

The Latitudinal Gradient in Niche Breadth: Concepts and Evidence

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Submitted December 5, 2003; Accepted March 24, 2004;
Electronically published May 28, 2004

ABSTRACT: We examine Robert MacArthur's hypothesis that niche breadth is positively associated with latitude (the latitude–niche breadth hypothesis). This idea has been influential and long standing, yet no studies have evaluated its generality or the validity of its assumptions. We review the theoretical arguments suggesting a positive relationship between niche breadth and latitude. We also use available evidence to evaluate the assumptions and predictions of MacArthur's latitude–niche breadth hypothesis. We find that neither the assumptions nor the predictions of the hypothesis are supported by data. We propose an alternative hypothesis linking latitude with niche breadth. Unlike previous ideas, our conceptual framework does not require equilibrium assumptions and is based on recently uncovered patterns of species interactions.

Keywords: environmental variability, latitudinal gradients, niche breadth, population variability, specialization, species richness.

The “economics of consumer choice” ... suggest that a productive, and above all a steady or predictable, environment will favor greater specialization. This clearly is the case in nature, and makes for greater specialization in the Tropics. (R. M. May 1973, p. 176)

The niche is arguably one of the central concepts in organismal biology. It is hard to think of any topic in ecology, evolutionary biology, or biogeography that does not involve, under one of its many labels, the niche concept. In spite of its relevance, however, the concept has been fre-

quently misinterpreted, and even its definition has been elusive (Real and Levin 1991; Leibold 1995; Chase and Leibold 2003). Many ideas about the niche have enjoyed long-standing acceptance in the form of untested assumptions.

One particularly influential idea is the purported latitudinal gradient in niche breadth. As exemplified by the above quote, biologists have often assumed that niche breadth decreases with decreasing latitude (hereafter the “latitude–niche breadth hypothesis”). Although tracking the origins of the latitude–niche breadth hypothesis is difficult, the work of Robert MacArthur, especially his 1972 book *Geographical Ecology*, has been particularly influential in bolstering this idea.

The hypothesis that niches become narrower toward the Tropics is intriguing in its own right, yet its importance stems mainly from its implications for several other important ideas in ecology, evolutionary biology, and biogeography. For example, a large proportion of the Earth's species are believed to be tropical herbivores. Erwin's (1982) famous estimate of 30 million arthropod species rests on the assumption that tropical herbivorous insects are highly specialized, much more so than their temperate counterparts. However, current evidence suggests greater generalization of tropical herbivorous insects than previously thought, which has led to revising the estimate of global species richness to approximately 5 million (Ødegaard 2000; Novotný et al. 2002). The idea of narrower niches in the Tropics has also been frequently considered as an explanation for latitudinal patterns in species richness. This gradient has been described on all continents except Antarctica throughout much of geological time and across most higher taxa of plants and animals (Willig et al. 2003; Hillebrand 2004). While the description of latitudinal patterns of diversity has been an active and productive area of ecological and biogeographic research, understanding the mechanistic bases for such patterns has developed much more slowly. More than 30 hypotheses have been proposed (Willig et al. 2003), several of which require that niches are narrower in the Tropics (Stevens 1989; Rohde 1992, 1999).

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Strong support for MacArthur's latitude–niche breadth hypothesis should come from evidence supporting both its assumptions and its predictions. Although there have been several studies examining the predictions of MacArthur's latitude–niche breadth hypothesis for particular taxa (see “The Central Question: Is There a Latitudinal Gradient in Niche Breadth?”), we know of no study that has evaluated the generality of the pattern. Furthermore, MacArthur's original hypothesis rests on a series of assumptions, most of which have been subject to little scrutiny. Here we review theoretical arguments about why we should expect a positive relationship between niche breadth and latitude. We also review the available evidence and use it to evaluate both the assumptions and the predictions of the latitude–niche breadth hypothesis. Last, we propose an alternative conceptual framework that we believe will help in making progress toward understanding whether and how niche breadth varies with latitude.

MacArthur's Latitude–Niche Breadth Hypothesis: Theoretical Arguments

MacArthur's thinking about the relationship between niche breadth and latitude can be summarized in the following statement: Because of greater stability and lower seasonality in tropical than in temperate regions, populations at low latitudes should be more stable than populations at higher latitudes; in turn, greater population stability should allow narrower niches. The first part of the argument (that environmental and population variability are lower in tropical than in temperate regions) has usually been assumed, and most theoretical discussion has concentrated on the second part of the argument (i.e., that greater stability leads to narrower niches).

MacArthur (1955) was probably the first to discuss the idea that greater population stability leads to narrower niches. He argued that populations of specialists should be more temporally variable than those of generalists. MacArthur (1972) later developed these arguments specifically in the context of latitudinal comparisons between tropical and temperate regions. As a way of explaining the latitudinal gradient in species richness, he argued that in tropical regions, coexistence of high numbers of species required at least one of the following conditions to be true: that the spectrum of resources, the overlap in resource utilization among species, or the dimensionality of the environment are greater in the Tropics or that the breadth of resource utilization per species (i.e., their niche breadth) is lower in the Tropics. If the last condition is true, we also expect that the proportion of extreme specialists (e.g., herbivores feeding on only one host plant species) increases toward the Tropics.

MacArthur argued that tropical regions were less en-

vironmentally variable, had lower levels of abiotic stress, higher productivity, and higher habitat heterogeneity than temperate regions (see also Stevens 1989; Brown and Lomolino 1998). He hypothesized that lower tropical environmental variability should allow species to attain narrower niche breadths and niche overlaps without increasing their risk of extinction. MacArthur's conceptual scheme implicitly assumes that there is a trade-off between the number of resources used and the efficiency with which an organism can process each resource, so that specialists use their narrow range of resources more efficiently than generalists do and thus are superior competitors in the overlapping portions of their niches. However, specialists are constrained to have smaller populations and hence are more susceptible to extinction than are generalists.

Surprisingly, these ideas have gone a long way without much scrutiny. The only previous attempt we know of to evaluate the generality of these theoretical arguments is by Price (1991). This author compared feeding specificity of insect herbivores between temperate and tropical areas for several groups, using data published in previous studies. His conclusion was that, for insect herbivores, specialization is very common and not a special attribute of tropical species. In the following sections we attempt a more systematic evaluation of the literature, examining available evidence for both the assumptions and predictions of MacArthur's latitude–niche breadth hypothesis. We first examine three critical assumptions, namely that environmental variability and population variability decrease toward the Tropics and that lower population variability allows narrower niches. We then evaluate the prediction of the latitude–niche breadth hypothesis, that is, that niche breadth increases with increasing latitude. Finally, we propose an alternative hypothesis leading to a latitudinal gradient in niche breadth, which we believe is more compatible with our current understanding of community assembly and of general latitudinal patterns of biodiversity.

Defining the Niche

Because of the importance of the niche concept throughout this article, we judged it necessary to define it clearly. We use a somewhat restricted definition: the breadth of the resources used by a species. By focusing on resource use, we overlook other important aspects of the niche considered by current definitions, such as the effect of enemies and the impact on the environment (Jeffries and Lawton 1984; Leibold 1995; Chase and Leibold 2003). Furthermore, most studies reviewed below measure breadth of resource use simply as the number of resource types (e.g., host species or families, habitats) without weighting them by the relative frequency of use or by the fitness effects of each resource type on the focal species. Fur-

thermore, all studies deal with one component (“axis”) of the niche, thus making the implicit assumption that all other components are less important. In spite of these limitations, this definition has the advantage of being more akin to the one used by MacArthur and by later workers discussing the relationship between niche breadth and latitude.

Evaluating MacArthur’s Latitude–Niche Breadth Hypothesis

In this section we evaluate three assumptions of MacArthur’s latitude–niche breadth hypothesis: that environmental variability decreases with decreasing latitude, that population variability decreases with decreasing latitude, and that niche breadth and population variability are negatively correlated. We then evaluate the prediction that niches become narrower as latitude decreases.

Is There a Latitudinal Gradient in Environmental Variability?

MacArthur (1972) argued that environmental variability was greater in temperate than in tropical regions. He showed plots with maximum and minimum daily temperatures and average monthly rainfall at two locations at contrasting latitudes: Belém, Brazil (1°28’N) and Toronto, Canada (43°40’N). These plots showed that minimum and maximum temperatures were virtually constant in Belém but greatly varied throughout the year in Toronto. Precipitation, however, showed the opposite pattern, being more variable throughout the year in Belém than in Toronto. Here we evaluate the generality of this pattern with current data from a large climatological database.

