Special Feature comprises six cutting-edge studies, illustrating where we stand with respect to explanations for broadscale patterns in ecology, highlighting both how much, and in some cases how little, we know.

The first four papers focus on the original question in geographical ecology; that is, what factors determine the number of species across large distances. Arguably, we know more about what drives tree diversity than any other group, and Field et al. present a powerful model for understanding the species richness of woody plants in regions for which we have data and for predicting richness patterns in areas where we do not. They also compare and contrast their model against an alternative generated to explain the global pattern of angiosperm family richness. What is most telling is that both models are based on the realization that elements of climate related to energy and water inputs represent the first-order driving forces of plant diversity. On the other hand, both models are designed to understand how currently existing taxa distribute themselves at broad scales, but they do not explicitly include speciation/extinction dynamics. The interplay between ecological and evolutionary processes represents the largest remaining challenge to a full explanation of diversity patterns, and Cardillo et al. take on this issue. They find, as many workers have suspected, that diversification rates (of birds) are generally higher in tropical com-

¹ Reprints of this 68-page Special Feature are available for \$10.25 each, either as PDF files or as hard copy. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1707 H Street, N.W., Suite 400, Washington, DC 20006.

pared to temperate clades. Why this might be is not clear in their analysis, but answering this question undoubtedly represents the future of research on diversity gradients.

The interaction between the past and the present as drivers of diversity is also the main focus of Rex et al., who take the question into the less well-documented oceans. Although there are extreme challenges in generating quantitative deep-sea data, the results so far again indicate that single-factor explanations (e.g., only the past or only the present drive diversity gradients) are almost certainly wrong, and more progress can be made by integrating their effects.

An independent test of the drivers of diversity gradients can be conducted using exotic species, which perhaps comes as close to a manipulative experiment as we can get in geographical ecology. Given that most modern introductions are directly or indirectly due to humans, we might expect environmental or biotic effects to be weaker determinants of exotic species richness than factors related to human activities. However, Stohlgren et al. find that the diversity of invasive plants in North America actually closely follows the pattern for native species; they conclude that biotic and environmental forces constrain both exotic and native plant diversity. This is an intriguing conclusion, and one likely to stimulate additional research based on human-influenced patterns of diversity.

Although it captures the lion's share of attention, species richness is certainly not the only ecological pattern across broad geographic scales. It has long been surmised that biotic interactions become stronger toward the tropics, and as a partial consequence, population dynamics are dominated by biotic effects in warm climates and abiotic effects in cold climates. The final two papers in the feature address these allied issues. Although the geographic span of such analyses is necessarily limited by the scope and complexity of the problem, it appears that interaction strengths do indeed increase toward the tropics as predicted (Pennings and Silliman). In the case of saltmarsh grass and its herbivores, interaction strengths vary independently of diversity or population densities, so one pattern cannot be predicted from the others. If general, this has important implications for attempts to generate a simple global theory of ecology and biogeography.

The notion that population dynamics vary systematically from north to south (in the Holarctic) was made famous by small mammals and their population cycles. Post demonstrates that two large mammal species also show latitudinal variability in population dynamics, arguing that density dependence is more pervasive in southern compared to northern populations. That this represents the first attempt to address the issue for any large-bodied species clearly indicates how little we know about global patterns other than diversity. If, indeed, geographical patterns in density dependence prove to be the rule, it may be that we are one step closer to an understanding of variation in the dynamics of populations.

We expect that this sample of papers, illustrating current questions and the data and methods being used to answer them, shows that geographical ecology is in fact making rapid progress. Understanding the factors that generate large-scale patterns is clearly more than just an abstract intellectual exercise. Species introductions, climate change, and other anthropogenic global changes will undoubtedly alter the face of ecological diversity and dynamics. We had best understand the patterns we have now to predict the future.

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GLOBAL MODELS FOR PREDICTING WOODY PLANT RICHNESS FROM CLIMATE: DEVELOPMENT AND EVALUATION

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Abstract. There have been few attempts to generate global models of climate–richness relationships, and fewer still that aim to predict richness rather than fitting a model to data. One such model, grounded on theory (biological relativity to water–energy dynamics) is the interim general model (IGM1) of the climatic potential for woody plant richness. Here we present a second-generation model (IGM2), and genus and family versions of both models. IGM1 describes horizontal climate–richness relationships based on climate station data and systematic species range maps, with IGM2 additionally incorporating vertical changes in climate due to topographic relief. The IGMs are mathematical transformations of empirical relationships obtained for the southern subcontinent of Africa, whereby the re-described regression models apply to the full range of global variation in all independent climate parameters. We undertake preliminary validation of the new IGMs, first by mapping the distribution and relative spatial variation in forecasted richness (per 25 000 km²) across the continent of Africa, then by evaluating the precision of forecasted values (actual vs. predicted) for an independent study system, the woody plants of Kenya. We also compare the IGMs with a recent example of purely statistical regression models of climate–richness relationships; namely, the “global” model of A. P. Francis and D. J. Currie for angiosperm family richness. We conclude that the IGMs are globally applicable and can provide a fundamental baseline for systematically estimating differences in (woody) plant richness and for exploring the hierarchy of subordinate relationships that should also contribute to differences in realized richness (mostly at more discrete scales of analysis). Further, we found that the model of Francis and Currie is useful for predicting angiosperm richness in Africa, on a conditional basis (somewhere, sometime); we examined the relationship that it describes between climate and richness. Lastly, we found that indices of available soil water used in “water-budget” or “water-balance” analyses are not proxies for available liquid water as a function of climatological dynamics.

Key words: Africa; climate; climatic potential for richness; diversity gradients; interim general model; Kenya; model evaluation; species richness; water–energy dynamics; woody plant diversity.

INTRODUCTION

It has long been known that global gradients in richness covary with global gradients in climate. The development of statistical models of this relationship that apply globally is an important but elusive goal for ecologists. In addition to improving our understanding of diversity patterns, such models could prove useful for predicting reasonable values of plant or animal richness where actual values are unknown, and for modeling how changes in climate could alter the richness (and vegetation) patterns we see today.

Attempts to apply models, developed in particular regions, to other regions have produced some success

but have tended not to result in globally applicable models (e.g., Currie and Paquin 1987). Such work tends to focus on mid to high latitudes; regions for which data availability is better, but which contain relatively few of the world's species. An exception is an interim general model (IGM) of the “climatic potential for (woody) plant richness” (O'Brien 1998). Rather than using a purely statistical approach, O'Brien worked from first principles to develop a first-order mechanistic explanation for covariation between climate and richness globally: biological relativity to water–energy dynamics (O'Brien 1989, 1993, 1998). This idea effectively links water–energy dynamics (work done by water) to fundamental parameters of both climatological and biological dynamics, at all scales of analysis: liquid water and solar energy (e.g., hydrologic cycle and photosynthesis, respectively). In accord with energy's dynamic relationship with the state of water, the model describes the relationship of climate to woody plant

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richness as a linear function of rainfall and an optimal (parabolic) function of insolation (O'Brien 1993, 1998).

Empirically, model development was based on climate and richness data for the southern subcontinent of Africa (from 15° S to 35° S latitude) at the macro scale (25 000 km² grain), which spans tropical to temperate climate and vegetation. Regression analyses suggested that the best climate variables for describing "available liquid water" and "optimal energy" conditions were annual rainfall (R_{an}) and minimum monthly potential evapotranspiration (PET_{min}), respectively: species richness $\propto R_{an} + (PET_{min} - (PET_{min})^2)$. An empirically based global model of this relationship depends on the availability of qualitatively similar "actual" richness data with global coverage. Because of the lack of such data (see Appendix B), the southern African model (SAF1) was mathematically transformed so that it applies to the full global range of variation in R_{an} and PET_{min} (O'Brien 1998). The transformation was necessary because energy's parabolic function prevents extrapolation to climates where energy values fall outside the range sampled in southern Africa. O'Brien (1998) showed that the resulting interim general model (IGM1) of the climatic potential for richness generates reasonable estimates for woody plant species richness elsewhere in the world (United States, South America, Africa, China) in terms of both relative differences (gradients) and actual values (for the United States).

Since development of the IGM1 for species richness, we have investigated two other implications of biological relativity to water–energy dynamics: (1) the same relationship should apply over time, and (2) inclusion of vertical changes in climatological dynamics as a function of topographic relief should improve model fit. First, if water–energy dynamics are fundamental to life, the same dynamics that apply over space today, should apply over time. If so, the same climate–richness relationships applying to species should apply to genera and families. O'Brien et al. (1998) found this to be true for southern Africa; the strength of the relationship being almost identical at species and genus levels, but significantly weaker for family richness. The last is unsurprising for the following reasons (see also Qian and Ricklefs 2004). Since terrestrial life began, both climatological and biological dynamics have been subject to change due to independent geological dynamics (e.g., plate tectonics and diastrophism). These processes necessarily alter the location of land and sea relative to both the horizontal and vertical vectors of climatological dynamics. The effects are evident today in continental disjunctions and taxonomic vicariance, and in the idiosyncratic effects of topography on the prevailing climate and richness of an area (e.g., orographic rainfall and rainshadows, and "hot spots" and refugia, respectively). Although the horizontal vector is inherent in IGM1, the vertical vector is not. The

second implication that we tested has two parts: (1) inclusion of the vertical vector should increase the strength and precision of climate–richness relationships; and (2) given the more recent evolution of modern genera and species, the increase should be greatest with regard to family richness. On adding topographic range to the species, genus, and family models for southern Africa, the strength and precision of climate–richness relationships increased from 78.8, 79.8, and 69.7% (SAF1 models) to 85.6, 86.8, and 81.5% (SAF2 models), respectively; the greatest improvement being in family richness (O'Brien et al. 2000). Herein we present IGMs for species, genus, and family richness that were developed from these findings.

This and other evidence reviewed elsewhere (e.g., Whittaker et al. 2001, Hawkins et al. 2003) has contributed to a growing shift from a traditional emphasis only on the relationship of energy with richness, to one whereby both liquid water and energy are considered when describing climate–richness relationships. One recent example of this shift is a "global" statistical model of the relationship of climate with angiosperm family richness developed by Francis and Currie (2003; hereafter, F&C model). They found that their model accounts for a greater portion of the variation in family richness (~84%) than does the IGM1 when its parameters are regressed using their data (~63%). However, such a discrepancy is expected given differences in richness (woody plant vs. angiosperm families) and climate data, and especially given that IGMs are explanatory regression models, rather than simply statistical regression models. In addition to meeting more stringent statistical criteria, the IGMs had to meet theoretical and empirical criteria, with the latter taking precedence over statistical strength (R^2) when selecting the "best" model. As a consequence, the best explanatory model may not be the "best-fit" statistical model. These and other important differences mean that the IGMs describe a general climate–richness relationship (everywhere, always); by comparison, given the a priori conditional nature of its water variable, the F&C model describes a conditional one (somewhere, sometime). (See *Results: Model terms and global application*.)

Our aims are therefore twofold. First, we present the second-generation IGMs (IGM2) for species, genus, and family richness, along with the hitherto unpublished IGM1s for genus and family richness. We examine their ability (1) to estimate absolute values of woody plant richness outside of southern Africa, specifically in Kenya, and (2) to describe the relative variation in predicted richness across the continent of Africa. The predicted pattern should reflect expected or known differences in richness and vegetation. The focus on Africa is in keeping with the paucity of convincing empirical relationships between richness and energy within the tropics, where rainfall seems to dominate. Africa is also suitable for generating a global

model since virtually the full range of variation in IGM climate parameters occurs there. Secondly, we compare the IGMs with the F&C model. We illustrate the similarities, but also the difference between explanatory and purely statistical regression models of climate–richness relationships. We focus attention on theoretical and empirical discrepancies between models, rather than purely statistical ones.

For reasons of limited space, and to save duplication, we do not attempt to review relevant literature. This has burgeoned in recent years, and contains richly contrasting views of controls on diversity (notably Huston 1994, Whittaker et al. 2001, 2003, Blackburn and Gaston 2003, Hawkins et al. 2003, Colwell et al. 2004, Currie and Francis 2004, Qian and Ricklefs 2004).

*Conceptual basis: biological relativity
to water–energy dynamics*

The following is drawn from E. M. O'Brien (*unpublished manuscript*) and briefly summarizes what is meant by biological relativity to water–energy dynamics and how it applies to terrestrial life.

Theoretically, the idea follows from first principles governing climatological, biological and ecological dynamics that can be gleaned from standard references and texts. The key is liquid water.

In terms of climatological first principles, given the Earth's energy regime, water is the only matter at the Earth's surface that is fully dynamic as a function of energy–matter exchange. Like all other matter at the Earth's surface, water is subject to changes in form and location. In addition, however, water occurs in and moves through all three states, primarily via climatological (atmospheric) dynamics—the hydrologic cycle. When this is combined with water's physical properties, the resulting water–energy dynamics (work done by water) account for almost all work done at the planet's surface throughout geological time. In terms of terrestrial life, climatological water–energy dynamics determine the very existence of water on landmasses, as well as its state, amount, duration and, in conjunction with topography, its distribution.

In terms of biological first principles, liquid water is the essential matter and matrix of life (see details in Franks 2000). Its physical properties make it the key agent of biological dynamics, driving all biological processes and functions, everywhere and always. Since the state of water varies as a function of ambient energy conditions, this a priori means that biological dynamics are restricted to optimal energy conditions—the range in which water is liquid and energy (light/heat) is still available for work. Outside this envelope biological dynamics cease (plant dormancy, aestivation, hibernation, death, etc.). Within this range the capacity for biological dynamics should vary as a function of both energy

and water availability, reaching maximum capacity where surface water from precipitation remains in a liquid state year-round and its amount exceeds the climatological demand (evaporation).

In terms of ecological first principles, the direct and primary relationship between climate and terrestrial life should be its relationship with plants, whereby raw energy, water and essential abiotic matter are transformed into biotic energy and matter. There should be a strong secondary relationship between climate and animal richness, via trophic plant–animal exchange, as found by Andrews and O'Brien (2000) for the distribution and richness of mammals in southern Africa. Finally, climatological dynamics are independent of life. Although secondary and tertiary feedbacks develop if life exists (e.g., vegetation cover decreasing albedo), life per se is not necessary to the operation of climatological dynamics. Crucially, however, climatological dynamics are necessary for terrestrial biological dynamics. Thus realized climate limits the capacity for terrestrial biological dynamics—and over time we expect richness to respond to this.

Other independent and dynamic parameters (e.g., geomorphological water–energy dynamics) also limit the capacity for biological dynamics (e.g., via dissolved nutrients), and must form part of a complete explanation for spatial richness patterns. However, given both the smaller distances over which these parameters exhibit measurable heterogeneity and their dependence on climatological water–energy dynamics, their inclusion must await the development of trans-scalar modelling (O'Brien 1989, O'Brien et al. 2000, Whittaker et al. 2001). In the interim the IGMs describe only the first-order “climatic potential for richness” and assume all else to be equal or non-limiting.

MATERIALS AND METHODS

The thrust of regression analysis can be explanation or simply statistical description. In either case, relationships need to be empirically plausible and based on analyses carried out at an appropriate scale (grain size). Sampling area should be held constant. If globally applicable predictive models are a goal, then the sampled variation in independent model parameters should be representative of (or reasonably extrapolated to represent) their full range of variation globally, and spatial autocorrelation in richness values should be minimized, if not eliminated, to avoid biasing model development, a priori, towards particular richness and associated climate conditions. Unlike purely statistical models, explanatory models explicitly test potential explanations for phenomena rather than simply documenting their existence. They should be both empirically and theoretically plausible in terms of how explanatory variables relate to each other and to the response variable. Correlation between explanatory

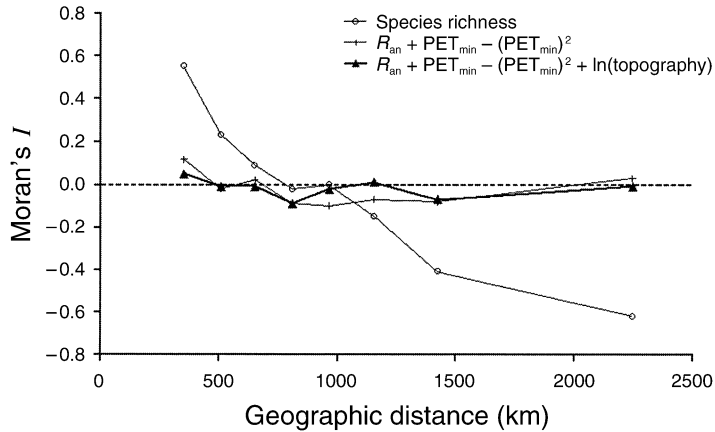


FIG. 1. Spatial correlograms for the southern African (SAF) data used in Interim General Model (IGM) development ($N = 65$ grid cells, each 25 000 km²): woody plant species richness; SAF1 residuals (rainfall [R_{an}] + PET model); and SAF2 residuals (rainfall + PET + topography model). The species richness correlogram is significant ($P < 0.001$, Bonferroni approximation), with the two smallest and two largest distance classes being significant at $P < 0.05$ after Bonferroni correction. The SAF1 correlogram is significant ($P = 0.011$), but the only significant point on this is the smallest distance class. The SAF2 correlogram is not significant ($P = 0.597$).

variables should be minimized to avoid (1) misleading (inflated) R^2 values resulting from redundancy, and (2) the problem of unstable parameter estimates, which can obscure the role of important “missing” environmental variables. Thereafter, selection of the “best” explanatory models should be based on theoretical criteria (plausibility, generality, simplicity, parsimony) and lastly on statistical strength.

Development of second-generation Interim General Models (IGM2s)

All of the southern African models (SAFs) and IGMs are explanatory regression models. Empirically they describe with minimal redundancy how water–energy dynamics relate to both climatological and biological dynamics. The capacity for atmospheric water–energy dynamics and biological water–energy dynamics (e.g., photosynthesis) should tend to increase with insolation (and evaporation off oceans), but only as long as available liquid water meets or exceeds the atmospheric energy demand for water and evapotranspiration off of landmasses. Theoretically the models describe one fundamental outcome of biological relativity to water–energy dynamics; that is, the relative capacity for changes in the form (richness) or location (distribution) of terrestrial life, over space and time.

Multicollinearity was minimized, first by restricting models to one water variable and one energy variable, both of which had to be dynamic first-order climatological parameters. Secondly, the energy and water variables used are as weakly correlated as possible ($r \approx 0.5$ in southern Africa, and in Africa in general), and empirically they are temporally independent of each other. The minimum monthly amount of potential evapotranspiration (PET_{min}) usually occurs in winter, when rainfall tends to be least. This is consistent with most seasonal changes in climate globally. The topography variable, $\ln(\text{topographic range})$, models the potential effects on richness of vertical variation in climate, such as environmental and adiabatic lapse rates. It is weakly correlated with the other explanatory variables ($r = 0.409$ and $r = -0.032$ [not significant] with

R_{an} and PET_{min} , respectively, in southern Africa). Note that the natural logarithm of topographic range is only slightly better statistically than a linear function; but it is more reasonable than the simpler linear function because of the increase in surface area (and habitats) that can be occupied as topographic relief increases (O’Brien et al. 2000).

The potential effects of spatial autocorrelation were first reduced by using only richness samples associated with climate stations (SAF1), and then eliminated by the addition of the topography variable, as indicated by the spatial distribution of residuals for SAF1 (O’Brien et al. 2000). No spatial autocorrelation remains in the residuals of SAF2 (Fig. 1).

Finally, we argue that the intercept should be negative, both theoretically and empirically. A negative intercept indicates that the relationship originates from the explanatory variables. Richness should be zero in the absence of liquid water, even when energy conditions are optimal (e.g., Peruvian coastal desert), since no life can exist without liquid water. Positive intercepts can be taken to indicate deficiency of the model, such as a missing variable. Negative predicted values should be treated as predictions of zero taxa. They can be taken to indicate the degree of increase in water and/or energy needed before any richness is expected (e.g., Antarctica).

Mathematical transformation of the best southern African models (SAF1 for genus and family; SAF2 for species, genus, and family) into IGMs followed exactly the same methods as those detailed in O’Brien (1998), except that topographic range was included in IGM2s (see Appendix B). For the mathematical transformation to be reasonable, there should be strong correlation ($r > 0.7$ and ideally $r > 0.9$) between forecasted richness values generated using the three empirical SAF models and those generated using IGMs, with minimal change in the unexplained variance. This was the case for IGM1 for species richness: $r \approx 0.97$ (O’Brien 1998). Thus it is reasonable to assume that the strength (R^2) and associated error term (RMSE) of the relationship of

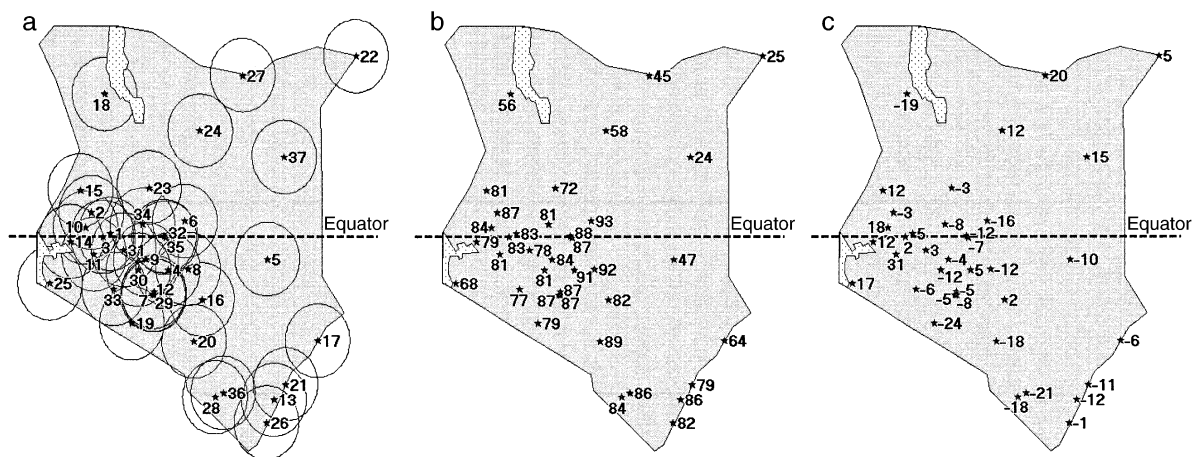


FIG. 2. Maps of Kenya showing: (a) the locations and identification numbers of the climate stations and the 25 000-km² circles surrounding them; (b) woody plant family richness per circle; and (c) “residuals” from IGM2 family level (i.e., forecast minus observed family richness). Large lakes (Turkana and Victoria) are indicated (stippled fill). Circles that have <80% of their area as land in Kenya, although shown here, are excluded from consideration in the paper; these are numbers 13, 17, 19, 21, 22, 25, 26, 27, and 28.

climate with richness in southern Africa also apply with respect to IGMs. As demonstrated for species richness by O’Brien (1998), this assumption is supported mathematically if there is little difference between the ideal SAF model (based on PET_{min}) and the corresponding IGM in terms of the coefficients for annual rainfall and, in the case of IGM2, topographic relief. (Compare ideal SAF models in O’Brien et al. [1998] with IGMs reported here.) Given the increased range in PET_{min} values, IGM coefficients for PET_{min} should markedly decrease relative to ideal SAF model coefficients. And, given the greater range of positive (potential) richness values, the intercept value should increase but remain negative.

African climate and topography data

We used Thornthwaite and Mather (1962–1965) for climate data from 980 stations in Africa (i.e., mean annual rainfall and potential evapotranspiration, both of which are dynamic climate variables). Thornthwaite’s PET is a proxy for the intensity of insolation at the Earth’s surface. It measures the energy demand for liquid water (mm), and thus the role of energy in climatological dynamics (evaporation and transpiration). The data were calculated using a formula he derived from experimental data on the amount of water evaporated and transpired from samples of grass-covered land never suffering from lack of water. The formula requires data on prevailing temperature and intensity of insolation at a given time (date) and place (latitude). Unlike many measures of PET, his is not adjusted to sea level and thus measures the energy (heat/light) regime actually influencing vegetation at the Earth’s surface.

Following O’Brien et al. (2000), topography data were extracted from the USGS DEM of Africa, and

resampled to 0.1° resolution, giving >200 elevation points/25 000-km² grid cell. The minimum value was subtracted from the maximum to give the “topographic range” (in meters), for each grid cell. Values were assigned to the 980 climate stations according to the grid cell that they occupied

Examination of the spatial pattern of model predictions

All IGMs were used to predict the climatic potential for richness across the continent of Africa, based on data from the 980 climate stations. The same was done for the F&C model at the family level (using the Thornthwaite climate data). Examination of the resulting patterns in forecasted richness, and how they relate to variation in vegetation and physiography, was undertaken following O’Brien (1998).

Actual vs. predicted richness for Kenya

All the IGMs forecast richness for a circular area of 25 000 km² (i.e., within a radius of 90 km of a climate station), the same area as the grid cells used in model development (e.g., O’Brien 1993). Actual woody plant richness data for Kenya were calculated accordingly, based on presence–absence data per circle, with each circle centered over a climate station (Fig. 2). Presence–absence data were obtained using a comprehensive set of distribution maps and site location data for Kenyan woody plants (Beentje 1994). Following the same criteria as in O’Brien (1993) to determine which species to include, 1417 out of 1862 species were retained; these represented the largest and longest lived of plant species, and thus those most likely to be robust indicators of climate conditions. Those eliminated were non-native species, plants ≤ 2.5 m in height, and/or plants that are not truly woody. The distributional rang-

es of higher taxa were determined by aggregating ranges of species within genera (635 genera in total), and within families (126 families).

Distribution maps from Beentje (1994) consist of presence/absence data per pixel, with pixel resolution of half a degree (30'). Given that Kenya lies on the equator, the spatial resolution of the distribution data is ~55.5 km and pixel area is effectively constant at ~3080 km². Distribution information for ~30% of the species in Beentje (1994) is given only as named collecting localities. For these, all the named places were assigned latitude and longitude coordinates using various sources, including Polhill's (1988) checklist of collecting localities, Microsoft Encarta CD-ROM, and a Kenyan postal districts booklet. These locations were then rasterized into the same 30' grid system. We calculated actual richness per circle using MapInfo Professional (MapInfo, Windsor, Berkshire, UK) by amalgamating the species data from those pixels whose centers lie within each circle. Circles with <80% of their area as land within Kenya's borders were removed from the data set, leaving a total of 28 circles (Table 2a).

We also calculated actual woody plant family richness for 34 900-km² circles (105-km radius) using the same protocol as for the 25 000-km² circles (Table 2b). This corresponds to the sampling area used by Francis and Currie (2003) for their model (see Table 1b for error terms). Of the 37 circles centered on Kenyan climate stations, 27 met the equal-area criterion at this grain size.

Woody plant family richness differs from angiosperm family richness, which includes nonwoody families and excludes gymnosperm and pteridophyte families. A comprehensive series of species range maps does not exist for Kenyan angiosperms. This prevents direct comparison between the IGMs and the F&C model, but some testable implications exist. We know there to be 245 plant families in Kenya (H. Beentje, *personal communication*). Excluding gymnosperm (3) and pteridophyte (31) families, this leaves 211 as a maximum for angiosperm family richness in any circle. According to the Francis and Currie richness data (not all derived from range maps) the global maximum angiosperm family richness in 34 900-km² grid cells is 201 (Francis and Currie 2003: Fig. 1). So, in the Kenyan test, predicted angiosperm family richness per 34 900-km² circle can be seen as reasonable if it is greater than actual woody plant family richness but <211 and preferably no more than 201. Similarly, for Africa in general, predicted family richness values using the F&C model should be <202. It is difficult to give a lower bound, but comparison with IGM forecasts could be informative.

The climate data used by Francis and Currie are from global climate databases (i.e., interpreted/interpolated data). The formulation of PET that they used is that of Ahn and Tateishi (1994). Annual water deficit (WD_{an}) was calculated as PET_{an} minus mean annual actual

evapotranspiration (AET_{an}). When using the F&C model to forecast richness in Kenya we used the climate data (and formulations) used by Francis and Currie. This was necessary because the two PET_{an} measures are very different, with ranges of 668–1938 mm and 1177–1727 mm, respectively (Appendix A: Fig. A1). Only in terms of the higher PET_{an} values, which occur in low-elevation interior (xeric) basins and coastal plains, are the two measures similar. For climate stations at higher elevations, and in the mountains and uplands of eastern Africa (>1000 m above sea level), Thornthwaite's PET_{an} is markedly lower than the PET_{an} values of Ahn and Tateishi. Each Kenyan climate station was assigned WD_{an} and PET_{an} values from the location closest to its geographic location (the Ahn and Tateishi data were kriged over a 0.5° grid; these climate data were kindly provided by A. P. Francis and D. J. Currie).

Many of the Kenyan circles overlap (Fig. 2). This would be a problem in model development, but is irrelevant in generating forecasted richness. It is also not important when we consider each circle individually: we simply compare the predicted richness with the actual richness. Similar to confidence intervals, forecasts within one error term (root mean square error) of the original model can be classed as a close fit; those out by 1–2 error terms, a reasonable fit; and those out by >2 error terms, a poor fit. Overlapping circles are a problem, however, if we try to compare predicted with actual values by considering more than one circle at a time (e.g., by correlation). To avoid such pseudoreplication when performing correlation, we generated 30 different random samples of the circles, such that no two circles in any sample overlapped; this produced sample sizes ranging from seven to nine. We correlated actual and forecasted richness values within each sample and report the mean results.

RESULTS

New IGMs

Model coefficients for IGM1 species richness (O'Brien 1998) and all new IGMs are reported in Table 1a, which also gives the *R*² and root mean square error (RMSE) values for the empirical southern African PET_{min} models. In addition, Table 1a gives correlation coefficients for the mathematical transformation of the southern African models into global models (IGMs). In all cases, statistical synonymy (*r* > 0.9) is indicated, making it reasonable to assume that empirical *R*² and RMSE for ideal PET_{min} models also apply to the respective IGMs. In all cases the expected mathematical changes occurred, supporting this assumption (see *Materials and Methods: Development of second-generation Interim General Models*; compare with SAF model coefficients in O'Brien et al. 2000). Furthermore, comparison between IGM1 and IGM2 model coefficients indicates that, consistent with comparisons between

empirical SAF1 and SAF2 models (O'Brien et al. 2000), the addition of topographic range independently increases precision and strength of the model. In all cases, this is shown by an increase in predictive power, reduction in unexplained variance, and the more negative intercept, while the R_{an} and PET_{min} coefficients remain nearly the same.

Statistical results

Spatial pattern of model predictions.—As expected (given the strong correlations between species, genus, and family richness in southern Africa), the patterns of predicted genus (especially) and family richness across Africa were very similar to those for species richness (Figs. 3, 4a, and Appendix A: Fig. A2). Visual comparison of these maps with topographic maps of Africa indicate, consistent with the changes in coefficients (see *Results: New IGMs* and Table 1), that IGM2 predictions result in an increase in forecasted richness values in areas with high topographic relief and a decrease for areas with relatively flat terrain, especially for family richness. For example, Mt. Cameroon, the African Rift Valley, the Ethiopian Highlands, and the Tibesti Dome all exhibit increases in predicted richness, while there are notable decreases in portions of the interior plateaus of eastern and southern Africa, and portions of the Congo and Chad Basins. In between these areas, predicted values remain similar to those generated by IGM1. This emphasizes the independent and idiosyncratic nature of vertical changes in climate and reflects the increased strength and precision of the models. Again in line with the greater contribution that topographic relief makes to the strength and precision of IGM2 for family richness, the most pronounced changes occurred for family richness.

