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RESEARCH PAPER

Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains

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ABSTRACT

Aim This research aims to understand the factors that shape elevational diversity gradients and how those factors vary with spatial grain. Specifically, we test the predictions of the species–productivity hypothesis, species–temperature hypothesis, the metabolic theory of ecology and the mid-domain effects null model. We also examine how the effects of productivity and temperature on richness depend on spatial grain.

Location Deciduous forests along an elevational gradient in Great Smoky Mountains National Park, USA.

Methods We sampled 22 leaf litter ant assemblages at three spatial grains, from 1-m^2 quadrats to 50×50 m plots using Winkler samplers.

Results Across spatial grains, warmer sites had more species than did cooler sites, and primary productivity did not predict ant species richness. We found some support for the predictions of the metabolic theory of ecology, but no support for the mid-domain effects null model. Thus, our data are best explained by some version of a species–temperature hypothesis.

Main conclusions Our results suggest that temperature indirectly affects ant species diversity across spatial grains, perhaps by limiting access to resources. Warmer sites support more species because they support more individuals, thereby reducing the probability of local extinction. Many of our results from this elevational gradient agree with studies at more global scales, suggesting that some mechanisms shaping ant diversity gradients are common across scales.

Keywords
Community structure, forests, Formicidae, Great Smoky Mountains National Park, productivity, scale, species richness, temperature, USA.

INTRODUCTION

What causes geographical variation in the number of species in local assemblages? This question has intrigued ecologists and biogeographers for more than 100 years, and dozens of mechanisms have been suggested to explain geographical variation in species richness (Gaston, 2000; Hawkins *et al.*, 2003; Currie *et al.*, 2004; Evans *et al.*, 2005; Rahbek, 2005). Many of these mechanisms fall into three broad classes of hypotheses: species–productivity hypotheses, species–temperature hypotheses and geometric constraints hypotheses.

Species–productivity hypotheses

Species–productivity hypotheses rest on a chain of causal links. The first link is that as productivity increases, so does the total abundance of a taxon in an area. Second, as abundance increases, so does richness. There are two mechanisms by which abundance can affect richness. The 'abundance–extinction' mechanism posits that more productivity leads to larger average population sizes, thereby reducing the probability of local extinction (Wright, 1983; Srivastava & Lawton, 1998; Kaspari *et al.*, 2000b). In contrast, the 'sampling mechanism' posits that more productivity increases the number of individuals in an assemblage. As more individuals are supported, the probability of a novel species being 'sampled' by a local assemblage from the regional species pool increases (Gotelli & Graves, 1996; Evans *et al.*, 2005). Distinguishing between the abundance–extinction and sampling mechanisms can be difficult, but one way to distinguish between them is to remove the effect of sampling by calculating Fisher's α. Fisher's α is a widely used estimate of diversity because it is independent of sample size and removes the sampling effect

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(Fisher *et al.*, 1943; Hubbell, 2001; Kaspari *et al.*, 2003; Evans *et al.*, 2005).

Species–temperature hypotheses

All species–temperature hypotheses predict that diversity is a positive function of temperature, but the mechanisms underlying that relationship differ. Temperature could indirectly limit diversity because it covaries with net primary productivity (NPP) (Rosenzweig, 1968; Leith, 1975), limits the physiology, behaviour or ranges of individuals (Kerr & Packer 1997; Kaspari *et al.*, 2000b), or drives speciation rates (Rohde, 1992; Allen *et al.*, 2002; Brown *et al.*, 2004).

One species–temperature hypothesis that is receiving increasing attention is the metabolic theory of ecology (MTE; Allen *et al.*, 2002; Brown *et al.*, 2004; Algar *et al.*, 2006; Hawkins *et al.*, 2006). Based on the biochemical kinetics of metabolism, the MTE makes two predictions. First, ln-transformed species richness should be linearly associated with an inverse rescaling of annual temperature (Allen *et al.*, 2002; Brown *et al.*, 2004). Second, and more specifically, the slope of the relationship between ln-transformed richness and $1/kT$, where k is Boltzmann's constant (0.0000862 eV K^{-1}) and T is temperature in Kelvin, should fall between −0.60 and −0.70 (Brown *et al.*, 2004). While many studies have tested for a relationship between temperature and diversity, only a handful of studies have tested whether observed richness patterns agree with the predictions of the MTE (Allen *et al.*, 2002; Brown *et al.*, 2004; Kaspari *et al.*, 2004; Algar *et al.*, 2006; Hawkins *et al.*, 2006).

Mid-domain null models

Geometric constraints along biogeographical domains can also influence patterns of species richness (Colwell *et al.*, 2004). These effects are often called mid-domain effect (MDE) null models. MDE null models predict a hump-shaped diversity curve that, due to spatial constraints, arises because the ranges of more species are expected to overlap by chance near the centre of the domain than at the edges of the domain. The concepts associated with MDE are controversial (Colwell *et al.*, 2004; Hawkins *et al.*, 2005), and some empirical studies show strong support for MDE while others do not (Dunn *et al.*, 2006).