Data. We used data on mean monthly ranges of temperature and precipitation coming from a $0.5^\circ \times 0.5^\circ$ global grid. These data come from the global climatology database developed by New et al. (1999; available at http://www.geog.ox.ac.uk/~mnew/research/data_download/index.html).

Statistical analysis. Latitudinal trends of temperature and precipitation ranges were quantified with Spearman’s rank correlation coefficients on mean ranges in 1° latitudinal bands.

Results. Our analysis of temperature and precipitation data from measuring stations throughout the world confirms the trend suggested by MacArthur: temperature ranges increase and precipitation ranges decrease with increasing latitude (fig. 1; see also Stevens 1989). What does this evidence tell us about the latitudinal gradient in environmental variability?

That temperature variability decreases but precipitation variability increases toward the Tropics implies that, for MacArthur’s hypothesis to be true, temperature variability

must be more relevant to population dynamics than precipitation variability. However, this assumption is difficult to justify. Even in the absence of seasonal fluctuations in temperature, moderate fluctuations in rainfall can impose a distinct seasonality (Ricklefs 1975; Boinski and Fowler 1989; Frith and Frith 1990). Furthermore, precipitation has been demonstrated to impose strong controls on population density (Polis et al. 1998; Ernest et al. 2000; Georgiadis et al. 2003) and can be associated with variability in population density (Post and Stenseth 1998; White and Garrott 1999; Matlack et al. 2002). In a recent study, Hawkins et al. (2003) conclude that water availability is a much stronger predictor of species richness than energy throughout most of the earth and that energy is a strong predictor only at high latitudes in the northern hemisphere. Rohde (1992) has raised similar concerns about the supposed environmental stability of tropical marine environments where extreme variations in temperature, salinity, and currents are apparently not uncommon. Therefore, until it can be demonstrated that temperature variability is the primary determinant of population dynamics, we must conclude that it is not possible to unambiguously argue that tropical regions are less environmentally variable than temperate regions.

Is There a Latitudinal Gradient in Population Variability?

A key requirement of MacArthur’s hypothesis of increasing niche specialization toward tropical areas is that population variability at lower latitudes results from lower environmental variability. Although, as we discussed above, it is difficult to argue that environmental stability is greater in the Tropics, it is at least plausible that environmental variables that are key for population dynamics are indeed less variable in tropical environments. This would be the case if, for example, temperature were more important in determining population dynamics than precipitation or if the quantification of climatic variability used (e.g., annual range of precipitation) was not the most relevant one for population dynamics. If environmental variability were indeed lower in the Tropics, then we should also observe less variable population dynamics in tropical regions. Testing for lower population variability in the Tropics is also key to the next part of the argument, that lower population variability allows greater specialization.

Several studies have analyzed latitudinal patterns in population variability. Probably the best-documented example of a latitudinal gradient in population variability is that of the Fennoscandinavian voles. Hansson and Henttonen (1985) showed that the population variability of the vole *Clethrionomys* increased with latitude. However, it is unclear whether this increase is a result of climatic seasonality or of other ecological processes such as changes

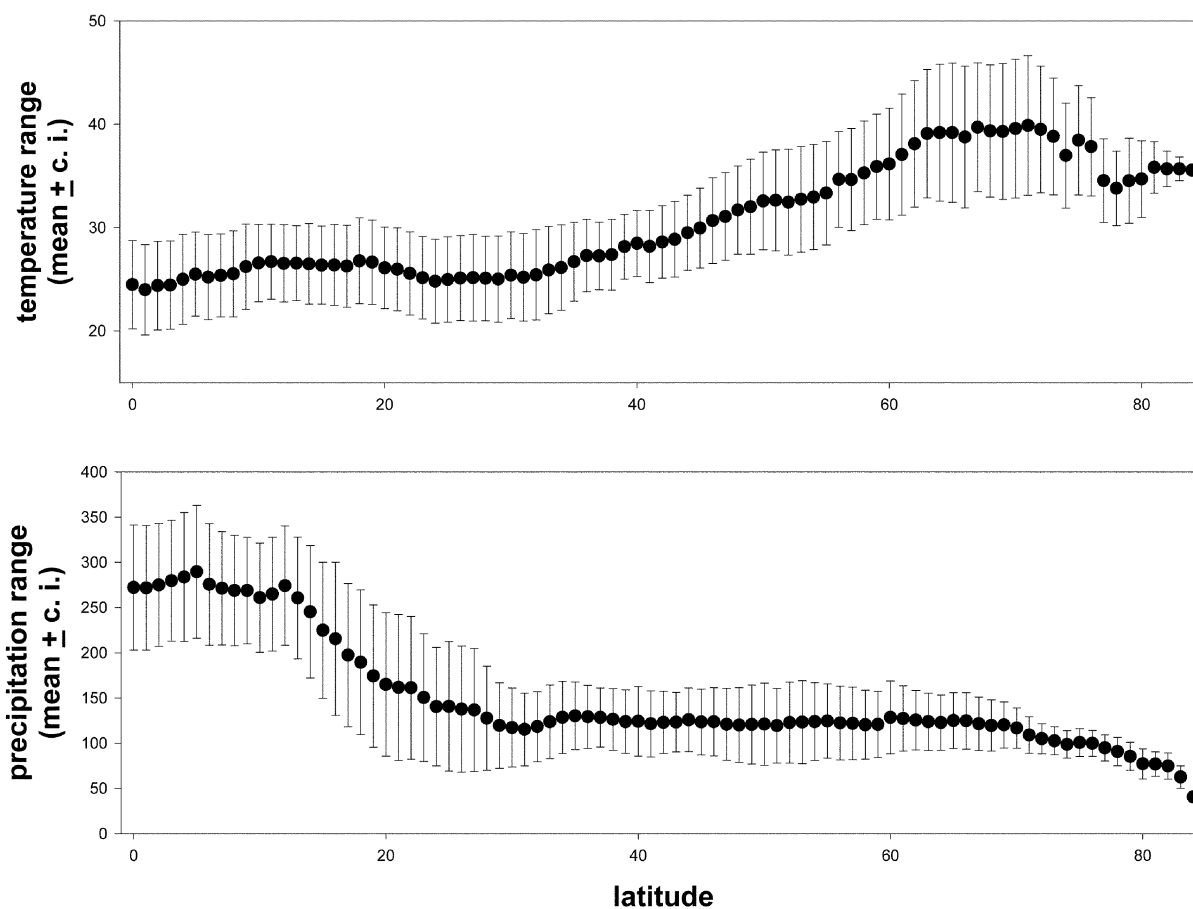


Figure 1: Ranges of temperature and precipitation and their relationship with latitude. Black circles represent the mean range at a particular latitude, and error bars represent confidence intervals. Spearman's rank correlation coefficient: mean temperature range versus latitude: $r_s = 0.88$, $N = 85$, $P < .0001$; mean precipitation range versus latitude: $r_s = -0.86$, $N = 85$, $P < .0001$. Data from New et al. (1999; available at http://www.geog.ox.ac.uk/~mnew/research/data_download/index.html).

in predator control of vole population dynamics that also vary consistently with latitude (Hanski et al. 1991; Sundell 2003). Furthermore, other vole species exhibit the opposite pattern, increasing in variability with decreasing latitude (Tkadlec and Stenseth 2001). Similarly, in a meta-analysis of population fluctuations of amphibian populations, Marsh (2001) found an increase in population variability toward the Tropics.

To further evaluate this hypothesis, we conducted an analysis of an extensive data set on latitudinal trends in population variability.

Data. We used population time series data to study latitudinal trends in population variability. Data came from the Global Population Dynamics Database (<http://cpbnts1.bio.ic.ac.uk/gpdd/>), a freely available database containing a large collection of population time series data (see Inchausti and Halley 2001). We used data for 12 major

taxa that met the following conditions: time series spanned at least 10 yr, taxa were unambiguously assigned to a species/morphospecies category, major taxa (orders) spanned at least 15° of latitude, and data were for major continental masses (i.e., we excluded island data).

Statistical analyses. For each data set, we calculated the coefficient of variation of population abundance among years as a measure of population variability. We calculated Spearman's rank correlation coefficient to quantify the relationship between latitude and the coefficient of variation for each of the 12 taxa. We then used meta-analysis to evaluate the generality of this relationship.

Meta-analysis is a set of statistical methods that allow the quantitative integration of results from multiple individual studies (Rosenthal 1991; Arnqvist and Wooster 1995; Osenberg et al. 1999). By defining a standardized measure of effect size, it is possible to gain insights about

the general outcome of studies. Although in the particular case of the relationship between latitude and population variability individual analyses were also conducted here, meta-analysis allowed us to summarize and integrate these results.