The pattern generated by the F&C model (using the climate station data) is similar to that generated by the IGMs for family richness in that the ordering of predictions is similar (compare Fig. 4a with Fig. 4b). When the 980 climate stations are ranked from lowest to highest predicted value for each model, the mean difference in ranks between the two models is only 65 (although this difference is significant; Wilcoxon signed rank test $Z = 3.6$, $P < 0.001$). The main distinction between the two sets of predictions is in the spread of values. The F&C model predicts high numbers of families under extremely arid conditions (see also Fig. 5). Indeed, all F&C model predictions for Africa are >50 angiosperm families and only 11 points are <70 . The maximum predicted value is 186.4, which is only just below the maximum possible from the model (186.8; Fig. 5); 55 predicted values are >175 (there would have been more had we used Ahn and Tateishi PET data in this exercise). In contrast, IGM1 produces 255 predictions below 35 woody plant families, the lowest being 5.8. The maximum predicted value for Africa is 263.9, but only 12 predictions are >175 . Some of these differences between the two models relate to the different response

variables, especially at the lowest predicted values. However, the fact that IGM1 predicts substantially more woody plant families in rich cells than the F&C model predicts angiosperm families is a notable difference. IGM2 produces lower predicted family richness at the top end (only six >175 , maximum 226.0), and also in the least rich cells (e.g., 12 predictions of zero), but not overall. Mean predictions for the 980 climate stations across Africa are 134.0 (F&C model), 62.6 (IGM1), and 63.0 (IGM2).

Kenyan test.—Predictions of actual woody plant richness values using the two generations of IGMs are mostly reasonable or close fits [within 2 or 1 error term(s), respectively], with a slight increase in precision being found among IGM2 predictions (Table 2a). Using the random sample protocol (see *Materials and Methods: Actual vs. predicted richness for Kenya*) to eliminate pseudoreplication caused by circle overlap, the mean values for “residuals” (forecast minus actual values) were very small. Mean observed species richness was 307.2 ± 3.0 (mean \pm SE); the mean residual of the species forecasts for IGM1 was -4.3 ± 3.7 (SD of residual sizes = 71.5 ± 2.4 [SD \pm SE]), and for IGM2 it was 23.1 ± 3.3 (75.2 ± 2.2). Mean genus richness was 172.5 ± 1.4 ; IGM1 mean residual was -1.4 ± 1.8 (34.0 ± 1.2), and IGM2 mean residual was 10.6 ± 1.6 (34.7 ± 1.0). Mean family richness was 65.4 ± 0.25 , IGM1 mean residual was -9.7 ± 0.45 (10.9 ± 0.19), and IGM2 mean residual was -2.7 ± 0.34 (6.2 ± 0.22).

The mean Pearson correlation coefficients between actual and forecast values were high: IGM1 species $r = 0.71 \pm 0.008$; IGM2 species $r = 0.78 \pm 0.007$; IGM1 genera $r = 0.72 \pm 0.007$; IGM2 genera $r = 0.80 \pm 0.006$; IGM1 families $r = 0.68 \pm 0.006$, IGM2 families $r = 0.81 \pm 0.005$. Significance values based on these mean r values and a sample size of eight are marginal for IGM1 ($P \approx 0.05$) and significant for IGM2 ($P \approx 0.02$). Further, the best-fit lines between observed and forecast values for IGM2 approximated the ideal 1:1 line in the cases of species and genera, suggesting no systematic errors in relation to richness levels: mean slope did not differ significantly from 1 nor mean intercept from 0. For families, and for all IGM1 forecasts, the slope (observed values arbitrarily on the y-axis) was flatter than 1. (For IGM2, species: mean slope = 0.95 ± 0.03 , mean intercept = -6.3 ± 7.3 ; genera: mean slope = 0.99 ± 0.03 , mean intercept = -7.8 ± 4.3 ; families: mean slope = 0.82 ± 0.02 , mean intercept = 14.0 ± 0.9 .) Thus the correspondence between observed and forecast richness values was good. Interestingly, $\ln(\text{topographic range})$ correlated very strongly with richness values in the random samples: $r = 0.80 \pm 0.005$, 0.83 ± 0.005 , 0.86 ± 0.003 , respectively, for species, genera, and families ($P \approx 0.01$).

Geographically there was a broad pattern of overprediction in west and northeast Kenya and underprediction in south and central Kenya (Fig. 2). Possible

TABLE 1. Predictive global model specifications for (A) Interim General Models (IGM1 and IGM2), and (B) F&C 2° potential evapotranspiration (PET) model, with values taken from Francis and Currie (2003) and residual mean square errors (RMSE) provided by D. J. Currie.

Model	IGM coefficients ($N = 980$)				ln(topographic range) (m)	Transformation (Pearson correlation r)†
	Intercept (constant)	R_{an} (mm)	PET _{min} (mm)	(PET _{min}) ² (mm ²)		
A) Interim general models of the climatic potential for richness: predicting number of woody plant taxa						
IGM1						
Species‡	-150	0.3494	5.6294	-0.0284		0.973
Genera	-70	0.1836	2.9008	-0.0141		0.974
Families	-1	0.0473	0.7197	-0.0039		0.963
IGM2						
Species	-371	0.2987	5.1186	-0.0257	42.7155	0.971
Genera	-170	0.1597	2.6250	-0.0127	19.6916	0.971
Families	-57	0.0372	0.6455	-0.0034	10.1120	0.966
B) Francis and Currie (2° latitude/longitude spatial resolution) global PET model: predicting the number of angiosperm families ($N = 4224$)						
Families	8.8	-0.0641§	0.2199	-6.79×10^{-5} ¶		

Notes: The correlation coefficients indicate statistical singularity ($r > 0.9$) between predictions generated using southern African (SAF) models and those generated using the IGMs, making it reasonable to assume that each IGM is a globally applicable redescription of the ideal empirical relationship obtained for southern Africa (see O'Brien 1998). For the southern African models, numbers in parentheses are the values when negative predictions are converted to zero values (see *Materials and Methods: Development of second-generation Interim General Models*); the first numbers result when the negative values are retained. R_{an} is annual rainfall; PET_{min} and PET_{an} are minimum monthly and annual potential evapotranspiration, respectively; WD_{an} is annual water deficit (see O'Brien 1998).

† Reported for the IGMs are both the empirical relationships obtained for the southern subcontinent of Africa (R^2 , adjusted R^2 , and RMSE; O'Brien et al. [1998]), and those obtained from mathematical transformation into global models (IGMs for the full range of variation globally in PET_{min}).

‡ See O'Brien (1998).

§ Value reported is WD_{an} (mm), not R_{an} .

|| Value reported is PET_{an}.

¶ Value reported is (PET_{an})².

contributing factors are likely to be edaphic ones, with underprediction being associated with richer-than-normal soils (basalt derived) and higher-than-normal soil moisture (presence of lakes, underground water resources, and/or exotic rivers [i.e., rivers bringing water from rainfall elsewhere]), and overprediction being associated with relatively poor soils and low soil moisture (high leaching, lack of exotic rivers or underground water resources). In some cases, overprediction could also be a function of undercollection of botanical specimens (e.g., from remote parts of Kenya), which were the basis for Beentje's maps.

The F&C model appears not to grossly underpredict angiosperm family richness in Kenya (Table 2b). Forecasted values are greater than the number of actual woody plant families in every 34 900-km² circle, and greater than the IGM-predicted woody plant family richness (for 25 000-km² circles). Given the maximum possible prediction of 187 associated with the F&C model, all forecasted values are less than the total number of angiosperm families known to occur in Kenya (211) and also less than the global maximum number (201) of angiosperm families per 34 900 km² reported by Francis and Currie.

Model terms and global application

In terms of global application, the range of variation in annual rainfall and PET_{min} across Africa is repre-

sentative of the global range of variation in these parameters. Even where PET_{min} = 0 (mid latitudes to poles) the IGMs plausibly describe how climate relates to richness, given the use of rainfall rather than precipitation (which includes solid water) as the measure of available liquid water. In other words, if there is rainfall then the energy conditions for liquid water necessarily exist at some time(s) during the year (e.g., summer). Thus R_{an} implicitly (and statistically) measures the amount and/or duration of optimal energy, as well as plant growth, under these conditions (see O'Brien 1998). Thus, where PET_{min} = 0, the IGMs still model water-energy dynamics, despite reducing to

$$\text{richness} \propto -a + R_{an} [+ \ln(\text{topographic range})]$$

where $-a$ is the (negative) intercept and R_{an} is the mean annual rainfall. Where R_{an} also equals zero, the IGMs reduce to

$$\text{richness} \propto -a [+ \ln(\text{topographic range})].$$

In this case zero woody plant richness is expected (e.g., Antarctic), which is empirically plausible.

The IGMs and the F&C model differ primarily in terms of the water variable used and in the sign of the intercept. Francis and Currie use a water-budget variable, water deficit, one of the basic indices of available soil moisture derived from climate (precipitation minus PET). Others are actual evapotranspiration (AET) and

TABLE 1. Extended.

Southern African model fits ($N = 65$)		
$R^2\dagger$	adj. $R^2\dagger$	RMSE†
0.788 (0.804)	0.778 (0.794)	73.7 (70.8)
0.798 (0.808)	0.788 (0.798)	36.7 (35.8)
0.697 (0.697)	0.683 (0.683)	11.8 (11.8)
0.856 (0.868)	0.846 (0.859)	61.2 (58.6)
0.868 (0.874)	0.859 (0.865)	29.9 (29.3)
0.815 (0.815)	0.803 (0.803)	9.3 (9.3)
0.837	0.837	17.40

water surplus. All are conditional indices of available soil moisture for plant growth; none is a dynamic climate variable. AET = precipitation only when precipitation < PET. Otherwise, when precipitation ≥ PET, AET = PET. WD = PET - AET when precipitation < PET. When precipitation ≥ PET, WD = 0, because AET = PET. Water surplus = precipitation - PET when precipitation > PET (i.e., when AET = PET and WD = 0). For a detailed analysis of how these indices statistically relate to richness, to climate variables, and

to each other in southern Africa or Africa in general, see O'Brien (1993, 1998).

Since $WD = 0$ when $PET = 0$ or when precipitation ≥ PET, the F&C model is a priori conditional. And when $WD_{an} = 0$, the model reduces to an optimal energy model of the relationship of climate with richness, with no water component. For Condition 1, the soil water-budget model, when P_{an} (mean annual precipitation) < PET_{an} , then $AET_{an} = P_{an}$ and $WD_{an} > 0$:

$$\begin{aligned} \text{richness} &\propto a - (PET_{an} - P_{an}) + [PET_{an} - (PET_{an})^2] \\ &= a - (PET_{an} - AET_{an}) + [PET_{an} - (PET_{an})^2] \\ &= a - WD_{an} + [PET_{an} - (PET_{an})^2]. \end{aligned}$$

For Condition 2, the optimal energy-only model, when $P_{an} \geq PET_{an}$ or when $PET_{an} = 0$, then $AET_{an} = PET_{an}$ and $WD_{an} = 0$:

$$\begin{aligned} \text{richness} &\propto a - (PET_{an} - PET_{an}) + [PET_{an} - (PET_{an})^2] \\ &= a - (PET_{an} - AET_{an}) + [PET_{an} - (PET_{an})^2] \\ &= a + [PET_{an} - (PET_{an})^2]. \end{aligned}$$

Thus the F&C model is a soil moisture-energy model where soil moisture deficits limit plant growth and is purely an energy model where water deficits do not occur. Where there is no available water, it predicts between nine and 98 angiosperm families (within the globally observed range of PET_{an} ; Fig. 5). This aspect of the model, which derives from both the positive

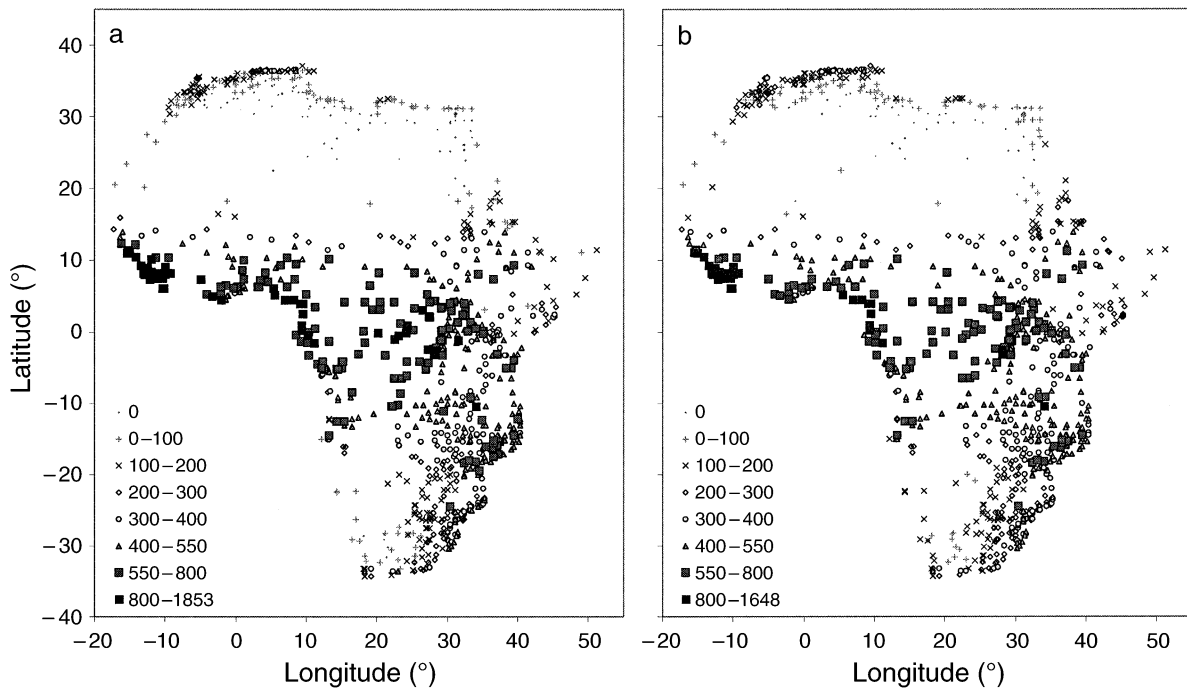


FIG. 3. Predicted species richness for Africa based on (a) IGM1 and (b) IGM2. Values were calculated using the Thornthwaite climate data for all 980 African climate stations (source of climate data: Thornthwaite and Mather 1962–1965). This figure is reproduced in color in Appendix A.

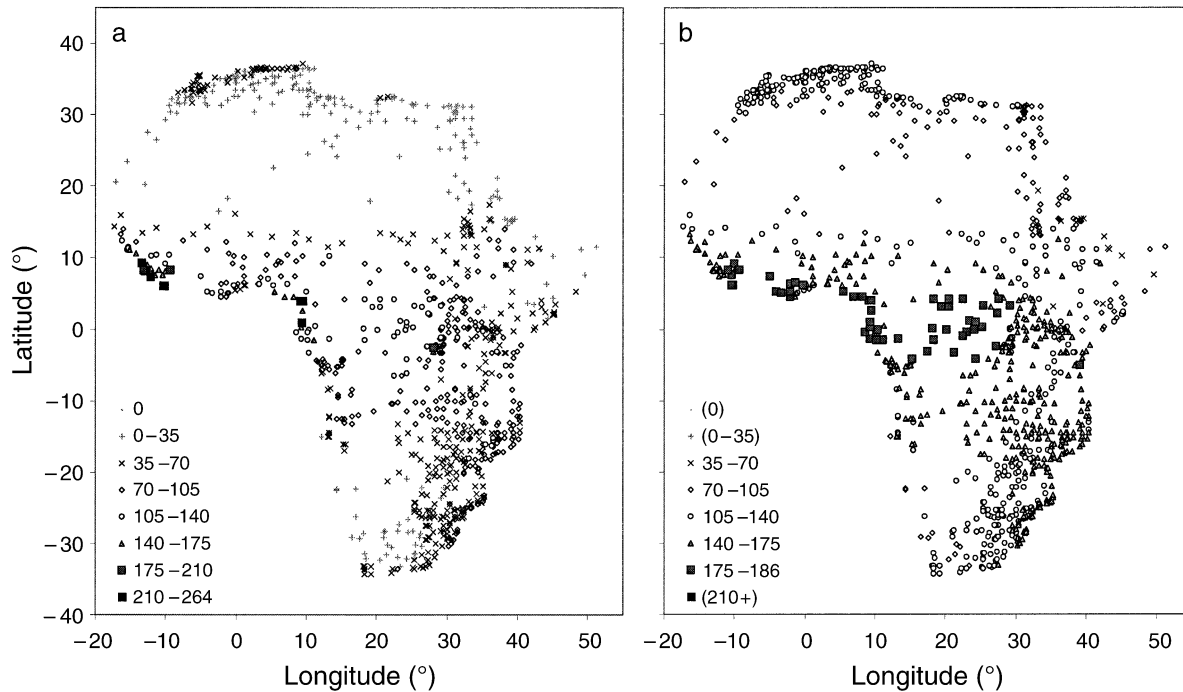


FIG. 4. Predicted family richness for Africa based on (a) IGM1 and (b) F&C model. Parentheses indicate that the category is empty, i.e., no climate stations in Africa have predicted richness within the specified range. Values were calculated using the Thornthwaite climate data for all 980 African climate stations (Thornthwaite and Mather 1962–1965). This figure is reproduced in color in Appendix A. Also, see Fig. A2 in Appendix A for IGM1 and IGM2 predictions at the genus and family levels.

intercept and the values of the other coefficients, suggests that unmodeled effects are subsumed within the statistical fit to the data, and is true for all the Francis and Currie global PET models (from 2° to 10° spatial resolution; Francis and Currie 2003: Table 2). Similarly, interpretation is hindered by the redundancy that results from the collinearity between PET_{an} and WD_{an} .

DISCUSSION

An empirical global model of the climatic potential for richness depends on the quality of the data on which it is based. Systematic and exhaustive species range maps do not exist for humid tropical regions of the world. They do exist for parts of mid to high latitudes (e.g., parts of Western Europe, United States). And they exist for the transition between them (southern Africa, Australia). However, model development also requires regions where we know or can reasonably assume species richness to be on a par with its environmental potential; where recolonization after deglaciation and major volcanic eruption, for example, is most likely to be complete. This assumption seems reasonable with regard to the flora of Africa, given the absence of major physical barriers to migration of species during Plio-Pleistocene ice-age oscillations. It is unreasonable in many parts of the mid to high latitudes. Thus the empirical basis for the IGMs can be considered reasonable.

Empirical performance of the models

The results support the global applicability of the new IGMs of the climatic potential for richness at three taxonomic levels. They support the idea that the relationship between climate and richness stems from the dependence of both climatological and biological dynamics on water–energy dynamics, and that consequent geographic variation in the climatic capacity for biological water–energy dynamics could cause the covariation between realized climate and realized richness. Given that the IGMs apply to the full range of global variation in R_{an} and PET_{min} , reasonable forecasting of the climatic potential for richness is possible for elsewhere in the world. The good fit between actual and predicted richness in Kenya supports this, as does the realistic pattern of relative variation in predicted richness across Africa (see O'Brien 1998). Empirically, the addition of vertical changes in climate in IGM2s alter forecasted richness values almost exclusively in areas of high or low topographic relief, in a positive or negative fashion, respectively. The same should apply globally. Since the IGMs only describe the climate potential for richness, gross over- or underprediction of richness by the models should highlight other variables that need inclusion in a more complete explanation (see *Discussion: Some applications and implications of predictive models*).

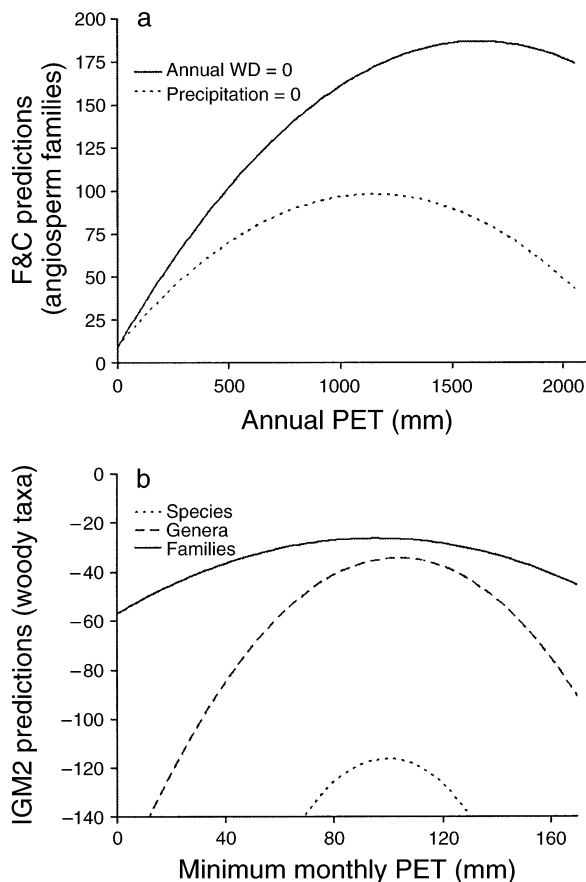


FIG. 5. (a) Envelope of possible predictions from the F&C model (Francis and Currie 2003). The solid line shows the condition of no water deficit (WD) and represents the upper limit of predictions for this model. The dashed line shows the condition of no precipitation and thus represents the lower limit of predictions for this model. All model predictions fall within the area bounded by the two lines. A plot showing the range of predictions of IGM1 can be found in Whittaker et al. (2003: Fig. 7.2b). (b) Predicted values from IGM2 plotted against minimum monthly potential evapotranspiration (PET_{min}) when there is no rainfall and no topography (i.e., completely flat terrain), at the species, genus, and family levels. Note that all are negative, which means that no woody plants are predicted to exist under such conditions, even when optimal energy conditions exist (see *Introduction: Conceptual basis: biological relativity to water–energy dynamics*)—in contrast to the F&C model.

Annual water deficits are common in Kenya and our findings support the predictive usefulness of the F&C model where annual water deficits occur, even in low latitudes.

Comparison of IGMs and the F&C model

To be a general, globally applicable description of the first-order (and ideally causal) relationship of climate with richness, a model should generate reasonable predicted richness values (without regional refitting), and the resulting distribution of relative predicted richness should be similar in pattern and relative magnitude

to observed or expected differences in richness, especially the latitudinal gradient in richness. All work to date suggests that the IGMs meet these and other empirical and theoretical criteria. Our results, together with those of Francis and Currie, suggest that the F&C model also tends to produce a good fit to empirical data in a range of climatic conditions. However, its upper prediction limit of 187 angiosperm families and its positive, often high lower limit (depending on PET_{an} ; Fig. 5) suggest that its predictive usefulness is best in moderate (e.g., temperate), rather than harsh (e.g., very arid) or benign (e.g., equatorial humid), climatic conditions.

The F&C model is a purely statistical regression model, which its authors interpret via the importance of secondary or tertiary biotic relationships to climate, such as the correlation of productivity with richness. We have only compared the F&C model with IGM1, since it applies only to the horizontal relationship of climate with richness. Like the other models, the F&C model was limited to a single water variable and a single energy variable (Table 1). In both cases the energy variables are similar (aspects of PET) and related to richness in a functionally similar fashion: an optimal (parabolic curve) function, modeled as $PET - PET^2$. Thus according to both sets of models, richness initially increases and then decreases as energy increases. In terms of climate, such an optimal relationship is empirically plausible with regard to rainfall: as we move from the poles to the tropics, rainfall increases as realized evaporation and the capacity for atmospheric saturation (dew point) increase up to some global optimum. At this point the capacity for evaporation continues to increase but subsequent condensation, saturation, and rainfall decrease as dew point increases. Instead, more and more (and eventually all) evaporated water is held in the atmosphere: the same amount of atmospheric moisture can keep Holland green, but the Sahara a desert.

These similarities between the F&C model and the IGM1 model are considerable and, along with other recent findings (e.g., Hawkins et al. 2003), could suggest that we are close to determining which climatic variables tend to be responsible for constraining plant richness. If so, the differences between the models may be even more instructive and important for advancing our knowledge. In the F&C model, a conditional, non-dynamic soil water-budget variable (WD_{an}) represents available liquid water, as opposed to the dynamic climate variable (R_{an}) in the IGMs. The result is a model of how energy, coupled sometimes with an insufficiency of soil moisture, relates to richness. The conditional rather than general nature of the F&C model can be attributed to at least two factors; (1) the lack of a theoretical or empirical explanatory framework in model development, and (2) statistical issues including multicollinearity between the variables chosen to define climate and how it relates to richness.

TABLE 2. (A) Interim General Models (IGMs): actual, predicted, and "residual" values for woody plant species, genus, and family richness/25 000 km² ($N = 28$ climate stations). (B) F&C model: actual woody plant richness and predicted angiosperm family richness/34 900 km² ($N = 28$ climate stations).

A) IGMs										
Climate station	Area (%)	Actual values			Model predictions					
		Woody plant richness			IGM1			IGM2		
		Species	Genus	Family	Species	Genus	Family	Species	Genus	Family
1	100	410	236	83	488	265	83	507	273	88
2	100	508	279	87	437	238	76	468	252	84
3	99	414	237	83	462	251	80	483	260	85
4	100	561	291	91	501	272	84	547	292	96
5	100	160	93	47	187	115	38	182	112	37
6	100	526	286	93	321	179	59	397	213	77
7	100	525	274	87	404	221	72	446	240	82
8	100	560	291	92	347	191	63	417	223	80
9	100	435	247	84	379	207	68	429	230	80
10	95	469	269	84	625	337	101	621	334	102
11	96	413	239	81	720	387	114	704	378	112
12	100	525	274	87	400	218	71	445	239	82
14	88	411	252	79	542	295	89	545	295	91
15	82	408	227	81	486	264	82	528	282	93
16	100	480	249	82	456	248	78	477	257	84
18	88	143	101	56	88	66	23	145	92	37
20	98	460	244	89	322	178	60	368	199	71
23	100	313	184	72	289	160	56	345	186	69
24	100	208	124	58	379	208	68	389	212	70
29	100	525	274	87	383	209	69	427	229	79
30	100	404	232	81	284	157	55	343	185	69
31	100	350	201	78	394	216	70	441	237	81
32	100	486	272	88	318	175	60	386	206	76
33	100	391	220	77	304	168	58	360	194	71
34	100	368	202	81	310	171	59	372	199	73
35	100	477	270	87	359	197	65	422	226	80
36	90	529	277	86	314	175	58	344	188	65
37	100	70	40	24	181	110	38	185	111	39

Notes: Area = percentage of the area of a circle that is land within Kenya. "Residuals" = predicted minus actual richness.

In the first case, given an explanatory framework, models can be accepted, rejected, or modified based on theoretical grounds (generality, parsimony, simplicity) and empirical observation, as well as on statistical criteria. Without an explanatory framework, only statistical descriptions of how input data relate to each other are generated, and discrimination of the "best" model is restricted to statistical criteria. Empirically the positive intercept of the F&C model suggests that the positive effect of some missing explanatory influence on richness is subsumed in the intercept (when there is no water and no energy, nine angiosperm families are modeled as being present). Within an explanatory framework, this would suggest model rejection, even if alternatives are less powerful statistically.

In the second case, we consider that the F&C model is biased by the fact that water deficit conditions dominate terrestrial systems, as does the vegetation associated with them, with associated richness values constituting the bulk of any global database on richness. A priori redundancy between WD_{an} and PET_{an} increases the statistical precision of this particular relationship at the expense of other possible relationships. Together these biases could account for the high statistical

strength of the F&C model, despite its poor performance under other climatic conditions. Climatic and water-budget variables are meaningful and these meanings need to be considered when modeling how climate relates to biological phenomena; rainfall always measures available liquid water as a function of climate.

Despite these issues, the Francis and Currie (2003) study contributes in several important ways to a better understanding of the relationship of climate with richness. First, their model emphasizes the negative effects of energy in its relationship with richness. It does so in a fashion that is empirically consistent with the optimal relationship between energy and the potential for rainfall (as energy increases, dew point increases while the potential for atmospheric saturation decreases). The same applies with regard to biological dynamics, as shown by the empirical increase and decrease in photosynthesis during the course of a day, and seasonally during the course of a year.

Second, their study highlights an assumption common to many studies of the relationship of climate with richness; that water-budget variables are climate variables. This assumption is similar to treating primary productivity as though it were a dynamic parameter of

TABLE 2. Extended.

A) IGMs						B) F&C model		
"Residuals"						Actual values	Model predictions	
IGM1			IGM2			Woody plant richness	Angiosperm richness	
Species	Genus	Family	Species	Genus	Family	Area (%)	Family	Family
78	29	0	97	37	5	100	85	175
-71	-41	-11	-40	-27	-3	98	88	179
48	14	-3	69	23	2	97	87	172
-60	-19	-7	-14	1	5	100	91	156
27	22	-9	22	19	-10	100	56	77
-205	-107	-34	-129	-73	-16	100	94	158
-121	-53	-15	-79	-34	-5	100	87	152
-213	-100	-29	-143	-68	-12	100	94	150
-56	-40	-16	-6	-17	-4	100	85	153
156	68	17	152	65	18	92	87	183
307	148	33	291	139	31	95	86	185
-125	-56	-16	-80	-35	-5	100	87	152
131	43	10	134	43	12	60	NA	NA
78	37	1	120	55	12	85	84	186
-24	-1	-4	-3	8	2	100	89	145
-55	-35	-33	2	-9	-19	88	59	87
-138	-66	-29	-92	-45	-18	95	89	130
-24	-24	-16	32	2	-3	100	79	151
171	84	10	181	88	12	100	69	155
-142	-65	-18	-98	-45	-8	100	87	152
-120	-75	-26	-61	-47	-12	100	85	151
44	15	-8	91	36	3	100	82	158
-168	-97	-28	-100	-66	-12	100	90	159
-87	-52	-19	-31	-26	-6	95	83	152
-58	-31	-22	4	-3	-8	100	87	150
-118	-73	-22	-55	-44	-7	100	90	157
-215	-102	-28	-185	-89	-21	85	87	141
111	70	14	115	71	15	99	25	95

photosynthesis. The fundamental, dynamic parameters of climate are atmospheric moisture, energy, wind, and pressure. Since derived water-budget variables are subordinate and conditional corollaries of realized climate-soil interactions, it follows that they should be conditional correlates of associated richness. But because they are not parameters of climatological dynamics, it does not follow that they should describe how climate per se relates to richness.

Third, the Francis and Currie (2003) study documents the fact that, when the global variation in PET_{an} is sampled, which is not possible using only African data, an optimal relationship between richness and energy pertains. Thus, Francis and Currie provide the first independent empirical corroboration of the optimal relationship between richness and energy first documented by O'Brien (1989, 1993). It is therefore puzzling that Francis and Currie (2003) argue that their findings refute the existence of such a relationship. Virtually all plant growth depends on liquid water, and since liquid water availability depends on ambient energy conditions, some form of optimal relationship between energy and richness should be expected (to account for the solid and gaseous states of water). It has

only recently been documented because few studies sample a sufficient range in climate and richness to obtain the relationship empirically. Most only examine portions of the curve, documenting positive, negative, or insignificant (humid tropics) statistical relationships between energy and richness. These results tend to be treated as competing hypotheses, but our findings and those of Francis and Currie show that they can be reconciled when energy is described as an optimal function.