Spatial scale and grain

Key to understanding the causes of spatial gradients in species richness is disentangling the relative importance of the underlying mechanisms and how they depend on spatial grain (Rahbek, 2005). One practical difficulty of disentangling the relative importance of temperature and productivity is that the two often covary in space. In addition, the effects of temperature and productivity may be masked by the influence of taxonomic composition, habitat structure and historical processes (Ricklefs & Schluter, 1993). Analyses at scales smaller than continental domains potentially include sites where temperature and productivity do not covary, thus minimizing the influence of habitat differences (if habitat type is controlled for) and regional historical processes. Therefore, examining the causes of spatial variation in richness at small spatial scales may better illuminate the mechanisms underlying gradients in species richness.

Spatial grain (the size of the sampling unit) can affect the form of and mechanisms underlying many spatial diversity gradients (Rahbek & Graves, 2001; Chase & Leibold, 2002; Hurlbert & Haskell, 2003; Kaspari *et al.*, 2003; Rahbek, 2005). At small grains, a multitude of biotic and abiotic factors might limit richness (Rahbek & Graves, 2001; Hurlbert & Haskell, 2003) and the relationship between richness and energy is often unimodal, with richness first increasing at low levels of productivity and then decreasing at high levels of productivity (Chase & Leibold, 2002; Mittelbach *et al.*, 2001). History and environmental factors will play larger roles as scale increases. Furthermore, at large spatial grains, species richness often increases monotonically with productivity (Mittelbach *et al.*, 2001; Chase & Leibold, 2002; Hawkins *et al.*, 2003). More recent analyses (Whittaker & Heegaard, 2003; Gillman & Wright, 2006), however, have shown that the unimodal relationship between species richness and productivity may not be as common as previous authors have suggested, and the relationship may not depend on spatial grain.

We sampled ant assemblages at 22 sites and three spatial grains along an elevational gradient in the southern Appalachian Mountains, USA. We use these data to: (1) test the predictions of the species–productivity hypothesis, the species–temperature hypothesis, the MTE and the mid-domain effects null model; and (2) examine how the effects of productivity and temperature on richness depend on spatial grain.

METHODS

Study sites and sampling

We sampled ant assemblages at 22 sites along an elevational gradient (379–1742 m) in Great Smoky Mountains National Park, USA (total area 2111 km^2) in June–August 2004 and 2005, during periods of peak ant activity (Dunn *et al.*, 2007b). The sites were all in mixed hardwood forests and located in areas away from roads, heavily visited trails or other recent human disturbances.

At each site, we randomly placed a 50 × 50 m plot. Within the corners of this plot, we placed a 10 m × 10 m subplot, and within the corners of each 10 m × 10 m subplot, we sampled ants in four 1-m^2 quadrats. Thus at each site there were 16 1-m^2 quadrats. At each 1-m^2 quadrat, we collected the leaf litter inside the quadrat and sifted it through a coarse mesh screen of 1-cm grid size to remove the largest fragments and concentrate the fine litter. The litter fragments that did not fit through the mesh, twigs and sticks in each 1-m^2 quadrat were inspected for colonies. The concentrated fine litter from each of the 16 1-m^2 quadrats was then suspended in 16 mini-Winkler sacks for 2 days in the laboratory. Winkler samplers are increasingly being used as common and efficient tools for sampling and quantifying ant diversity (Fisher, 1996, 1998, 2005; Ward, 2000; Longino *et al.*, 2002; Kaspari *et al.*, 2004). All worker ants that were extracted from the 1-m^2 quadrats

were identified and enumerated and are stored in N.J.S.'s ant collection at the University of Tennessee. A species list is available from N.J.S. At eight of the sites, we also collected ants using an array of 10 pitfall traps over 2 years. The number of species collected by pitfall traps did not differ from the number collected by the Winkler samplers (paired $t = 1.88$, $n = 8$, $P = 0.11$). Similarly, the fauna sampled by the pitfall traps was similar to the fauna sampled by the Winkler samplers (mean Jaccard similarity index = 0.70) (Lessard *et al.*, 2007).

We estimated richness at three spatial grains: the average number of species in a 1-m^2 quadrat; the number of species in 50 × 50 m plots (the number of species detected in the 16 1-m^2 quadrats at the site); and the Chao2 estimate of richness for the site assuming sampling went to completion. Counts of observed species may reflect total species richness, but they are also sensitive to total abundance and the number of individuals collected in the sample (Gotelli & Colwell, 2001). For these reasons, species richness estimators such as Chao2 are recommended (Gotelli & Colwell, 2001). The Chao2 estimate is spatially ambiguous, but represents the number of species occurring in some area larger than the 50 × 50 m plot (Colwell & Coddington, 1994). Because estimators such as the Chao2 are sensitive to sample size (Colwell & Coddington, 1994), we used ESTIMATES 7.50 (Colwell, 2005a) to construct 500 randomized accumulation curves for each site to calculate the standard deviation of the estimated species richness.