We used the correlation coefficient (r) as a measure of effect size in all meta-analyses. In each meta-analysis, we used the 95% confidence intervals of the correlation coefficient to test the null hypothesis that $r = 0$. To this end, correlation coefficients were first normalized by applying Fisher's z transform, $z = 0.5 \ln [(1 + r) / (1 - r)]$ (Zar 1999). In meta-analysis, it is advisable to weight the effect sizes by the inverse of the sampling variances (Rosenthal 1991; Gurevitch et al. 2001) so that individual z values with small variances have a greater influence than those with greater variances. Because the variance of the correlation coefficient is defined as $v = 1 / (N - 3)$ (Zar 1999), weights can be defined as $w = N - 3$ (Rosenthal 1991). The weighted mean of z_r is thus defined as $\bar{z}_w = \sum w_i z_i / \sum w_i$. We used bootstrap to calculate the mean and 95% percentile confidence limits of \bar{z}_w (Manly 1997), with a bootstrap sample size of 10,000. Calculations were performed using an algorithm written in Matlab (MathWorks 1999).

A limitation of meta-analysis is that results can be heavily influenced by publication bias. Publication bias can occur as a result of selective reporting, for example, when researchers and editors are more likely to publish highly significant results or results that support a particular hypothesis (Palmer 1999). Although in the particular case of the latitudinal trend of population variability this bias is probably a relatively minor issue (because data were gathered for the database with purposes other than testing for this relationship), it is a good practice to verify that this is the case; furthermore, we describe the general problem here because we will refer to it below when analyzing the relationships between population dynamics and niche breadth and between latitude and niche breadth. We used a graphical method for detecting publication bias known as the "funnel graph" (Light and Pillemer 1984; Palmer 1999). This approach relies on three basic statistical principles: that the variation about the "true" effect size should increase because of increased sampling error as sample size decreases, that average effect size should be independent of sample size, and that, regardless of sample size, individual effect sizes should exhibit a normal distribution about the "true" mean effect size because of random sampling error. When effect sizes are plotted against sample sizes in the absence of selective reporting, we expect data points to exhibit a funnel-shaped distribution with a wide dispersion at small sample sizes and a tapering of the distribution as sample size increases but with no apparent trend in mean effect size. Conversely, underreporting of

nonsignificant results resulting from low sample sizes may result in a V-shaped distribution, whereas underreporting of results inconsistent with a hypothesis would result in a correlation between sample size and effect size so that the highest effect sizes are observed at low sample sizes (for an example, see Palmer 1999).

Results. If the effects of latitude on population variability are indeed general, then a majority of taxa evaluated should exhibit a positive relationship between population variability and latitude. This is not the case; of 12 major taxa examined (which included orders of mammals, birds, and insects), only two showed a significant increase in population variability with latitude, five showed a significant decrease, and five showed no significant pattern (fig. 2). Furthermore, a meta-analysis shows that the 95% confidence limit for the correlation coefficient does not allow the rejection of the null hypothesis that $r = 0$ (fig. 3). As expected, the funnel plot shows no strong bias in the distribution of effect sizes (fig. 3). Thus, we conclude that available evidence does not support the assumption that population variability increases with increasing latitude.

Is There a Relationship between Population Variability and Niche Breadth?

Another condition for a latitudinal effect on niche breadth through environmental and population stability as envisioned by MacArthur (1972) is a relationship between population variability and niche breadth. MacArthur (1955) argued that population variability should be lower for species that are immersed in more complex food webs. For example, population variability should be lower for a predator with several prey items than for one that feeds on only one prey species (see also Pimm 1991). An important assumption of MacArthur's idea is that high population variability was the result of severe decreases in average population numbers during periods of scarcity of food or other resources; species would mitigate the effects of variability by becoming more generalized. Thus, lower variability should allow greater specialization: if the Tropics are less environmentally variable than temperate regions, tropical populations should exhibit lower population variability than their temperate counterparts; low variability would allow specialists to persist, thus displacing generalists.

An argument diametrically opposed to MacArthur's was proposed by Watt (1964). Discussing the population dynamics of herbivorous insects, he argued that polyphagous species could be more variable than monophagous species. The rationale of Watt's argument was that natural enemies and inclement weather usually keep population levels below those set solely by the availability of their food supply. The ability of polyphagous species to exploit a greater

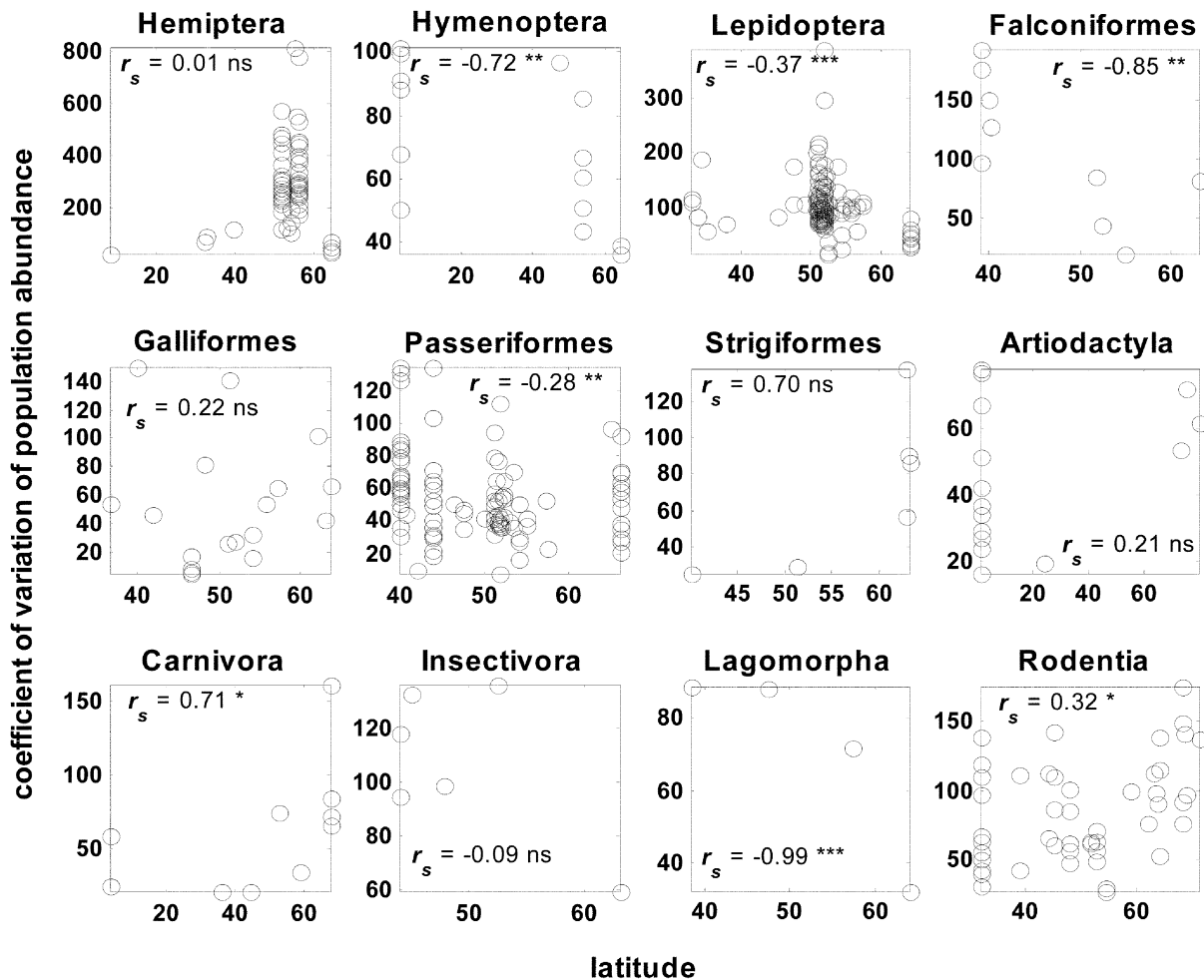


Figure 2: Coefficient of variation of population dynamics versus latitude for 12 major taxa. Data are from the Global Population Dynamics Database (<http://cpbnts1.bio.ic.ac.uk/gpdd/>). In each panel, Spearman's rank correlation coefficient is reported together with its statistical significance (*ns* = not significant; *one asterisk* = $P < .05$; *two asterisks* = $P < .01$; *three asterisks* = $P < .001$).

spectrum of resources should allow them to reach higher population levels during benign periods than monophagous species.