Fourth, the Francis and Currie study highlights the issue of using only statistical strength to refute a hypothesis. To test the global applicability of IGM1 in principle (see Appendix B), they regressed their family richness data accordingly, as a function of increasing annual rainfall and optimal energy (PET_{min}) conditions. (Note that Francis and Currie cite Legates and Willmott [1992] and Ahn and Tateishi [1994] as the sources of their data; the IGM was derived using climate data from Thornwaite and Mather [1962–1965]). Despite the discrepancies in climate and richness data, they found that this relationship accounted for 63% of the global variation in angiosperm family richness (Francis and Currie 2003:530). This is close to the 68% accounted for

by SAF1/IGM1 for woody plant family richness (O'Brien et al. 1998). Although they rejected IGM1 in favor of the statistically stronger F&C model in this case, their study can be seen as providing the first independent evidence that the IGMs are globally applicable and empirically plausible in principle.

*Some applications and implications
of predictive models*

The most obvious use of predictive models is to predict richness where actual values are unknown. Other applications are also possible. First, if Africa's flora is assumed to be near equilibrium with its climatic potential, the IGMs provide a line of evidence for evaluating whether or not this is the case elsewhere in the world. Second, given that they invoke dynamic climatological parameters, the IGMs can be linked directly to Global Climate Models (GCMs) and used to examine how past and/or future changes in climate could alter present-day richness patterns. Alternatively, being independent of GCMs, they could be used for testing GCM predictions. Perhaps most importantly they can contribute to the development of trans-scalar models, and to making hierarchy theory operational. In essence, when working at more discrete scales of analysis, predictions at the macro scale can be incorporated as constants ("potential richness") in analyses of how other variables and factors (e.g., edaphics, shade) relate to richness (O'Brien 1989, O'Brien et al. 2000, Whittaker et al. 2001, 2003). In so doing, the first-order effects of climate can be eliminated as active factors, focusing analyses on the residual variation not explained by climate.

In terms of future test implications, gross differences between predicted and actual richness values in Kenya emphasize that climate is not the only factor influencing richness. Consistent with findings for southern Africa (O'Brien et al. 2000), visual examination of topographic, hydrological, and soil maps for Kenya points to edaphic and associated hydrological factors as the next independent parameters that need to be included in a more complete explanation of global variations in plant richness, especially exotic rivers, permanent and ephemeral lakes (pans), ground water reserves, soil parent material, and nutrient content. Of these, exotic rivers, ground water reserves, and soil parent material probably make the most important edaphic contribution to woody plant richness in Africa today, as in the past (O'Brien and Peters 1999a, b). IGMs should grossly overpredict richness where extant richness is below its climatic potential (e.g., where soils are poorer than normal or lower in moisture than that expected as a function of rainfall, and especially where perennial lakes and rivers are scarce). Gross underprediction is expected where perennial lakes and rivers (especially exotic rivers) exist, soils are richer than normal, or soil moisture is greater than that expected as a function of rainfall alone (e.g., due to meltwater).

CONCLUSIONS

The results of this study both support and extend the global applicability of O'Brien's (1998) interim general model of the climatic potential for woody plant richness, thereby providing operational versions at three taxonomic levels, for use with or without topographic data. They also support the idea that biological relativity to water-energy dynamics explains the covariation between climate and richness globally, one outcome of which should be a "latitudinal gradient" in richness. IGM2 invokes parameters that reflect both the horizontal and vertical vectors of change in climate and should contribute to a better understanding of observed elevational gradients in richness in mountainous regions, as well as idiosyncratic "hot spots" of high diversity. Lastly, by providing a systematic and globally applicable model of how first-order differences in climate relate to woody plant richness, we are now in a position to eliminate it as an active factor (hold it constant) when analyzing other causes for differences in richness at more discrete scales of analysis.

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APPENDIX A

Figures showing the relationship between PET data used for IGMs and PET data used for the F&C model for Kenyan climate stations (Fig. A1), the predicted genus richness for Africa based on (a) IGM1 and (b) IGM2 (Fig. A2), color reproductions of Figs. 3 and 4, and associated literature citations are available in ESA's Electronic Data Archive: *Ecological Archives* E086-120-A1.

APPENDIX B

A description of the general methodological constraints, a summary of transformation of southern African models into IGMs, and associated literature citations are available in ESA's Electronic Data Archive: *Ecological Archives* E086-120-A2.

TESTING FOR LATITUDINAL BIAS IN DIVERSIFICATION RATES: AN EXAMPLE USING NEW WORLD BIRDS

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Abstract. Study of the latitudinal diversity gradient to date has focused largely on pattern description, with relatively little work on the possible mechanisms underlying the pattern. One proximate mechanism is a latitudinal bias in the discrepancy between speciation and extinction rates, leading to higher rates of species diversification toward lower latitudes. Despite being central to many explanations for high tropical diversity, this mechanism is tested very rarely. We discuss some of the problems involved in testing for latitudinal bias in diversification rates and present an example phylogenetic analysis for endemic bird genera of the New World. The results provide evidence for higher diversification rates in clades inhabiting lower latitudes, both when genera are considered independent and when phylogeny is controlled for using independent contrasts. High rates of diversification are also associated with larger geographic area and higher net primary productivity, although these do not fully account for the latitudinal effect. The latitudinal pattern is stronger in younger clades, supporting the prediction of a simple model in which the signal of latitudinal bias in diversification rates diminishes as clades age and become saturated with species. Our study demonstrates that a clade-based approach can help answer important questions that a geographic approach cannot, but large phylogenies and geographic databases are needed to cope with the large amount of noise inherent in this type of analysis.

Key words: diversification; extinction; latitudinal diversity gradient; New World birds; speciation; species richness.

INTRODUCTION

Explaining why there are more species in the tropics compared to higher latitudes is one of the great contemporary challenges of ecology. The continuing strong interest in the latitudinal diversity gradient is demonstrated by the large number of papers recently published on the topic, the frequent publication of reviews (Rohde 1992, 1999, Rosenzweig 1995, Gaston 2000, Willig et al. 2003), and the regular emergence of novel hypotheses to explain the pattern (Stevens 1989, Colwell and Hurtt 1994, Dynesius and Jansson 2000, Guernier et al. 2004). Although the pattern remains famously poorly explained, slow progress towards a solution is being made. For example, recent analyses of large data sets point increasingly towards climate rather than geographic area as the major driving force of higher tropical species richness (Hawkins and Porter 2001, Macpherson 2002, Francis and Currie 2003, H-Acevedo and Currie 2003, Hawkins et al. 2003a, b, Hawkins and Porter 2003). However, much uncertainty remains. In particular, the mechanisms by which latitudinal variation in climate determines species numbers largely remain a mystery: far less effort

has been spent on empirical testing of possible mechanisms than on pattern description and correlative tests.

In this paper, we focus on the idea that the proximate mechanism for the latitudinal diversity gradient is a higher rate of species diversification at lower latitudes, where diversification is defined as the discrepancy between speciation and extinction rates. A latitudinal bias in diversification rate is central to a number of high-profile explanations for high tropical species richness. Rosenzweig's (1992, 1995) area hypothesis states that the larger geographic distributions attainable by tropical species serve both to elevate speciation rates (by increasing the likelihood of allopatric subdivision) and reduce extinction rates (by providing a buffer against range or population decline). The species–energy hypothesis (Wright 1983, Wright et al. 1993) proposes that extinction rates are reduced in lower latitude species as a result of the higher populations sustainable by the greater amount of available energy. Rohde (1992, 1999) suggests that speciation rates at lower latitudes are elevated by shorter generation times driven by higher temperatures. Other authors have predicted higher extinction rates at high latitudes due to “harsher” or more variable climatic conditions (Cracraft 1985, Dynesius and Jansson 2000).

Despite being central to many explanatory hypotheses, faster diversification is not a necessary precondition for higher species richness at lower latitudes.

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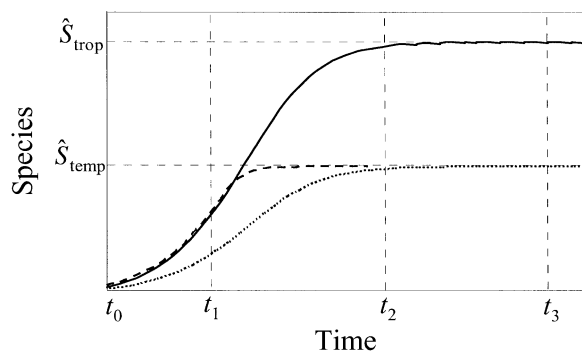


FIG. 1. Simple model of the growth in the number of species in tropical and temperate regions or clades, from zero to saturation levels (\hat{S}_{trop} and \hat{S}_{temp}). The solid curve represents diversification of tropical groups, the dotted curve represents diversification of temperate groups when a latitudinal bias in diversification rate exists, and the dashed curve represents diversification of temperate groups when there is no latitudinal bias.

This can be visualized using the simple model shown in Fig. 1. The number of species in a region increases from zero to a saturation level where rates of speciation and extinction are in equilibrium. The inherent diversification rate of the temperate region may be equal to (dashed line) or lower than (dotted line) that in the tropics, but a lower saturation level keeps temperate species richness below that in the tropics. This model can be applied equally to the growth of individual clades. A regional assemblage of species consists of numerous clades, at different stages along this trajectory. Below saturation (e.g., at time t_1), any inherent variation in diversification rate between tropical and temperate clades should be easily detectable as latitudinal differences in mean diversification rates over the lifetime of clades (the period from t_0 to t_1). When saturation is reached (time t_2), the diversification rate of temperate and tropical clades at that point in time will be equal (speciation minus extinction = 0), but comparisons of mean diversification rates over the lifetime of clades (the period from t_0 to t_2) should still carry the signal of any inherent latitudinal bias. This signal will diminish in strength after long periods at saturation (time t_3). This model therefore predicts that any latitudinal bias in diversification rates should be most strong among younger clades, which have yet to become, or have only recently become, saturated with species. It also demonstrates that latitudinal variation in species numbers can arise without any latitudinal bias in diversification rates. Establishing whether or not diversification rates show latitudinal bias, therefore, is an important step in understanding the origin of the latitudinal diversity gradient.

TESTING FOR LATITUDINALLY BIASED DIVERSIFICATION RATES

Given its central position in many hypotheses to explain the latitudinal diversity gradient, it is surprising

that direct empirical tests for latitudinal bias in diversification rates are relatively scarce. Previous tests are almost entirely confined to the paleontological literature, and these have tended to support higher diversification rates in the tropics. Faster tropical diversification has been implied by lower average taxon ages or higher rates of first appearances in the tropics (Stehli et al. 1969, Durazzi and Stehli 1972, Hecht and Agan 1972, Jablonski 1993, Flessa and Jablonski 1996), or from a higher rate of diversity accumulation through time in tropical groups (Crame 2000, 2001, Buzas et al. 2002).

An alternative approach is to infer diversification rates using the information contained within phylogenies of extant taxa. Using phylogenetic methods allows tests to be done for groups with a poor or unreliable fossil record (e.g., the majority of terrestrial vertebrates). Whereas paleontological analyses are usually geographic (involving the comparison of assemblages across different geographic regions or grid cells), phylogenetic analyses are explicitly clade based. The mean diversification rate of a clade throughout its history is a function of its age and number of extant species. In the absence of dated phylogenies, sister-clade comparisons are often used to infer relative diversification rates, an approach that is now standard practice in comparative tests of the effects of life history or ecological traits on diversification rates (see Barraclough et al. 1998).

However, testing for geographic variation in diversification rates by this method presents additional difficulties and has received very little attention. As far as we are aware, only three times has latitude been tested explicitly as a predictor of diversification rates using phylogenetic methods. Farrell and Mitter (1993) attempted the first such test by identifying five tropical-temperate pairs of sister clades of phytophagous insects, but with such a small sample their result was inconclusive. Cardillo (1999) extended this approach to passerine birds and swallowtail butterflies, and increased the number of useful sister-clade comparisons by treating latitude as a continuous variable, measured as the midpoint between the northern and southern limits of the geographic range of each species. This study suggested that lower latitudes were indeed associated with higher rates of diversification. Most recently, Davies et al. (2004b) used a similar approach on a much larger data set for angiosperm families (see also Davies et al. 2004a). Again, this analysis suggested a link between latitude and diversification rates, although the test for latitudinal variation of Davies et al. (2004b) was incidental to an analysis of the effects of environmental energy. Taken together these three studies serve to highlight a number of challenges in doing comparative tests that are both phylogenetically and geographically explicit. These challenges may be summarized as follows. (1) *Phylogenetic accuracy*. As with any phylogenetic comparative analysis, the reliability of sister-

clade groupings and branch lengths (where used) are contingent on the quality of the phylogeny used. Different types of data and methods of phylogeny reconstruction may give conflicting results. However, the need for large phylogenies to identify a sufficient number of comparisons usually means there is little or no choice available in the selection of a phylogeny, and the limitations of the phylogeny used must be acknowledged and accepted. This is changing with the routine application of robust phylogenetic reconstruction methods. (2) *Loss of data*. In Cardillo's (1999) analysis, the use of pairwise comparisons required the imposition of strict criteria of latitudinal separation and overlap between sister clades. As a result, only a small subset of available sister-clade contrasts were permissible, so even with a large phylogeny, sample sizes were small and statistical power low. Restricting an analysis to comparisons between non-overlapping tropical-temperate sister clades, as attempted by Farrell and Mitter (1993), is unlikely to produce enough comparisons for an acceptable statistical test, even with the largest phylogenies currently available. However, this is changing with the increasing use of supertree methods to construct large phylogenies (e.g., Davies et al. 2004b). (3) *Summarizing clade latitude*. For use as a continuous predictor variable in statistical models, the range of latitudes inhabited by each clade must be summarized as a point estimate. Cardillo (1999) did this by using the mean of the latitudinal midpoints of all member species within a clade. Latitudinal midpoint is a relatively accurate point estimate for a species where its geographic range is small and circular, with a low perimeter:area ratio. However, many species have ranges that are irregularly shaped with respect to latitude. For example, a species may be found almost entirely in the tropics where it occupies a circular range, but with a narrow coastal band extending into high latitudes. In this case, latitudinal midpoint is a misleading summary of where the bulk of the area of the range of a species lies. (4) *Latitudinal overlap*. Even where latitudinal point estimates differ between two clades, there may still be substantial latitudinal overlap in their geographic ranges, although this probably elevates Type 2 rather than Type 1 statistical error (Cardillo 2002). The likelihood of substantial latitudinal overlap will be lower where geographic ranges are mostly relatively small. (5) *Accuracy of geographic range estimates*. Although distributions are well-known for some well-studied taxa in some parts of the world, other taxa have relatively few records and some parts of the world are poorly surveyed. Geographic distributions are often presented as the extent of occurrence (i.e., polygons drawn around a number of occurrence records from single, often widely separated, locations). This implies that the species inhabits a continuous distribution within the polygon boundaries, which may not be true. Even so, extent of occurrence maps may reflect historical distributions if the isolated populations have become

separated from a once continuous distribution (e.g., as a result of habitat fragmentation). (6) *Dynamic range boundaries*. Geographic ranges are unlikely to be static over long periods of time, but expand and contract in response to environmental changes or as the result of speciation events (Price et al. 1997, Gaston 1998). Even if the contemporary range of a species is mapped with accuracy, is difficult to know how well it represents the range that the species has occupied throughout its history. (7) *Environmental drivers of latitudinal patterns*. Although Cardillo's (1999) analysis supported a latitudinal bias in diversification rate, it went no further in testing possible causes of this pattern. Ultimately, it is not latitude itself, but the underlying environmental gradients or historical factors that are of interest in explaining the geographic distribution of species richness (Hawkins and Diniz-Filho 2004). As with latitude, there may be substantial error variance around a point estimate of the range of environmental conditions experienced by a species.

AN EXAMPLE USING NEW WORLD ENDEMIC BIRD CLADES

Methods

We present here an example of an approach to testing for latitudinal bias in diversification rates using phylogenetic methods, which attempts to improve on the analysis of Cardillo (1999) by dealing with some of the challenges (2, 3, and 7) shown in the previous section. We focused on endemic bird clades of the New World, since the geographic distributions of birds in the New World are relatively well-known, and restricting the analysis to the endemics of a single region provided a measure of control for possible biogeographic and historical influences (Hawkins et al. 2003b). We chose genus as the taxonomic level of the analysis, primarily for the larger number of endemic New World clades (hence larger sample size) available at lower taxonomic levels. In addition, species within genera tend to occupy a more restricted range of latitudes than species within higher taxa, so the problems of latitudinal overlap among clades and variation around the point estimate of the latitude of a clade are likely to be less severe.

To avoid the loss of data involved with choosing latitudinally separated pairs of sister clades from a phylogeny, we estimated absolute rates of species diversification of clades using a dated phylogeny. Using this approach allowed us to treat each clade as an independent observation in the analysis. Of course, any phylogenetic bias in diversification rates and latitude would violate this assumption of independence, so we repeated analyses using phylogenetically independent contrasts. We estimated clade ages using the DNA hybridization phylogeny of Sibley and Ahlquist (1990). The differences in melting temperatures of hybridized DNA between pairs of taxa (ΔT_{50H}) were converted to

millions of years (10^6 yr) using the calibration factors suggested by Sibley and Ahlquist: $\Delta T_{50}H 1.0 = 2.3 \times 10^6$ yr for passerines and $\Delta T_{50}H 1.0 = 4.2 \times 10^6$ yr for nonpasserines. Species diversification rate was then estimated for each clade as $\ln(\text{number of species})/\text{age}$ (Purvis 1996). We only accepted an age estimate for a clade from the Sibley and Ahlquist phylogeny if its sister clade was also present in the phylogeny, as the absence of the sister clade means that the age of a clade will appear artificially high, giving misleadingly low estimates of diversification rates. We established whether the sister of each clade was present in the Sibley and Ahlquist phylogeny by using the Sibley and Monroe (1990) classification of birds to determine the full list of genera within the next most inclusive taxon (usually a tribe or subfamily). If all other genera within the next most inclusive taxon were represented in the Sibley and Ahlquist phylogeny, we accepted the age estimate of the clade because its sister clade must be present. In some cases, if not all genera were present in Sibley and Ahlquist, we were able to refer to independent phylogenies to determine the sister of a clade. In this way, we were able to estimate ages for 37 New World endemic genera. We are conscious of the uncertainty of date estimates derived from DNA hybridization data, and of criticisms of some of the methods used by Sibley and Ahlquist (see O'Hara 1991). However, this phylogeny is currently the largest available for birds built using a single method, and thus the only one with which a test such as this can be carried out (see Bennett and Owens 2002). We emphasize that the analysis we present here is illustrative, and that the same approach can be applied with new and perhaps more rigorous dated phylogenies as they become available.

All geographic data were processed within a geographic information system. This had several important advantages over the analysis of Cardillo (1999): it allowed species latitudes to be measured more accurately, and it allowed us to include geographic area and climatic factors as covariates in the analysis. The geographic range characteristics for the clades were measured as follows, using polygon range data from Ridgley et al. (2003). First, we measured the latitude of the centroid of the breeding range of each species, a more accurate characterization of the latitude of a species than latitudinal midpoint when ranges are irregularly shaped. The latitude of each clade was then summarized as the mean of the species latitudinal centroids; effectively providing a measure that is weighted by species richness. We then measured the total geographic area occupied by each clade, a factor shown to be a significant predictor of diversification rates among bird families (Owens et al. 1999, Bennett and Owens 2002). The non-overlapping breeding ranges of species were combined into a single range for each clade, which was then reprojected into a Lambert Azimuthal Equal Area projection with central meridian and parallel set to the

centroid of the clade range. The area of the reprojected range was then recorded in km^2 . We included measures of three climatic factors, in order to test possible underlying causes of any latitudinal bias in diversification rates: mean annual temperature, annual actual evapotranspiration (AET), and annual net primary productivity (NPP), all of which have previously been shown to be correlated with species richness at large scales (Currie 1991, Wright et al. 1993, H-Acevedo and Currie 2003, Hawkins et al. 2003a, b) or suggested to influence rates of speciation or extinction (Currie 1991, Rohde 1992, 1999, Wright et al. 1993). All three climatic variables were recorded as raster data on geodesic grids. The temperature and AET data (0.5° resolution) were from the United Nations Environment Program GRID databases (UNEP 2003), and the NPP data (1° resolution) were from Woodward et al. (1995). Estimates of climatic variables for each species were obtained by converting the breeding range for the species and each climatic variable onto a 0.05° grid and then calculating the mean value across the cells occupied by the species. We then summarized the variable for each clade as the mean of the member species values. All the above analyses were performed using ArcMap 8.2 (ESRI 2002).

We tested for associations between diversification rate and predictor variables using multiple linear regressions. We first examined histograms of all variables and univariate plots against diversification rate to determine the most suitable transformations to stabilize variances and normalize error distributions, and to test for second- and third-order polynomial effects. A minimum adequate model (MAM) was found by fitting all predictors, then sequentially removing each predictor that contributed the smallest amount of marginal variance to the model until all remaining predictors were significant at $P \leq 0.05$. We then reintroduced predictors, and interaction terms, one at a time and tested the model for significance each time.

Because of the possibility of phylogenetic bias in diversification rates, we repeated these tests using phylogenetically independent contrasts, calculated using software written in R by A. Purvis (*available online*).⁵ All regressions on independent contrasts were forced through the origin (Garland et al. 1992). Because we did not use a complete phylogeny, we could not test clade area as a predictor of diversification rate using independent contrasts calculated for internal nodes. Our independent-contrasts tests using clade area are therefore restricted to contrasts calculated for terminal nodes only.

A prediction of the model presented in the *Introduction* is that the strength of any latitudinal bias in diversification rates, measured as the mean rate over the lifetime of a clade, will depend on the point at which most clades appear along the trajectory shown in Fig.

⁵ <http://www.r-project.org/>

TABLE 1. (A) Cross-taxon results and (B) independent-contrasts results for separate effects of latitudinal centroid, clade area, mean annual temperature, annual actual evapotranspiration (AET), and net primary productivity (NPP) on bird diversification rates.

Variable	Entire data set			Monospecifics excluded		
	Coefficient	<i>t</i>	<i>r</i> ²	Coefficient	<i>t</i>	<i>r</i> ²
A) Cross-taxon results						
Latitude (degrees from equator)	-0.06	-2.31*	0.108	-0.04	-1.5	0.054
Clade area (km ² × 10 ⁶)	0.008	1.8†	0.059	0.007	1.68	0.077
Temp (°C)	0.05	0.61	0	0.05	0.56	0
AET (mm)	0.09	1.52	0.035	0.08	0.98	0
NPP (kg C/m ²)	0.11	1.93†	0.07	0.11	1.19	0.018
B) Independent-contrasts results						
Latitude (degrees from equator)	-0.06	-2.38*	0.118	-0.04	-1.64	0.074
Clade area (km ² × 10 ⁶)	0.02	3.02*	0.447			
Temp (°C)	0.05	0.57	0	0.04	0.59	0
AET (mm)	0.1	1.55	0.039	0.05	0.77	0
NPP (kg C/m ²)	0.16	2.83**	0.167	0.07	1.01	0.001

Notes: Results are shown for regressions of each variable using the entire data set ($n = 37$ clades and 35 contrasts for cross-taxon and independent-contrasts tests, respectively), and with monospecific clades excluded ($n = 23$ clades and 21 contrasts). Independent-contrasts results for clade area are for terminal nodes only ($n = 10$ contrasts; degrees of freedom was too low for the test with monospecific clades excluded). All predictors except clade area are ln-transformed; the diversification rate is square-root transformed.

* $P \leq 0.05$; ** $P \leq 0.01$.

† $P \leq 0.1$.

1. We expect the signal of any latitudinal bias in diversification rate to be weaker among older clades that are more likely to have been at saturation levels for a long time, and stronger among younger clades. To test for any such age effects, we included clade age and latitude × clade age interaction terms in the models together with latitude. We also tested the effect of latitude on diversification rate separately for clades younger and older than the median genus age of 23.52×10^6 yr for cross-taxon tests, and the median nodal age of 39.48×10^6 yr for independent-contrasts tests.

Results

Latitude, clade area, and net primary productivity (NPP) were significantly associated with diversification rate as single predictors (Table 1, Figs. 2, 3). Diversification rate was significantly higher in clades with lower latitudinal centroids, both in cross-taxon tests ($P = 0.027$) and independent-contrasts tests ($P = 0.023$). For both clade area and NPP, positive associations with diversification rate were marginally nonsignificant in cross-taxon tests ($P = 0.08$ for clade area and $P = 0.062$ for NPP), but significant when independent contrasts were used ($P = 0.015$ and $P = 0.008$). Area explained a substantial proportion of the variance in diversification rate when independent contrasts were used (44.7%), although because only terminal nodes were used, the power of this test was low. Actual evapotranspiration (AET) and temperature were not significantly associated with latitude as single predictors in cross-taxon tests or in independent-contrasts tests.

One feature of our data set is the large proportion of genera with only one species, which tend to have higher latitudinal centroids than the majority of genera (Fig. 2). To examine the degree to which these genera

drive the negative association between latitude and diversification rate, we repeated the tests with the 14 monospecific genera dropped from the analysis. For most predictors, slopes became slightly flatter and the significant associations with diversification rate disappeared, although the power of the tests to detect significant associations also declined substantially (Table 1).

Latitude was significantly associated with diversification rate when included with other variables in multiple regression models (Table 2). In cross-taxon analyses, the only independent predictors included in the final minimum adequate model (MAM) were latitude, clade age, and a positive latitude × clade age interaction term. The positive interaction indicates that the slope of the latitudinal effect on diversification rate is more steeply negative for younger clades, supporting the prediction of the model shown in Fig. 1. In analyses using independent contrasts, the MAM included latitude and a positive, nonlinear effect of NPP on diversification rate.

The effect of clade age on the strength of the latitude–diversification rate association was corroborated by separate tests on young and old clades (Table 3, Fig. 2). In both cross-taxon tests and independent-contrasts tests, there was a significant positive association between latitude and diversification rate among young clades, but no significant association among old clades.

DISCUSSION

The analysis we present here is an example of how phylogenetic methods can be used to test for latitudinal or other geographic trends in species diversification rates. Within the limitations of the data set, our analysis points to faster diversification in clades of New World

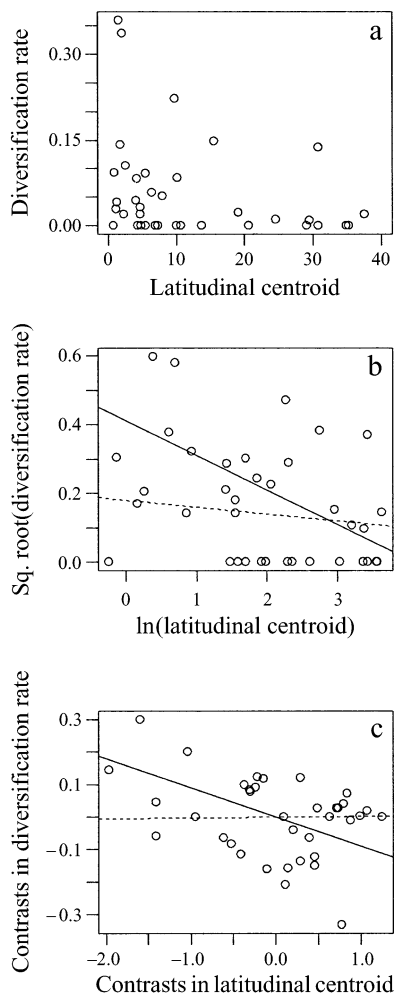


FIG. 2. Association between latitude (mean latitude of species geographic centroids) and diversification rate ($\ln[\text{species}]/10^6 \text{ yr}$), among New World endemic bird clades: (a) the association in arithmetic space; (b) the association with axes square-root transformed as in the analysis, with regression lines for young clades (solid line) and old clades (dashed line); (c) the association using phylogenetically independent contrasts, with regression lines for young and old clades.

endemic birds that inhabit lower latitudes. This pattern is found regardless of whether diversification rates are considered to be independent of phylogeny, or phylogeny is controlled for using independent contrasts. It also appears that the association between latitude and diversification rate is stronger among younger clades, supporting the prediction that the association should diminish as clades age beyond the point at which they become saturated with species.

The pattern of higher rates of diversification at low latitudes that we have detected here does appear to be driven, at least in part, by the tendency for monospecific clades to inhabit higher latitudes. Although clades that are currently monospecific may well have undergone periods of rapid cladogenesis, they have an ap-

parent diversification rate of zero, since any speciation events have been balanced by extinctions. However, because these clades do vary in age and we have no way of knowing how imminent the next bifurcation event might be, any real variation in diversification rate among monospecific clades may be obscured. Nevertheless, weakening of the latitude–diversification rate association when monospecific clades are dropped does not, in our view, necessarily nullify the result obtained when all clades are included in the analysis. The tendency for monospecific clades to be found at higher latitudes than most other clades in our data set is consistent with latitudinal variation in diversification rates. Furthermore, there is still a positive latitude–diversification rate slope with monospecific clades excluded, and the fact that this slope is not significantly different from zero may result simply from the substantially reduced power of the test. This underscores the importance of large phylogenetic and geographic data sets in testing for geographic variation in diversification rate: with larger data sets, the influence of monospecific clades on patterns of diversification rate will be testable with more power.

A potential problem of using molecular data to estimate the ages of bird clades is the possibility of latitudinal bias in rates of molecular evolution, and thus in estimates of diversification rate. For example, higher temperatures at low latitudes may lead to faster individual growth rates and shorter generation times, which could speed the rate of molecular evolution (Rohde 1992). However, Bromham and Cardillo (2003) have recently examined this possibility and found no evidence for latitudinal bias in rates of molecular evolution in birds, using both DNA hybridization data and molecular sequence data. In any case, any such bias would be likely to be conservative, as a higher rate of molecular evolution at lower latitudes would increase estimates of node ages, making diversification rates of lower latitude clades appear artificially low. Therefore, we do not believe that our result could have been an artifact of latitudinal bias in rates of molecular evolution.

