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LETTER

Assessing latitudinal gradients in speciation rates and biodiversity at the global scale

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Abstract

The mechanisms responsible for latitudinal biodiversity gradients have fascinated and perplexed biologists since the time of Darwin. Ecological theory has yielded two general classes of mechanisms to account for variation in biodiversity: dispersal–assembly mechanisms that invoke differences in stochastic rates of speciation, extinction and dispersal; and niche–assembly mechanisms that invoke species differences, species interactions and environmental heterogeneity. Distinguishing between these two classes of mechanisms requires explicit consideration of macroevolutionary dynamics. Here, we assess the importance of dispersal–assembly mechanisms in the origin and maintenance of biodiversity using fossil data that encompass 30 million years of macroevolution for three distinct groups of ocean plankton: foraminifera, nannoplankton and radiolaria. Applying new methods of analysis to these fossil data, we show here for the first time that latitudinal biodiversity gradients exhibit strong positive correlations with speciation rates even after explicitly controlling for variation in sampling effort and for increases in habitat area towards the equator. These findings provide compelling evidence that geographical variation in macroevolutionary dynamics is a primary determinant of contemporary biodiversity gradients, as predicted by dispersal–assembly theory.

Keywords

Latitudinal gradient, metabolic theory of ecology, neutral theory of biodiversity, niche conservatism, speciation rate, species–area relationship.

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INTRODUCTION

Biologists have been fascinated by the latitudinal gradient of increasing biodiversity from the poles to the equator since the time of von Humboldt (1808), Darwin (1859) and Wallace (1878). Contemporary data indicate that this gradient holds for nearly all major groups of terrestrial, aquatic and marine taxa (Rohde 1992; Allen *et al.* 2002; Willig *et al.* 2003; Currie *et al.* 2004), and fossil data indicate that this gradient has been maintained for at least 270 Myr (Stehli *et al.* 1969). The mechanisms responsible for biodiversity gradients remain poorly understood despite nearly two centuries of inquiry (Allen *et al.* 2003; Storch 2003), but many hypotheses have been proposed to explain them (Allen *et al.* 2003; Huston *et al.* 2003; Storch 2003; Currie *et al.* 2004).

Ecological theory has yielded two general classes of mechanisms to account for the amount of biodiversity maintained in a community (Hubbell 2001): (i) dispersal–assembly mechanisms that focus on how species richness is determined by stochastic rates of speciation, extinction and dispersal in a community whose species composition is continually changing (MacArthur & Wilson 1967; Hubbell 2001); and (ii) niche–assembly mechanisms that focus on how functional differences among species, species interactions and environmental heterogeneity combine to determine the equilibrium number and composition of species in a community (Hutchinson 1959; Chesson 2000). These two classes of mechanisms are not necessarily mutually exclusive. For example, according to dispersal–assembly theory, an increase in the speciation rate, due to some environmental factor such as temperature (Rohde 1992; Allen *et al.* 2006) or habitat area (Rosenzweig 1995; Losos & Schluter 2000), will serve to increase the number of species maintained in a community at macroevolutionary time scales (Hubbell 2001). However, increases in species number may be accompanied by natural selection for narrower niches and/or different modes of interspecific interaction, thereby allowing more species to coexist at ecological time scales. To further complicate matters,

theoretical work demonstrates that dispersal–assembly and niche–assembly models can generate similar species–abundance distributions (Chave *et al.* 2002). Consequently, evaluating the importance of these two classes of mechanisms in the origin and maintenance of biodiversity gradients requires explicit consideration of macroevolutionary dynamics.