Redfearn and Pimm (1988; see also Pimm 1991) argued that these hypotheses are not mutually exclusive and that variability is probably a consequence of both unusually low (MacArthur) and unusually high (Watt) population levels. Thus, it would be the relative importance of each of these two processes that determines the overall variability in a given environment and its relationship to niche breadth. Therefore, there are theoretical reasons to argue that the relationship between population variability and niche breadth could exhibit any possible form and direction. Below we present results of a meta-analysis of published studies assessing the relationship between population variability and niche breadth.

Data. We combined data from previous studies analyzing the relationship between population variability and niche breadth. Most of these data had been reviewed by Redfearn and Pimm (1988); however, these authors did not use meta-analytical techniques to evaluate the overall pattern, which makes their results difficult to interpret and weakens their conclusions. We therefore reanalyze the same data using formal meta-analytical techniques, combining them with additional data coming from two recent studies (Koenig and Haydock 1999; Petchey 2000).

Data can be classified in two broad categories (table 1). One consists of data on long-term population abundance and niche breadth measured at particular localities for multiple species of herbivorous insects. The assumption in these studies is that niche breadth is a rigid property of species expressed throughout the study sites. A second

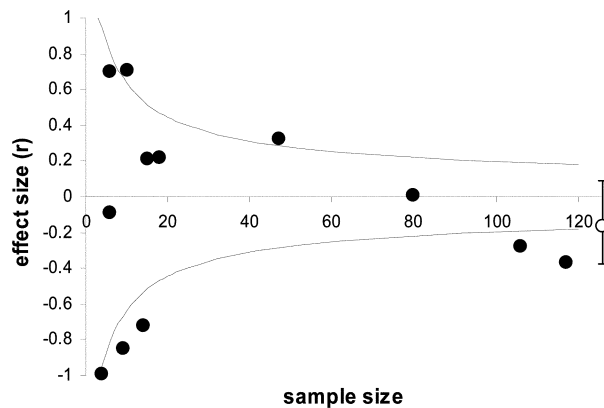


Figure 3: Funnel graph of latitude versus population variability. Black circles represent effect size (r) and sample size corresponding to each taxon (see fig. 2). White circle with error bars on right represents back-transformed mean and 95% bootstrap confidence interval of mean effect size.

kind of study consists of data for a single species at multiple sites (or laboratory microcosms) that are able to feed on different numbers of prey items, thus assuming that niche breadth varies among populations. Although the assumptions and simplifications of these two kinds of studies are quite different, the predicted outcome under the latitude–niche breadth hypothesis would be the same; therefore, we include them in a single meta-analysis. In all cases, niche breadth was measured quantitatively as the number of food items (prey species, host plant genera, or families) or qualitatively on specificity categories based on the number of food items.

Data may have important limitations. First, some data may suffer from nonindependence. The aphid data used by Redfearn and Pimm (1988) were collected from six sites throughout Britain; it is possible that population dynamics at these sites are spatially autocorrelated. A similar problem applied to the acorn woodpecker data used by Koenig and Haydock (1999). Second, the measures of niche breadth used in all studies are problematic both because they are too simplistic (e.g., relative frequency of different food items was not taken into account) and because they may be biased (e.g., abundant species may appear more generalized than rare species; see Redfearn and Pimm 1988). Because of these limitations, results should be interpreted with caution.

Statistical analyses. For each dataset, we calculated Spearman’s rank correlation coefficient between population variability and niche breadth. We then calculated the 95% bootstrap confidence interval and analyzed publication bias using the meta-analytic techniques described

above (see “Statistical Analyses” in “Is There a Latitudinal Gradient in Population Variability?”).

Results. Twelve of 13 correlation coefficients were negative, which would agree with the hypothesis that species with less variable populations tend to have narrower niches. However, the 95% weighted bootstrap confidence interval of the correlation coefficient overlapped with 0, and thus the null hypothesis that $r = 0$ cannot be rejected; this is the case even when each of the six aphid and the two woodpecker data sets are considered independent (fig. 4).

The funnel graph shows that sample size and effect size are negatively correlated, which suggests underreporting of studies with nonsignificant results or with results contrary to the hypothesis that population variability and niche breadth. However, the small number of studies available for the meta-analysis calls for a cautious interpretation of the funnel graph; it is also possible that the two studies with the largest sample sizes are outliers and that the remaining studies do represent the “true” effect size. The only way of distinguishing between these two possibilities is with further studies that allow stronger inference.

The Central Question: Is There a Latitudinal Gradient in Niche Breadth?

We have examined the assumptions of MacArthur’s original hypothesis and have shown that they are at best equivocally supported by data. We now evaluate the main prediction of the latitude–niche breadth hypothesis: that niches become narrower toward the Tropics. We present results of a literature survey in which we summarized the studies that have attempted to evaluate the prediction of MacArthur’s hypothesis.

Data. We conducted a literature review and gathered all the articles we found examining the relationship between niche breadth and latitude. To conduct our review, we searched the Web of Science database covering 1945–2003 for the terms “latitud*” or “latitudinal pattern” and “specializ*” or “niche*”. We also searched a variety of other sources such as the literature cited in articles found in our search. We found 11 articles attempting to quantitatively evaluate the latitude–niche breadth hypothesis (table 2). Studies vary greatly in their taxonomic scope, quality of data, and quantification of niche breadth. Most studies considered as the dependent variable either mean niche breadth (i.e., mean number resource types used) or the proportion of extreme specialists (i.e., proportion of species using only one resource type). Under MacArthur’s latitude–niche breadth hypothesis we expect an increase of mean niche breadth and a decrease in the proportion of extreme specialists with increasing latitude. Most studies directly measured one or both of these variables, whereas

Table 1: Studies evaluating the relationship between population variability and niche breadth

| Taxon | Geographical location | Period (yr) | No. species | Measure of variability | Measure of niche breadth | ES | <i>N</i> | References |
|---|---|-------------|-------------|------------------------|--|------|----------|---------------------------|
| Moths | Multiple localities in Canada (pooled for analysis) | 18 | 204 | SD of log abundance | No. host plant genera in Canada | −.05 | 151 | Redfearn and Pimm 1988 |
| Moths | 15 localities in U.K. (pooled for analysis) | 16 | 25 | SD of log abundance | Qualitative assessment of feeding specificity in Britain | −.12 | 25 | Redfearn and Pimm 1988 |
| Aphids | High Mowthorpe, U.K. | 13 | 26 | SD of log abundance | No. host plants in Britain | −.04 | 22 | Redfearn and Pimm 1988 |
| Aphids | Wye, U.K. | 13 | 26 | SD of log abundance | No. host plants in Britain | −.39 | 25 | Redfearn and Pimm 1988 |
| Aphids | Newcastle, U.K. | 13 | 26 | SD of log abundance | No. host plants in Britain | −.33 | 20 | Redfearn and Pimm 1988 |
| Aphids | Dundee, U.K. | 13 | 26 | SD of log abundance | No. host plants in Britain | −.32 | 23 | Redfearn and Pimm 1988 |
| Aphids | Elgin, U.K. | 13 | 26 | SD of log abundance | No. host plants in Britain | −.37 | 18 | Redfearn and Pimm 1988 |
| Aphids | Silwood Park, U.K. | 13 | 26 | SD of log abundance | No. host plants in Britain | −.49 | 25 | Redfearn and Pimm 1988 |
| Noctuid moths | South Bohemia, Czech Republic | 12 | 142 | CV of abundance | Categories based on no. host plant genera and families | .16 | 123 | Rejmánek and Spitzer 1982 |
| Moths | Southern British Columbia, Canada | 11 | 5 | SE of log abundance | No. tree host species in Canada | −.50 | 5 | Watt and Craig 1986 |
| Syrphid flies | English suburban garden | 15 | 38 | SD of log abundance | Categories of no. host plant genera and families | .32 | 38 | Owen and Gilbert 1989 |
| <i>Dileptus anser</i> (ciliate) | Laboratory | 14–20 d | 1 | SD of abundance | No. prey species per experimental unit | −.80 | 7 | Petchev 2000 |
| <i>Melanerpes formicivorus formicivorus</i> (southwestern acorn woodpecker) | Multiple sites in Pacific coast of U.S. | 17 | 1 | CV of abundance | No. oak species producing acorns per study site | −.98 | 8 | Koenig and Haydock 1999 |
| <i>Melanerpes formicivorus bairdii</i> (Pacific acorn woodpecker) | 150 sites in southwestern U.S. | 17 | 1 | CV of abundance | No. oak species producing acorns per study site | −.67 | 8 | Koenig and Haydock 1999 |

Note: ES = effect size, defined as Spearman's rank correlation coefficient, except for Petchev (2000), which reported Pearson's correlation coefficient; SD = standard deviation; CV = coefficient of variation; *N* = sample size.