One assumption that many phylogenetically based analyses of geographic patterns must make is that contemporary geographic ranges of species represent, at least approximately, the distributions species have occupied throughout their histories. Unfortunately, we do not know the extent to which this is true, given that geographic ranges expand, contract, and shift over time (Price et al. 1997, Gaston 1998). Furthermore, climatic zones are also nonstatic: within the lifetimes of many of the genera included in our analyses, there have been periods when climatic conditions we now consider “tropical” extended to far higher latitudes than they do today (Brown and Lomolino 1998). Ideally, an analysis such as ours would make use of reliably reconstructed paleodistributions and paleoclimates to summarize the mean latitudinal position and climatic con-

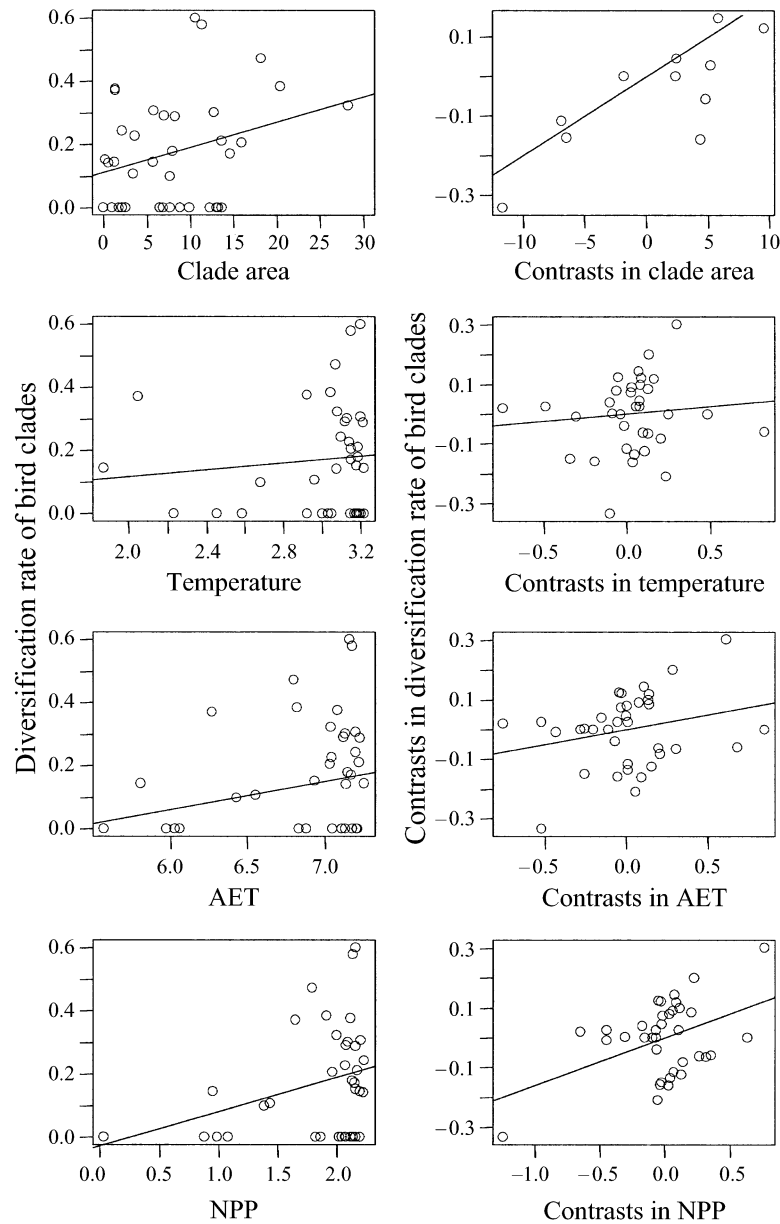


FIG. 3. Associations between clade area (millions of km²), mean annual temperature (°C), annual actual evapotranspiration (AET, mm), and net primary productivity (NPP, kg C/m²), and diversification rate of bird clades. Left-hand column: associations with bird genera treated as independent observations. Right-hand column: associations using phylogenetically independent contrasts. All predictors except area are ln-transformed; diversification rate is square-root transformed.

ditions within the range of each species throughout its history. For some groups that have a high-quality fossil record, such as marine bivalves, this may indeed be possible (e.g., Flessa and Jablonski 1996). For birds and other terrestrial vertebrates, however, the fossil record is relatively poor, and reconstructing paleodistributions for large numbers of species will never be possible. However, if there is a tendency for phylogenetic conservatism of ecological niches, as has been suggested (Peterson et al. 1999, Wiens 2004), it seems likely that geographic ranges track long-term expan-

sions and contractions of climatic zones; this has been demonstrated in birds (Price et al. 1997). Even if latitudinal positions of species have been dynamic, therefore, current distributions may at least provide a reasonable summary of climatic conditions experienced by species throughout their lifetimes.

If variation in diversification rates is a proximate mechanism for the origin of the latitudinal diversity gradient, what are the environmental gradients that underlie this mechanism? The two major contenders are geographic area and climate. Rosenzweig (1992, 1995)

TABLE 2. Cross-taxon tests ($n = 37$ clades) and independent-contrasts tests ($n = 35$ contrasts) for combined effects of latitudinal centroid, mean annual temperature, annual actual evapotranspiration (AET), and net primary productivity (NPP) on bird diversification rates.

Predictor	Cross-taxon results			Independent-contrasts results		
	Coefficient	t	Partial r^2	Coefficient	t	Partial r^2
Intercept	0.51	6.23***				
Latitude (degrees from equator)	-0.14	-3.91***	0.133	-0.06	-1.84†	0.143
Clade area ($\text{km}^2 \times 10^6$)						
Temp ($^{\circ}\text{C}$)						
AET (mm)						
NPP (kg C/m^2)				0.55	2.7*	0.065
(NPP) ²				-0.18	-2.42*	0.108
Clade age	-0.007	-3.48**	0.089			
Latitude \times AET						
Latitude \times clade age	0.002	2.74**	0.145			

Notes: Results shown are for minimum adequate models (see *An example using New World endemic bird clades; Methods*). Clade area was not fitted in the model using independent contrasts.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

† $P \leq 0.1$.

has argued that because the tropics are the largest of the world's major bioclimatic zones, tropical clades are able to occupy larger areas, which promotes a higher speciation rate and a lower extinction rate. The area hypothesis has been controversial: for example, it has been argued that land area does not even increase towards low latitudes (Rohde 1997). The balance of empirical evidence seems not to favor the area hypothesis, with recent large geographic analyses offering little support for area as a major driver of the latitudinal diversity gradient (Hawkins and Porter 2001, Macpherson 2002). Climate, on the other hand, varies unarguably across latitudes, and there is strong support for associations between climatic factors and species richness of birds and other major taxonomic groups across latitudes (Currie and Paquin 1987, Currie 1991, Francis and Currie 2003, H-Acevedo and Currie 2003, Hawkins et al. 2003a, b, Hawkins and Porter 2003).

Our study has taken a different approach from the majority of previous studies by examining area, climate, and latitude as properties of clades rather than of geographic entities such as grid cells. Although our data set is small and subject to a number of limitations, our results suggest that diversification rates may be influenced by both area and climate. The tendency for clades occupying larger areas to have higher diversification rates is consistent with previous findings for bird families (Owens et al. 1999, Bennett and Owens

2002), and may reflect an increased potential for population divergence or a greater buffer against extinction. The influence of climate on diversification rates is supported by a positive association with net primary productivity (NPP), but not with actual evapotranspiration (AET) or temperature. Compared to AET or temperature, NPP may be a closer indicator of the habitat features that promote speciation in birds, such as the structural complexity of tropical forests. It should be kept in mind, however, that NPP and AET are highly correlated across bird clades, that diversification rate also showed a positive trend against AET (Fig. 3), and that the overall power of the data set to detect significant patterns was relatively low.

If large clade area and high NPP are associated with high rates of diversification among bird clades, are these the factors driving the increase in diversification rates towards lower latitudes? Both clade area and NPP increase strongly towards lower latitudes (clade area: $P = 0.008$, $r^2 = 0.16$; NPP: $P < 0.0001$, $r^2 = 0.82$), so these two factors must certainly account for at least some of the latitudinal bias in diversification rates. However, the association between latitude and diversification rate is independent of clade area (Table 2), and largely independent of NPP, although when independent contrasts were used, the addition of NPP reduced the slope of the latitudinal effect considerably (Table 2). Clearly, there is a component of latitudinal

TABLE 3. Effects of clade age on the latitudinal bias in diversification rate, for young and old clades, using cross-taxon tests ($n = 18$ and 19 clades, respectively) and independent-contrasts tests ($n = 17$ and 18 contrasts, respectively).

Predictor	Cross-taxon results				Independent-contrasts results			
	Young clades		Old clades		Young clades		Old clades	
	Coefficient	t	Coefficient	t	Coefficient	t	Coefficient	t
Intercept	0.41	3.99**	0.18	4.41***				
Latitude	-0.1	-2.31*	-0.02	-1.05	-0.09	-2.52*	0.003	0.12

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

variation in diversification rate that is not accounted for by the environmental measures we have examined. It is possible that this is simply because our data set is prone to high Type 2 statistical error resulting from summarizing heterogeneous climatic conditions to a point estimate for each clade. Another possibility is that latitudinal variation in speciation or extinction rates are driven by environmental features we have not examined. For example, extinction rates may be elevated by a high degree of temperature variation, either annually or over longer time periods (Dynesius and Jansson 2000).

Our finding that the slope of the association between latitude and diversification rate was steeper in younger clades is consistent with the prediction derived from the model presented in Fig. 1. Although our division of clades into “young” and “old” was arbitrary, the model does not predict a discrete division of young and old clades. Rather, it predicts that the strength of any latitudinal bias in diversification rate should decline smoothly with clade age. Hence, the precise definition of young and old clades is relatively unimportant, and almost any division should produce a similar result. In fact, with a sufficiently large and robustly dated phylogeny, it may even be possible to estimate the function of the decline in slope with clade age, perhaps providing insight into the age (or range of ages) at which clades tend to reach saturation.

Hypotheses for the latitudinal diversity gradient assume either equilibrium or nonequilibrium regional species richness. If the former, the gradient must arise from latitudinal differences in the geographic equilibrium (saturation) level; if the latter, it must arise from latitudinal differences in diversification rate or clade ages (Rohde 1992). By focusing on clades rather than geographic entities, the model in Fig. 1 unites these opposing viewpoints by assuming simply that clades of a range of ages are present, that each has its own saturation level of species richness, and that some have reached saturation and some have not. The model therefore implies that among older, saturated clades, it is latitudinal variation in equilibrium levels of species richness, rather than diversification rates, that determine the latitudinal diversity gradient. Hence, the opposite prediction to that for diversification rate applies (i.e., that latitudinal variation in species richness per unit area among clades should be stronger among older clades). This should be another matter for investigation when larger phylogenies and geographic data sets become available.

CONCLUSION

There are two central messages that arise from the illustrative analysis we have presented. First, there should be more emphasis on clade-based approaches, to complement geographic approaches, in studying the latitudinal diversity gradient and other geographic patterns of diversity. Work to date has been dominated by

geographic analyses, whereas phylogenetic analyses, provided the limitations are recognized, can address different and important questions. As we have shown, latitudinal variation in diversification rates cannot be assumed to underlie the gradient in species richness, and must be explicitly demonstrated. At present, the best developed methods for doing so use clades rather than regions as the units of analysis. Second, there is an urgent need for large phylogenetic and geographic data sets. The data sets used in this type of study are inherently noisy, since clade diversification rates are likely to be determined by numerous environmental and biological factors, as well as unpredictable factors such as dispersal events or the evolution of key innovations. Hence, detecting the component of variation in diversification rates explained by latitude, then further decomposing this into components accounted for by different environmental factors, is a task best suited to large databases.

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LARGE-SCALE BIOGEOGRAPHIC PATTERNS IN MARINE MOLLUSKS: A CONFLUENCE OF HISTORY AND PRODUCTIVITY?

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Abstract. Large-scale biogeographic patterns in marine systems are considerably less well documented and understood than those in terrestrial systems. Here, we synthesize recent evidence on latitudinal and bathymetric gradients of species diversity in benthic mollusks, one of the most diverse and intensively studied marine taxa. Latitudinal gradients in coastal faunas show poleward declines in diversity, but the patterns are highly asymmetrical between hemispheres, and irregular both within and among regions. The extensive fossil record of mollusks reveals that latitudinal gradients have become steeper during the Neogene, partly because of a rapid diversification in tropical coral reefs and their associated biotas. Much of the inter-regional variation in contemporary latitudinal trends depends on the longitudinal distribution of reefs and major Neogene vicariant events. Thus, coastal faunas reveal a strong evolutionary–historical legacy. Bathymetric and latitudinal gradients in the deep ocean suggest that molluscan diversity is a function of the rate of nutrient input from surface production. Diversity may be depressed at abyssal depths because of extremely low rates of organic carbon flux, and at upper bathyal depths and high latitudes by pulsed nutrient loading. While the deep-sea environment is not conducive to fossilization, relationships between local and regional diversity, and the distribution and age of higher taxa indicate an evolutionary signal in present-day diversity gradients. Marine invertebrate communities offer tremendous potential to determine the relative importance of history and ecological opportunity in shaping large-scale patterns of species diversity.

Key words: bathymetric gradients; history; latitudinal gradients; marine mollusks; productivity; species diversity.

INTRODUCTION

Making sense of large-scale marine biogeography remains a difficult challenge. The oceans represent a huge and complex ecosystem that supports Earth's richest diversity of animal phyla. Much of the marine realm has been inaccessible to exploration until quite recently, particularly polar regions and the deep sea. Yet the very distinctiveness of the marine fauna and environment, when compared to terrestrial systems, holds the promise of discovering the common underlying causes of global biogeographic patterns.

In this paper, we take a fresh look at two major biogeographic trends in the oceans: latitudinal and bathymetric gradients of species diversity. We focus on gastropod and bivalve mollusks, important faunal components of virtually all major marine habitats. We examine past and present latitudinal gradients of species diversity in coastal assemblages, and contemporary latitudinal gradients in the deep sea. Coastal and deep-sea systems have fundamentally different ecologies. The two worlds are linked by depth gradients of diversity in which pattern and scale become compressed

to help reveal the potential causes of variation in diversity at large horizontal scales. We stress from the outset that latitude and depth per se are not environmental variables; they are merely geographic gradients that define macroecological patterns (Hawkins and Diniz-Filho 2004). However, as we will see, large-scale marine biogeography is still very much in a descriptive phase. Establishing pattern is a primary objective. In the case studies that we present, we do not consider species richness to be a response variable, or depth and latitude to be explanatory variables. Rather we document geographic gradients of diversity in a variety of environmental circumstances, and attempt to identify factors that begin to provide consistent explanations.

Patterns of species diversity in time and space present a multivariate problem. Of the welter of hypotheses proposed to explain them, recent attention has centered on energy and history as potential unifying themes (Ricklefs and Schluter 1993, Hawkins et al. 2003). It is mainly in this context that we explore marine molluscan diversity. Whittaker and Field (2000) point out that the energy–diversity theory makes specific predictions about patterns of diversity, but that history cannot; the evolution and subsequent geographic spread of taxa are inherently stochastic processes that can only be inferred a posteriori. They propose reconciling the two explanations by testing contem-

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porary trends against expectations of the energy–diversity theory, and then determining if residual variation can be attributed to historical contingency. Of course, given sufficient information about history, the opposite approach seems equally plausible. Historical development may be modulated by present-day ecology. One disadvantage of working with terrestrial organisms is their relatively poor fossil record, especially for plants that have figured so importantly in energy–diversity studies. By contrast, marine invertebrates have an impressive fossil record that includes proxy variables for climate reconstruction.

The theory that energy limits diversity has two basic versions (Hawkins et al. 2003). One is the reductionist view that ambient energy in the form of heat from solar radiation regulates the biochemical kinetics of metabolism, and consequently organism abundance and evolutionary rates (e.g., Allen et al. 2002, Vermeij 2005). This theory predicts that diversity should be a positive function of temperature. A second version is the productivity hypothesis, which is more concerned with the rate of energy fixation for food and its effect on population growth (Huston 1994, Rosenzweig 1995). The relationship between diversity and productivity is expected to be either unimodal or positive and linear (Mittelbach et al. 2001). Presumably, water availability, an integral part of the energy–diversity theory as it pertains to terrestrial biotas, is not relevant in the oceans. A comparison of molluscan diversity patterns suggests strong roles for both history and productivity in the development of large-scale marine biogeographic patterns.

LATITUDINAL GRADIENTS OF DIVERSITY IN THE SHALLOW SEAS

Contemporary spatial patterns

Studies of both bivalves and gastropods have been fundamental in developing our concept of taxonomic diversity gradients in the shallow marine realm. Initially, the patterns they revealed seemed to be simple and regular (Fischer 1960, Stehli et al. 1967, Schopf 1970), but as the scale of investigations expanded, and more comprehensive databases were assembled, it became apparent that regional gradients were much more complicated than originally envisaged (Roy et al. 1994, 1998, Flessa and Jablonski 1995, Crame 2000a, b, Valdovinos et al. 2003). In particular, the decline in taxonomic diversity values from low to high latitudes is much less regular than is often portrayed and there are significant inter-regional differences in gradients on a variety of spatial scales.

Fig. 1 shows the contemporary latitudinal gradient of species richness in gastropods of the East Pacific along the continental shelves of North, Central, and South America. It combines data for the northern hemisphere from Roy et al. (1994, 1998), the southern hemisphere from Valdovinos et al. (2003), and new Ant-

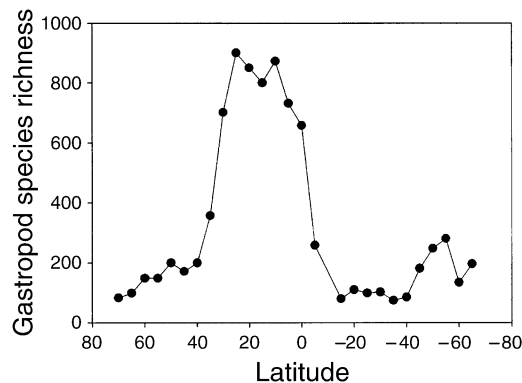


FIG. 1. Latitudinal variation in species richness of gastropod molluscs from the Pacific continental shelf of North and South America and Antarctica. Data are from Roy et al. (1994, 1998) and Valdovinos et al. (2003), with Antarctic data from British Antarctic Survey records. Data are pooled by bins of 5°. Negative latitudes are southern. This figure was modified with permission from the journal *Ecography*.

arctic records from the British Antarctic Survey's SOMBASE database. This is the most well-documented and geographically controlled latitudinal pattern known for marine benthic organisms. Apart from the fact that diversity is markedly higher within tropical and subtropical latitudes than at higher latitudes, there are a number of unexpected features. The pattern is asymmetrical with peak diversity occurring at northern subtropical latitudes rather than near the equator. One of the most striking discoveries to emerge from recent studies is the high variability of diversity within the tropics (Flessa and Jablonski 1995, Crame 2000a, b). Tropical latitudes contain among the highest and lowest values of diversity shown in Fig. 1. In parts of the vast Indo-Pacific province there is no obvious latitudinal gradient between the equator and approximately 30° N and 30° S, and this is particularly so in the western Indian Ocean for both benthic mollusks and hermatypic corals (Sheppard 1998, Mackie et al. 2005).

Much of the variation in tropical shallow diversity, and hence the overall shape of latitudinal gradients, is controlled by the distribution of coral reefs. Reefs are the sites of highest diversity in a wide range of marine invertebrate, vertebrate, and plant taxa (Briggs 1996, Ellison et al. 1999, Bellwood and Hughes 2001, Roberts et al. 2000), and wherever they are absent or only poorly developed tropical diversity is much reduced. The northern and southern limits of hermatypic coral growth are sharply defined (Veron 1995) and have in turn served to delimit the latitudinal ranges of many reef-associated bivalves, gastropods, and other taxa. It is likely that these very sensitive outer boundaries to reef growth were accentuated by intense Late Neogene (i.e., the last 10–15 × 10⁶ yr) glacioeustatic sea-level cycles that left the reef tract repeatedly and abruptly stranded (Rosen 1981, Paulay 1990). This is particularly so in regions such as the western Atlantic and

western Pacific (Veron 1995). The marked reduction in coral reefs around the South American and African continents has been attributed, at least in part, to the presence of cold boundary currents on tropical western coasts and large river outflow on tropical eastern coasts (Crame 2000b Fig. 1).

Gastropod diversity falls precipitously at the northern edge of the tropics (Fig. 1). This pattern is mirrored in a number of other taxonomic groups (Clarke and Lidgard 2000, Crame 2000b) and is significantly steeper than the accompanying latitudinal temperature gradient (Rosen 1981, Valdovinos et al. 2003). The northern hemisphere gradient becomes much shallower at 35–40° N where it forms a distinct bench-like feature into the highest latitude regions (Roy et al. 1998, Crame 2000b, Fig. 1).

There has been considerable debate about the similarity between latitudinal gradients in the northern and southern hemispheres (e.g., Gaston 1996, Crame 2000b). In a weighted meta-analysis based on a large data set from both the shallow and deep marine systems, Hillebrand (2004a, b) was unable to detect a significant difference in either the strength or slope of the gradient between hemispheres. In many respects this is a surprising result, for even though the southern gradients have been much less intensively studied, there are strong indications that they may be significantly different in form. For example, in East Pacific gastropods, diversity is relatively low and constant at ~100 species from 10° to 40° S (Fig. 1). Thereafter values increase sharply to the south, reaching 300 species at Cape Horn, and remain high in the Antarctic Peninsula region (55–65° S). There are indications of a steeper gradient in bivalve diversity on the eastern coast of South America (Crame 2000b), but this still in no way matches any of its northern counterparts. Our knowledge of African tropical bivalve diversity is incomplete, but regional gradients from either West or East Africa, through South Africa, to Antarctica appear to be very flat. The only strong molluscan gradients detected so far in the southern hemisphere are those that run from Northern Territory/Queensland through South Australia and New Zealand to Antarctica (Crame 2000b). There is even a hint of a sharp inflection in this gradient comparable to that seen in the strongest gradients in the northern hemisphere.

Along the East Pacific coast of the northern hemisphere, molluscan diversity is positively correlated with sea-surface temperature but uncorrelated with area of the continental shelf (Roy et al. 1998). In the southern hemisphere, just the opposite occurs (Valdovinos et al. 2003). Thus, while the potential effects of temperature and area on marine diversity have not been evaluated on a global basis, the current evidence seems contradictory. Similarly, the effect of productivity on coastal diversity at large spatial scales remains unclear. Valdovinos et al. (2003) note that low diversity between 10° and 40° S (Fig. 1) coincides with one of the most

productive regions in the ocean. Polar regions also support high and seasonal productivity. Later, we suggest that nutrient loading can depress diversity in marine systems by accelerating population growth and biological interactions. Exceptionally high productivity can produce an oxygen minimum zone in which benthic diversity is greatly reduced, as occurs in some regions of the southeastern Pacific coast at outer continental shelf depths.

Historical development

Some evidence suggests that coastal marine latitudinal diversity gradients have been persistent features through geological time (summarized in Crame 2001). If this is the case, then it may be possible to attribute their generation to some time-invariant feature of the Earth's surface, such as the greater area or habitat complexity of the tropics, or some form of species–energy hypothesis (e.g., Rosenzweig 1995, Brown and Lomolino 1998). Although such processes are undoubtedly important, we also need to consider the effects of time. Have there been any significant shifts in the form or strength of the latitudinal gradient and, if so, can we pinpoint when?

One of the most striking paleontological trends to emerge in recent years is the marked rise in global taxonomic diversity through the Cenozoic Era; estimates range from a three-fold to a >10-fold increase in species diversity during this time (Valentine et al. 1978, Jackson and Johnson 2001). While the existence of such a trend has not gone unchallenged (Alroy et al. 2001), it is now generally recognized that it cannot be attributed to preservational or other biases alone, and represents one of the most spectacular phases of diversification in the entire Phanerozoic (Valentine 2001, Jablonski et al. 2003b).

Two particular features of the Cenozoic diversification are beginning to emerge: it was largely but not exclusively tropical in nature, and it was concentrated in the last 23×10^6 yr during the Neogene and Quaternary (Vermeij 1987). The main phase of coral reef development in the Cenozoic occurred in the Early to Middle Miocene (~23–17 $\times 10^6$ years ago). This was a period of pantropical diversification of scleractinian corals (Veron 1995, Wilson and Rosen 1998), bivalves (Flessa and Jablonski 1996, Crame 2000a), gastropods (Taylor et al. 1980, Kohn 1990), and a range of other reef-associated taxa (Vermeij 1987). In other words, latitudinal gradients of species diversity in the marine environment became more pronounced during the Neogene through rapid development of tropical and subtropical diversity.

As the latitudinal temperature gradient steepened through the Neogene, the once homogeneous tropical biota was disrupted by a series of vicariant events that led eventually to the formation of the discrete Indo-West Pacific (IWP) and Atlantic–Caribbean–East Pacific (ACEP) high-diversity foci (Crame and Rosen

2002). The split between these two realms can be traced back to no earlier than the collision between Africa/Arabia and Eurasia 20×10^6 years ago. Prior to that, in the Paleogene ($\sim 65\text{--}30 \times 10^6$ years ago), there is evidence of coral, mollusk, and mangrove taxa that had essentially pantropical distributions (Vermeij 1987, Wilson and Rosen 1998, Ellison et al. 1999). In the Eocene–Early Oligocene ($\sim 50\text{--}30 \times 10^6$ years ago) coral reef diversity was centered in the Mediterranean and Caribbean, and IWP faunas were comparatively sparse. However, in the Early Miocene there was a fourfold increase in IWP coral genera, and reefs proliferated in the shallow-water habitats created by the collision of Australia/New Guinea with Southeast Asia (Crame and Rosen 2002).

Although the tropical marine fauna is of great antiquity, it is apparent that the distinctive IWP and ACEP high-diversity foci of the present day may be no more than $15\text{--}20 \times 10^6$ years old. Tropical biotas retracted significantly in areal extent through the early part of the Cenozoic Era, but from approximately 20×10^6 years ago the two high-diversity faunas developed on discrete clusters of continental and oceanic islands (Crame and Rosen 2002). As the steepest latitudinal gradients of the present day are all associated with either the IWP or ACEP foci, it can be concluded that they are no more than $15\text{--}20 \times 10^6$ years in age. Some may be substantially younger (Vermeij 1987, Crame and Rosen 2002). Clearly, the development of latitudinal gradients in coastal marine mollusks and their highly variable expression between hemispheres and oceans can only be fully understood in an historical context.

BATHYMETRIC GRADIENTS OF DIVERSITY

Bathymetric gradients of community structure on the sea floor are counterparts to elevation gradients in terrestrial systems. Both exhibit strong environmental changes over relatively short distances (10s to 100s of km). Species diversity along vertical gradients is easier to measure and interpret than global-scale latitudinal trends that are often interrupted by major geographic barriers and confounded by complicated inter-regional differences in basic ecology. Because of the smaller spatial scales involved, and consequently greater dispersal potential, vertical gradients of diversity are apt to be caused more by contemporary ecological forces than by the evolutionary–historical processes of diversification and subsequent geographic spread of taxa; although as we point out later, it is regional-scale radiations that create the species pools from which vertical diversity gradients are formed.

Diversity–depth gradients in the deep-sea benthos coincide with a wide range of biotic and abiotic environmental gradients (reviewed in Etter and Mullineaux 2001, Levin et al. 2001, Stuart et al. 2003), and are attended by rapid faunal turnover (Gage and Tyler 1991) and clinal effects within individual species

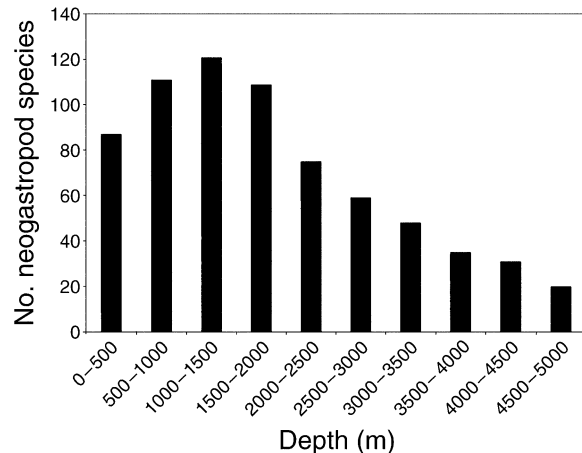


FIG. 2. The bathymetric pattern of species richness of deep-sea neogastropods in the eastern North Atlantic. Diversity is estimated as the number of coexisting species ranges in 500 m depth increments. Data are from Bouchet and Warén (1980, 1985).

(Chase et al. 1998, Rex and Etter 1998). They are best documented in the North Atlantic Ocean where benthic communities have been sampled extensively from the continental shelves to abyssal depths. Diversity appears to increase from the shelf–slope transition (~ 200 m) to a peak at upper- to mid-bathyal depths on the continental margin, and then decrease toward the abyssal plain (Sibuet 1977, Rex 1981, Etter and Grassle 1992, Paterson and Lamshead 1995, Cosson-Sarradin et al. 1998). The exact shape of the curves varies among taxa and ocean basins (Stuart et al. 2003).

Our knowledge of these unimodal diversity–depth patterns is based almost entirely on estimates of alpha (α) diversity along sampling transects. Here we present an alternative way of illustrating them that is similar to the use of long-term biotic surveys to detect biogeographic trends in terrestrial and coastal systems. We compiled data on ranges of neogastropods, the largest taxon of deep-sea snails, from two comprehensive systematic monographs that cover the eastern North Atlantic fauna (Bouchet and Warén 1980, 1985). The data represent 189 species in over 1300 samples collected through a century of deep-sea dredging in a region east of the Mid-Atlantic Ridge from the Azores to the Norwegian Sea. To assess the diversity–depth pattern, we summed the number of coexisting species within 500 m depth increments. The results indicate that diversity has a unimodal relationship with depth on regional as well as local scales (Fig. 2). The curve is asymmetrical with a maximum at upper bathyal depths (1000–1500 m), and is skewed to the right with a long tapering decline to very low levels in the abyss (>4000 m). A conservative interpretation might be that diversity simply decreases with depth; but depressed diversity at upper continental slope depths, while less pronounced,

is a persistent feature of diversity–depth curves that may provide an important clue about their causes.

Many ecological explanations have been proposed to account for diversity–depth trends (Rex 1981, Levin et al. 2001). While deep-sea diversity is surely influenced by numerous factors that operate on different scales of time and space, much recent attention has focused on the potential importance of energy availability (Stuart et al. 2003, McClain et al. 2004, Rex et al. 2005). The prediction that temperature affects diversity is not borne out in a consistent way in the deep sea where diversity increases with depth and decreasing temperature (Sanders 1968) across the upper bathyal zone (Fig. 2). Below the permanent thermocline, the decrease in diversity is dramatic, while the drop in temperature is minute, implying that either diversity is acutely sensitive to temperature or that other factors are involved. Productivity does seem to be important. Apart from chemosynthetic communities, there is no *in situ* primary production in the deep-sea ecosystem. Food originates as surface production and sinks through the water column. Because production is highest near coasts, and sinking phytodetritus is partially remineralized in the water column, the average rate of nutrient input to the benthos decreases with distance from shore and depth. This accounts for the exponential decrease in benthic standing stock with depth that is found throughout the World Ocean (Rowe 1983). Standing stock is probably the most accurate indicator available for the average rate of organic carbon flux to the benthos (Smith et al. 1997). Standing stock in the deep sea decreases by 2–3 orders of magnitude from 10 000s of individuals/m² and 10s of g/m² at upper bathyal depths to 10s–100s of individuals/m² and <1 g/m² in the abyss (Gage and Tyler 1991). If standing stock can be accepted as a proxy for organic carbon flux to the benthos, then species diversity has a unimodal relationship to productivity in the deep North Atlantic.

Although unimodal diversity–productivity relationships appear to be common (though not universal) in nature, the actual mechanism through which productivity influences diversity remains uncertain. Tilman and Pacala (1993:19) point out that any number of equilibrium or nonequilibrium processes can permit persistence of high diversity. “Thus the question becomes not ‘Why are there so many species?’ but ‘Why are there a particular number of species, and not many, many more?’” It is not surprising, given the large species pool and dispersal ability of deep-sea mollusks, that a rich community has accumulated in the relatively productive and physically benign environment found at intermediate depths. What requires explaining most is why diversity is depressed at upper bathyal and abyssal depths.