Here, we propose a test for assessing whether dispersal–assembly mechanisms contribute to the origin and maintenance of biodiversity gradients. The test entails correlating species richness with the absolute rate of speciation (species Myr^{-1}) for different communities in plots of equal area. When performing this test, the absolute rate of speciation, and not the per-species rate of speciation (species species^{-1} Myr^{-1}), should be used because dispersal–assembly theory predicts that the speciation rate controls the number of species maintained in a community, and not vice versa (Hubbell 2001). Furthermore, plot area should be controlled for because it is known to be a primary determinant of species richness (Rosenzweig 1995; Barnosky *et al.* 2005), and may influence speciation rates through its effects on total community abundance (Hubbell 2001; Allen *et al.* 2006) and the potential for geographical isolation of populations (Rosenzweig 1995; Losos & Schluter 2000). We will return to these important issues in the *Discussion*.

If spatial variation in demographic rates maintains geographical gradients in biodiversity, as predicted by the dispersal–assembly hypothesis, our proposed test should yield a positive correlation between species richness and the speciation rate. Remarkably, we would expect this positive correlation regardless of whether different communities comprising the gradient are at dynamic equilibrium. For the dynamic equilibrium case, where the rates of speciation and extinction are equal for each community (Alroy *et al.* 2001), dispersal–assembly theory predicts that species richness will be positively correlated with the speciation rate. This is because increasing the speciation rate, while holding total community abundance constant, increases species number (Hubbell 2001), but in doing so reduces average population size (Allen *et al.* 2002), thereby resulting in higher rates of stochastic extinction (Levinton 1979; Lande *et al.* 2003). For the non-equilibrium case, where communities are in the midst of adaptive radiation (Schluter 1996), variation in species richness will directly reflect variation in net rates of taxon diversification, consistent with the dispersal–assembly hypothesis, provided that lineages in different communities have been radiating for comparable periods of time starting from similar levels of biodiversity (e.g. Buzas *et al.* 2002).

Here, we evaluate the dispersal–assembly hypothesis by applying new methods of analysis to fossil data compiled for three distinct groups of ocean plankton (planktonic foraminifera, nannoplankton and radiolaria) in Neptune, a microfossil database of global extent (Spencer-Cervato 1999). The Neptune data analysed for this study encompass *c.* 180 000 records of morphospecies occurrence, compiled from >150 deep-sea drilling holes that collectively span 30 Myr of macroevolution for 220 morphospecies of foraminifera, 313 morphospecies of nannoplankton and 457 morphospecies of radiolaria (Spencer-Cervato 1999). Using these data, we assess how the rate of first occurrence (FO), a surrogate measure for the speciation rate (Jablonski 1993; Allen *et al.* 2006), varies across latitudes at the global scale. Our analysis explicitly accounts for variation in sampling effort across space and time. Therefore, we begin by discussing how variation in sampling effort can affect the estimated dates and locations of FOs in the fossil record. We then discuss how standardized data, which control for this source of variation, can be used to assess the importance of dispersal–assembly mechanisms in the origin and maintenance of biodiversity gradients.

METHODS

Effects of variation in sampling effort on latitudinal distributions of FOs

Previous work has demonstrated the importance of standardizing sampling effort to evaluate biodiversity dynamics in the fossil record (Alroy *et al.* 2001; Barnosky *et al.* 2005). Using order statistics from probability theory, we now show how sampling effort can influence the estimate dates and locations of FOs in the fossil record. To begin, let us assume that a new species first arose through speciation at low latitudes τ, Myr ago, that N_1 samples of 'true' age $-\tau_1$ Myr have been taken from low-latitude sites where the species first appeared, and that the age estimates of samples are unbiased with error variance σ^2 Myr^2. Given that older ages and dates correspond to increasingly negative values, the estimated date of FO is equal to the minimum age estimate for the N_1 samples. The probability of obtaining any given FO estimate is therefore equal to the first-order statistic (i.e. the minimum) of the N_1 age estimates:

$$f(t,\tau_1,N_1)\mathrm{d}t = N_1\Phi(t,-\tau_1) \times \left(1 - \int_{t'=-\infty}^{t'=t} \Phi(t'-\tau_1)\mathrm{d}t'\right)^{N_1-1} \mathrm{d}t, \quad (1)$$

where $f(t,\tau_1,N_1)\mathrm{d}t$ is the probability that the date of FO is in the interval $(t - \mathrm{d}t/2,\ t + \mathrm{d}t/2)$, and

$$\Phi(t,-\tau_1) = \frac{\exp(-(t+\tau_1)^2/2\sigma^2)}{\sigma\sqrt{2\pi}}$$

is a normal distribution with mean $-\tau_1$ Myr and standard deviation σ Myr. It can be shown using eqn 1 that the

estimated date of FO gets progressively earlier as sample size N_L increases.