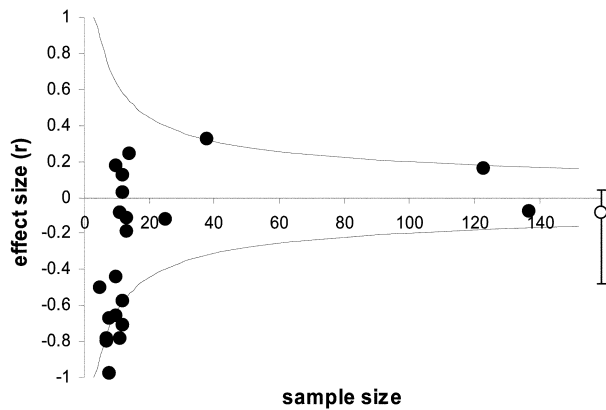


Figure 4: Funnel graph of population variability versus niche breadth. Black circles represent effect size (r) and sample size corresponding to each study (listed in table 1). White circle with error bars on right represents back-transformed mean and 95% bootstrap confidence interval of mean effect size.

others presented enough information to allow us to calculate them. As before, we defined niche breadth as the number of resource categories used by a particular species, which is the definition used in a majority of studies (with the exception of the study by Korpimäki and Marti [1995], which also reported Levin’s diversity index of prey species).

Studies also varied in terms of the geographical scope of the analysis (table 2). Some used data from multiple locations at different latitudes. Other studies defined latitudinal bands (e.g., 5° or 10° of width) and used all available information within each band. Some studies reported the correlation coefficient between latitude and mean niche breadth or the proportion of extreme specialists; in studies where correlation coefficients were not reported, we calculated them from the original data or from data extracted from figures. One study (Fiedler 1998) compared one temperate region with one tropical region; we discarded this study because it was not possible to calculate the correlation coefficient, and thus it could not be incorporated in the meta-analysis. In all studies, data came from literature surveys or field studies originally conducted for purposes other than testing the specialization–latitude hypothesis.

It is noteworthy that there are potential biases in the data that could serve to spuriously generate some of the patterns reported in the literature. The most important bias is that data tend to be less complete in tropical than in temperate regions. Several authors have explicitly expressed this concern (e.g., Beaver 1979; Ollerton and Cranmer 2002). For example, in Beaver’s (1979) study, information on host specificity was available for 98% of species in temperate areas but only for 54% and 69% for the two

tropical areas studied. Another similar bias is that the number of available studies in tropical regions is, in most cases, much lower than that in temperate regions, and some studies entirely lack tropical coverage (e.g., the European dataset used by Korpimäki and Marti [1995]; see table 2). If anything, these sampling artifacts should bias results in the direction predicted by the latitude–niche breadth hypothesis; it should lead to an increase in niche breadth with increasing latitude.

Statistical analyses. To evaluate the generality of the relationship between latitude and specialization, we calculated the 95% bootstrap confidence interval of the correlation coefficient between latitude and mean niche breadth and between latitude and the proportion of extreme specialists and analyzed publication bias using the meta-analytic techniques described above (see “Statistical Analyses” in “Is There a Latitudinal Gradient in Population Variability?”). Most data sets reported Spearman’s rank correlation coefficient or contained information that allowed its calculation. However, a few studies reported Pearson’s product-moment correlation coefficient or the coefficient of determination (R^2) used in regression analysis and did not provide data that allowed us to calculate Spearman’s coefficient. In these cases, we included Pearson’s coefficient and the square root of R^2 as estimates because they can be thought of as standardized effect sizes comparable to Spearman’s coefficient (Rosenthal 1991).

Results. Both for mean niche breadth and for the proportion of extreme specialists the bootstrap confidence interval overlapped with 0 (fig. 5). Thus, results of the meta-analysis do not allow us to reject the null hypothesis of no correlation between latitude and niche breadth.

For mean niche breadth, effect sizes tend to increase with decreasing sample size, indicating underreporting of negative correlation coefficients (fig. 5a); thus, this result suggests a publication bias against results contrary to the prediction of the latitude–niche breadth hypothesis. For the proportion of extreme specialists, the distribution of sample sizes is more symmetrically distributed, suggesting weaker publication bias (fig. 5b).

Conclusions of Examination of MacArthur’s Hypothesis

Our examination of MacArthur’s (1972) hypothesis of a latitudinal gradient in niche breadth suggests that it rests on a series of assumptions for which support is at best equivocal. Furthermore, our analysis shows that available evidence does not provide support for the general pattern predicted by the hypothesis that niche breadth increases with increasing latitude.

Of course, it is important to consider that the fact that we found no support for MacArthur’s hypothesis does not necessarily mean the hypothesis is false. Several factors

Table 2: Empirical studies evaluating the relationship between latitude and niche breadth

| Taxon | Geographic extent | Definition of niche breadth | Dependent variable | ES measure | ES | <i>N</i> | References |
|---------------------------|--|--|-----------------------------------|--|-------------------|----------|---------------------------|
| Catarrhine primates | 500 × 500-km grid across sub-Saharan Africa | No. food types consumed | Mean niche breadth | Pearson's <i>r</i> | .58 | 102 | Eeley and Foley 1999 |
| Catarrhine primates | 500 × 500-km grid across sub-Saharan Africa | No. habitat types occupied | Mean niche breadth | Pearson's <i>r</i> | .17 | 102 | Eeley and Foley 1999 |
| Milkweeds | Multiple locations around the world (1°–43°) | No. flower visitor species | Mean niche breadth | Spearman's <i>r</i> | .33 | 91 | Ollerton and Cranmer 2002 |
| Flower visitors | Multiple locations around the world (0°–82°) | No. plant species visited | Mean niche breadth | Pearson's <i>r</i> | .33 | 33 | Ollerton and Cranmer 2002 |
| Plants | Multiple locations around the world (0°–82°) | No. flower visitor species | Mean niche breadth | (<i>R</i> ²) ^{1/2} | .23 | 29 | Olesen and Jordano 2002 |
| Terrestrial mammals | 19 equidistant latitudinal bands in North America (<10°–>80°N) | No. habitats occupied | Mean niche breadth | Spearman's <i>r</i> | .96 | 19 | Pagel et al. 1991 |
| Diurnal raptors | Multiple locations in Europe (37°–71°N) | No. prey species | Mean niche breadth | Spearman's <i>r</i> | .26 | 108 | Korpimäki and Marti 1995 |
| Diurnal raptors | Multiple locations in North America (19°–69°N) | No. prey species | Mean niche breadth | Spearman's <i>r</i> | –.01 | 115 | Korpimäki and Marti 1995 |
| Owls | Multiple locations in Europe (37°–71°N) | No. prey species | Mean niche breadth | Spearman's <i>r</i> | –.15 | 191 | Korpimäki and Marti 1995 |
| Owls | Multiple locations in North America (19°–69°N) | No. prey species | Mean niche breadth | Spearman's <i>r</i> | –.10 | 176 | Korpimäki and Marti 1995 |
| Papilionid butterflies | 10° latitudinal bands (70°N–50°S) | No. host plant families | Proportion of extreme specialists | Spearman's <i>r</i> | –.93 ^a | 7 | Scriber 1973 |
| Licaenid butterflies | 5° latitudinal bands in Palearctic (30°–>70°N) | No. host plant families | Proportion of extreme specialists | Spearman's <i>r</i> | –.54 | 9 | Fiedler 1997 |
| Licaenid butterflies | 5° latitudinal bands in East Asia (30°–>70°N) | No. host plant families | Proportion of extreme specialists | Spearman's <i>r</i> | .76 | 8 | Fiedler 1997 |
| Macrolepidoptera | 10 × 10-km squares throughout Britain | No. host plant species | Proportion of extreme specialists | Pearson's <i>r</i> | –.65 | 10 | Loder et al. 1998 |
| Bark and ambrosia beetles | France, California, Malaysia, and Fiji | No. host plant species, genera, and families | Proportion of extreme specialists | Spearman's <i>r</i> | .32 | 10 | Beaver 1979 |
| Digenean fish parasites | 13 sites throughout the world's oceans (4°–70°) | No. host fish species | Proportion of extreme specialists | Spearman's <i>r</i> | –.77 | 11 | Rohde 1978 |
| Monogenean fish parasites | 13 sites throughout the world's oceans (4°–70°) | No. host fish species | Proportion of extreme specialists | Spearman's <i>r</i> | –.10 | 10 | Rohde 1978 |
| Plants | Multiple locations around the world (0°–82°) | No. flower visitor species | Proportion of extreme specialists | Spearman's <i>r</i> | –.26 | 23 | This study ^b |
| Flower visitors | Multiple locations around the world (0°–82°) | No. plant species visited | Proportion of extreme specialists | Spearman's <i>r</i> | –.06 | 23 | This study ^b |

Note: ES = effect size; *N* = sample size.