Estimating temperature and productivity

To estimate mean annual temperature at each of our 22 sites, we used data from one or two HOBO data loggers placed on the ground at 11 sites over 2 years from 2002 to 2003. These 11 sites ranged in elevation from 531 to 1944 m. Initially there were two data loggers at each site, but one data logger at each of three sites was damaged, presumably by bears. Temperature measurements differed little between the two data loggers at any one site, so it is unlikely that data lost from the three data loggers influenced our estimates of temperature. Temperature data were recorded hourly. Mean January minimum temperature, mean July maximum temperature and annual temperature were strongly correlated ($r \geq 0.97$ in all cases), so here we use mean annual temperature. To obtain estimates of mean annual temperature for the 22 sites in this study, we used common linear interpolation techniques (e.g. Lieberman *et al.*, 1996; Allen *et al.*, 2002). Hereafter, we refer to mean annual temperature simply as 'temperature'.

We generated NPP values for each site by overlaying site localities on a GIS NPP data layer obtained from the NASA MODIS Land Algorithm (MOD17A3) at 1-km spatial resolution (data acquired in 2004 and 2005) (Running *et al.*, 2004). Because the resolution at which the NPP data were collected is much greater than the scale at which the ant species richness data were collected, and because the NPP estimates are derived from an algorithm with a series of assumptions that might not necessarily hold, we also used the normalized difference vegetation index (NDVI) as an estimate of NPP. NDVI is a measure of greenness calculated from reflectance in the near-infrared and red portions of the electromagnetic spectrum. The values of NDVI range from –0.2 to +1 globally. Within our study region, NDVI ranged from +0.32 to +0.44. Here, NDVI correlates strongly with NPP, and is frequently used as an estimate of productivity (Oindo, 2002; Hurlbert & Haskell, 2003; Kerr & Ostrovsky, 2003; Hurlbert, 2004). We generated NDVI values at a 250-m resolution for each site by overlaying site localities on a GIS NDVI data layer obtained from the NASA MODIS data base (data acquired in 2004 and 2005).

Analyses

To test whether the species–temperature or species–productivity hypotheses were supported across three spatial grains, we used separate stepwise multiple regressions (P to enter = 0.10) to ask whether log-transformed NPP, log-transformed NDVI and log-transformed mean annual temperature predicted species richness at each spatial grain. To remove the effect of sampling on species richness, we also calculated Fisher's α for each site. After tallying the number of occurrences of each species in the 16 1-m^2 quadrats, we used ESTIMATES (Colwell, 2005a) to calculate Fisher's α for each site. Using a stepwise linear regression, we then tested how well log-transformed NPP, log-transformed NDVI and log-transformed mean annual temperature predicted Fisher's α. To reiterate, relating Fisher's α to the environmental variables allows us to test whether these environmental factors affect richness in some way other than by the sampling mechanism. We used JMP 6.0 (SAS, Cary NC) to conduct all regressions.

Because spatial autocorrelation can cause non-significant relationships to appear significant when using traditional statistical approaches, we assessed the potential effects of spatial autocorrelation in several ways. First, we used SAM 1.1 (Rangel *et al.*, 2006) to calculate the modified t-test developed by Dutilleul (1993) and promoted by others (Legendre *et al.* 2002; Diniz-Filho *et al.*, 2003). The modified t-test tests for significant relationships between the environmental variables and the dependent estimates of ant species richness, factoring out the effects of spatial autocorrelation. In the results we indicate when we used these corrected probabilities by labelling the P-values as 'corrected P'. Second, as a test of whether any of the response or predictor variables were spatially autocorrelated (Diniz-Filho *et al.*, 2003), we used SAM 1.1 (Rangel *et al.*, 2006) to calculate Moran's I. We calculated Moran's I across eight spatial distance classes for ant species richness at each of three spatial grains (1-m^2 quadrats, 50 × 50 m plots, Chao2 estimated richness) and for Fisher's α. Third, we asked whether the residuals from the stepwise regression models described above were spatially autocorrelated by calculating Moran's I on them. If no spatial autocorrelation is found in the residuals of the model including the environmental factors, then there is no statistical bias introduced by spatial autocorrelation in the original regression (Legendre *et al.*, 2002; Diniz-Filho *et al.*, 2003).