As a direct consequence of this sampling effect, variation in sampling effort can influence the estimated latitudinal distribution of FOs. To illustrate this point, let us assume that this same species, which first arose through speciation τ_1 Myr ago at low latitudes, subsequently evolved to occupy high latitudes $\tau_1 - \tau_2$ Myr later. Following eqn 1, the probability that the estimated date of FO at high latitudes is in the interval $(t'-\mathrm{d}t'/2,\ t'+\mathrm{d}t'/2)$ is equal to $f(t',\tau_2,N_2)\mathrm{d}t'$ for N_2 high-latitude samples of true age $-\tau_2$. By taking the convolution of $f(t',\tau_2,N_2)$ and $f(t,\tau_1,N_1)$ using standard methods of integration, we can calculate the probability, P_s, that this species is incorrectly identified as having speciated at high latitudes rather than low latitudes:

$$P_s = \int_{u=0}^{u=\infty} \int_{t=-\infty}^{t=\infty} f(t,\tau_1,N_1) f(t-u,\tau_2,N_2)\mathrm{d}t\,\mathrm{d}u, \qquad (2)$$

where P_s is the probability that the age estimate of at least one high-latitude sample is older than all of the low-latitude age estimates. Integration of eqn 2 shows that this probability is negligible, regardless of the sample sizes N_1 and N_2, if $\sigma \ll \tau_1 - \tau_2$, but that P_s is sensitive to differences between N_1 and N_2 if σ and $\tau_1 - \tau_2$ are of comparable magnitude. For example, if $\tau_1 - \tau_2 = \sigma$, the error probability is low ($P_s = 0.14$) if the sample sizes are equal ($N_1 = N_2 = 5$), but increases dramatically ($P_s = 0.55$) if sampling is an order of magnitude greater at high-latitude sites ($N_1 = 5$, $N_2 = 50$). Overall, eqns 1 and 2 demonstrate the importance of standardizing sampling effort across space and time to assess latitudinal distributions of FOs. Below we discuss how the Neptune data can be standardized to control for this issue.

Selection criteria for Neptune samples

The latitudinal distributions of FOs were separately analysed for three groups of ocean plankton (planktonic foraminifera, nannoplankton and radiolarians) using morphospecies-level occurrence data compiled in Neptune (Spencer-Cervato 1999). This database is now publicly available thanks to two major initiatives, Chronos (http://www.chronos.org) and the Paleobiology Database project (http://www.paleodb.org). For this study, we analysed morphospecies-level data for all taxa marked as valid in the February 2005 version of Neptune downloaded from the Paleobiology Database website. Each Neptune sample was dated using biostratigraphy events that have an estimated precision of ± 0.36 Myr (Spencer-Cervato 1999). To help control for issues associated with this method of age estimation, samples within 0.36 Myr of hiatuses (periods of negligible sediment accumulation) were excluded based on a published delineation (Spencer-Cervato 1998). Furthermore, data from the following drilling cores were excluded because inspection of published biostratigraphy plots (Spencer-Cervato 1999) indicated that the age estimates of samples were too imprecise for our purposes: 62A, 64, 356, 369A, 433A, 470A, 588C, 700B and 738B. Another issue of concern is taxonomic misidentifications, which will tend to bias the FO estimates towards older dates. This issue cannot easily be quantified, but should not affect our results provided that taxonomic misidentifications show no systematic trends with respect to the geographical locations of samples. A final issue of concern is the uneven distribution of Neptune samples across space and time. Samples > 30 Myr old were excluded from analysis because sample availability declines substantially beyond this date. We now discuss methods used to standardize effort for the remaining samples.