Low diversity in the abyss has been attributed to an Allee effect (Rex 1973); population densities of many species are so sparse that they may be reproductively

unsustainable and suffer chronic local extinction from inverse density dependence. Most abyssal mollusks in the North Atlantic represent deeper range extensions for a subset of bathyal species with high dispersal ability (Rex et al. 2005). This suggests that bathyal and abyssal populations may function as a source–sink system, and that much of the abyssal molluscan fauna exists as a mass effect from bathyal sources. Most ecologists agree that this kind of phenomenon explains low diversity at extremely low levels of productivity, and that diversity increases with more available energy. The decline in diversity at very high levels of productivity is more difficult to account for (Rosenzweig and Abramsky 1993). The rate of nutrient input is not only much higher at upper bathyal depths, but also presumably more temporally variable because of the close proximity to seasonal phytoplankton blooms. Rex (1983) proposed that upper bathyal diversity is depressed because high productivity accelerates population growth and competitive displacement, and because variable productivity might limit the ability of predators to diversify by specialization in diet. There is no direct evidence for this; although, as we point out later, pulsed nutrient loading always seems associated with high abundance and depressed diversity in deep-sea benthic habitats. Chown and Gaston (1999) suggested, for similar reasons, that unimodal diversity–productivity curves may result from a positive relationship between the mean and variance of productivity at high levels in marine systems. One advantage of bathymetric patterns of diversity for exploring the productivity–diversity relationship is the large range of productivity spanned, including the most extreme values in marine systems.

The consistent relationship between diversity and productivity in the deep-sea benthos does not deny the action of other potential causes such as environmental heterogeneity, metapopulation dynamics and dispersal, boundary constraints, or disturbance (reviewed in Levin et al. 2001). All of these may modify the effects of productivity, or vice versa! The areal extent of major physiographic features in the deep sea within basins is uncorrelated with diversity; indeed, the abyssal plain that supports the lowest diversity is by far the largest region (Rex 1981).

LATITUDINAL GRADIENTS OF DIVERSITY IN THE DEEP SEA

Until the last few decades the deep-sea benthic environment was assumed to be uniform throughout and insulated from surface climatic variation by the thick overlying water column. However, it is now clear that the deep-sea fauna shows differences in both the level of diversity and species makeup at large interbasin scales (Allen and Sanders 1996, Wilson 1998). Gastropods and bivalves show evidence of latitudinal gradients of species diversity at bathyal depths in the North Atlantic and Norwegian Sea (Rex et al. 1993, 2000,

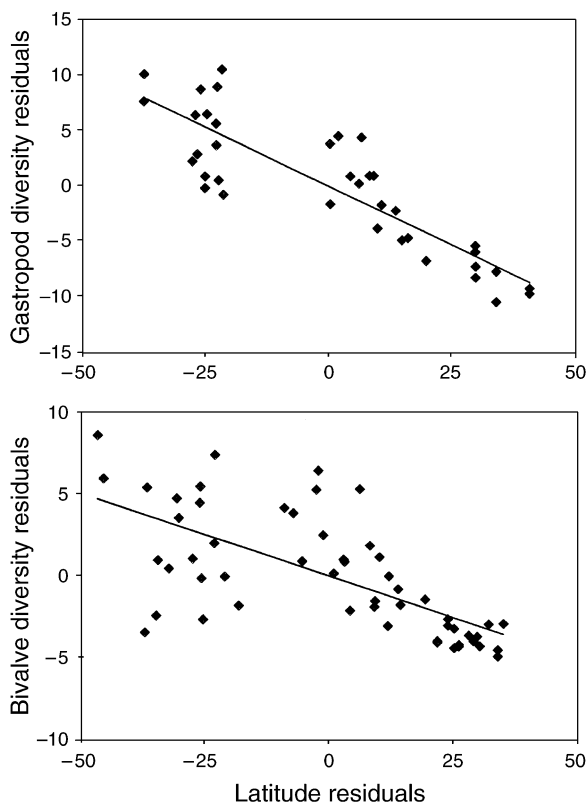


FIG. 3. The relationships of the residuals of diversity vs. depth against the residuals of latitude vs. depth for gastropods and bivalves in the deep North Atlantic Ocean. The analyses show the relationship between diversity and latitude with the effect of depth statistically removed. Diversity was measured as the Sanders-Hurlbert Expected Number of Species. The figure has been adapted and modified with permission from *Nature* (Rex et al. 1993). Regression statistics: gastropods $Y = -0.211X$, $r = -0.865$, $F = 104.4$, $P = 0.0001$, $N = 37$; bivalves $Y = -0.101X$, $r = -0.672$, $F = 42.9$, $P = 0.0001$, $N = 54$.

Stuart and Rex 1994). Since diversity varies with depth (Fig. 2), it is necessary to statistically remove the effect of depth by partial regression to detect an independent latitudinal relationship (Fig. 3). Rex et al. (2000) showed that turrid gastropods in the deep eastern North Atlantic also show a latitudinal gradient of species diversity when the number of coexisting species ranges is summed over latitudinal bands within depth increments. It must be stressed that the apparent latitudinal gradients illustrated in Fig. 3 are based on limited sampling in both the eastern and western corridors of the deep North Atlantic (see Rex et al. 1993, 2000, for maps of sampling localities). Both taxa also show weak, but statistically significant, latitudinal gradients in the South Atlantic where geographic coverage is even more restricted and inter-regional variation pronounced (Rex et al. 1993). Also, unlike terrestrial and coastal habitats where latitudinal gradients are well established and general (Hillebrand 2004a, b), it remains to be seen whether diversity of the deep-sea fauna as

a whole responds to environmental gradients that parallel latitude (Stuart et al. 2003).

Why is deep-sea species diversity depressed toward the poles? Rex et al. (1993) suggested that it might be related to the higher and more seasonally variable surface production at high latitudes (Campbell and Aarup 1992). The resulting pulsed nutrient loading to the benthos may reduce diversity for the same reasons invoked in the section on bathymetric gradients of diversity for upper bathyal depths. High organic carbon flux to the seabed from intense upwelling (Sanders 1969), lateral advection (Blake and Hilbig 1994), oxygen minimum zones (Levin and Gage 1998), concentrating bottom topography (Vetter and Dayton 1998), and reactive sediments introduced by disturbance (Aller 1997), is typically associated with elevated standing stock and lower diversity. Chemosynthesis at hydrothermal vents and cold seeps, the only source of in situ production in the deep sea, also results in much higher biomass and lower diversity than in adjacent soft-sediment habitats (Van Dover 2000). There is no immediate indication that temperature is related to variation in diversity at these very large scales, but this has never been examined statistically.

Several indirect lines of evidence suggest that evolutionary-historical factors also come into play at interbasin and global scales. Because of low temperatures and high pressure, the deep-sea environment is not conducive to fossilization. However, Stuart and Rex (1994) demonstrated a positive relationship between local and regional diversity in contemporary deep-sea gastropod assemblages that is also related to the dispersal potential of constituent species. This suggests that local diversity reflects enrichment from the regional species pool, which is generated by basin-scale speciation and adaptive radiation as in other marine environments (Karlson et al. 2004, Witman et al. 2004). Allen and Sanders (1996) argued that the modern distribution of deep-sea protobranch bivalves in the Atlantic shows a Tethyan influence. The distribution and diversity of other taxa also seem to bear the imprint of history. For example, deep-sea foraminifera show latitudinal gradients in the North and South Atlantic (Culver and Buzas 1998), and the gradual development of foraminiferan latitudinal gradients since the Eocene is evident in seabed cores (Thomas and Gooday 1996). Wilson (1998) proposed that the higher diversity of deep-sea isopods in the South Atlantic and the poleward decrease of diversity in the North Atlantic is partly an historical consequence of a fairly recent invasion of the deep sea in the southern hemisphere superimposed on a much earlier in situ radiation.

Area may also be implicated at very large scales, but it is difficult to separate its potential role from historical events and unusual ecological circumstances. For example, the deep Mediterranean (Bouchet and Taviani 1992) and Norwegian (Bouchet and Warén 1979) Seas support much lower molluscan diversity

than the adjacent Atlantic. Both are considerably smaller than the Atlantic and are partially isolated by shallow sills. They also have experienced catastrophic physical disturbances during the Neogene. The Mediterranean was separated from the Atlantic and dried out in the Messinian salinity crisis of the Late Miocene ($5\text{--}6 \times 10^6$ years ago), and was inundated from the Atlantic in the Early Pliocene (Duggen et al. 2003). During the Pleistocene, much of its deep seabed was buried by a massive submarine landslide (Rothwell et al. 1998). The Norwegian Sea was affected by Quaternary glaciation and experienced huge sediment slumps as recently as $6\text{--}8 \times 10^3$ years ago (Bugge et al. 1988). While relatively small basin size and recovery from recent mass extinction events could certainly limit diversity, differences in nutrient input may also be important. The Mediterranean has low surface production and elevated bottom temperatures that intensify biodegradation of sinking phytodetritus. Consequently standing stock of the deep benthos is very low (Tselepidis et al. 2000). By contrast, the frigid Norwegian Sea has high and very seasonal surface production, and high benthic standing stock (Dahl et al. 1976). The two seas may represent the near extremes of the unimodal diversity–productivity curve on an among-basin scale.

CONCLUSION AND PROSPECTS FOR FUTURE RESEARCH

Currently, it is not possible to undertake a comprehensive global analysis of marine biogeography, as it is for continental biotas (e.g., Hawkins et al. 2003). What we attempt to do here is provide insight into pattern and process by comparing new databases on the diversity of one widespread and dominant marine taxon, the mollusks. In general, mollusks provide evidence that history and energy availability have interacted to form large-scale patterns of diversity, just as they appear to have in other ecosystems. This in no way precludes the importance of other factors. For example, in a series of major syntheses, Vermeij (1978, 1987, 2004) has stressed the potential role of competition in the generation of taxonomic diversity. In his view, the higher temperatures and more prolific and predictable resources of tropical regions create the variation that is the essential raw material for diversity. Competition for locally limiting resources within these tropical systems then promotes a division of labor that in turn leads to functional differentiation and specialization. The richer the resource base, the more intense this process becomes (Vermeij 2005).

The surprising variability of taxonomic diversity patterns observed between hemispheres and regions obviously will require a more specific and complicated explanation. Knowledge of the oceans, past and present, is developing very rapidly with the compilation of much more extensive databases on existing and fossil faunas, the availability of paleoceanographic methods to interpret past climates, and satellite imagery to

measure environmental variables such as temperature and productivity. This will make it possible to directly correlate biodiversity trends with environmental variables on very large scales. New information and technology promise to help answer some of the most fundamental problems in biogeography, especially concerning historical driving forces that are hard to discern in other systems.

We urge two new approaches to broaden future research on marine diversity gradients. First, the quest to explain diversity has centered almost exclusively on identifying independent environmental variables to account for a single response variable, the number of taxa. Alternative, but as yet little investigated, ways of exploring the nature of latitudinal gradients might be to analyze patterns of either morphological or functional diversity (Jablonski et al. 2003a). For example, Roy et al. (2001) compared the variation in regional patterns of species richness within the Indo-Pacific gastropod family Strombidae with those of morphological disparity. In certain regions, high taxonomic diversity was clearly linked with low morphological disparity, and in others the reverse was true. The very striking latitudinal gradient in gastropod diversity along the west coast of North America is now being reanalyzed in terms of functional groups. One of the largest of these, the carnivores, when plotted as a proportion of the total gastropod fauna, clearly shows a marked rise into the high-latitude regions and departure from the flat-bench profile (Valentine et al. 2002). A very similar complex gradient has been demonstrated in the northeastern Atlantic for predatory prosobranch gastropods (Taylor and Taylor 1977). The relationships between species richness, abundance, and body size also provide a promising avenue of research (McClain 2004).

Second, it will be important in future investigations to focus more attention on the taxonomic composition of latitudinal diversity gradients (Roy et al. 2000, Jablonski et al. 2003a). For example, it is apparent that the marked Cenozoic expansion in bivalve gradients was underpinned largely by just one (the heteroconchs) of seven component clades and that of the gastropods by just one (the neogastropods) of nine component clades (Crame 2000a, 2001, 2002). Asymmetric clade expansion may be pointing to the importance of some form of evolutionary interaction in promoting global diversification such as escalation (Vermeij 1987), rather than an extrinsic factor such as energy or climate change, which might be expected to have had an equal effect on all clades. The concentration of diversification in reef areas points to factors other than just tropicity in generating modern patterns of diversity. Phylogeographic analyses ultimately may be the key to understanding large-scale biogeographic patterns.

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PLANT SPECIES INVASIONS ALONG THE LATITUDINAL GRADIENT IN THE UNITED STATES

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Abstract. It has been long established that the richness of vascular plant species and many animal taxa decreases with increasing latitude, a pattern that very generally follows declines in actual and potential evapotranspiration, solar radiation, temperature, and thus, total productivity. Using county-level data on vascular plants from the United States (3000 counties in the conterminous 48 states), we used the Akaike Information Criterion (AIC) to evaluate competing models predicting native and nonnative plant species density (number of species per square kilometer in a county) from various combinations of biotic variables (e.g., native bird species density, vegetation carbon, normalized difference vegetation index), environmental/topographic variables (elevation, variation in elevation, the number of land cover classes in the county, radiation, mean precipitation, actual evapotranspiration, and potential evapotranspiration), and human variables (human population density, cropland, and percentage of disturbed lands in a county). We found no evidence of a latitudinal gradient for the density of native plant species and a significant, slightly positive latitudinal gradient for the density of nonnative plant species. We found stronger evidence of a significant, positive productivity gradient (vegetation carbon) for the density of native plant species and nonnative plant species. We found much stronger significant relationships when biotic, environmental/topographic, and human variables were used to predict native plant species density and nonnative plant species density. Biotic variables generally had far greater influence in multivariate models than human or environmental/topographic variables. Later, we found that the best, single, positive predictor of the density of nonnative plant species in a county was the density of native plant species in a county. While further study is needed, it may be that, while humans facilitate the initial establishment invasions of nonnative plant species, the spread and subsequent distributions of nonnative species are controlled largely by biotic and environmental factors.

Key words: native plant species; non-indigenous plant species; patterns of invasion; species densities.

INTRODUCTION

General ecological theories about the patterns of biological diversity provided competing hypotheses for this study. On one hand, von Humboldt (1808), Currie (1991), Huston (1979, 1994), Rosenzweig (1995), and Hawkins et al. (2003) described a fairly consistent trend of decreasing richness of vascular plants, birds, mammals, amphibians, and reptiles with increasing latitude and co-varying environmental factors. The pattern followed declines in actual and potential evapotranspiration (AET, PET) and solar radiation, with optimal conditions for growth and productivity associated with the peaks in richness (Currie 1991; but see Huston

[1999]). The theory that species richness is largely determined by environmental factors is sometimes called “local determinism” (Ricklefs 2004). It logically follows that these relationships might be similar for both native and nonnative plant species, assuming they respond similarly to energy and resource availability. We refer to this as the “environment-matching hypothesis.”

On the other hand, it also follows from theories of plant invasions that competition for available resources and subsequent resource limitations could constrain species coexistence, especially if newly arriving small seeds of nonnative species must compete with well-established, mature, native plants (Stohlgren et al. 2003). If available niches are filled with many native species, and if competition for resources were a strong, broad-scale force in nature, we might expect to see negative relationships between native and nonnative species richness (or densities) in local or regional flo-

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ras. This has been broadly termed “competitive exclusion theory” (Grime 1973).

Humans increase the complexity of the issue and, potentially, the uncertainty associated with any analyses of patterns of native and nonnative species plant richness. Humans may have settled in native species-rich areas or may have introduced nonnative species to those areas or adjacent species-poor areas. Further establishment and spread of invasive nonnative species may be a complex function of human-caused and natural disturbances, land-use change, and environmental conditions, along with the complex traits and autecology of the invading and resident species.

Understanding the patterns of native species richness at local, landscape, and regional scales may further our understanding of invasion by nonnative species. Some landscape-scale surveys of plant diversity in the United States have shown significant positive relationships between native and nonnative plant species richness in 0.1-ha plots in the Central Grasslands, Rocky Mountains of Colorado, and arid ecosystems in southern Utah (Stohlgren et al. 1997, 1998, 1999a, 2001, 2002). In many cases, native and nonnative species richness was positively correlated to soil fertility and water availability. Preliminary county-level data showed that native plant species richness was positively correlated to nonnative species richness in 45 of 46 states (Stohlgren et al. 2003). Still, little is known about the abiotic and biotic factors associated with national-scale patterns of plant species distributions.

It is intuitive that factors other than latitude more directly influence plant species richness and that latitude is cross-correlated with AET, PET, precipitation, mean annual temperature, solar radiation, and other factors (Currie 1991, Rosenzweig 1995, Hawkins et al. 2003). Given the complex topography of the United States, predominantly north-south mountain ranges, and elevation and rain shadow effects, productivity may be a better surrogate of optimum growth conditions than latitude. We anticipate that native and nonnative plant species densities may be affected by optimal combinations of warm temperatures, high light, water, and nutrient availability (for carbon accumulation) and by avoiding high stress, extreme environments such as very high latitudes and elevations, or extremely arid or low-light environments. Habitat heterogeneity and moderate levels of disturbance also may increase species richness (Huston 1994, 1999), so we included the variation in elevation and the number of land cover classes in a county as simple measures of habitat variation.

The role of modern humans in altering species distributions cannot be denied. Direct habitat loss and intentional invasive species introductions have been directly linked to human habitation (Soulé 1991a, b, Wilcove et al. 1998), and approximately 60% of humans live within approximately 170 km of the ocean (or sea; Hindrichson 1997). Since the introduction of

non-indigenous species is largely human-induced (via trade, modern transportation, and urbanization patterns), we included human population density and road density in the list of potential drivers of the patterns of species introductions. Approximately 60% of the invasive nonnative plant species were escaped horticultural or agricultural products (Reichard and White 2001). Since many nonnative plant seeds arrived as contaminants with forage crops and are thought to become initially established on disturbed sites (Reichard and White 2001), we included percentage of cropland area in a county and percentage of disturbed lands (e.g., cultivated land, mining, urban areas) as “human” variables in regression analyses. Currie (1991), Huston (1994), Rosenzweig (1995), and Hawkins et al. (2003) do not directly discuss modern patterns of diversity resulting from the exchange of species among continents and habitats. Our analysis may complement these works by evaluating native and nonnative plant species densities at a large spatial scale.

We assessed preliminary trends in native and nonnative plant species densities with a large county-level data set on vascular plant distributions in the United States. Our objectives were to: (1) evaluate simple patterns of native and nonnative plant species density (number of species per square kilometer in a county) related to latitude and productivity (total vegetation carbon) gradients in the continental United States; and (2) use the Akaike Information Criterion and information-theoretical model selection to provide a more detailed evaluation of competing models explaining native and nonnative plant species density relative to various combinations of biotic, environmental/topographic, and human variables.

METHODS AND STATISTICAL APPROACH

The plant data set was gathered over the past 35 years by the Biota of North America Program (BONAP). The taxonomic accuracy and completeness of the collection have made it the standard plant data set for many government and nongovernment agencies. The data set included the occurrence of over 22 800 native and 3726 nonnative plant taxa in 3114 counties in the 48 conterminous states. Nonnative plant species were defined as those plant species with origins in other countries. This distinction is nonambiguous and well accepted. Nonnative plant species records reflect all past introductions, including some species that have not been recently reported. Due to incomplete data on current species distributions, we assumed that the patterns of past introductions are only a first approximation of current introduction patterns. To further protect against the influence of incomplete data in some counties, all counties with fewer than 100 native plant species recorded were removed from analyses, leaving 3000 counties in the continental United States.

Because counties vary greatly in area (from 59 km² for New York County, New York, to over 52 000 km²

for San Bernadino County, California), we used the density of native and nonnative plant species as primary dependent variables in regression analyses. We investigated several models of species densities. Preliminary species–area analyses showed that “area” explained little of the variation in native species richness ($r^2 = 0.16$) and nonnative species richness ($r^2 = 0.001$), while equal or lesser amounts of variation were explained by relationships to $\log_{10}(\text{area})$ ($r^2 = 0.11$ and 0.0001 , respectively). Thus, many other factors related to the environment, habitat heterogeneity, land-use change, disturbance history, and evolutionary history may be more important than area in influencing species richness. Still, because there were significant effects of area (in a statistical sense), it could not be ignored. We concluded that simple measures of species density (number of species per square kilometer) would work as well or better than more complex models of density at these spatial scales. This reduced the effect of area when comparing data among counties, but we realize that eastern U.S. counties were considerably smaller on average and that finer resolution analyses (below the county level) would have been preferred, but the data do not exist for such analyses.

We initially considered 13 environmental/topographic variables including latitude, mean elevation, and variation in elevation in a county, mean minimum temperature, mean annual temperature, mean annual precipitation, actual and potential evapotranspiration, solar radiation, humidity, and the number of frost-free days and growing degree-days. However, to reduce statistical problems related to multicollinearity (Neter et al. 1990, Burnham and Anderson 2002), we screened out variables that were highly cross-correlated ($r > \pm 0.80$; Bonferroni tests, transformed data where necessary; Appendix). For example, latitude and mean temperature were highly related to PET ($r > 0.91$), and PET was considered a more direct driver of plant diversity, so latitude and mean temperature were dropped from further analysis. Likewise, minimum temperature, humidity, frost days, and growing degree-days were excluded, leaving seven environmental/topographic variables (Appendix).

Human factors included human population, road density, percentage of cropland in a county, and an index of habitat disturbance (ratio of area disturbed [developed, cultivated, and surface mines] to total county area; Appendix). However, since road density was highly correlated with human population density ($r = 0.85$), it was excluded from further analysis (Appendix).

Biotic variables initially included vegetation carbon and the normalized difference vegetation index (NDVI). Plant productivity is difficult to measure because it involves aboveground and belowground components, changes seasonally and annually, and is prohibitively expensive to measure at large spatial scales. We relied on two surrogates for productivity (potential

aboveground total vegetation carbon) based on a 30-yr annual mean (1961–1990) measured as grams of carbon per square meter at 3168 locations in the United States, then kriged to county centroids (VEMAP2 DATA, 2000, National Center for Atmospheric Research, Boulder, Colorado, USA; Hof et al. 2004) and NDVI (see Appendix for details). Vegetation carbon provided a commonly used estimate of a productivity gradient to compare with latitude and other variables.

An additional biotic measure of habitat heterogeneity included native bird species density. In another paper (Stohlgren et al. 2005), we demonstrated that the density of native bird species in a county (nesting birds only) integrated elements of high productivity, high habitat heterogeneity, and moderate disturbance as has been found in other studies (Rosenzweig 1995). Because the density of bird species also integrates many aspects of the environment at global scales (Currie 1991), we used the density of native bird species in a county as an independent variable in models to predict native and nonnative plant species densities. Native bird species data were compiled at the USGS Patuxent Wildlife Research Center, Maryland, USA, producing species richness data for 3079 counties across 50 states. For 36 states, distribution data were obtained from published breeding bird atlas projects conducted between the mid-1970s and the late 1990s. Various state and regional publications provided county-level distribution information for states lacking published atlases.

We hypothesized that mean native and nonnative plant species density within counties for the conterminous United States would be more closely associated with productivity gradients rather than latitude gradients. We further hypothesized that because biota may integrate coarse- and fine-scale environments and habitat heterogeneity, biotic variables would more strongly predict native and nonnative plant species densities compared to either environmental/topographic variables or human variables. We tested only two models on a preliminary set of data (Stohlgren et al. 2005), so we updated the data set and expanded the analysis to an a priori suite of models designed to test our primary hypothesis that biotic variables would better describe patterns of native and nonnative species densities at county scales compared to environmental/topographic and human variables.

We assessed cross-correlations among vegetation carbon, NDVI, bird species density, and the environmental/topographic and human variables using pairwise comparisons and Bonferroni tests of significance (Systat version 10; SYSTAT Software, Port Richmond, California, USA), and no egregious cross-correlations were found ($r > 0.80$). We conducted stepwise multiple regressions to remove insignificant predictors from the models ($P > 0.15$), to remove additional variables with high tolerance levels (>0.95 ; none were found), and to assure that no significant predictors were ignored. Lastly, model residuals were inspected for underlying

patterns (Zar 1974), and none were found. Significant values in all cases were determined using the SYSTAT statistical software (version 10).

We used the Akaike Information Criterion (AIC) and information-theoretical model selection (Burnham and Anderson 2002) to evaluate multiple regression models related to the specific hypotheses above. While this approach may not produce the “best” model as compared to other computationally intensive approaches, it does allow for direct comparisons among multiple models.

For least-squares regressions, we assumed normally distributed errors (a fair first approximation in our case), and AIC was computed as

$$\text{AIC} = n \log(\text{RSS}/n) + 2K \quad (1)$$

where n was the sample size, RSS was the residual sum of squares in the model such that RSS/n is the maximum likelihood estimator, and K was the number of estimable parameters in the model (including the intercept and residual variance; Burnham and Anderson 2002:63). The differences in AIC values between the best model (lowest AIC) and other models were used to rank the models in relation to their support based on the data.

RESULTS

Latitudinal gradients of plant species density

Regression analyses showed no relationship between latitude and native plant species density ($r^2 = 0.0001$, $P = 0.60$; Fig. 1). There was a statistically significant but biologically meaningless positive relationship between latitude and nonnative plant species density ($r^2 = 0.01$, $P = 0.0001$; Fig. 1).

Productivity gradients of plant species density

Plant species density was more strongly correlated to total vegetation carbon than to latitude. Higher native and nonnative plant species densities were associated with areas of high total vegetation carbon (Fig. 2). Total vegetation carbon explained approximately 22% of the variation in native species densities and 7% of the variation in nonnative species densities. There were several counties moderately high in vegetation carbon with high values of native and nonnative plant species density, but these were offset by a large number of counties with low densities of species (Fig. 2).

Cross-correlations among variables

We found many cross-correlations among factors related to latitude and total vegetation carbon that can confound or help interpret patterns of plant species density (Table 1). Native and nonnative plant species density were strongly positively correlated to bird species density, and these three biotic variables were positively correlated to vegetation carbon and NDVI. All the biotic variables were positively correlated to pre-

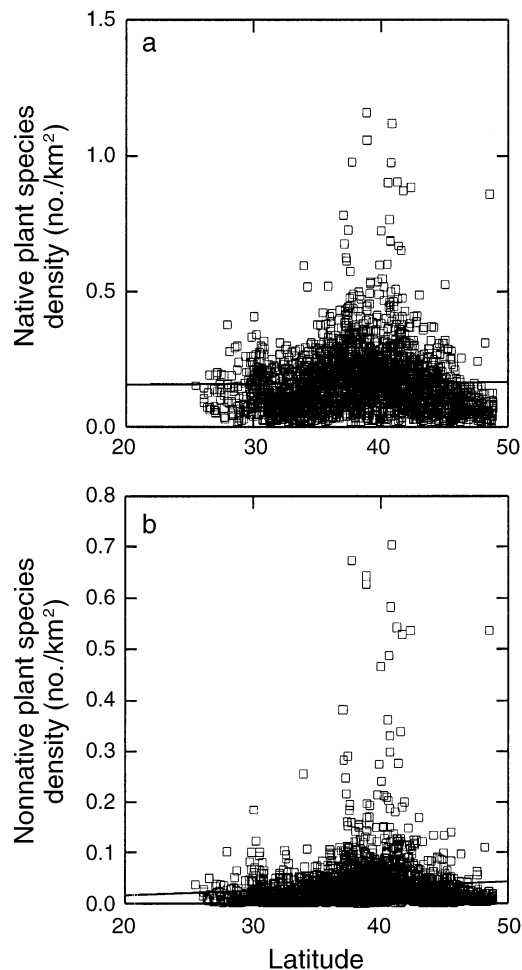


FIG. 1. Regressions of species density in a county on latitude for (a) native plant species ($r^2 = 0.0001$, $P = 0.60$) and (b) nonnative plant species ($r^2 = 0.01$, $P = 0.0001$) ($n = 3000$ counties in 48 states of the United States). Data were log transformed.

cipitation and negatively correlated to radiation, elevation, and the variation in elevation in a county. Potential evapotranspiration, which was strongly correlated to latitude, and AET were positively correlated to one another and to precipitation and negatively correlated to elevation and variation in elevation (Table 1).

Solar radiation was negatively correlated to vegetation carbon. This shows the potentially confounding geographic patterns in the United States where there are significant positive correlations between latitude and elevation and between latitude and the variation in elevation in a county. This describes the geography and topography of the United States due to north-south-oriented mountain ranges (e.g., Rocky Mountains, Sierra Nevada, Cascade, and Appalachian ranges), which intercept precipitation and cause rain shadow effects with west-to-east-moving jet streams.

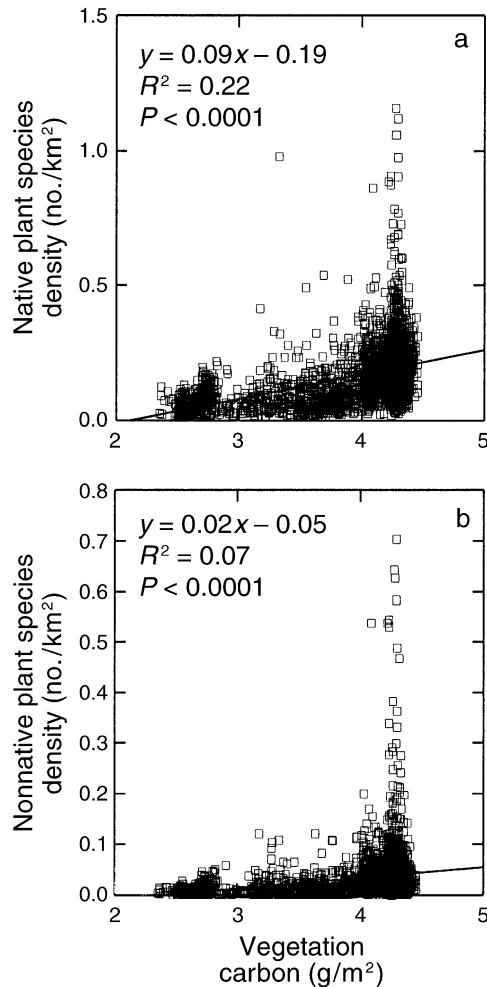


FIG. 2. Regressions of species density in a county on productivity (total vegetation carbon) for (a) native and (b) nonnative plant species ($n = 3000$ counties in 48 states). Data were log transformed.

Human population was strongly positively correlated to native and nonnative plant species density, native bird species density, and vegetation carbon, while cropland area was negatively correlated with these variables. The percentage of disturbed habitat in a county was weakly but positively associated with native and nonnative plant species density and with bird species density in a county (Table 1).

In the initial screening of the variables, growing degree-days, minimum and mean annual temperature, precipitation, PET, and AET were all significantly negatively correlated with latitude. However, latitude and temperature variables were replaced with PET for the multivariate models that follow.

Information-theoretical models of plant species density

The best single model describing the density of native plant species included all biotic, environmental/

topographic, and human variables (Table 2, model 1). This model had the smallest (most negative) AIC value of -16691 and explained 69% of the variation in native plant species density. Of the 15 individual variables used in the model, the most important predictors based on standardized partial regression coefficients (S_b) included a positive relationship to native bird species density ($S_b = 0.50$) and negative relationships to elevation ($S_b = -0.24$ and PET $S_b = -0.24$; also read latitude).