^a Calculated for data on the total number of species and the number of specialists in each 10° latitudinal band (using absolute latitude, without distinguishing between northern and southern hemispheres) for data for four subfamilies pooled.

^b Calculated from data in appendix A.

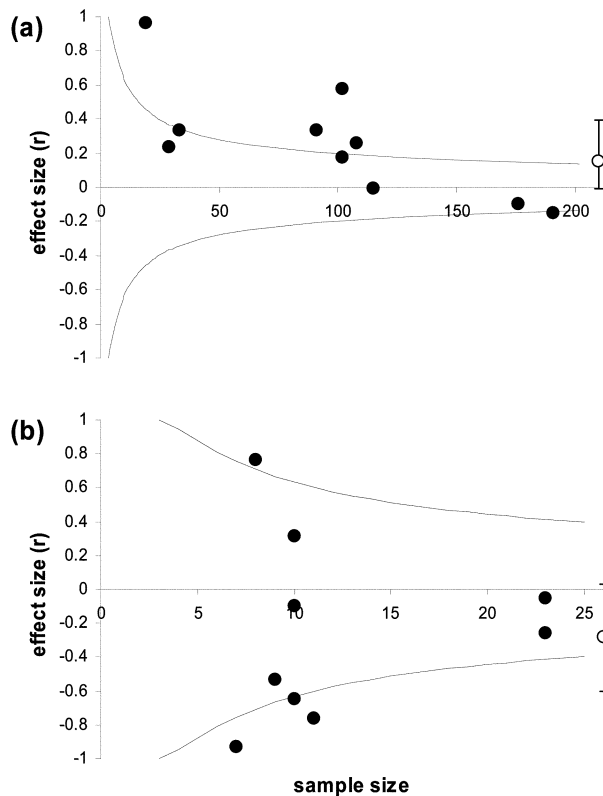


Figure 5: Funnel graphs of latitude versus mean niche breadth (a) and latitude versus proportion of extreme specialists (b). Black circles represent effect size (r) and sample size corresponding to each study (listed in table 2). White circles with error bars on right represent back-transformed mean and 95% bootstrap confidence interval of mean effect size.

could lead to acceptance of the null hypothesis of no effect even if it were false (i.e., a type II error). First, we cannot exclude the possibility that this general lack of significant effects is partly because of the low power resulting from the small number of studies that were available for the meta-analyses. In fact, despite nonsignificant results, in two cases (i.e., the relationships between population variability and niche breadth and between latitude and mean niche breadth) most of the published studies did have effects in the direction predicted by MacArthur’s hypothesis. However, the patterns observed in funnel graphs suggest that such a trend could have resulted from publication bias against studies that did not agree with the expectations of MacArthur’s latitude–niche breadth hypothesis.

Second, we cannot exclude the possibility that the general lack of significant effects stems from how the niche was defined in most of the studies reviewed here. As we argued above, this definition has many limitations, and it would not be surprising that future studies that use better quantifications of the niche lead to different conclusions

from those reached by us. All we can say at present is that current evidence does not provide support for either the assumptions or the predictions of MacArthur’s latitude–niche breadth hypothesis.

In spite of the apparent lack of generality of the latitudinal gradient in niche breadth, we argue that such a gradient can be expected under some circumstances. However, evidence presented above suggests that such a pattern is unlikely to result from the mechanism suggested by MacArthur. We provide an alternative hypothesis next, which may partly explain the diverse results obtained by the studies that have sought to investigate the latitudinal gradient in niche breadth.

An Alternative Hypothesis

There is ample evidence that species richness increases toward the Tropics for many taxa (Rohde 1992; Willig et al. 2003; Hillebrand 2004). This pattern has been observed for a great variety of groups; yet, it is not universal, and a number of exceptions exist. Although many mechanisms have been proposed to explain this pattern, there is still no consensus as to which one is more likely to operate. Regardless of the mechanism leading to a negative relationship between species richness and latitude, we suggest that, on the basis of ways species interact to form communities, latitudinal increases in specialization can result solely as a by-product of increases in species richness. Under this view, latitude would affect niche breadth only indirectly through species richness, and thus, a latitudinal gradient in niche breadth would be observed only when there is a latitudinal gradient in species richness and an effect of richness on niche breadth.

It is important to clarify here what we mean by an effect of latitude on species richness. “Latitude” is defined in Merriam-Webster’s dictionary (Merriam-Webster Online; <http://www.m-w.com>) as the “angular distance north or south from the earth’s equator measured through 90 degrees.” Such latitudinal position results in a particular angle of incoming solar radiation relative to the earth’s surface, which in turn affects the quantity of heat absorbed; the most intense heating will occur when incident solar radiation is perpendicular to the earth’s surface (both because travel of radiation through the atmosphere and the ratio of surface area to quantity of energy received are minimal). Solar radiation affects local climatic variables (particularly temperature and humidity). Thus, in reality, latitudinal position has an indirect effect on climate through an effect on incoming solar radiation; climate, in turn, affects species richness. By just drawing an arrow between latitude and species richness, we are ignoring much of this complexity and implying a direct causal relationship between two variables that is actually indirect.

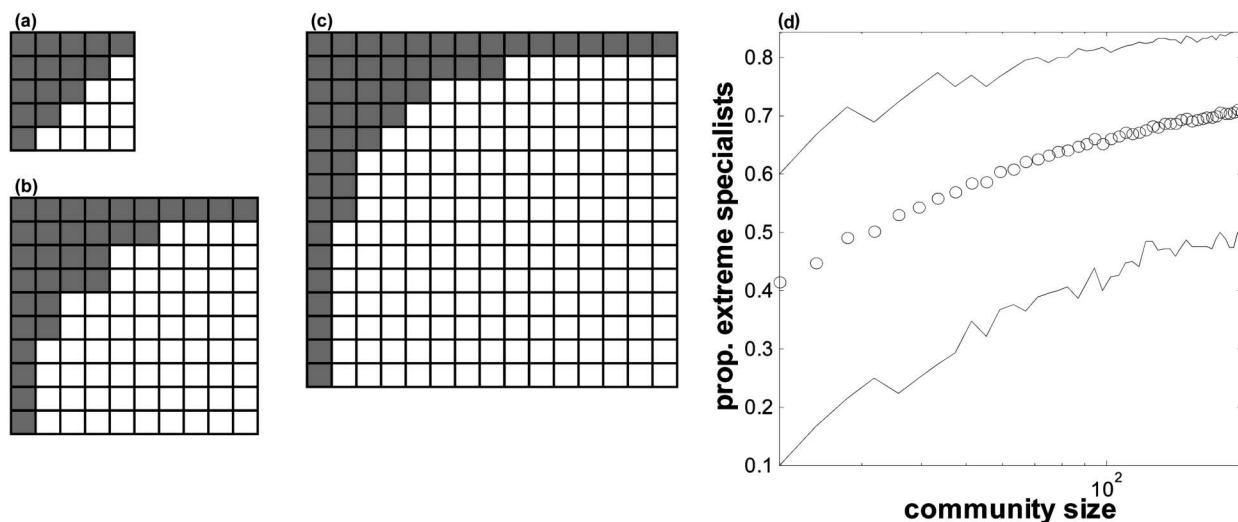


Figure 6: Example of how nested structure of interaction networks resulting from asymmetric specialization can lead to an increase in the proportion of extreme specialists as the number of species in the community increases. *a–c*, Each panel represents a community matrix in which rows represent a group of species (e.g., hosts) and columns represent another group (e.g., parasites). The total number of interactions (*filled cells*) in the matrix was calculated from an empirical relationship between community size (S) and the number of links (L ; table 2; see also Olesen and Jordano 2002). In the smaller community (*a*), only one-fifth of species in each group are extreme specialists (i.e., interact with only one other species), whereas this proportion increases to two-thirds in the intermediate community (*b*) and to seven-fifteenths in the largest (*c*). *d*, Results of simulation showing how extreme specialization tends to increase with community size, for communities of sizes 20–200. Circles represent mean proportion of extreme specialists calculated for 1,000 simulated communities for each community size; lines above and below circles are the 95% percentile confidence limits of the randomization (see app. B for simulation details).