Standardizing sampling effort

The Neptune samples meeting the selection criteria above varied substantially among latitudinal bands and time intervals for all three taxonomic groups (Table 1). To simultaneously control for the effects of variation in sampling effort on the estimated dates and locations of FOs (eqns 1 and 2), and for the pronounced increase in ocean coverage towards tropical latitudes (Fig. 1), we separately analysed occurrence data for each of the three taxonomic group using the following procedure: (i) we assigned each sample to one of four equal area latitudinal bands of *c.* 9.1×10^7 km^2 (Fig. 1), and to one of six 5-Myr time intervals spanning the last 30 Myr (Table 1), using age and paleolatitude estimates in Neptune; (ii) we selected fixed numbers of samples (Table 1) at random and without replacement from each latitudinal band and time interval, yielding a standardized data set; (iii) we repeated steps (i–ii) 100 times to generate 100 standardized data sets for subsequent statistical analyses. For step (ii), the target number of samples per latitudinal band and time interval varied among taxonomic groups (Table 1), and represented a compromise between maximizing the sizes of standardized data sets and equalizing sampling effort across latitudinal bands and time intervals. Some latitudinal band/time interval categories had fewer samples than these target values (numbers in bold in Table 1). For those categories, all samples were included in the standardized data sets.

Statistical analyses of standardized data

For each standardized data set, we performed the following procedure: (i) to obtain an overall estimate of species richness for each latitudinal band, we first tallied the number of species recorded in each band and time interval, and then took an average of the six 5-Myr richness estimates for each band; (ii) to obtain a speciation-rate estimate for each latitudinal band, we first determined the paleolatitude of FO

Table 1 Total numbers of Neptune samples per equal area latitudinal band (Fig. 1) and time interval for the three taxonomic groups analysed

Group/band	Target sample size	Time interval (Myr) 0–5	5–10	10–15	15–20	20–25	25–30
Planktonic Foraminifera							
90° S–36.1° S	40	123	42	109	98	58	110
36.1° S–8.2° S	40	363	175	93	51	47	116
8.2° S–18.9° N	40	437	316	139	40	74	70
18.9° N–90° N	40	947	105	92	**18**	56	49
Nannoplankton							
90° S–36.1° S	70	171	76	162	205	73	176
36.1° S–8.2° S	70	471	238	128	**63**	79	97
8.2° S–18.9° N	70	778	507	227	214	180	144
18.9° N–90° N	70	1170	225	157	92	116	134
Radiolaria							
90° S–36.1° S	25	235	130	153	99	**22**	51
36.1° S–8.2° S	25	55	84	25	28	**23**	**3**
8.2° S–18.9° N	25	582	494	137	137	104	95
18.9° N–90° N	25	526	151	135	46	46	**19**

The target sample sizes refer to the numbers of samples taken at random and without replacement from each equal area latitudinal band and time interval (see Methods). Numbers in bold correspond to band/time interval categories that fell below the target sample sizes used to standardize sampling effort.