Three other models explained 63–67% of the variation in native plant species density (models 2–4; Table 2), but strict adherence to information-theory modeling would suggest that the data do not support models 2 through 7 because the AIC differences ($\Delta AIC_i = AIC_i - AIC_{\min}$, where i indexes competing models) greatly exceed 10 (see Burnham and Anderson [2002:70]). In the models that included biotic factors (models 1–4), the strongest single predictor variable was native bird species density ($S_b \geq 0.50$). In the models that included environmental/topographic variables, negative relationships with PET and elevation were strong predictors of native plant species diversity. In general, for the seven models describing native plant species density, models including biotic variables performed better than models including human variables or environmental/topographic variables (Table 2).

Initially, the best single model describing the density of nonnative plant species also included biotic, environmental/topographic, and human variables (Table 3, model 8). In predicting nonnative plant species density, we could use the native plant species density as an independent variable because the native species were well entrenched for millennia prior to the arrival of nonnative species from other countries. Model 8 had the smallest (most negative) AIC value of -24055 , explained 86% of the variation in non-native plant species density, and was driven largely by the positive relationship with native plant species density ($S_b = 0.66$). This is a stronger model (in terms of R^2 values) than model 1 for native plant species density, but the models included different independent variables, so a direct comparison of models is impossible. Model 8 excluded NDVI, mean precipitation, land cover, and variation in elevation ($P > 0.15$). In the five models that used biotic factors (models 8–12; Table 3), the most important predictor was the positive relationship to native plant species density ($S_b \geq 0.66$), and four models also included the density of native bird species in the top three predictors ($S_b \geq 0.21$).

Four other models explained 75–85% of the variation in nonnative plant species density, models 9–12, the latter being a simple linear model (Table 3). However, strict adherence to information-theory modeling again would suggest that the data do not support these other models.

Lastly, in a post hoc model, we found a highly significant positive, nonlinear relationship between native

and nonnative plant species density, with 90% of the variation in nonnative plant species density explained solely by the density of native plant species in a county (Fig. 3). Had we included this model in our original suite (Table 3), its AIC = $-25\,125$ would have made it the “best model.” We tested the model regionally in selected areas of the United States and found that between 64% and 98% of the variation in nonnative species densities could be explained solely by the density of native plant species (Table 4).

It is worth noting that model rank order based on AIC from best to least supported given our data is identical to the ranking based on adjusted R^2 (Tables 2, 3). In fact, the correlation between those two statistics exceeds 0.96 for both native and nonnative species density response variables (unreported data). Although we were initially surprised by this pattern, it is clear from Eq. 1 that when dealing with consistently large sample sizes ($n = 3000$) and K s that vary little (3–15) most of the variation in AIC will be captured by the residual sum of squares. Since that term is shared by AIC and adjusted R^2 the common rank orders should have been anticipated.

DISCUSSION

Understanding optimal conditions for plant species density

The weak relationship between latitude and native species density in the conterminous United States (Fig. 1) might be expected due to north-south-oriented mountain ranges, which affect precipitation patterns and cause rain shadow effects with west-to-east-moving jet streams. That is, sites of similar latitude on the western and eastern sides of a mountain range will have very different environments, species compositions, and likely species densities. Several authors discuss the limitations of latitude as an environmental predictor of species richness (Huston 1999, Hawkins et al. 2003, Hawkins and Diniz-Filho 2004). However, the observed productivity gradient with native and nonnative plant species densities more strongly suggests that native and nonnative plant species may be responding to similar environmental constraints (Fig. 2), providing a link to similar global-scale energy patterns (Rosenzweig 1995) and water-driven patterns of plant diversity (see Hawkins et al. [2003] for a review). Because vegetation carbon was correlated more strongly with precipitation ($r = 0.78$) than with radiation ($r = -0.20$), mean annual temperature ($r = 0.31$), PET ($r = 0.24$), or AET ($r = 0.61$; all $P < 0.0001$), our data corroborate the Hawkins et al. (2003) conclusion that water may be a major driver of species richness in the continental United States.

However, energy (solar radiation and temperature) also may play an important role in plant species density. The consistent significant negative relationships between all the biotic variables and both elevation and

radiation, negative relationship between mean annual temperature and elevation ($r = -0.62$; $P < 0.0001$), and positive relationship between mean annual temperature and vegetation carbon ($r = 0.31$; $P < 0.0001$) suggest that optimal conditions for productivity involve the interactions of energy and water (Hawkins et al. 2003). There is growing evidence that diversity peaks at those places with optimal conditions for growth and productivity (Currie 1991, Rosenzweig 1992, Badgley and Fox 2000, Hawkins et al. 2003; but see Huston [1979, 1994]).

Multiple models and multiple variables associated with plant species density

Multiple models of native plant species diversity included all the variables inserted in the models (Table 2, model 1), initially complicating our understanding of the factors predicting patterns of native plant species diversity. All the subsequent models (Table 2, models 2–7) would be dismissed based on the Δ AIC criterion, and we did not expect the model based on environmental/topographic variables (model 6) to perform the worst of the seven models. It was instructive that models that included biotic factors performed better than models based strictly on environmental/topographic and human variables. The importance of humans might be dismissed on the grounds that humans settled in species-rich areas rather than “causing” species-rich areas (Stohlgren et al. 2005). In this study, the best model of nonnative plant species density ultimately supported by the data (Fig. 3) also excluded human variables. It was more informative to recognize that the primary predictor variables in the best model of native plant species density (Table 2, model 1) were native bird species density, elevation, and PET (biotic and environmental variables).

Biotic factors may integrate complex and coarse-resolution environmental/topographic data. In loosely comparing the models for native plant species density (models 1–7; Table 2) and the models for nonnative species density (models 8–15, excluding model 12; Table 3), the AIC rankings of two sets of models were unexpectedly identical, suggesting: (1) generally biotic variables \gg human variables \approx environmental/topographic variables in describing patterns of native and nonnative plant species density, and (2) the dominant predictor biotic variable for native plant species density was always native bird species density, while the dominant predictor biotic variable for nonnative plant species density was always native plant species density. It may be that native plant and bird species densities summarize species richness data from rare and common habitats in a county and, as such, integrate micro- and macroenvironments, and disturbed and undisturbed habitats that are not adequately represented by mean environmental/topographic or human variables at county scales.

TABLE 1. Cross-correlations (Pearson coefficients) among selected biotic, environmental/topographic, and human variables.

Variable	Native plant density	Nonnative plant density	Native bird density	Vegetation carb.	NDVI	Elevation	Variation in elevation
Native plant density	1.00						
Nonnative plant density	0.86	1.00					
Native bird density	0.76	0.77	1.00				
Vegetation carbon	0.46	0.26	0.34	1.00			
NDVI	0.26	0.14	0.18	0.38	1.00		
Elevation	-0.33	-0.27	-0.29	-0.49	-0.14	1.00	
Variation in elevation	-0.20	-0.14	-0.23	-0.29	-0.25	0.76	1.00
Land cover	-0.15	-0.11	-0.20	NS	-0.44	-0.11	0.13
Radiation	-0.28	-0.26	-0.25	-0.20	-0.72	0.15	0.21
Precipitation	0.35	0.18	0.26	0.78	0.41	-0.57	-0.33
AET	0.24	NS	0.18	0.61	0.26	-0.70	-0.66
PET	-0.06‡	-0.10	NS	0.24	-0.27	-0.61	-0.47
Human population density	0.59	0.70	0.55	0.23	NS	-0.28	-0.13
Crop area	-0.37	-0.25	-0.34	-0.50	0.09	0.20	-0.11
Disturbance	0.12	0.15	0.12	-0.07	0.37	-0.11	-0.46

Notes: Transformed data were used where it was appropriate. Correlations are significant at $P < 0.05$ except where noted; NS = $P > 0.1$. NDVI, normalized difference vegetation index; AET, actual evapotranspiration; PET, potential evapotranspiration.

† $P = 0.06$.

‡ $P = 0.09$.

The post-hoc nonlinear model of native to nonnative plant species density (Fig. 3), the new best model examined in terms of both AIC and adjusted R^2 , further suggests that the total environmental conditions conducive to high native plant species densities may create environmental conditions conducive to the establishment of nonnative species. Since many factors are significantly cross-correlated with latitude, including productivity, solar radiation, AET, PET, mean annual temperature, mean minimum temperature, and precipitation, it's not surprising that native and nonnative plant species densities also are significantly cross-correlated to these same variables. And, despite the fact that all these factors vary enormously in various regions of the country, a single, strong predictor of nonnative species density in selected regions (Table 4), and in the conterminous United States (Fig. 3), is the density of native plant species.

Patterns that cross spatial scales

There is growing evidence that a few environmental factors may explain species richness patterns at landscape scales (Stohlgren et al. 1997, 2002, Chong et al. 2001), continental and regional scales (Stohlgren et al. 2005a), and global scales (Currie 1991, Huston 1994, Rosenzweig 1995, Kleidon and Mooney 2000, Allen et al. 2002, Hawkins et al. 2003). For example, in Rocky Mountain National Park, Colorado, mesic mountain meadows and aspen (*Populus tremuloides*) habitats that were high in light, nitrogen, and water had higher native and non-plant species densities (per 0.1-ha plot) and overall richness based on multiple plots (Stohlgren et al. 1997, 1999a). High-elevation sites had far fewer nonnative species than low-elevation sites. Likewise, mesic vegetation types in the xeric Grand

Staircase-Escalante National Monument, Utah, with soils high in nitrogen and phosphorus, had higher native and nonnative plant species densities (per 0.1-ha plot) and overall richness based on multiple plots (Stohlgren et al. 2002). From the shortgrass steppe sites to tallgrass prairie sites in the central grasslands of the United States, native-species-rich areas were more heavily invaded (i.e., in nonnative plant species richness and foliar cover) than species-poor sites (Stohlgren et al. 2001). At statewide scales, California has the greatest number of native and nonnative plant species, coinciding with high habitat heterogeneity, large area, complex topography and paleobotany, and mix of climate zones (Dobson et al. 1997, Stein et al. 2000; Table 4). The richness of plant species and many other biological groups (e.g., bird species density in this study) is often associated with high habitat heterogeneity (Rosenzweig 1992, 1995), but coarse-scale measures like land cover classes and variation in elevation (Table 1) may not sufficiently describe important microhabitats at county scales. At national scales, there is an overwhelming positive relationship between native and nonnative plant species richness (Stohlgren et al. 2003) and densities (Stohlgren et al. 2005) in counties, states, and regions.

Our study seems to support some aspects of what Ricklefs (2004) called "local determinism," despite some unexplained variation potentially due to local and regional species pools, patterns of endemism, varying levels of disturbance, and human factors (Huston 1999). Other studies also report that native plant species density in a region may be a complex function of habitat heterogeneity, warm temperatures, and/or precipitation (Rosenzweig 1995, Hawkins et al. 2003, Venevsky and Veneskaia 2003).

TABLE 1. Extended.

Land cover	Radiation	Precipitation	AET	PET	Human population density	Crop area	Disturbance
1.00							
0.38	1.00						
-0.10	-0.23	1.00					
-0.06†	NS	0.73	1.00				
0.24	0.49	0.38	0.67	1.00			
NS	-0.14	0.17	0.08	NS	1.00		
-0.12	-0.16	-0.42	-0.23	-0.15	-0.23	1.00	
-0.29	-0.38	-0.10	0.08	-0.10	0.16	0.64	1.00

Local determinism has notable exceptions, typically where unique evolutionary history plays a significant role (Gentry 1986, Venevsky and Veneskaia 2003). Some arid landscapes with infertile soils, such as the fynbos region of South Africa (Bond 1983, Cowling et al. 1998), southwest Australia (Abbott 1977, Abbott and Black 1980), and the southwestern United States (Dobson et al. 1997), are hotspots of high plant endemism and diversity. However, more of the globe conforms to the general “hotspots” pattern closely associated with tropical and subtropical areas with abundant solar radiation and rainfall (Rosenzweig 1995, Myers et al. 2000). At landscape scales, some endemic species may be associated with arid environments such as desert habitats in southern Utah (Stohlgren et al. 2004), but in these and other areas throughout the United States, species-rich habitats also are common in highly productive areas with fertile soils, mesic habitats, and low-elevation areas. In the continental United States and at county scales, this pattern is corroborated by our finding that native species densities are positively correlated with potential vegetation carbon (Tables 1 and 2, Fig. 2). However, highly productive sites that have not been recently disturbed and where trees gain dominance may have low understory plant and bird diversity. These sites may rarely cover entire counties,

and they may be less common (in terms of area) at regional scales.

Realizing that exceptions exist, this present study now provides a framework to evaluate general patterns of plant density. The relatively high predictability of native and nonnative species densities at subcontinental scales ($R^2 = 0.68$ and 0.90 , respectively; Table 2 and Fig. 3) strongly supports similar global patterns and proposed mechanisms reported where declining diversity predictably coincides with harsh environments (Currie 1991, Rosenzweig 1995, O’Brian 1998, Francis and Currie 2003, Hawkins et al. 2003, Venevsky and Veneskaia 2003, Stohlgren et al. 2005).

*Predictable patterns of invasions
of nonnative plant species*

The patterns and relationships presented here are preliminary. Additional data on native and nonnative plant distributions may improve our findings. Most counties are incompletely surveyed, and the additions of vegetation plot data, species lists from parks and refuges, and other point locations of plant species will improve sparsely surveyed counties (Crosier and Stohlgren 2004). We would also benefit from new systematic and periodic plant surveys, especially for invasive plant species, and better information on plant species mi-

TABLE 2. Models evaluated for native plant species density (NatSpDen).

Model no.	Native plant species density models	AIC	Δ AIC	Percentage difference	Adjusted R^2	K
1	NatSpDen = biotic, environmental/topographic, human variables	-16 691	0	0	0.69	15
2	NatSpDen = biotic, human variables	-16 525	165	1.0	0.67	8
3	NatSpDen = biotic, environmental/topographic variables†	-16 320	370	2.2	0.65	9
4	NatSpDen = biotic variables	-16 174	517	3.1	0.63	5
5	NatSpDen = environmental/topographic, human variables	-15 622	1069	6.4	0.56	11
6	NatSpDen = human variables	-14 553	2138	12.8	0.37	5
7	NatSpDen = environmental/topographic variables	-14 215	2475	14.8	0.29	9

Notes: AIC is the Akaike Information Criterion; K is the number of estimable parameters in the model.

† The normalized difference vegetation index, radiation, and land cover were removed from model 3 ($P > 0.15$).

TABLE 3. Models evaluated for nonnative (or nonindigenous) plant species density (NISpDen).

Model no.	Nonnative plant species density models	AIC	Δ AIC	Percentage difference	Adjusted R^2	K
8	NISpDen = biotic, environmental/topographic, human variables†	-24 055	0	0	0.86	12
9	NISpDen = biotic, human variables†	-23 889	166	0.7	0.85	6
10	NISpDen = biotic, environmental/topographic variables†	-23 435	619	2.6	0.82	11
11	NISpDen = biotic variables	-23 142	913	3.8	0.80	5
12	NISpDen = NatSpDen (linear model)	-22 378	1677	7.0	0.75	3
13	NISpDen = environmental/topographic, human variables†	-20 806	3248	13.5	0.57	11
14	NISpDen = human variables	-20 335	3720	15.5	0.52	5
15	NISpDen = environmental/topographic variables	-18 962	5093	21.2	0.21	9

Notes: AIC is the Akaike Information Criterion; K is the number of estimable parameters in the model.

† Variation in elevation, land cover, precipitation, and the normalized difference vegetation index, (NDVI) were removed from model 8; NDVI, crop area, and disturbance were removed from model 9; land cover and precipitation were removed from model 10; radiation and actual evapotranspiration were removed from model 13 ($P > 0.15$).

grations, persistence, and extirpations at the county scale and at finer resolutions. Despite the needed improvements in the data set, the patterns and relationships discussed below serve as reasonable working hypotheses.

The very high predictability of nonnative species densities at regional scales ($R^2 = 0.64$ – 0.98 ; Table 4) and subcontinental scales ($R^2 = 0.90$; Fig. 3) strongly supports the same global patterns and proposed mechanisms contributing to native plant diversity (Huston 1999, Hawkins et al. 2003, Ricklefs 2004). In the conterminous United States, nonnative plant species diversity can be expected to be greatest in low-latitude areas, in high-precipitation areas, at low elevations, and in warm temperatures, factors associated with “the good life”: low environmental stress, high productivity, and high heterogeneity (assuming bird species density is a good indicator of habitat heterogeneity). It is unlikely that competition, imagined to be a strong force inhibiting invasions at the scale of plant neighborhoods (e.g., Tilman 1999), is a strong force inhibiting inva-

sions at landscape and regional scales. The more general principal in ecology (and widespread in terms of area) is that regions high in native species richness and density are particularly prone to invasions (Fig. 3, Table 4). Increasing invasions in productive environments would continually add to the regional species pool of nonnative species, facilitating future invasions in productive and less productive environments. Human factors may play an important role in the observed patterns of nonnative plant diversity via initial establishment locations. However, environmental factors may determine the ultimate distributions and densities of nonnative species.

CAUTIONS, CONCLUSIONS, AND NEXT STEPS

Local (Ricklefs 2004) and regional determinism may play an extremely important role in the invasion of nonindigenous species because: (1) the strongest predictor of the densities of nonnative plant species was the density of their native cohorts (Fig. 3, Table 4); (2) native and nonnative species densities generally tracked the same factors in a consistent way (Tables 2 and 3); and (3) models that included human factors were not strongly supported by the data using AIC (Table 3). Even stronger than we reported earlier for the richness

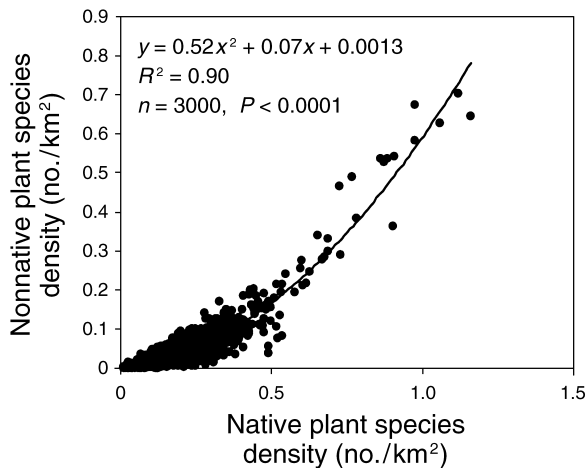


FIG. 3. Relationship between native plant species density and nonnative plant species density in 3000 counties in the United States. Data were log transformed.

TABLE 4. Regional tests of the polynomial model ($y = x^2 + x + c$) predicting nonnative plant species density (y) from native plant species density (x) as in Fig. 3.

State groups	Adjusted R^2	No. counties
CA (by itself)	0.98	58
AZ, NM, UT, CO	0.64	140
FL, GA, MS, LA	0.64	125
NY, NH, PA, ME	0.95	155
MT, WY, ND, SD	0.72	195
WA, OR, ID	0.96	118

Note: State abbreviations are: CA, California; AZ, Arizona; NM, New Mexico; UT, Utah; CO, Colorado; FL, Florida; GA, Georgia; MS, Mississippi; LA, Louisiana; NY, New York; NH, New Hampshire; PA, Pennsylvania; ME, Maine; MT, Montana; WY, Wyoming; ND, North Dakota; SD, South Dakota; WA, Washington; OR, Oregon; ID, Idaho.

of vascular plants in counties (Stohlgren et al. 2003) and a linear model comparing native and nonnative plant species densities (Table 3, model 12), we found additional evidence to support “the rich get richer” pattern (Fig. 3, Table 4). There is little evidence of a saturation of nonnative plant species densities at county, regional, or continental scales. But because the density of nonnative plant species generally tracks hotspots of native plant and bird species diversities and a subset of environmental factors, areas of high native plant and bird species diversity near current invasions should be specifically targeted for early detection and rapid response programs. We need to carefully monitor invasions in species-rich areas.

One next step will be to include information on species identity and characteristics. For example, Brazilian pepper tree, Australian melaleuca, and Asian cogon-grass were pre-adapted to the climatic conditions they found in Florida. Climate matching (Huston 1979, 1994, Currie 1991, Rosenzweig 1995) and habitat matching, where nonnative annual plant species target habitats high in native annual plant species (Stohlgren et al. 2005), may support increasing invasions by nonnative species facilitated by trade and transportation. We need to better predict the interactions of species traits and the vulnerability of habitats to invasion. Several nonnative plant species may benefit from continued introduction into many habitats each year by trade and transportation (Reichard and White 2001). This will complicate the development of site-specific predictive models of invasion.

There are many additional factors that could affect the success of nonnative species in species-rich areas including weak competition for resources from native species, use of previously underused resources, or escape from natural predators (see Mack et al. [2000]). Native and nonnative plant species may simply be responding to similarly inviting habitats and resources (Stohlgren et al. 2005a, b), coexisting due to habitat heterogeneity (Huston 1994), high species turnover, increased pulses of available resources from continued large and small disturbances (D’Antonio et al. 1999), and thus, more opportunities for the establishment of nonnative plants (Abbott 1977, Abbott and Black 1980, Rosenzweig 1995, Stohlgren et al. 1997, 2003). This is the case for plants in Rocky Mountain National Park, Colorado, and throughout the Central Grasslands of the United States (Stohlgren et al. 1999a, 2002). Identifying specific mechanisms and processes associated with invasion is beyond the scope of this correlative study. However, the highly significant nonlinear patterns that we observed (Fig. 3, Table 4) and the highly significant cross-correlations and models are reason for concern.

Disturbances such as wildfire and hurricanes, land use change, and altered disturbance regimes may facilitate invasions. However, many fairly undisturbed areas have been successfully invaded, such as ungrazed

grassland sites, tree fall gaps, small-mammal mounds, and throughout many natural areas (Stohlgren et al. 1999a, b).

In many areas, the richness and foliar cover of nonnative plant species are strongly positively correlated (Stohlgren et al. 1998, 1999a, 2003, 2005b), so habitats vulnerable to establishment may also be vulnerable to successful invasion by nonnative species. However, despite the generalized patterns shown here where nonnative plant species have successfully established in native species-rich counties, many nonnative plant species also have been successful in species-poor areas (e.g., cheatgrass in some arid shrublands). Additional research is needed on the multiple factors associated with successful species invasions. Predictive models may be improved by using many of the factors identified here (Tables 1–3, Fig. 3) to begin forecasting where species will move in space and time. Theories pertaining to rates of species invasions will have to accommodate extensive coexistence of native and nonnative species at large spatial scales, lag times, and highly dominant native species or superinvaders in certain habitats (not all species are equivalents [Hubbell 2001]).

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APPENDIX

A table presenting species richness and ancillary data used in this analysis is available in ESA's Electronic Data Archive: *Ecological Archives* E086-121-A1.

LINKING BIOGEOGRAPHY AND COMMUNITY ECOLOGY: LATITUDINAL VARIATION IN PLANT–HERBIVORE INTERACTION STRENGTH

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Abstract. Ecological interactions may vary geographically as a function of diversity, density, or per capita interaction strengths, but we know little about the relative importance of these three mechanisms. We examined variation in species richness, abundance, and interactions among leaf-chewing herbivores and the dominant salt-marsh plant *Spartina alterniflora* along the Atlantic Coast of the United States. High-latitude *S. alterniflora* plants are more palatable to herbivores than are low-latitude plants. Within this range of latitude, diversity and density of the dominant leaf-chewing consumers, snails and grasshoppers, in *Spartina*-dominated portions of the marsh varied little. Low-latitude plants, however, experienced much greater levels of leaf damage from consumers than did high-latitude plants. Per capita feeding rates of low-latitude snails (*Littoraria irrorata*) and grasshoppers (*Orchelimum fidicinum*) in the laboratory were greater than feeding rates of high-latitude snails (*Melampus bidentatus*) and grasshoppers (*Conocephalus spartinae*). In field experiments, low-latitude snails strongly suppressed *S. alterniflora* growth, but high-latitude snails had no effect on primary production. Thus, latitudinal differences in the effect of herbivores on plants (i.e., interaction strength), driven by differences in per capita effects among species, rather than differences in diversity or density, may contribute to selection for latitudinal differences in plant palatability. Because geographical differences in interaction strength can occur in the absence of differences in diversity or density, linking biogeography with community ecology will require experimental studies that explicitly measure interaction strength at multiple geographic locations.

Key words: gastropods; grasshoppers; interaction strength; latitude; plant–herbivore interactions; salt marsh; *Spartina*; top-down effects.

INTRODUCTION

Over the past several decades, ecologists have increasingly appreciated the insights that can be gained by examining ecological questions from a geographic perspective (MacArthur 1972, Brown and Maurer 1989, Brown 1995, Gaston and Blackburn 2000). At the same time, there has been increasing interest in the variable nature of interactions among species (Thompson 1988, 1994, Dunson and Travis 1991, Bertness and Callaway 1994, Travis 1996, Callaway and Aschehoug 2000, Callaway et al. 2002). Together, these two lines of inquiry have stimulated studies that have examined geographic variation in interaction strength.

The strength of biological interactions is not uniform across space and time. Rather, interactions vary as a function of abiotic conditions, population densities, genetic structure, and a host of other factors (Thompson 1988, Thompson and Cunningham 2002, Harley 2003, Menge 2003), all of which are likely to vary across

latitude. Ecologists have examined latitudinal variation in the strength and nature of interactions between predators and prey (Vermeij 1978, Jeanne 1979, Fawcett 1984, Stachowicz and Hay 2000, Sanford et al. 2003), between herbivores and plants (Coley and Aide 1991, Bolser and Hay 1996, Pennings et al. 2001, Sotka and Hay 2002, Post 2005), and among competitors (James et al. 1997, Bertness and Ewanchuk 2002, Pennings et al. 2003). This growing list of studies is laying the foundation for a general theory of latitudinal variation in interaction strength, which generally is supporting the intuition of early naturalists that biological interactions are more intense towards the tropics.

Because many factors can vary across latitude, a major task for this developing theory will be to disentangle the relative contributions of different causal factors to variation in interaction strength. Consider the case of herbivores and plants. The nature of the interaction between these two groups of organisms may vary across latitude as a function of plant and herbivore species richness, population density, and/or intra- or interspecific variation in per capita interaction strength. To the best of our knowledge, the relative importance of these factors in mediating latitudinal variation in plant–herbivore interactions has not been explored for any plant–herbivore system. Here we consider these

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issues for salt marshes along the Atlantic Coast of the United States, focusing on the impact that herbivores have on plants.

Salt marshes are the dominant intertidal habitat along the Atlantic Coast of the United States, from central Florida through Maine. Throughout this range, the most abundant marsh plant is the grass *Spartina alterniflora*, which dominates the middle to lower intertidal zones, often in monospecific stands. The wide range of *S. alterniflora* provides a rare opportunity to make intraspecific comparisons across latitude, thus minimizing artifacts that might be associated with comparing distantly related taxa. In Atlantic Coast marshes, *S. alterniflora* is attacked by a variety of consumers, including stem-boring insects (Stiling and Strong 1984), sap-sucking leafhoppers (Denno 1977), tettigoniid grasshoppers (Smalley 1960), snails (Silliman and Ziemann 2001), and mammals (Pfeiffer and Wiegert 1981). Here, we will focus on the two most common groups of leaf-chewing invertebrates, snails and grasshoppers, because these are geographically widespread and relatively easy to count in the field, leave easily quantifiable feeding marks, and account for the vast majority of chewing damage to *S. alterniflora* leaves on the Atlantic Coast of the United States (S. C. Pennings and B. R. Silliman, *personal observations*).

Biogeographic theory predicts that plant-herbivore interactions will be more intense and thus plant defenses better developed at low vs. high latitudes (MacArthur 1972, Gaines and Lubchenco 1982, Coley and Aide 1991). Studies in both terrestrial (Coley and Aide 1991) and marine (Bolser and Hay 1996) systems have generally supported this hypothesis, although many exceptions exist (Targett et al. 1992, Swihart et al. 1994). Some early studies suffered from limitations in experimental design and scope, including limited replication of sites within regions, working with processed rather than fresh plant material, and comparing between distantly related plant taxa (reviewed in Pennings et al. [2001]). These limitations have been largely overcome by recent work in salt marshes along the Atlantic Coast of the United States, which has documented that, across most of the plant community (the 10 most common and widespread species), plants from replicated low-latitude sites are less palatable to (i.e., less readily eaten by) 13 species of leaf-chewing herbivores than are conspecifics from high-latitude sites (Pennings et al. 2001). The proximal factors governing this variation in palatability include latitudinal variation in nitrogen content, toughness, and chemistry (Siska et al. 2002), and these latitudinal differences appear to be constitutive rather than induced (Salgado and Pennings 2005). The ultimate drivers creating variation in these plant traits remain unexplored.

Here we focus on the most abundant of these 10 plants, *S. alterniflora*, and examine whether latitudinal variation in herbivore richness, herbivore abundance, and/or herbivore impacts on plants might be driving

latitudinal patterns in palatability. In past work, 19 of 21 trials, conducted both early and late in the growing season with five different herbivores from Rhode Island and Georgia, indicated significant and strong feeding preferences for high- vs. low-latitude *S. alterniflora* leaves (Pennings et al. 2001). Both early and late in the growing season, high-latitude *S. alterniflora* leaves were softer and contained fewer phenolics than low-latitude leaves (Siska et al. 2002). Leaves from high-latitude plants were also higher in nitrogen, consistent with a widespread tendency for leaf nitrogen to increase with latitude (Reich and Oleksyn 2004). Latitudinal differences in palatability and plant traits persisted over five clonal generations in a greenhouse, suggesting genetic control of fixed differences (Pennings and Salgado 2005). Across intertidal elevation within a single marsh, *S. alterniflora* varies in height as a function of edaphic conditions: plants immediately adjacent to creekbanks are taller and more palatable than plants throughout the marsh platform (the short-*Spartina* zone) (Valiela et al. 1978, Goranson et al. 2004, Richards et al. 2005). Here we focus on the short-*Spartina* zone because this comprises the vast majority of the acreage of *S. alterniflora*. To explore latitudinal variation in the effects of consumers on *S. alterniflora* and the mechanisms underlying these effects we ask three questions: (1) How do grasshopper and snail diversity, density, and feeding damage vary across latitude? (2) Do northern and southern consumers differ in per capita feeding rates in the laboratory? (3) Does the impact of consumers on *S. alterniflora* vary across latitude?

METHODS

Study species

Spartina alterniflora (henceforth, *Spartina*) is a wind-pollinated, perennial grass. One of the most widespread and locally abundant plants in salt marshes along the Atlantic and Gulf Coasts of the United States, it spreads rapidly and extensively via belowground rhizomes. Seedlings are rarely observed in undisturbed vegetation, but new sites are colonized both by seed and by drifting rhizome fragments (Travis et al. 2002).

The tettigoniid grasshoppers *Conocephalus sparti-nae* and *Orchelimum fidicinum* are the most abundant Orthoptera found on *Spartina* in high- and low-latitude Atlantic Coast marshes, respectively (Pfeiffer and Wiegert 1981, Bertness et al. 1987, Bertness and Shumway 1992). Like most tettigoniids, they are omnivores. In addition to feeding on leaves, both also eat insect prey, and *Conocephalus* is known to feed on flowers and seed heads. Adults are abundant in the months of July and August.