To test the predictions of the MTE, for each spatial grain we used JMP 6.0 to implement Model I OLS linear regression (following Brown *et al.*, 2004) to relate ln(species richness) at each spatial grain to $1/kT$. The first prediction is that the relationship

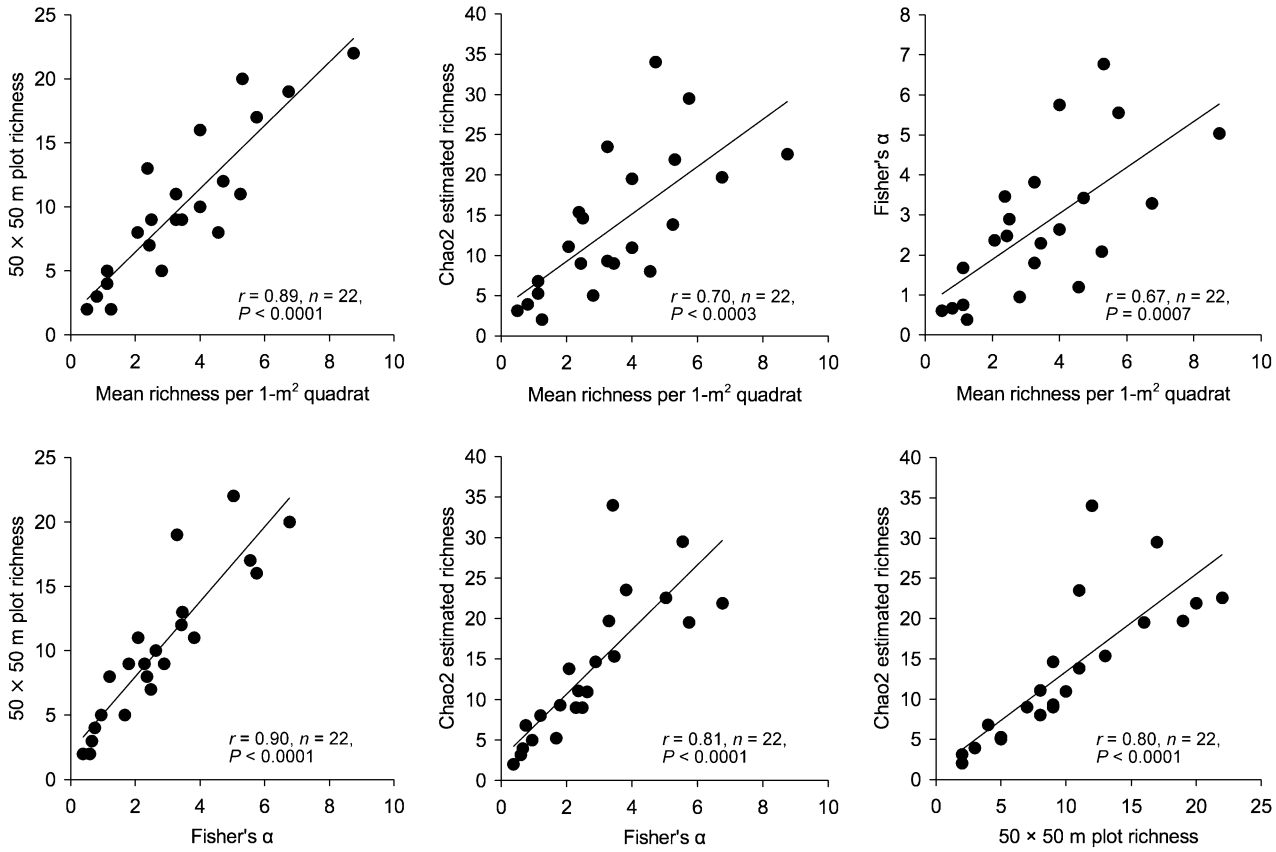

Figure 1 Relationships between richness at three spatial grains and Fisher's α: the mean number of species detected per 1-m² quadrat, the number of species detected in the 50 × 50 m plot at each site, the Chao2 estimate of richness and Fisher's α.

is linear and negative. The second prediction is that slope is somewhere near −0.65. In addition, we also use Dutilleul's (1993) *t*-test to test the significance of slopes based on the geographically effective degrees of freedom, though the original investigators (Allen *et al.*, 2002; Brown *et al.*, 2004) did not take this additional precaution. A key assumption of the MTE is that the abundance and average body mass of ectotherms are constant among samples. This assumption is not met here, nor was it met in the original tests of the theory (Allen *et al.*, 2002; Brown *et al.*, 2004) or more recent tests (Algar *et al.*, 2006, Hawkins *et al.*, 2007). Prior to analysis, richness at the smallest spatial grain was $\ln(x + 1)$-transformed to prevent negative species richness values.

To test whether the observed richness pattern at each grain was predicted by the MDE, we used RANGEMODEL 4.0 (Colwell, 2005b) to estimate predicted richness under the assumption of random placement of species ranges along the elevational gradient. RANGEMODEL 4.0 randomly reassigns the location of each species' range (1000 times) within the domain (379–1742 m), then generates a mean predicted richness value for each of the 22 sites. We then examined the relationship between predicted richness at each grain and observed richness using simple linear regression. We defined the domain as the elevational range considered in this study. When we defined the domain as ranging from 0 to1742 m, the results did not qualitatively differ.