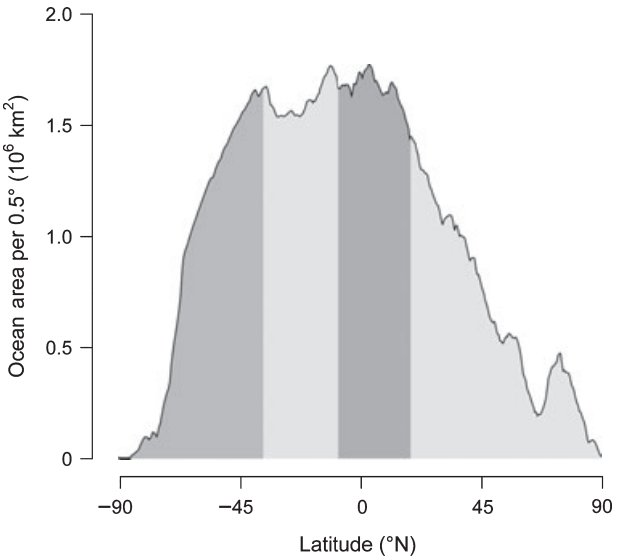

Figure 1 Latitudinal distribution of ocean surface area per 0.5° latitude, calculated based on the sea surface coverage of Casey & Cornillon (1999). The different shades of grey are used to represent four equal area latitudinal bands of *c.* 9.1×10^7 km^2 ocean area each.

for each morphospecies arising through speciation over the past 30 Myr, and then tallied the total number of FOs for each band; (iii) using the species-richness and speciation-rate estimates obtained in steps (i–ii), we fitted an ordinary least squares (OLS) regression slope. By performing steps (i–iii) for each of the 100 standardized datasets, we were able to estimate 95% CI for the species-richness and speciation-rate estimates, and to assess whether the fitted OLS-regression slopes differed significantly from 0. Importantly, in step (i), we excluded morphospecies whose dates of FO occurred within a given 5-Myr time interval from the richness calculations in that time interval to ensure statistical independence of the species-richness and speciation-rate estimates. For step (ii), we excluded morphospecies with FO estimates > 27.5 Myr old in the full set of Neptune samples to prevent taxa that may have arisen > 30 Myr ago from entering into our calculations.

RESULTS

We begin by evaluating the influence of variation in sampling effort (eqns 1 and 2) on latitudinal trends in speciation rates. We do so by comparing the latitudinal distributions of FOs observed for the full data sets to those observed for subsets of data that have been standardized to control for variation in sampling effort across space and time (Table 1, see Methods). For both the planktonic foraminifera and nannoplankton, the number of FO events per 20° latitudinal band peaks at or near the equator (−30° N to 10° N) for both the complete (panels 1 and 2 of Fig. 2a) and standardized data sets (panels 1 and 2 of Fig. 2b). Furthermore, for both groups, the relative fractions of FOs between paleolatitudes −50° N and −10° N increased after data standardization, reflecting latitudinal

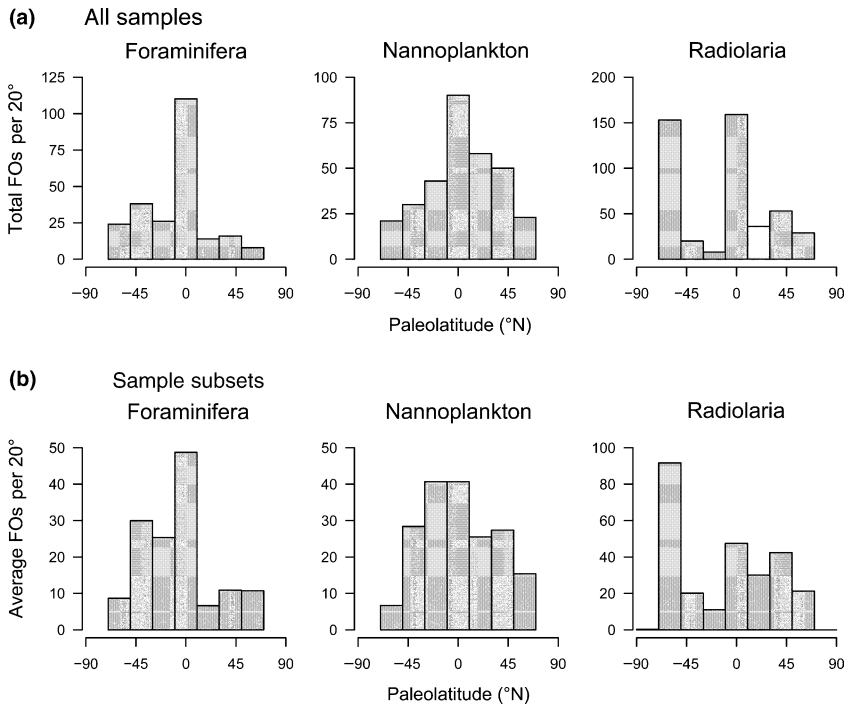

Figure 2 Numbers of taxonomic first occurrences (FOs, bars) per 20° paleolatitude for (a) all samples in the Neptune database that met our selection criteria (see Methods), and (b) standardized subsets of samples that control for variation in sampling effort across time and space (see Methods and Table 1).