The snails *Littoraria irrorata* (salt marsh periwinkle) and *Melampus bidentatus* (coffee bean snail) are the most abundant gastropods in Atlantic and Gulf Coast U.S. salt marshes. Both species may live for several years. *Melampus*, the smaller species (up to 1.3 cm in

shell length), is distributed along the entire U.S. East Coast and is particularly abundant at higher latitudes, although it can be locally common at low-latitude sites as well (S. C. Lee and B. R. Silliman, *unpublished manuscript*). *Littoraria* is larger (up to 3.2 cm in shell length) and occurs only at lower latitude sites (New Jersey through Florida). Both are detritivore-omnivore grazers, feeding on organic matter and algae on the marsh surface at low tide and consuming standing-dead plant material and associated fungi as they ascend marsh grass stems during high tide (Daiber [1982] and references therein). At high densities, *Littoraria* also grazes live *Spartina* and can strongly suppress marsh grass growth and reproduction (Silliman and Zieman 2001, Silliman and Newell 2003). Field observations and gut content analysis suggest that *Melampus*, like *Littoraria*, grazes live marsh grass through direct radular contact and contains both detrital and green *Spartina* material in its gut (Hauseman 1932, Thompson 1984; B. R. Silliman, *personal observation*). Whether radular grazing by *Melampus* affects the growth of living *Spartina*, however, has not been evaluated.

Grasshopper abundance and feeding damage

Grasshoppers were counted visually on 10×2 m transects ($n = 6-8$ grasshoppers/site) in the short-*Spartina* zone at 10 sites each in New England (Maine, Massachusetts, Rhode Island, and Connecticut) and the South Atlantic Bight (South Carolina, Georgia, and Florida) in July and August of 2002. A single plant stem was haphazardly selected following each transect, and grasshopper grazing damage to the two youngest, fully expanded leaves was visually estimated to the nearest 10% of leaf area. Grasshopper density and feeding damage data were averaged across leaves, transects, and/or months to yield a single value for each variable at each site.

Snail abundance and feeding damage

Snails were counted in 0.0625- or 0.25-m² quadrats ($n = 8-20$ snails/site) in the short-*Spartina* zone at nine sites each in New England (Rhode Island and Connecticut) and in the mid-Atlantic and the South Atlantic Bight (Maryland, Virginia, North Carolina, South Carolina, Georgia, and Florida) in the summers of 2000–2002. Snail feeding on *Spartina* plants results in characteristic longitudinal grazing scars that cut through the entire leaf, termed “radulations” (Silliman and Zieman 2001). At a subset of the sites, five plant stems were haphazardly selected and snail radulation damage to the whole stem (i.e., total area, in centimeters, of radulations per stem) was measured with a ruler. Snail density and radulation damage data were averaged across plots or plants, sites, and/or months to yield a single value for each variable at each site.

Per capita feeding rates in the laboratory

To test the hypothesis that latitudinal differences in feeding damage could be generated by differences in

per capita feeding rates, we compared feeding rates of northern and southern consumers in laboratory experiments using common diets. To estimate feeding rates of grasshoppers, we reanalyzed data from feeding preference experiments reported in Pennings et al. (2001). Individual grasshoppers from the north (Rhode Island, mostly *Conocephalus spartinae*, 76 replicate animals in three different assays) and the south (Georgia, mostly *Orchelimum fidicinum*, 113 replicate animals in eight different assays) were each offered one leaf of a northern and one leaf of a southern *Spartina*. Cut leaves were placed upright with their bases in a vial of water. Assays in both Rhode Island and Georgia were run indoors at approximately 22–24°C. Individual replicates ran until substantial feeding (ca. 30% of one leaf) occurred or 72 h had elapsed. To standardize for duration, we divided the total amount of both leaves eaten by the number of elapsed hours. Autogenic controls were not run because cut leaves neither grew nor shrank appreciably in the absence of herbivory. The vast majority of feeding was on northern leaves (Pennings et al. 2001), so data were not corrected for any potential differences in leaf mass/area between northern and southern leaves.

To estimate per capita feeding rates of the two snail species, we offered undamaged leaves of *Spartina* (two 10-cm pieces), from either the short-*Spartina* zone or the tall-*Spartina* zone, to groups of four *Littoraria* or four *Melampus* (both collected from Georgia; $n = 16$ leaves per snail species per zone). We used plants from both zones to confirm previous results that plants from the tall-*Spartina* zone are more palatable than those from the short-*Spartina* zone (Silliman and Bertness 2002, Goranson et al. 2004). After 72 h, leaves were removed and radulations measured. This experiment involved the assumption that *Melampus* from Georgia would have a similar ability to feed on *Spartina* as *Melampus* from high-latitude sites, an assumption that was supported by the field experiments described below.

Snail–Spartina interaction strength in the field

To test the hypothesis that the effect of snails on *Spartina* varies across latitude, we compared the results of parallel snail enclosure experiments conducted in the short-*Spartina* zone of two high- (Rhode Island) and four low- (Virginia, Georgia) latitude sites. Results from one of the two sites in Virginia and methods for these experiments have been previously published (Silliman and Zieman 2001). Briefly, roofless cages were constructed of zinc-coated hardware cloth to a height greater than that of the vegetation (6.35-mm mesh, 0.25 or 1 m² in area). Partial cage controls indicated no effect of caging on vegetation, snails, or the snail–plant interaction at any site. Snails (*Melampus* in Rhode Island, *Littoraria* in Virginia and Georgia) were stocked in enclosures at low (zero), moderate, and high densities to represent the lowest, typical, and highest densities

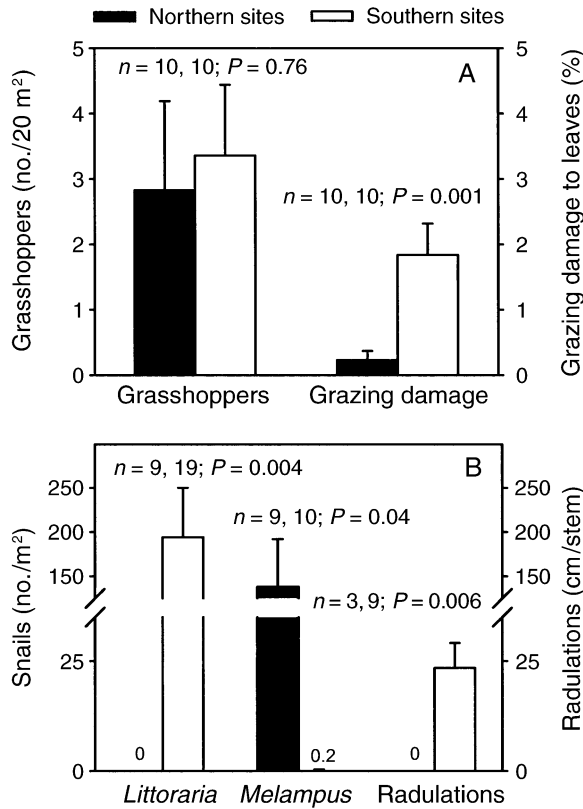


FIG. 1. (A) Density of grasshoppers (mostly *Conocephalus* and *Orchelimum*) and grasshopper grazing damage to leaves of *Spartina alterniflora* in the short-*Spartina* zone of marshes in New England (northern sites: Maine, Massachusetts, Rhode Island, Connecticut) vs. the South Atlantic Bight (southern sites: South Carolina, Georgia, Florida), USA. (B) Density of snails (*Melampus*, *Littoraria*) and radulation damage to leaves of *Spartina alterniflora* in the short-*Spartina* zone of marshes in southern New England (Rhode Island, Connecticut) vs. the mid-Atlantic and South Atlantic Bight (Maryland, Virginia, North Carolina, South Carolina, Georgia, Florida). Data are means + SE, and sample sizes and P values are given above bars. Data were analyzed with two-sample t tests or with one-sample t tests vs. zero, treating sites as replicates.

found at each site. Each snail density treatment was replicated three or six times. After 6 mo (May–October), live vegetation was harvested from a 0.0625-m² quadrat centered in each plot. Total radulations were measured on 10 haphazardly chosen stems from each plot.

RESULTS

Grasshopper density was similar among geographic regions (Fig. 1A). Most individuals observed were tettigoniids, primarily *Conocephalus spartinae* in New England and *Orchelimum fidicinum* in the South Atlantic Bight (these two species cannot be distinguished on visual transects, but relative abundance was determined by representative collections and accords with previous studies). A small proportion (<10%) of grass-

hoppers were acridids (mostly *Dicromorpha elegans*, *Orphulella pelidna*, and *Paroxya clavuliger*), which were transients from other marsh zones. Although grasshopper densities were similar between geographic regions on the dates we sampled, feeding damage was almost 10 times greater in the South Atlantic Bight than in New England (Fig. 1A), suggesting that high-latitude grasshoppers have a smaller per capita effect on *Spartina* foliage than low-latitude grasshoppers.

Two snail species were present in quadrats. *Littoraria irrorata* was absent in New England but common at most mid- and south Atlantic sites, with mean densities ranging from zero to over 800 snails/m² at different sites (Fig. 1B). (*Littorina littorea* and *L. saxatilis* occur in some New England salt marsh sites in small numbers but were not present in our quadrats.) *Melampus bidentatus* showed the opposite distribution pattern: it was common at many sites in southern New England, with mean densities ranging from zero to over 400 snails/m², but rare at mid- and south Atlantic sites. In these low-latitude sites, *Melampus* can potentially reach high densities but is typically excluded by exploitative competition and habitat modification by *Littoraria* (S. C. Lee and B. R. Silliman, unpublished manuscript). Radulation damage to *Spartina* was observed only at mid- and south Atlantic sites (Fig. 1B), where it positively correlates with snail density (Silliman and Zieman 2001). Thus, as with the grasshoppers, the geographical differences in damage were much more striking than the differences in snail abundance or diversity, suggesting that high-latitude snails have a smaller per capita effect on *Spartina* than low-latitude snails.

In the laboratory, southern grasshoppers ate more than three times as much leaf material per hour as did northern grasshoppers (Fig. 2). *Littoraria* fed on *Spartina* leaves from both marsh zones, producing visible

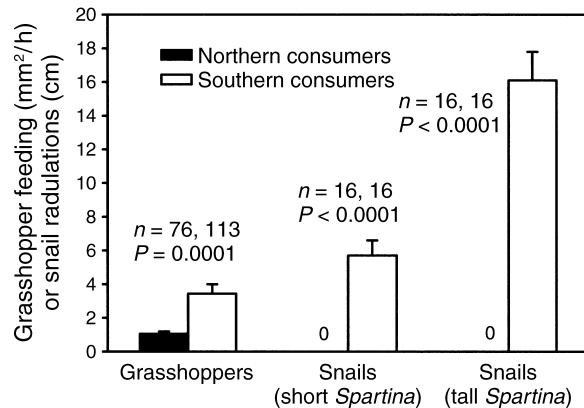


FIG. 2. Per capita grazing rates of northern and southern grasshoppers (*Conocephalus* and *Orchelimum*, respectively) and snails (*Melampus* and *Littoraria*, respectively) feeding on *Spartina alterniflora*. Data are means + SE; sample sizes and P values are given above bars. Data were analyzed with two-sample t tests or with one-sample t tests vs. zero.

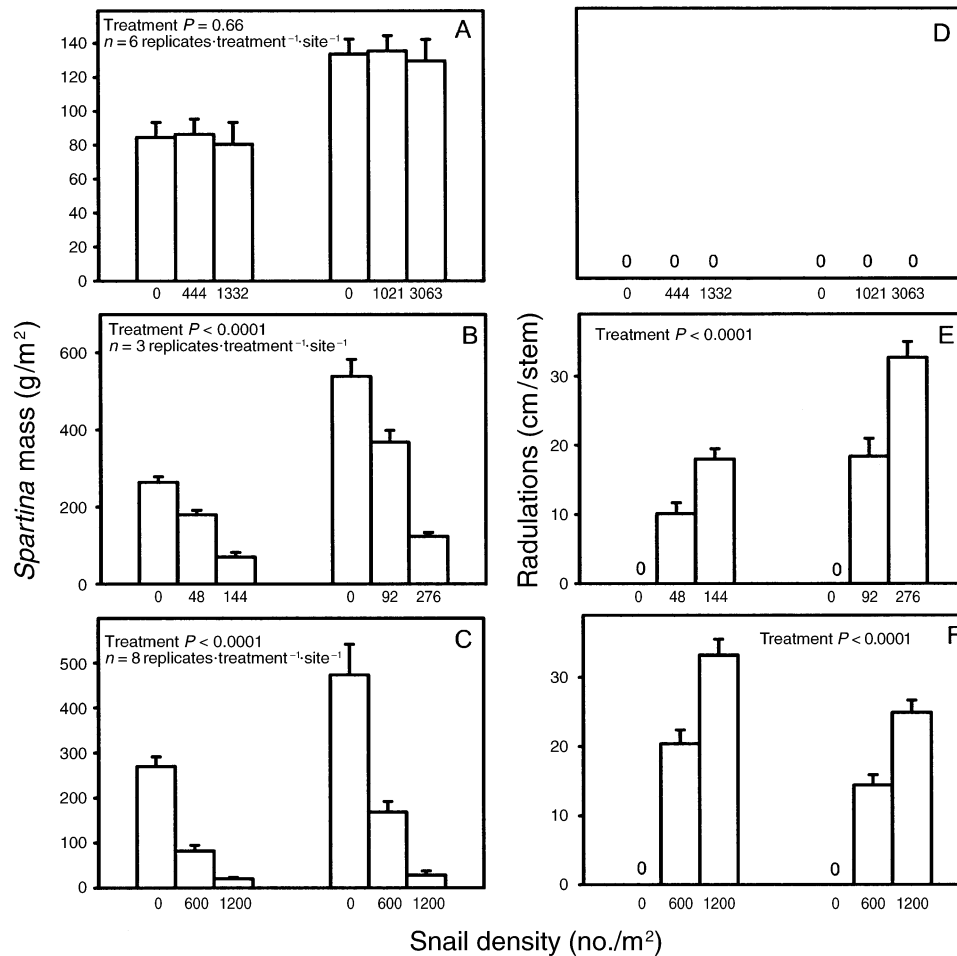


FIG. 3. Impacts of snails on biomass of *Spartina alterniflora* in experiments at two sites each in (A) Rhode Island (*Melampus*), (B) Virginia (*Littoraria*), and (C) Georgia (*Littoraria*); and snail damage (radulations) on plants in (D) Rhode Island, (E) Virginia, and (F) Georgia (damage was zero in all treatments in Rhode Island). Snail densities are given below bars. Data are means + SE and were analyzed with ANOVA, treating sites as blocks. Results of one of the Virginia experiments (panel B, Broadwater marsh, bars on left) were previously published (Silliman and Zieman 2001).

radulations, but as expected (Silliman and Bertness 2002, Goranson et al. 2004), fed most heavily on leaves from the tall zone (Fig. 2). *Melampus* produced no visible radulations on leaves from either zone.

Manipulating *Melampus* density in the field had no effect on live *Spartina* biomass at the two sites in Rhode Island (Fig. 3A). No radulations were observed in the *Melampus* manipulations, even at the highest snail densities (Fig. 3D). In contrast, manipulating *Littoraria* density had strong effects on *Spartina* biomass at the four sites in Virginia and Georgia, with *Spartina* biomass often reduced several-fold at moderate and high snail densities compared to low (zero) densities (Fig. 3B, C). At these sites, radulations increased with snail densities (Fig. 3E, F).

DISCUSSION

On the Atlantic Coast of the United States, salt marsh plants from high-latitude sites are more palatable to

consumers than are conspecific plants from low-latitude sites (Pennings et al. 2001). Data presented here for the most abundant salt marsh plant, *S. alterniflora*, indicate that the less-palatable low-latitude plants also receive more damage from herbivores, suggesting that latitudinal differences in palatability could be selected for by latitudinal differences in the intensity of herbivory. Moreover, latitudinal differences in herbivore damage appear to be driven more by differences between herbivore species in per capita effects than by differences in herbivore diversity or density. These results have important implications for attempts to link community ecology and biogeography.

Our sampling data indicated that *Spartina* plants in the South Atlantic Bight accumulate far more herbivore damage than conspecific plants in New England. Similar latitudinal gradients in herbivore damage have been documented for broad-leaved forests (Coley and Aide 1991). To the extent that this difference in grazing pres-

sure selects for plant defenses against herbivores, it may contribute to the latitudinal differences in plant traits (Seliskar et al. 2002, Siska et al. 2002) and palatability (Pennings et al. 2001) that have been documented previously. Other factors, such as differences in soil type, porewater chemistry, or the length of the growing season, may also select for differences in plant traits (Reich and Oleksyn 2004, Wright et al. 2004), perhaps with indirect effects on palatability, and the relative importance of these different, putative selective forces has yet to be determined. Nevertheless, the striking difference in herbivore damage across latitude argues that variation in herbivore damage could be one important factor selecting for different plant phenotypes across latitude. Consistent with this suggestion, *Spartina* introduced to San Francisco Bay appears to have rapidly lost defenses to herbivores in the absence of herbivore pressure (Daehler and Strong 1997).

The latitudinal differences in damage that we documented were much larger than latitudinal differences in consumer density. Moreover, for the leaf-chewing guild of herbivores on *Spartina*, there are not striking latitudinal differences in diversity. *Conocephalus* and *Orchelimum* are both widely distributed along the East Coast of the United States, although *Conocephalus* is more common at high latitudes and *Orchelimum* at low latitudes. The richness of common marsh snails increases from zero in northern New England to one (*Melampus*) in southern New England to two (*Melampus* and *Littoraria*) at lower latitudes. At low latitudes, however, *Melampus* is functionally absent from the short-*Spartina* zone at many sites (S. C. Lee and B. R. Silliman, unpublished manuscript), so it may be more correct to think of this as a species replacement at low latitudes than as an increase in diversity. Moreover, *Littorina littorea* and *L. saxatilis* are occasionally present in high-latitude marshes in New England (Bertness 1984, Barlocher and Pitcher 1999), although we did not record them in our quadrats. In addition, we have observed lepidopteran larvae feeding on *S. alterniflora* only at high-latitude sites in northern New England, although these were also rare (Pennings et al. 2001). In sum, the diversity of the leaf-chewing guild on *Spartina* is low and varies little across latitude within the range of latitude considered here. We have not examined latitudinal patterns in the sap-sucking or stem-boring guilds, however, and it is possible that diversity and/or density of these herbivores changes across latitude. We have also not examined latitudinal patterns in feeding on seeds and flowers; latitudinal variation in these processes might affect the ability of plants to colonize new sites, but would likely not affect vegetation dynamics within a site where growth is primarily vegetative.

Although we did not find strong differences in herbivore abundance or diversity across latitude, we did find strong differences in per capita impacts. Laboratory feeding rates of low-latitude grasshoppers and

snails on leaves of *Spartina* were several times those of high-latitude consumers. In field experiments, low-latitude snails (*Littoraria*) strongly suppressed live biomass of *Spartina*, but high-latitude snails (*Melampus*) had no effect on live biomass, despite being stocked at higher densities. It is likely that these differences in interaction strength are linked to interspecific differences in feeding ecology. *Conocephalus spartinae*, the grasshopper most abundant at high latitudes, feeds heavily on flowers and seeds of marsh plants (Bertness et al. 1987, Bertness and Shumway 1992) and may be poorly adapted to feeding on leaves. It is also smaller than the grasshopper that is most abundant at low latitudes, *Orchelimum fidicinum*. Similarly, the ability of snails to feed on the tough leaves of *Spartina* is size-dependent. Very small *Littoraria irrorata* individuals cannot feed on live *Spartina* (B. R. Silliman, personal observation), probably because their radulas are too small and weak. Because *Melampus* is smaller than *Littoraria* and possesses a weaker radula at a given size (B. R. Silliman, personal observation), it may be unable to feed on living leaves and be limited to a diet of detritus (Rietsma et al. 1988), fresh *Spartina* fragmented by other mechanisms (e.g., other grazers), and microalgae (Thompson 1984).

Why herbivore morphology and per capita impacts should vary across latitude is an interesting question deserving of attention. It is possible that these herbivore traits are driven by the impacts of temperature on physiology, growth rate, and activity levels. Alternatively, herbivore traits may be determined by plant traits, in an evolutionary arms race (Vermeij 1987) that is proceeding at different rates in different geographic regions. Finally, phylogenetic history undoubtedly both predisposes and constrains species traits. For example, most species of *Littoraria* can graze on vascular plants (typically mangroves), but to our knowledge no species of *Melampus* does so, suggesting that the differences in interaction intensity for snails that are reported here are at least in part due to phylogenetic constraints.

At first glance, the strong effects of snails on live biomass of *Spartina* at low-latitude sites (Fig. 3B, C) might appear difficult to reconcile with the fact that low-latitude marshes are dominated by *Spartina*. Four points likely explain how *Spartina* persists as a dominant plant in the face of such strong consumer pressure. First, the highest snail density treatment represents the high end of densities observed in the field. Although we do observe areas in which snails reach these high densities and *Spartina* is completely or almost completely suppressed, these areas are patchy and represent a small percentage of the total marsh surface. Second, although the intermediate snail density treatment, which represents more typical snail densities, also produced moderate to strong suppression of *Spartina*, the plants were not completely eradicated. We argue that this treatment represents typical conditions

TABLE 1. Latitudinal variation in ecological processes in salt marshes on the Atlantic Coast of the United States.

Process	Pattern	References
Abiotic		
Disturbance	ice disturbance most intense at higher latitudes wrack disturbance most intense at higher latitudes due to seasonality of plant growth	Redfield (1972), Hardwick-Witman (1985), Pennings and Bertness (2001) Bertness and Ellison (1987), Pennings and Richards (1998), Pennings and Bertness (2001)
Salt stress	salt stress at intermediate marsh elevations most intense at lower latitudes due to higher temperatures, increased evapotranspiration	Pennings and Bertness (1999, 2001)
Biotic		
Competition/facilitation	within New England, facilitation among plants increases at lower latitudes due to increased salt stress across entire coast, competition among plants increases at lower latitudes due to per capita differences in stress tolerance or competitive ability	Bertness and Ewanchuk (2002) Pennings et al. (2003)
Predation	crab predation on mussels may increase at lower latitudes due to increased crab densities and activity	Bertness and Grosholz (1985), Lin (1989), Stiven and Gardner (1992), Pennings and Bertness (2001)
Herbivory	herbivore damage to plants increases at lower latitudes due to increased per capita effects (but geese can be locally important at high latitudes) plants less palatable to herbivores at lower latitudes due to lower N content, increased toughness and polar chemistry	this paper; S. C. Pennings, <i>unpublished data</i> Kerbes et al. (1990), Srivastava and Jefferies (1996) Pennings et al. (2001), Siska et al. (2002)

across vast areas of *Spartina* marsh at low latitudes. Snails are present at moderate densities, radulation damage to plants is readily observed, and *Spartina* is suppressed (~30–70%) but not eradicated (Silliman and Bortolus 2003). Third, low inorganic nitrogen availability in the short-*Spartina* zone likely shields cordgrass from overgrazing and local extirpation, which can occur at intermediate snail densities (200–600 snails/m²) when nitrogen availability is greatly enhanced through fertilization (Silliman and Zieman 2001; B. R. Silliman, *unpublished manuscript*). Fourth and finally, *Spartina alterniflora* is the only species of plant physiologically capable of occupying the lower intertidal zone in these salt marshes. Thus, regardless of how much *Spartina* is suppressed by herbivores, it will not be replaced by other species of plants and can remain a near-monoculture throughout much of the marsh.

Latitudinal variation in the strength of species interactions in Atlantic Coast salt marshes

A survey of the literature suggests that, in general, biological interactions of all types in Atlantic Coast salt marshes are more intense at lower latitudes (Table 1). Within New England, competition among plants decreases with increasing physical stress at lower latitudes. Across the entire coast, however, the facilitative interactions often found in New England are replaced by strong competitive interactions in the South, likely because of differences among individual plants in stress

tolerance and competition (i.e., per capita effects). In New England, predation on mussels by crabs is modest and limited to the marsh edge, and mussels are most abundant at lower marsh elevations. Crabs appear more abundant and more active at warmer, southern sites, and crab predation appears correspondingly more intense, essentially eradicating mussels at lower marsh elevations and limiting them to higher marsh elevations. Parallel studies of crab–mussel interactions across latitude, however, have not been done to test this hypothesis. Herbivory on higher plants is more intense at lower latitudes, despite a decrease in plant palatability at lower latitudes. A notable exception to this pattern is the heavy herbivory near goose nesting grounds at some high-latitude marshes. In contrast to these biotic interactions, physical disturbance from ice and wrack (mats of floating dead plant stems) is more intense at higher latitudes. By definition, all salt marshes suffer chronic abiotic stress from flooding and salinity, but salinity levels are somewhat higher in low-latitude marshes. In sum, the publications cited in Table 1 suggest a general pattern for disturbance to increase at higher latitudes and biological interactions to be stronger (more negative) at lower latitudes in coastal salt marshes. In all these cases, biological interactions appear to change with latitude primarily due to differences in densities or per capita effects, not species diversity.

Results from other nearshore marine habitats generally support, with some exceptions and caveats, the

hypothesis that both predation (Vermeij 1978, Bertness et al. 1981, Menge and Lubchenco 1981, Fawcett 1984) and herbivory (Horn 1989, Bolser and Hay 1996, Cronin et al. 1997) are more intense at lower latitudes. In contrast to salt marsh studies, however, work on rocky shores has emphasized the importance of upwelling (Connolly and Roughgarden 1998, Sanford 1999, Connolly et al. 2001, Menge 2003), which affects delivery of nutrients, larvae, and food items. This likely reflects a fundamental difference between rocky coasts and salt marshes, where much of the food web, even for filter feeders (Stiven and Kuenzler 1979, Kreeger et al. 1988, Langdon and Newell 1990), is derived from marsh or estuarine sources, rather than from oceanic sources.

Linking biogeography and community ecology

Our results have important implications for any attempt to link the fields of biogeography and community ecology. One major focus of biogeography is documenting and understanding geographical patterns in biodiversity (Hillebrand 2004). All else being equal, variation in diversity is likely to affect community function (Loreau et al. 2002); however, all else will not be equal across latitudinal gradients. Across latitudinal gradients, the large differences in climate and productivity that produce patterns in diversity are likely to also directly affect ecological processes, perhaps more strongly than variation in diversity does. In the case of *Spartina* along the Atlantic Coast of the United States, we argue that there are strong latitudinal differences in interaction strength, driven by the traits of particular herbivore species, in the absence of strong differences in diversity. In other cases, the reverse might be true: herbivore diversity or density might matter more than per capita interaction strength. It would be interesting to conduct studies similar to ours but in higher-diversity systems. At this point, however, we simply are not yet capable of inferring community process from diversity patterns alone at the geographic spatial scale. Even at the local scale, interaction strength cannot be inferred from a knowledge of feeding ecology or abundance, but must be measured directly (Paine 1980, 1992). Thus, forging a robust link between biogeography and community ecology will require studies that explicitly measure interaction strength at a geographic scale.

Because plants make up so much of the world's biomass and herbivores so much of the world's biodiversity, understanding interactions between plants and herbivores is central to understanding both ecosystems and community ecology. Interactions between herbivores and plants, however, have a wide variety of mechanisms and outcomes. In order to make sense of the rich diversity of interactions between plants and herbivores, we must understand the variables that mediate the nature and strength of these interactions. Meta-analyses comparing different types of herbivores and different habitats have shown that herbivore type and habitat

account for much of the variation in interaction strength between plants and herbivores (Bigger and Marvier 1998, Cebrian 1999). We would argue that latitude (or more specifically some underlying environmental variable[s] that correlate with latitude) may explain much of the remaining variation in interaction strength between plants and herbivores. This is not a new idea (MacArthur 1972, Coley and Aide 1991), but there are few rigorous tests. Incorporating latitude into meta-analytical approaches (Post 2005) and conducting explicit geographical comparisons of plant-herbivore interaction strength, as others have done with predation (Harley 2003, Menge 2003), would both be profitable approaches.

In general, ecologists who are interested in biogeography document patterns but not interactions. Community ecologists, in contrast, often study interactions but usually do not know how these vary geographically. When examined, however, geographic differences in interactions often turn out to be large, indicating that they cannot be ignored if we hope to develop generalities (Thompson 1994, Travis 1996, Bertness and Ewanchuk 2002, Thompson and Cunningham 2002, Sanford et al. 2003). Merging the approaches of biogeography and community ecology is logistically challenging, but we argue it will lead to a new level of understanding and generality. Because geographic variation in interactions may be driven either by ecological factors (e.g., resource availability, species richness or densities, and temperature) or by evolutionary factors (traits of species that alter per capita effects or responses to ecological factors), understanding geographic variation in interaction strength may be a challenging task. Our understanding of geographical variation in community ecology has grown to the point, however, that it is no longer satisfying either to uncritically generalize from single studies or to treat each study as unique. Rather, we must seek to develop an explicit understanding of how ecological interactions vary geographically, one that incorporates not only geographic mosaics (Thompson 1994, 1999) but also predictable large-scale clines such as those discussed here and that will allow us to integrate results obtained from different parts of the world. Developing and testing such an understanding will be a critical step towards more robust generalizations in ecology.

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LARGE-SCALE SPATIAL GRADIENTS IN HERBIVORE POPULATION DYNAMICS

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Abstract. Spatial gradients in density dependence and cyclicity are familiar features of the population dynamics of small mammals, particularly Fennoscandian rodents. The most well-documented of such gradients is a weakening of direct density dependence and an increase in the tendency of populations to cycle the farther north they occur, a phenomenon that has been attributed to gradients in predation and seasonality. Among large mammals, however, for which evidence of cyclicity is less clear, geographic gradients in population dynamics are limited to spatial variation in the strength of density independence. The population dynamics of caribou and muskoxen in Greenland, for example, display latitudinal gradients in the response of populations to large-scale climatic fluctuation. To my knowledge, the existence of spatial gradients in density dependence has not been explicitly investigated in large mammals. Here I present an analysis of the dynamics of 27 populations of caribou and reindeer in Greenland, Finland, and Russia, spanning 21 degrees of latitude (51.7°–72.7° N) and 215 degrees of longitude (56.4° W–159.5° E), to identify spatial gradients in density dependence and independence.

Results of autoregressive time series analysis show a clear gradient in the strength of direct density dependence exhibited by these populations that declines from southern to northern latitudes. Although this pattern mirrors the latitudinal gradient evident in Fennoscandian rodent dynamics, an analysis of the dimensionality of these time series suggests that few, if any, of the populations are limited by predators. The existence of an inverse latitudinal gradient in the magnitude of the influence of large-scale climate on the dynamics of these populations suggests there may be a tension in the strength of density-dependent vs. density-independent limitation experienced by them.

Key words: caribou; density dependence; density independence; latitude; longitude; Rangifer tarandus; reindeer.

INTRODUCTION

The earliest body of ecological theory concerning animal population dynamics focused on competition as the primary, if not sole, factor regulating populations (Elton 1927, Nicholson 1933). The exemplar of population limitation by intraspecific competition for food (Lack 1954) persisted nearly unchallenged for decades, until the publication of a paper demonstrating the influence of temperature on population growth in the rice weevil (*Calandra oryzae*) (Birch 1948) signaled a change in thinking among ecologists about density dependence and population dynamics. Birch's paper was followed that year, in the same journal and volume, by a seminal paper quantifying the population dynamics of apple blossom thrips (*Thrips imagines*) solely in terms of density-independent, environmental factors (Davidson and Andrewartha 1948). With the subsequent publication of the classic work by Andrewartha and Birch (1954), ecologists were provided a framework for quantifying density-independent population

dynamics that was comparable in authority to the density-dependent models of Lotka (1925) and Nicholson and Bailey (1935).