RESULTS

In total, we detected 38 leaf litter ant species at the 22 sites. The number of species per m² ranged from 0–10, and the number of species per 50 × 50 m plot varied from 2–22. The Chao2 estimates of site richness ranged from 4–34 species. In 20 of the 22 sites, the estimators reached an asymptote, indicating that further sampling with the same methods would probably have added no new species. The four estimates of ant species richness (average number per m², number per 50 × 50 m plot, Chao2 estimated richness and Fisher's α) were correlated with one another ($r = 0.67$ to 0.90, $n = 22$, $P \leq 0.0007$; Fig. 1). Richness at each spatial grain declined with elevation ($r = -0.83$ to -0.64, $n = 22$, corrected $P \leq 0.015$). Mean annual temperature decreased with elevation ($r = 0.99$, corrected $P < 0.0001$). However, there was no relationship between elevation and NPP ($r = 0.34$, corrected $P = 0.17$) or NDVI ($r = 0.50$, corrected $P = 0.12$). NPP, temperature and NDVI did not covary with one another across the elevational gradient (corrected $P > 0.12$ in all cases).

At the 1-m² quadrat spatial grain, standard multiple regression indicated that log(temperature) explained 42.7% of the variation in the mean number of species per m², and log(NPP) explained an additional 10% of the variation (Table 1). At the 50 × 50 m plot grain, log(temperature) explained 66% of the variation in species richness, with log(NPP) explaining an additional 9% of

Table 1 Results of stepwise multiple regression examining the effects of log[mean annual temperature (°C)], log[NPP (g C m^{-2} $year^{-1}$)] and log(NDVI) on ant species richness at three spatial grains and Fisher's α.

Variable	Parameter	Partial r^2	Model r^2	F	Probability
m^2 quadrat richness					
log(temperature)	10.69	0.43	0.52	10.86	0.001
log(NPP)	−7.53	0.10		3.78	0.07
50 × 50 m plot richness					
log(temperature)	38.28	0.66	0.74	33.93	<0.001
log(NPP)	−20.65	0.09		6.92	0.02
Chao2 estimated richness					
log(temperature)	27.97	0.62	0.62	32.42	<0.001
Fisher's α					
log(temperature)	11.72	0.67	0.79	39.25	<0.0001
log(NPP)	−7.31	0.12		10.73	0.004

the variation in richness (Table 1). At the largest spatial grain, log-transformed temperature explained 62% of the variation in the Chao2 estimate of richness, and no other variable entered the model. Log-transformed (temperature) explained 67% of the variation in Fisher's α, with log(NPP) explaining an additional 12% of the variation (Table 1). When log(NPP) entered the model at each spatial grain, the parameter estimate was negative.

There was little evidence that species richness was spatially autocorrelated, except at the largest distance classes, where richness was negatively spatially autocorrelated (see Table S1 in Supplementary Material). Fisher's α was positively spatially autocorrelated at the smallest spatial grain, indicating that assemblages with high values of Fisher's α tended to be close to one another (Table S1). Fitting the climate model including log-transformed NPP, log-transformed NDVI and log-transformed mean annual temperature removed all of the significant spatial autocorrelation in the richness data across all distance classes (see Table S2 in Supplementary Material). This confirms that the spatial variation in the environmental variables, most notably mean annual temperature, drives these diversity gradients at each spatial grain.

Table 2 Summary of the relationship between ln(species richness) and the inverse of temperature (K) at three spatial grains.

Grain	Slope	95% CI	r^2	Corrected probability
1-m^2 quadrat	−0.51	−0.76 to −0.27	0.49	0.001
50 × 50 m plot	−0.95	−1.21 to −0.69	0.74	0.001
Chao2 estimate	−1.04	−1.31 to −0.77	0.77	0.001

Consistent with a prediction of the MTE, at each spatial grain, ln(species richness) decreased with inverse temperature ($1/kT$) (Fig. 2). In no case did the slope of the relationship fall between −0.60 and −0.70, as the MTE predicts (Table 2). However, the large confidence intervals encompassed −0.60 and −0.70 at the m^2 grain and the 50 × 50 m plot grain, but not at the largest spatial grain (Table 2).

The MDE did not predict richness at any grain in any of the models ($r^2 < 0.01$ in all cases).

DISCUSSION

Our key result is that, across three spatial grains from 1-m^2 quadrats to approximately 50 × 50 m plots, warmer sites have more species than cooler sites, but sites with higher primary productivity do not have higher species richness. In addition, the relationship between diversity and temperature is not driven by the sampling mechanism, as Fisher's α was predicted by temperature but not primary productivity. We found some support for the predictions of the MTE, but no support for the mid-domain effects null model. Thus, our data are best explained by some version of a species–temperature hypothesis.