However, this representation should not be regarded as erroneous. In causal modeling, a “direct cause” is always defined with reference to vertices (variables) within a particular causal graph, and it is not a claim that the cause is direct with respect to any other variable that might exist (Shipley 2000). Furthermore, we are not claiming that radiation resulting from latitudinal position is (directly or indirectly) the only cause of climate; other environmental factors will also affect climate, such as proximity to oceans and elevation. Nor are we claiming that climate is the only determinant of species richness; other factors such as history and species interactions may also contribute to determine local species richness. All we are suggesting is that latitudinal position can have some sort of measurable effect on climate and on species richness.

Likewise, we must explain how an effect of richness on niche breadth can be brought about. We propose that such a relationship can occur when species interactions are structured in an asymmetrically specialized, nested fashion. Recent studies in plant-animal mutualistic networks have shown that pairs of interacting species usually are asymmetrically specialized so that specialists tend to interact with generalists (Bascompte et al. 2003; Vázquez and Aizen 2004). Such asymmetry leads to a nested structure of the interaction network whereby specialized species

interact with a subset of the interaction partners of more generalized species (Bascompte et al. 2003). A nested structure of interspecific interactions has also been observed in parasite host interactions (Morand and Guégan 2000; Morand et al. 2002). However, we know of no studies that have evaluated this pattern in other kinds of interactions, and thus we cannot assess the generality of the mechanism we are proposing.

An important property of nestedness and asymmetric specialization in species interactions is that they tend to increase with the number of species in the network (Bascompte et al. 2003; Vázquez and Aizen 2004). As shown in figure 6 and appendix B, this increased asymmetric specialization among species suggests that the number of extreme specialists increases faster than community size; thus, higher species richness can lead to greater extreme specialization. This effect on extreme specialization could occur even if average niche breadth remained unchanged (asymmetric specialization translates into many species being extremely specialized and few extremely generalized; thus, niche breadth variance will increase with community size but not necessarily its mean). A similar argument can also be made for nonorganismal niche components such as habitat types (e.g., Pagel et al. 1991); in this case, a nested distribution of species among habitat types (Wright

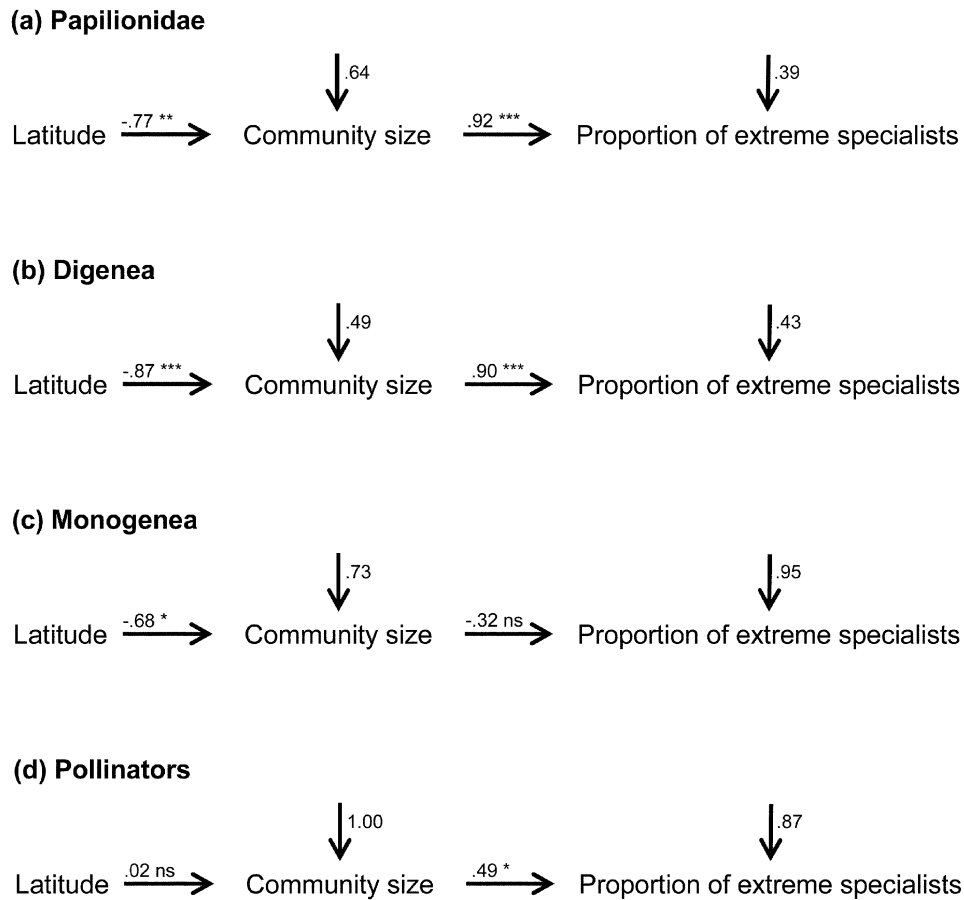


Figure 7: Path analysis of effect of latitude on species richness and of richness on the proportion of extreme specialists and on mean niche breadth. Horizontal arrows represent causal effects of one variable on another; vertical arrows indicate unexplained variability of endogenous variables. Magnitude of path coefficients (i.e., standardized regression coefficients) is given next to each arrow (statistical significance is indicated as in fig. 2). Community size was log transformed for analyses.

et al. 1998) would also result in an increasing proportion of extreme specialists with increasing species richness.

Is there evidence for a richness-mediated effect of latitude on extreme specialization? Four of the data sets listed in table 2 contain enough information (i.e., community size and proportion of extreme specialists at different latitudes) to allow us to examine this chain of effects: papilionid butterflies, digenean and monogenean parasites of fish, and pollinators. We use path analysis to evaluate the effect of latitude on community size and of community size on the proportion of extreme specialists (by “community size” we mean the number of species in the focal taxa and of their hosts, except for the papilionid butterflies, where we use only the number of butterfly species because the number of host plant species was not available). We use this analysis heuristically to illustrate how the alternative mechanism we are proposing could operate; a rigorous test would require the use of an independent dataset.

There was a significant, positive correlation between latitude and niche breadth (table 2) only for papilionid butterflies and digenean parasites. For both data sets, latitude has a negative, significant effect on community size; in turn, community size has a positive effect on the proportion of extreme specialists (fig. 7a, 7b). Thus, the observed effect of latitude on niche breadth reported in the original studies is consistent with an indirect effect of latitude on niche breadth through its effect on species richness. With path analysis it is possible to quantify the magnitude of this indirect effect as the product of the path coefficients along the pathway. For example, the indirect effect of latitude on the proportion of extreme specialists is $-0.77 \times 0.92 = -0.71$ for papilionid butterflies and $-0.87 \times 0.90 = -0.78$ for digenean parasites.

In contrast, no significant relationship between latitude and niche breadth was observed for monogenean parasites

or pollinators (table 2). For monogeneans, there is an increase of richness with decreasing latitude but no effect of richness on the proportion of extreme specialists (fig. 7c), making the indirect effect of latitude on niche breadth substantially low (0.22). The lack of effect of richness on specialization may be explained by the fact that most parasite species in this group are extremely specialized, where most of them interact with only one host species (Rohde 1978, 1992).

For pollinators, there is an effect of community size on the proportion of extreme specialists (fig. 7d), but there is no effect of latitude on community size; thus, the indirect effect of latitude on specialization is virtually 0 (-0.01). Although it is possible that the lack of effect of latitude on community size is real, it is also possible that it is a consequence of lower sampling effort in tropical communities. Indeed, species richness of most taxa (including most groups of flowering plants and insects) does increase toward the Tropics; however, researchers' decisions about sampling effort and number of plant species included in studies of local communities may weaken the correlation between local and regional species richness. Plant-pollinator data sets coming from tropical communities do seem to be less intensively sampled than their temperate counterparts (see Ollerton and Cranmer 2002); thus, we cannot ignore the possibility that the lack of effect of latitude on community size could have resulted from lower sampling effort in tropical communities.

The hypothesis we are proposing is an alternative to MacArthur's latitude–niche breadth hypothesis. Although the predictions of both hypotheses are similar (a positive relationship between niche breadth and latitude), the mechanisms hypothesized to lead to this pattern are entirely different. Whereas MacArthur's hypothesis is based on equilibrial mechanisms that assume a limiting similarity among coexisting species, the alternative hypothesis we are proposing does not require making any of these assumptions. Rather, we suggest that a latitudinal gradient in niche breadth will occur if two conditions are met, namely, if there is a latitudinal gradient in species richness and if interactions (or, more generally, resource use) are structured in an asymmetrically specialized, nested fashion. Thus, the generality of the latitudinal gradient in niche breadth will depend on the generality of these two conditions.