An elegantly unifying treatment of the roles of density dependence and independence in population limitation has emerged over the past decade in the study of spatial gradients in population dynamics. Although many examples exist, by far the most well-studied and familiar gradients in population dynamics are those evident in the spatial heterogeneity of the small mammal cycles in northern environments. In Europe, for instance, there is a clear tendency for the degree of cyclicity displayed by populations of rodents to increase from southern to northern latitudes (Hansson and Henttonen 1985). As well, the dynamics of small mammals in Fennoscandia display an increase in the length of the population cycle with increasing latitude (Hanski et al. 1991) that is associated with a weakening of the strength of direct density dependence along the same gradient from south to north (Bjørnstad et al. 1995).

Among the many hypotheses that have been proposed to explain the latitudinal gradient in density dependence and cyclicity apparent in the dynamics of small mammals in northern Europe, the two most commonly invoked are the "generalist predator" hypoth-

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esis (Hanski et al. 1991) and the “seasonality” or “snow cover” hypotheses (Hansson and Henttonen 1985). According to the former, the abundance of generalist predators at southern latitudes and the dominance of specialist predators at northern latitudes explain the increase in cyclicity and the weakening of direct density dependence as one moves from south to north (Hanski et al. 1991, Bjørnstad et al. 1995, Hanski and Korpiimäki 1995). By contrast, the latter hypotheses predict that the greater persistence of snow cover at northern latitudes limits the vulnerability of small mammals to predation, thereby producing dynamics that are dominated more by reproduction (and, hence, delayed density dependence) than by mortality due to predation (and, hence, direct density dependence) (Hansson and Henttonen 1985, Steen 1995).

Although the Fennoscandian rodent cycles have been by far the most closely scrutinized (Stenseth 1999), they constitute by no means the only such examples of latitudinal gradients in density dependence and cyclicity. On the Japanese island of Hokkaido, for example, the dynamics of the grey-sided vole (*Clethrionomys rufocanus*) are characterized by a transition from stability in the southwestern populations to cyclicity in the northeastern populations (Saitoh et al. 1998). Notably, however, in contrast to the pattern seen in Fennoscandian rodent cycles, the gradient on Hokkaido is due to a cline in delayed rather than direct density dependence (Stenseth et al. 1996, Saitoh et al. 1998) that has been attributed to spatial variation in the length of winter across the island (Stenseth et al. 1998).

Despite clear evidence for spatial gradients in the strength of density dependence and cyclic behavior of rodent dynamics, similar patterns have not, to my knowledge, been explicitly investigated or clearly documented in large mammals. This may lead some to question whether there is something inherently different about the biology, ecology, and dynamics of small vs. large mammals that would explain the presence of strong dynamical gradients in rodents but their absence in, for example, ruminants (Caughley and Krebs 1983, Sæther 1997). If so, are the hypotheses developed in the study of rodent population dynamics unsuited to the study of the dynamics of large mammals? It has been suggested, for example, that large mammal populations may be limited more by extrinsic than by intrinsic factors, while the reverse may often be the case for small mammals (Caughley and Krebs 1983). In northern environments, in particular, harsh environmental conditions and extreme weather during winter may result in stronger limitation of large herbivore populations by density-independent than by density-dependent factors (Albon and Clutton-Brock 1988), though the two are often likely to operate in concert (Forchhammer et al. 1998, Milner et al. 1999, Post and Stenseth 1999).

The potential for tension between density-independent and density-dependent influences on population

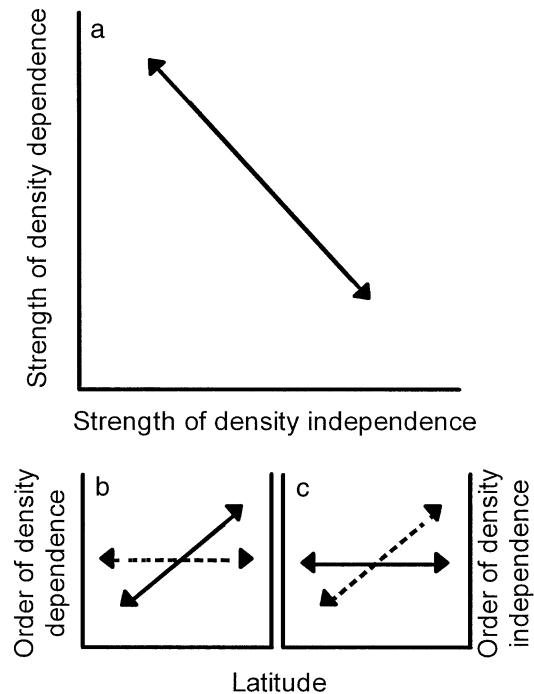


FIG. 1. (a) Hypothetical tension between the strength of density dependence and density independence in population dynamics. Populations limited mainly by abiotic, environmental, or other density-independent factors may be prevented from reaching densities at which density-dependent factors limit population growth. Conversely, populations under favorable environmental conditions may be limited more by density-dependent processes. If these conditions hold, then spatial gradients in population dynamics may be attributable to similar gradients in biotic interactions or abiotic conditions. For example, (b) gradients in population dynamics attributable to spatial variation in the strength or importance of biotic interactions should be discernible in latitudinal and/or longitudinal gradients in the order of density dependence (solid line) but not in the order of density independence (dashed line). Conversely, (c) gradients in population dynamics attributable to spatial variation in abiotic conditions influencing dynamics should be characterized by latitudinal and/or longitudinal variation in the order of density independence (dashed line) but not density dependence (solid line).

dynamics may be visualized as a continuum along which the relative influence of each varies inversely with that of the other (Fig. 1a). According to this hypothesis, populations inhabiting favorable environments with, for instance, mild or relatively stable weather conditions may be more likely to increase to the carrying capacity of the environment and experience density-dependent regulation than would populations limited by abiotic conditions in harsh environments (Elliott 1987, Albon and Clutton-Brock 1988).

Such a tension would mean that spatial gradients in the dynamics of large herbivores, if present, would be difficult to attribute to biological interactions vs. spatial variation in abiotic conditions. Inferences might be drawn, however, on the basis of the signatures that biotic and abiotic influences leave on the autoregressive

structure of the time series data (Post and Forchhammer 2001). The order (i.e., temporal lag) of density dependence, or the number of steps backward in time at which densities are correlated, increases with the complexity of trophic interactions or time lags in reproduction influencing population dynamics (Royama 1992, Bjørnstad et al. 2001). Similarly, the number of lags at which abiotic conditions influence population dynamics may be thought of as the order of density independence. Applying these definitions, we can expect that spatial gradients in dynamics attributable to clines in density dependence would be evident in, for example, latitudinal or longitudinal gradients in both the strength and the order of density dependence, and, potentially, inverse gradients in the strength of density independence, but no such gradient in the order of density independence (Fig. 1b). In contrast, spatial gradients in dynamics attributable to variation in the response of populations to abiotic conditions would be evident in spatial gradients in both the strength and order of density independence and inverse gradients in the strength of density dependence but the lack of such a gradient in the order of density dependence (Fig. 1c).

The existence of spatial gradients in the strength of density independence in the dynamics of large herbivores has, indeed, been documented recently. The magnitude of the influence of a large-scale climate system, the North Atlantic Oscillation (NAO; Hurrell 1995) on the population dynamics of caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*) in Greenland varies with latitude among the populations in each species (Forchhammer et al. 2002, Post and Forchhammer 2004). Hence, given widespread evidence for a role of the NAO in the population dynamics of numerous species (Ottersen et al. 2001, Walther et al. 2002, Forchhammer and Post 2004), and considering the tremendous variation in the strength of the influence of the NAO on local weather conditions along both latitudinal and longitudinal gradients throughout the Northern Hemisphere (Hurrell et al. 2003; Fig. 2a), there is considerable potential for similar gradients in the population dynamics of large herbivores over the same spatial scale. Here I expand upon the analyses of Forchhammer et al. (2002) and Post and Forchhammer (2002) in an attempt to investigate the potential for large-scale spatial gradients in the population dynamics of large herbivores. My analysis focuses on the dynamics of 27 populations of caribou, semi-domestic reindeer, and wild reindeer (all *Rangifer tarandus*) spanning 21 degrees of latitude (51.7°–72.7° N) and 215 degrees of longitude (56.4° W–159.5° E), from west Greenland to eastern Russia (Fig. 2b).

MATERIAL AND METHODS

Population data and time series analysis

Following methods described earlier (Forchhammer et al. 2002), I analyzed the population dynamics of

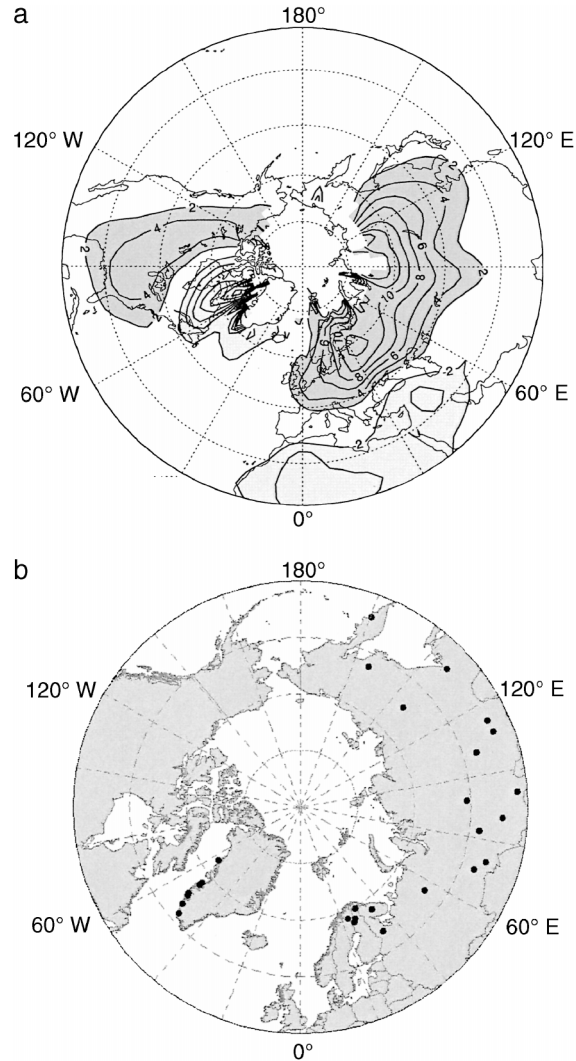


FIG. 2. (a) Spatial patterns of the influence of the North Atlantic Oscillation (NAO) on local temperatures throughout the Northern Hemisphere. Shown are the magnitudes of the changes in mean surface temperatures (in tenths of degrees Celsius) during winter for the months December through March in response to a unit change in the NAO index for the period 1900–2003 (see also Hurrell et al. [2003]). (b) Approximate locations of the populations of caribou and reindeer analyzed in this paper. Locations of the Finnish populations were extracted from the Global Population Dynamics Database (a collaboration of the Natural Environment Research Council [NERC] Centre for Population Biology, Ascot, UK; the National Center for Ecological Analysis and Synthesis, Santa Barbara, California, USA; and the Department of Ecology and Evolution, University of Tennessee, Knoxville, Tennessee, USA). For the Russian populations, the dots represent the centroids, located using ArcView version 3.0 (Environmental Systems Research Institute, Redlands, California, USA), of the regions denoted by the Main Administration of Hunting and Game Preserve of the former USSR (Syroechkovskii 1995).

caribou and reindeer in seven populations in Greenland (Post and Forchhammer 2002), four populations in Finland, and 16 populations in Russia (Syroechkovskii 1995; Fig. 2b). To my knowledge, this comprises the most spatially extensive analysis of the population dynamics of a species of large mammal. Data from the Greenlandic populations consist of numbers of caribou shot annually from 1908 through 1981 in each population (Meldgaard 1986), before hunting quotas were introduced there (Linnell et al. 2000). As such, these data do not constitute actual counts of individuals in the populations, but interannual variation in the numbers shot have not been determined or constrained by quotas and thus are assumed to match interannual variation in actual population sizes (Forchhammer et al. 2002). Moreover, our previous analyses of these data, using a subset of the time series for which independent estimates of population size are available in the form of aerial counts of caribou in two of the focal populations, have revealed a positive, linear correlation between numbers of caribou shot and population counts (Post and Forchhammer 2004). The Finnish populations comprise semi-domesticated reindeer (Helle and Kojola 1994), while the Russian populations are wild reindeer (Syroechkovskii 1995). Data from the Finnish and Russian populations represent population estimates based on actual counts of animals (Helle and Kojola 1994, Syroechkovskii 1995). The Finnish populations have been counted annually during roundups in September–January each year, and variation in accuracy of the counts among years is reportedly small (Helle and Kojola 1993). Data on annual population densities of all four Finnish populations cover the period 1968–1990. Annual counts of wild reindeer in the Russian populations span 1961–1984, but are continuous temporally only from 1975 to 1984. Although data were available for an additional six populations of wild reindeer in Russia, I restricted my analysis of the Russian populations to those for which annual estimates of population size were temporally continuous from 1975 to 1984. Use of continuous data was necessary to avoid spurious estimates of statistical density dependence in the autoregressive approach described below (Royama 1992).

Using an established approach (Forchhammer et al. 1998, 2002), I applied autoregressive (AR) time series analysis to identify or confirm previous reports (Forchhammer et al. 2002, Post and Forchhammer 2002) of the best fit AR models including the NAO as a covariate. I used the same approach that has been applied recently in the development of models of plant–herbivore–climate (Forchhammer et al. 1998) and predator–herbivore–plant–climate (Post and Forchhammer 2001) interactions that have focused on the dynamics of red deer (*Cervus elaphus*); and wolves (*Canis lupus*), moose (*Alces alces*), and balsam fir (*Abies balsamea*), respectively. The general form of this model for any

focal population is as follows (Forchhammer et al. 2002):

$$N_t = N_{t-1} \exp \left(\beta_0 + \sum_1^{i=d} \beta_i X_{t-i} + \sum_1^{j=k} \omega_j U_{t-j} \right) \quad (1)$$

in which abundance at time t is represented by N_t , and in which $X_t = \log_e(N_t)$, U_{t-j} represents the influence of climate, and β_0 is the intrinsic growth rate of the population (Forchhammer et al. 1998, Post and Stenseth 1999). After taking the natural logarithm of both sides of Eq. 1, a generalized autoregressive model with summed climatic components is obtained (Forchhammer et al. 2002):

$$X_t = \beta_0 + (1 + \beta_1)X_{t-1} + \beta_2 X_{t-2} + \beta_3 X_{t-3} + \dots + \beta_d X_{t-d} + \sum_1^{j=k} \omega_j U_{t-j} + \varepsilon_t \quad (2)$$

in which the coefficients $(1 + \beta_1)$ and β_2 quantify direct and delayed density dependence, respectively, ω_j quantifies the direct and/or delayed climatic influences on population dynamics, and ε_t represents the remaining variance not quantified by the model parameters.

It is important to note that Eq. 2 is a candidate model specifying all potential direct and delayed density-dependent and climatic influences on population dynamics, but not necessarily the form of the most parsimonious AR model for any particular population. Because the strength of trophic interactions and, hence, direct and delayed density dependence, may vary along large-scale spatial gradients (Pennings and Silliman 2005), the form of the most parsimonious model will likely vary among the focal populations.

Applying the model in Eq. 2 to the caribou data from West Greenland covering 1980–1981, the semi-domestic reindeer data from Finland covering 1968–1990, and the wild reindeer data from Russia covering 1975–1984, I identified the most parsimonious (i.e., best fit) model for each population. The most parsimonious order or dimension of each time series was identified by choosing the AR model with the lowest corrected Akaike Information Criterion (AICc) score (Sakamoto et al. 1986) among all possible models for each population and values of d from 0 to 3, but no covariates. Because estimation of the AR coefficients may be biased if the time series are not stationary (i.e., if they possess a significant trend over time; Royama 1992), the term “year” was included in analyses of all time series with a significant temporal trend (Forchhammer et al. 1998). After identifying the most parsimonious order of each time series, further improvement of the fit of each model was then tested for by inclusion of a term quantifying the influence of the NAO on dynamics at lags of 0–3 yr; reduction of the AICc score of any model by a value of 1 or more was considered significant improvement of the model (Bjørnstad et al. 1995). None of the best-fit models contained more than one NAO term, and the

mean number of parameters in the best fit models was 2.6 among the Greenlandic time series, 2.8 among the Finnish time series, and 2.06 among the Russian time series.

Finally, because the natural log transformation of the Finnish time series produced zeros in 13% of the total observations, I analyzed those data in both the transformed and nontransformed states for comparison. Results using AR coefficients from the analysis of the transformed and nontransformed Finnish data did not differ, and both are reported.

Spatial analyses

Coefficients of the AR models quantify the strength of statistical direct density dependence and climatic influences on population dynamics (Royama 1992, Forchhammer et al. 2002), while the highest lagged density and NAO terms indicate the most parsimonious orders of density dependence (Bjørnstad et al. 1995) and density independence (Forchhammer et al. 2002, Post 2004), respectively. Spatial gradients in the strength of density dependence and density independence were analyzed using linear regression with the respective coefficients from the statistical AR models as dependent variables and with latitude/longitude coordinates of the populations as predictor variables. Both latitude and longitude were included in the analyses because there is clear variation in the strength of the effect of the NAO on local temperatures throughout the Northern Hemisphere along both gradients (Fig. 2a). Across Finland and Russia, in particular, local temperatures display strong latitudinal and longitudinal variation in their response to unit deviations in the NAO index (Fig. 2a; Hurrell et al. 2003), whereas in the area of West Greenland inhabited by caribou, local temperatures vary with the NAO along primarily a latitudinal gradient (Post and Forchhammer 2002) because the populations are confined to an area of narrow longitudinal variation (Forchhammer et al. 2002).

In conducting statistical tests of the significance of spatial gradients in the strength of density dependence and independence in the dynamics of these populations, I used stepwise linear regression with backward elimination of nonsignificant covariates. In addition to the coordinates mentioned above, I included as potential predictor variables terms quantifying the order of density dependence and independence for each population. Coefficients of predictor variables were estimated using the linear model function in S-plus version 6.0 (Insightful Corporation 2001), and in each step of the analysis the term with the lowest nonsignificant ($P > 0.05$) t value was eliminated until a reduced model was achieved containing only significant ($P \leq 0.05$) predictor variables. I repeated these analyses using forward stepwise regression to confirm the composition of these best-fit models.

To determine whether any potential latitudinal and/or longitudinal gradients in the strength of density de-

pendence or independence in the dynamics of the focal populations might be attributable to spatial variation in biotic interactions vs. abiotic influences on population dynamics, I first tested for a correlation between the coefficients of direct density dependence and density independence from the most parsimonious models for all 27 populations (sensu Fig. 1a). Next I tested for spatial gradients in the order of density dependence and density independence using linear regression with terms quantifying those orders as the dependent variables and the following predictor variables: latitude, longitude, and the coefficients of density dependence and independence. Additionally, in the analysis of spatial variation in the order of density dependence, I included a term for the order of density independence as a potential predictor variable and likewise included a term for the order of density dependence in the analysis of spatial variation in the order of density independence. Here as well I used stepwise linear regression with backward elimination of nonsignificant predictor variables until a reduced model with significant predictors only was achieved. These models were likewise confirmed with a forward stepwise analysis. All linear spatial analyses were repeated using generalized additive models (GAMs) (Hastie and Tibshirani 1999) to test for potentially significant nonlinear gradients in density dependence, density independence, and the orders of both; however, none of the GAM results were significant (all P values > 0.10). Analyses were performed using S-plus version 6.0.

RESULTS

The dynamics of 22 (81%) of the populations analyzed were best described by first-order autoregressive (AR) models, while a second-order model best described the dynamics of four of them, and a third-order model best described the dynamics of only one population. The lag at which the NAO entered the best fit model, quantifying the order of density independence, was 0 (i.e., direct) for 10 populations, 1 for nine populations, and 2 for the remaining eight populations.

There was a clear, inverse relationship between the coefficients of density dependence and density independence describing the dynamics of the focal populations ($r = -0.54$, $P < 0.005$; Fig. 3a). The coefficient of direct density dependence covaried positively with latitude (Fig. 3b), indicating stronger density dependence at southern latitudes and weaker density dependence at northern latitudes (Bjørnstad et al. 1995). The best-fit model describing variation in the strength of density dependence across populations included latitude ($t = 3.67$, $P = 0.001$), strength of density independence ($t = -2.91$, $P = 0.008$), and the dimension of density independence ($t = 2.36$, $P = 0.03$) as predictors. When natural log-transformed Finnish data were used instead of raw data, the best-fit model contained the same variables (latitude, $t = 3.80$, $P < 0.001$; strength of density independence, $t = -2.96$, $P =$

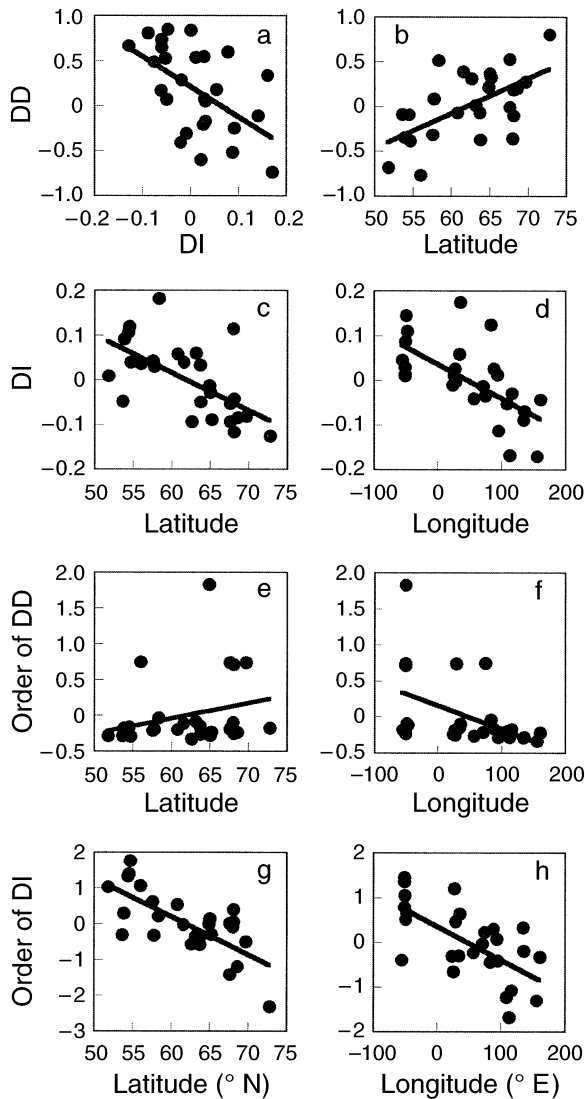


FIG. 3. Partial residual correlation plots from multivariate regression analyses of (a) the strength of density dependence (DD) vs. density independence (DI) in the population dynamics of caribou and reindeer in Fig. 2b, (b) density dependence vs. latitude, (c) density independence vs. latitude, (d) density independence vs. longitude (negative values indicate longitudes west of the Prime Meridian), (e) order of density dependence vs. latitude, (f) order of density dependence vs. longitude, (g) order of density independence vs. latitude, and (h) order of density independence vs. longitude.

0.007; dimension of density independence, $t = 2.53$, $P = 0.02$).

Although these partial correlations are fairly strong, a certain degree of caution may be warranted because the time series derive from three distinct sets of populations under different harvest and management regimes. If the hypothesized tension in Fig. 1a is a general phenomenon, however, it should be apparent in data from each of the three regions separately. Considering these regions individually reveals the same

general pattern of inverse correlation between the strength of density dependence and density independence in Greenland ($r = -0.64$, $df = 5$, $P > 0.10$), Finland ($r = -0.58$, $df = 2$, $P > 0.20$), and Russia ($r = -0.55$, $df = 14$, $P < 0.05$), although with considerably lower degrees of freedom. Combining the Greenlandic and Finnish data reveals the same inverse association ($r = -0.60$, $df = 9$, $P = 0.05$). Furthermore, a generalized linear model with populations assigned to one of three categories (Greenland, Finland, Russia) revealed no difference among them in the strength of the correlation between density dependence and independence ($F = 0.75$, $df = 2, 24$, $P = 0.48$).

In accordance with the patterns of spatial variation in the strength of the influence of the NAO on local temperatures throughout the regions inhabited by the focal populations (Fig. 2a), the coefficient of density independence varied along gradients of both latitude ($r = -0.62$, $P < 0.001$; Fig. 3c) and longitude ($r = -0.64$, $P < 0.001$; Fig. 3d). The best-fit model describing variation in the strength of density independence across populations included longitude ($t = -2.64$, $P = 0.01$), latitude ($t = -2.59$, $P = 0.02$), and the dimension of density independence ($t = -2.21$, $P = 0.04$) as predictors. When natural log-transformed Finnish data were used instead of raw data, the best-fit model contained the same variables (longitude, $t = -2.40$, $P = 0.03$; latitude, $t = -2.49$, $P = 0.02$; dimension of density independence, $t = -2.04$, $P = 0.053$).

The dimension of density dependence did not vary significantly with latitude ($t = 0.52$, $P = 0.61$; Fig. 3e), but did show weak variation with longitude ($t = -2.30$, $P = 0.03$; Fig. 3f). The dimension of density independence displayed significant variation with both latitude ($r = -0.72$, $P < 0.001$; Fig. 3g) and longitude ($r = -0.66$, $P = 0.01$; Fig. 3h).

DISCUSSION

Although time series on the population fluctuations of lynx (*Lynx canadensis*) throughout the boreal forest of Canada display large-scale spatial structure (Stenseth et al. 1999), the analysis reported here constitutes, to my knowledge, the first documentation of spatial gradients of density dependence and independence in the population dynamics of large mammals. The latitudinal gradient in density dependence of caribou and reindeer dynamics documented here matches the pattern reported for microtine rodents in Fennoscandia (Bjørnstad et al. 1995): direct density dependence is stronger among populations inhabiting southern latitudes than among those at more northern latitudes. While strikingly similar, the relationships generating this pattern in microtine rodents vs. caribou and reindeer are likely distinct. Among Fennoscandian populations of microtine rodents, the weakening of density dependence from southern to northern populations appears to relate to a transition from limitation by gen-

eralist predators among southern populations to limitation by specialist predators in northern populations (Hanski et al. 1991). This hypothesis is also consistent with an increasing tendency for populations of Fennoscandian rodents to undergo clear multi-annual cycles in northern environments but not in southern environments (Bjørnstad et al. 1995); presumably, the numerical tracking of rodent density fluctuations by specialist predator populations is a major contributing factor to such cycles (Hanski and Korpimäki 1995).

My analysis of the dimensionality of the dynamics of caribou and reindeer indicates, however, that few, if any, of these populations are limited by predation. Such limitation should be apparent as higher-order autoregressive processes or dependence among densities separated by more than one time step (Royama 1992, Bjørnstad et al. 2001). Most of the populations analyzed, however, were best described by first-order autoregressive models, containing only direct density dependence. On a cautionary note, the time series quantifying the dynamics of Russian wild reindeer may be too short to detect higher-order dynamics; only one of 16 Russian populations displayed second-order density dependence. Notably, however, wolves (*Canis lupus*) and other large predators capable of limiting caribou populations are absent from West Greenland (Bøving and Post 1997), yet the Greenlandic populations themselves display a clear latitudinal gradient in density dependence (Forchhammer et al. 2002).

Rather than concurring with the specialist-generalist predator hypothesis, therefore, the patterns documented here appear to agree more with the snow cover hypothesis of microtine rodent dynamics (Hansson and Henttonen 1985). In the case of large mammals, however, snow cover is not likely to influence population dynamics by providing refuge from predation; instead, it may buffer overexploitation of winter forage. Caribou and reindeer populations at higher latitudes where snow cover is more persistent may, for instance, be less likely to overgraze fragile winter lichen beds and therefore less likely to experience density-dependent population crashes (Klein 1968, 1999). Such spatial variation in the strength of herbivore–plant trophic interactions has been documented in salt-marsh systems involving gastropod and insect herbivores (Pennings and Silliman 2005).

The inverse relationship between density dependence and density independence evident in the cross-population comparison (Fig. 3a) appears to support the hypothetical tension depicted in Fig. 1a. While it does not constitute evidence for a causal relationship, this correlation does suggest, as with red deer (*Cervus elaphus*) in Scotland (Albon and Clutton-Brock 1988), that populations limited strongly by density-independent factors may be prevented from reaching carrying capacity and/or sufficiently high densities to be limited by population-intrinsic processes (Elliott 1987). If so, the latitudinal gradient in density dependence apparent

in these data may actually be attributable to an inverse gradient in the strength of density independence, which in fact appears to be the case (Fig. 3c). Furthermore, the existence of strong latitudinal and longitudinal gradients in the order of density independence and the lack of such clear gradients in the order of density dependence would appear to support the hypothesis that the mechanisms underlying the large-scale gradients in the population dynamics of caribou and reindeer across much of the Northern Hemisphere reflect spatial variation in abiotic conditions and their influences on local populations. Notably, recent empirical work on the population dynamics of aphids (*Aphis nerii*) documenting an inverse relation between the strength of density dependence and the rate of population growth has concluded that in species in which the rate of increase is influenced differentially by climate along spatial gradients, the strength of density dependence should vary accordingly along the same gradients (Agrawal et al. 2004). The results reported here may indeed represent such an example.

I hasten to emphasize that this analysis is not intended to argue that the NAO is the main population limiting factor for caribou and reindeer, nor is it intended to argue that density independence is more important than density dependence in the dynamics of this species. The relative roles of intrinsic and extrinsic forces, or biotic and abiotic factors, in animal population dynamics have been debated nearly ad nauseum (Elton 1927, Andrewartha and Birch 1954, Mech et al. 1987, Messier 1991, Turchin 2003), and my purpose is not to advocate one position over the other. Certainly, both density-dependent and -independent processes are at work in the dynamics of these populations and those of other large mammals in northern environments (Forchhammer et al. 1998, 2001, Post and Stenseth 1999, Coulson et al. 2001), although time series analysis alone may be insufficient to capture the signatures of both types of process (Kaitala and Ranta 2001) where experimental approaches are also feasible and tractable (Karels and Boonstra 2000, Bjørnstad et al. 2001).

I do, however, wish to stimulate new thinking about the consequences of large-scale spatial variation in both the magnitude and direction of climatic forcing of local weather for spatial gradients in population dynamics. Classically, density dependence has been regarded as potentially stabilizing for population dynamics if it is not over-compensatory (May 1973a, b), while density independence is considered destabilizing (Ives 1995), so what might the patterns revealed here indicate about potential ecological consequences of climate change? Observing the tremendous degree of variation throughout the Northern Hemisphere in the extent to which local temperatures vary with changes in the NAO (Fig. 2a) calls into question the extent to which we can hope to predict the distribution-wide response of any quasi-cosmopolitan species to future changes in climate. The

analyses reported here indicate, however, a tension between the two processes and suggest a potential for the climatic signal in local population dynamics to strengthen with future warming, as has been reported in the dynamics of cholera outbreaks (Rodó et al. 2002). Such a strengthening might lead the dynamics of these populations to be governed more by abiotic than by biotic factors, a condition that may lead to population instability (Ives 1995, Mueller and Joshi 2000). Whether the tension between density dependence and independence hypothesized to operate in the dynamics of large mammals also plays a role in spatial gradients in the dynamics of other animal species, including small mammals, will require at a minimum comparably large-scale analyses (Forchhammer and Post 2004).

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