Species–temperature and species–productivity hypotheses

Though productivity is often positively correlated with species richness (Mittelbach *et al.*, 2001), we found that productivity and

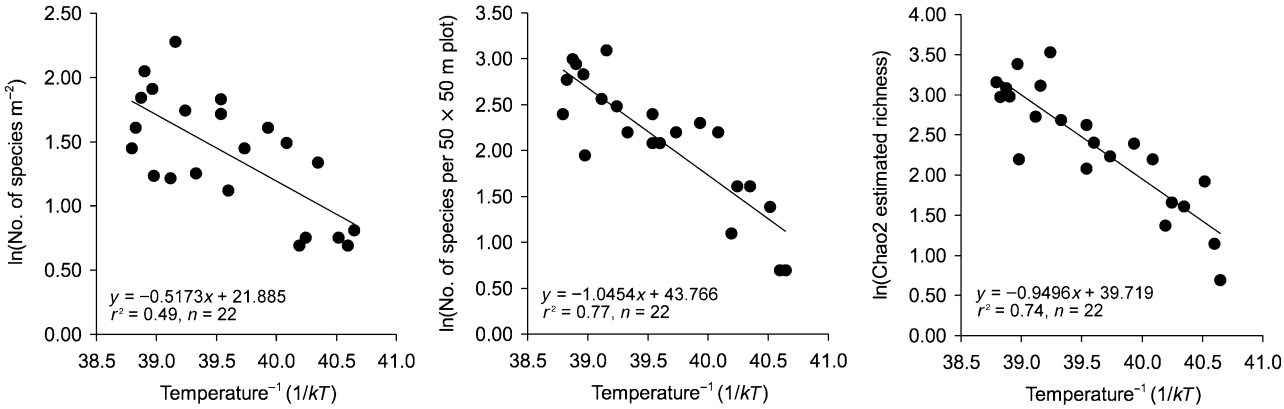

Figure 2 The relationships between ln(richness) at three spatial grains and the inverse of temperature.

ant species richness were negatively correlated. Why might the relationship between productivity and richness or abundance be negative? Hurlbert (2004) recently found a negative relationship between the abundance of birds and a proxy for productivity (NDVI) in North American forests, but a positive relationship in grasslands. To explain this unlikely result, he suggested that the effective survey area was smaller in forests than in grasslands, but he did not rule out the possibility that there might be real differences in the way that individuals in forests and grasslands respond to increasing productivity. We also cannot rule out the possibility that forest assemblages respond to productivity differently than do assemblages in other habitat types. This seems to us to be a rich area for future research. Another possibility for the negative richness–productivity relationship is that at high levels of productivity, other factors limit richness (Hawkins *et al.*, 2003). This might be a likely explanation for our result because of the relatively high levels of productivity in the southern Appalachians and because so little variation in productivity existed among our study sites. That is, the range of NPP is still relatively small compared with global gradients in NPP. So it could be the case that NPP is positively correlated with richness at global scales (Kaspari *et al.*, 2000a, 2003; Pautasso & Gaston, 2005), but at smaller spatial extents, such as along elevational gradients where the range of NPP is smaller, it is not.

In addition, productivity on its own may not be an accurate predictor of ant species diversity for several reasons. First, productivity might not be the best measure of resource availability to ants, or any heterotroph for that matter (Clarke & Gaston, 2006). That is, it is unclear whether traditional estimates of the energy available, such as productivity or biomass production, really equate to the resources that ants require. For example, much of that biomass will be tied up in lignin and cellulose, which the ants cannot use directly, even if they were strictly herbivores. Second, ants generally forage in only a narrow portion of their thermal range (Cerdá *et al.*, 1997, 1998). The greater number of days when foraging is possible at warmer sites means that ants can access a higher proportion of available resources and thus the energy available to them is greater. The richness of a local community might then be a function of productivity on those days warm enough, but not too warm, for ants to be active. This simple and intuitive mechanism is akin to the mechanism Turner *et al.* (1987) proposed for why temperature is correlated with the local richness of butterflies and moths in Great Britain and Currie's (1991) notion that 'benign environments permit more species'. Such straightforward hypotheses might have multiple underlying mechanisms, but the key point is that warmer temperatures might allow access to available resources. Thus, for any such temperature–resource mechanisms, the key prediction is that, when productivity is held constant, richness should increase with increasing numbers of days warm enough to be active.

It is unlikely that sites with higher temperature have more species only because local assemblages are simply sampling from the regional species pool, as the sampling mechanism predicts. Fisher's α, which removes the effect of sampling, still tracked temperature. This result suggests that some sites are more species rich because those sites have higher abundance, and thus lower probabilities of extinction. In fact, if we tally the number of occurrences (the number of 1-m^2 quadrats a species is detected in) as an estimate of abundance (following previous authors: Kaspari *et al.*, 2000a,b, 2003; Longino *et al.*, 2002) and plot richness against abundance, the relationship is strong and positive at each spatial grain and for Fisher's α (Table 3), indicating that some sites have more species because the probability of local extinction is reduced. This result, along with the positive relationship between Fisher's α and temperature, supports the abundance–extinction mechanism.