Conclusions

Our study shows that there is little evidence for a general effect of latitude on niche breadth. Recently Price (2002, p. 3) argued that “one of the major problems with ecology today is the existence of too much data and not enough theory, too many hypotheses and not enough testing, too many models and not enough verification”; in other words, in some cases there seems to be a disconnection between theoretical development and empirical testing of theory. Along the same lines, Graham and Dayton (2002) suggested that empirical testing of some ecological ideas lags far behind theory development, with models gaining paradigm status on the basis of very few empirical tests. This seems to have been the case with MacArthur's latitude–niche breadth hypothesis. We hope our synthesis will help to move beyond these early ideas.

In spite of the failure of MacArthur's hypothesis to receive support from available evidence, we have argued that a latitudinal gradient in niche breadth is likely to occur in some circumstances, namely when there is a latitudinal gradient in species richness, and when species interactions are organized in an asymmetrically specialized, nested fashion. We believe this new hypothesis merits further attention, especially rigorous tests that employ new data sets independent from the ones used in the present study.

Acknowledgments

We are grateful to the many field biologists who have produced the data used here to evaluate the latitude–niche breadth hypothesis and to the Global Population Dynamics Database, the Interaction Web Database, and M. Newman's Climatic Data Web site for providing access to data. S. Floeter, B. Hawkins, G. Mittelbach, A. Moles and an anonymous reviewer made useful comments on the manuscript. Postdoctoral fellowships to the authors at the National Center for Ecological Analysis and Synthesis (funded by National Science Foundation grant DEB-0072909, the University of California, and the University of California, Santa Barbara) provided the ideal conditions for conducting this work.

APPENDIX A

Table A1: Data sets used to calculate proportion of extreme specialists in plant-pollinator interactions reported in table 2 and figure 7 and to calculate the relationship between number of links (L) and community size (S , the number of plant and pollinator species in the data set) reported in appendix B and figure 6

| Data set | No. plant species | No. pollinator species | L |
|--|-------------------|------------------------|-------|
| Arroyo et al. 1982 (3 webs) | 87 | 99 | 365 |
| | 42 | 61 | 183 |
| | 41 | 28 | 87 |
| Barrett and Helenurm 1987 | 12 | 102 | 167 |
| Clements and Long 1923 | 96 | 275 | 923 |
| Elberling and Olesen 1999 | 23 | 118 | 238 |
| Hocking 1968 | 29 | 86 | 184 |
| Kato et al. 1990 | 89 | 678 | 1,202 |
| Kevan 1970 | 32 | 115 | 312 |
| Inouye and Pyke 1988 | 42 | 91 | 281 |
| McMullen 1993 | 105 | 54 | 204 |
| Medan et al. 2002 (2 webs) | 21 | 45 | 83 |
| | 23 | 72 | 125 |
| Memmott 1999 | 25 | 79 | 299 |
| Mosquin and Martin 1967 | 11 | 18 | 38 |
| Motten 1982 | 13 | 44 | 143 |
| Olesen et al. 2002 (2 webs) | 14 | 13 | 52 |
| | 10 | 12 | 30 |
| Ramírez and Brito 1992 | 28 | 53 | 109 |
| Schemske et al. 1978 | 7 | 32 | 59 |
| Small 1976 | 13 | 34 | 141 |
| Vázquez and Simberloff 2002, 2003 ^a | 14 | 93 | 169 |
| C. Smith-Ramírez et al., unpublished data ^b | 24 | 111 | 300 |

Note: Linear regression of $\ln L$ versus $\ln S$ rendered the following relationship: $L = \exp(0.31 + 1.05 \ln S)$; $P < .001$, $N = 23$, $R^2 = 0.91$. Data are available from the Interaction Web Database (<http://www.nceas.ucsb.edu/interactionweb>).

^a This data set includes data from eight sites with the same community type within a 25-km radius. To avoid pseudoreplication, we report results for the number of plants, pollinators, and links with the data for the eight sites combined into a single data set.

^b This data set is not included in the Interaction Web Database.

APPENDIX B

Relationship between Community Size and Proportion of Extreme Specialists: A Simulation

We conducted a simulation to study the relationship between community size (number of species in a community) and the proportion of extreme specialists (i.e., species interacting with only one other species) when the interaction matrix exhibits a moderate to highly nested structure and species interactions are asymmetrically specialized. Although we present this simulation in the context of two groups of interacting species (e.g., insect herbivores or pollinators and their host plants), the same reasoning can be applied to other cases such as a set of species using several habitat types.

Simulation procedure. We generated $m \times n$ binary interaction matrices, $\mathbf{A}_{m \times n} = [a_{ij}]$, with m species in one group and n species in the other (we worked under the special case of $m = n$ for simplicity). A binary interaction matrix is one in which columns represent species in one group (e.g., plants), rows represent species in the other group (e.g., pollinators), cells with 1's represent interactions between a pair of species, and cells with 0's represent no interaction (see Jordano et al. 2003; Vázquez and Aizen 2003). For each simulated matrix, we generated $\mathbf{F}_{m \times 1} = [f_j]$ and $\mathbf{G}_{n \times 1} = [g_j]$ lognormally distributed vectors of interspecific interaction probabilities, with entries in each vector ordered in decreasing magnitude; these vectors were generated by drawing from a lognormal distribution with mean = 1 and SD = 2. In this way, few species had a high probability of having interspecific interactions, and

many had a low probability, as frequently observed in many real communities (Bascompte et al. 2003; Montoya and Solé 2003; Vázquez and Aizen 2003). The total number of interspecific interactions (“links”) in a given matrix was calculated according to the following empirical scaling relationship between species richness (S) and the number of links (L), derived for a dataset on plant-pollinator interactions: $L = \exp(0.31 + 1.05 \ln S)$ (see app. A for details). Although the parameters of this relationship are probably different for other types of interactions, the qualitative form of the relationship is likely to be similar (see, e.g., Martinez 1992). We then used two different procedures to generate simulated matrices.

Under the first matrix-generating procedure, we started by assigning 1’s to the first column and row of the matrix, so that one species in each group had a maximum number of interactions, and interactions of all other species in each group were “nested” within the interactions of these maximally generalized species. We then assigned the χ remaining interactions the remaining cells of the interaction matrix according to the product of the interspecific interaction probabilities, $P_{ij} = f_i g_j$; cells with the highest χ associated probabilities were assigned 1’s, and the remaining cells were assigned 0’s. This procedure generated matrices with a high degree of nestedness.

The second matrix-generating procedure was based on a previously published null model of interspecific interactions (referred to as “null model 2” in Vázquez and Aizen 2003, 2004). Briefly, for each species one interaction partner is selected among the pool of possible interaction partners according to their probabilities of interspecific interaction. Once each species has one (and only one) link, the remaining χ links are randomly assigned according to probability $P_{ij} = f_i g_j$. Thus, whereas in the first procedure randomness operates only once (i.e., for the generation of the probability vectors \mathbf{F} and \mathbf{G}), in the second procedure randomness operates twice (once for the generation of probability vectors \mathbf{F} and \mathbf{G} and again for the assignment of links according to the probabilities P_{ij}). Therefore, this second procedure generates matrices with a moderate degree of nestedness and exhibiting a structure less orderly than those produced by the first procedure but still more orderly than in a completely random matrix. This procedure has been shown to generate topological patterns resembling those observed in plant-pollinator interaction networks (Vázquez and Aizen 2003, 2004) and can thus be considered a more realistic model than the first procedure.

One thousand sets of simulated matrices were generated for a range of community sizes ($S = m + n$) of 20–200 ($m = n$ in all cases) under each simulation procedure. Mean and 95% percentile confidence limits of the proportion of extreme specialists were calculated for each

community size. Pearson’s correlation coefficient between community size and the proportion of extreme specialists was calculated for each of the 1,000 sets; confidence limits of the correlation coefficient were calculated as the 95% percentiles of the distribution of the 1,000 correlation coefficients.

Simulation results. Both matrix-generating procedures resulted in a positive relationship between community size and the proportion of extreme specialists. For the first matrix-generating procedure, mean Pearson’s correlation coefficient was positive and relatively high (fig. 6*d*; mean correlation coefficient: 0.50; 95% confidence limits: [0.21, 0.67]). The relationship between community size and the proportion of extreme specialists obtained with the second matrix-generating procedure was weaker but still positive (mean correlation coefficient: 0.38; 95% confidence limits: [0.15, 0.58]). These simulation results suggest that the proportion of extreme specialists may increase with increasing community size when interspecific interactions are asymmetrically specialized and community interaction matrices exhibit moderate to high degrees of nestedness.

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