Table 3 Results of linear regression of richness at three spatial grains and Fisher's α against abundance.

Spatial grain	r^2	Probability
m^2 quadrat richness	0.99	<0.0001
50×50 m plot richness	0.78	<0.0001
Chao2 richness	0.48	0.0004
Fisher's α	0.45	0.0007

The metabolic theory of ecology

The results from our study support one prediction of the MTE, namely that ln-transformed species richness should be linearly associated with an inverse rescaling of annual temperature (Allen *et al.*, 2002; Brown *et al.*, 2004). At the smallest grain a second prediction was supported, namely that the slope we observed did not differ from the slope predicted by the MTE. However, the confidence intervals were large and would have included any slope from −0.76 to −0.27. At the largest grain, the confidence intervals did not include values between −0.60 and −0.70. Do other elevational diversity gradients follow the predictions of the MTE? Apparently they do (Allen *et al.*, 2002; Brown *et al.*, 2004). Allen *et al.* (2002) show that elevational gradients in both Costa Rican trees and Ecuadorian amphibians support the predictions of an earlier version of the MTE, and Brown *et al.* (2004) report that amphibians on the Volcan Barva transect in Costa Rica support the predictions of the MTE. To our knowledge, there have been no other tests of whether the MTE can explain elevational diversity gradients.

Although we cannot reject the MTE, at least at small grains, we question whether the MTE alone can be expected to adequately and consistently explain most elevational diversity gradients [note that Allen *et al.* (2002) emphasize that factors other than the MTE can influence diversity gradients]. First, the MTE posits that temperature and richness are correlated because temperature influences speciation rates. Species richness might be a function of temperature because temperature increases mutation rates, speeds up molecular evolution and thereby increases speciation rates (Rohde 1992; Allen *et al.*, 2002). However, to our knowledge, there remains relatively little empirical support for the notion that temperature limits mutation and recombination rates, and that these rates limit speciation (Bromham & Cardillo, 2003; Currie *et al.*, 2004; Cardillo *et al.* 2005; Evans & Gaston, 2005).

Even if there were convincing evidence (see Allen *et al.*, 2006), it seems unlikely that incipient speciation events along the elevational gradient studied here could drive patterns of diversity or that they would do so identically on elevational and latitudinal gradients.

One criticism of our work presented here might be that in an area this small, it is unlikely that there will be sufficient variation in speciation rates for the ants in the regional species pool to be an appropriate system for investigating the relative contribution of the MTE. We agree that attempting to link speciation rates to elevational diversity gradients might not be fruitful. However, we note that in the two key papers (Allen *et al.*, 2002; Brown *et al.*, 2004) outlining how the MTE shapes diversity gradients, data from elevational gradients make up half of the diversity gradient figures. Brown *et al.* (2004) note that 'This result holds true not only along latitudinal gradients, but also along elevational gradients where variables such as photon flux, seasonal changes in day length, and biogeographic history are held relatively constant'. We argue that the theory was developed, at least in part, to explain elevational gradients and latitudinal gradients.

A second reason why we question whether the MTE alone can explain elevational diversity gradients is that a number of geographical data sets find little support for the predictions of the MTE (Hawkins *et al.*, 2007). Of 46 geographical data sets analysed by Hawkins *et al.* (2007) (none of which were elevational gradients), nine at most hinted at some support for the specific predictions of the MTE, and the relationship between temperature and richness was both taxonomically and geographically variable (Hawkins *et al.*, 2006). In our data set, the strongest support for the MTE as an explanation for elevational diversity gradients occurs when diversity is estimated as the number of species per m^2 quadrat. At larger grains, the predictive power weakens, and the slope does not fall between −0.60 and −0.70 when we use the Chao2 estimate of richness. Species richness estimators such as the Chao2 are sensitive to the sampled data, but one view (Gotelli & Colwell, 2001) is that it makes little sense to compare communities, or what structures them or determines the number of species in them, unless sampling is complete. To our knowledge, only one previous test (Kaspari *et al.*, 2004) of the predictions of the MTE has used estimated richness. All other studies assumed that species were completely sampled from communities.

In one of the first independent tests of the predictions of the MTE, Kaspari *et al.* (2004) found that broad-scale patterns of ant diversity supported the earlier predictions of Allen *et al.* (2002), namely that the slope of ln(richness) against $1000/T$ would approximate −9.0. Since Allen *et al.*'s (2002) development of the theory, the activation energy underlying the MTE has been altered from 0.78 in Allen *et al.* (2002) to *c.* 0.65 in Brown *et al.* (2004), as has the independent variable [Allen *et al.* (2002), $1000/T$; Brown *et al.* (2004), $1/kT$]. Thus, it is unclear whether the analysis by Kaspari *et al.* (2004) would still find strong support for the MTE using the updated formulation of the theory, or whether the results presented here would agree with those presented in Kaspari *et al.* (2004). Furthermore, in the meta-analyses by Hawkins *et al.* (2007), the ln-transformation of ant species richness in 1° × 1° quadrats in Colorado and Nevada (data from Sanders, 2002) regressed against $1/kT$ was actually positive, not negative as the MTE predicts. Taken together, it seems unlikely that patterns of ant diversity are consistently predicted by the MTE across either spatial grains or extents.

Mid-domain effects

We found no support for mid-domain null models in this system. Mid-domain effect null models have received increasing attention as potential explanations for patterns of species richness along a variety of domains (e.g. Colwell *et al.*, 2004; Dunn *et al.*, 2006). Mid-domain effect null models predict the pattern of richness expected in the absence of strong gradients on the location of species ranges. Other studies have found support for MDE null models, often to the exclusion of other candidate variables (e.g. Sanders 2002; Colwell *et al.*, 2004; Dunn *et al.*, 2007a). Several recent authors have suggested that both the predictions of the MDE and its underlying assumptions lack empirical support (e.g. Zapata *et al.*, 2003, 2005; Hawkins *et al.*, 2005). Recent work suggests that the explanatory power of the MDE can depend on the size of the domain, with the MDE explaining little of the variation in species richness along small domains (e.g. Dunn *et al.*, 2006). We suspect that at least for ants in this study, the strength of the gradient in temperature is such that it swamps the effects of geometric constraints.

Spatial grain and species richness

Temperature had an over-riding influence on richness at each spatial grain in this study, perhaps because it limits abundance. There was some evidence that the explanatory power of temperature was limited at the smallest 1-m^2 quadrat spatial grain. This suggests that some other factor, such as the availability of nest sites (e.g. Armbrecht *et al.*, 2004) limits richness at the smallest grains (Table 3). At this grain, local interactions for these limiting resources might limit abundance, and therefore richness. However, as grain increases, more heterogeneity in the environment is introduced, and environmental factors, such as temperature, begin to control diversity. This agrees with previous work on global ant diversity gradients (Kaspari *et al.*, 2000a, 2003). Taken together, our results may suggest a switch from direct local control on ant species richness by competition for limiting resources at small grains to regional control on richness by temperature at large grains. That is, at both small and large grains, abundance is likely to limit richness. But at the largest grain, we suggest that temperature limits abundance, and therefore richness. At the smallest grain, limiting resources regulate abundance, and therefore richness.

CONCLUSIONS

Comprehensive analyses of global data sets by Kaspari and colleagues (Kaspari *et al.*, 2000a,b, 2003, 2004) have highlighted the role that NPP and temperature play in limiting ant diversity. The work presented here builds on these global analyses by focusing on the determinants of ant species richness at a smaller

spatial extent along elevational gradients where productivity and temperature do not covary. Two of the key findings from Kaspari's work on global ant diversity are: (1) spatial grain matters; and (2) abundance, temperature and NPP, but not geometric constraints, predict diversity. Our results are congruent with results from global scales in that we find that temperature (Kaspari *et al.*, 2000a, 2003, 2004) and perhaps abundance (Kaspari *et al.*, 2000a, 2003) limit diversity. However, in contrast to previous work at global scales, we found no effect of NPP on diversity. The development of mechanistic theories of geographical diversity gradients will be enhanced as we learn more about how the mechanisms that generate and maintain diversity vary among spatial grains, from m^2 quadrats to biomes, and among spatial extents, from elevational gradients to latitudinal gradients. Nevertheless, it seems that, at least with the ants, some general mechanisms are beginning to emerge.

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BIOSKETCHES

Nathan J. Sanders uses a combination of experimental and descriptive approaches to pursue research into the determinants of diversity and community organization of ants, the causes and consequences of biological invasions, and how biotic and environmental factors influence species diversity at local and regional scales.

Jean-Philippe Lessard is beginning his PhD at the University of Tennessee with Nathan J. Sanders where he will pursue questions about the macroecology and community ecology of ants.

Robert R. Dunn is an Assistant Professor at North Carolina State University. He studies the ecology and evolution of ant-mediated plant dispersal in south-western Australia, and patterns of diversity and ecological and evolutionary causes and consequences more generally.

Matthew C. Fitzpatrick is a PhD candidate at the University of Tennessee with Nathan J. Sanders. Matt is interested in modelling biological invasions and the impacts of global change on biodiversity, and is investigating how seed dispersal mode affects the broad-scale distribution of plants.

Editor: Tim Blackburn

SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Tests of spatial autocorrelation in ant diversity at three spatial grains and Fisher's α.

Table S2 Tests of spatial autocorrelation on the residuals of the multiple regression model including log(NPP), log(NDVI) and log(temperature) on ant species richness at three spatial grains and Fisher's α.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1466-8238.2007.00316.x
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