variation in sampling effort and its effects on geographical trends in FO rates (eqns 1 and 2). The number of FO events per 20° latitude also exhibits a peak at the equator for the radiolaria, but with an additional peak at extreme southern latitudes (−70° N to −50° N; panel 3 in Fig. 2a). The relative fraction of FOs at southern latitudes increases substantially after data standardization (panel 3 in Fig. 2b), indicating that the southern latitude peak is not a statistical artefact of sampling.

Using standardized data for each of the three taxonomic groups, we evaluate the dispersal–assembly hypothesis by plotting average species richness per equal area latitudinal band against the time-averaged speciation rate over the past 30 Myr (Fig. 3). Three features of this figure are worthy of

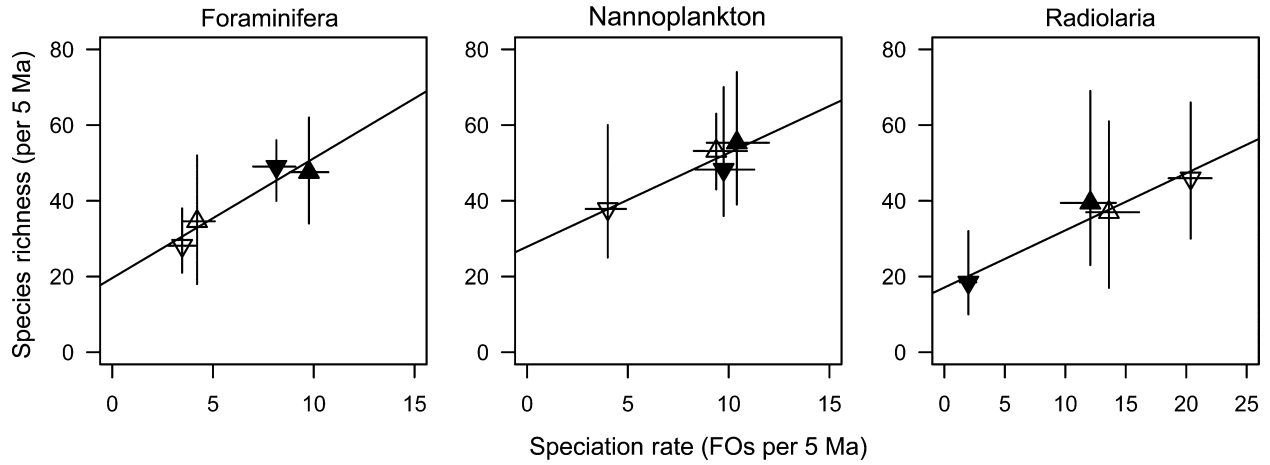

Figure 3 Relationship between species richness and the speciation rate per equal area latitudinal band (Fig. 1) for three distinct groups of ocean plankton. The averages of the estimates are depicted using different symbols for each band: 90° S–36.1° S (▽), 36.1° S–8.2° S (▼), 8.2° S–18.9° N (▲), 18.9° N–90° N (△). Speciation rates were calculated based on the latitudinal distributions of first occurrence events (FOs) over the past 30 Myr using fossil data compiled in the Neptune database (Spencer-Cervato 1999); 95% CI (vertical and horizontal lines) were generated using a randomization procedure (Table 1) that explicitly controls for the effects of variation in sampling effort (eqns 1 and 2), and for the substantial increase in ocean coverage towards the tropics (Fig. 1). The ordinary least squares-fitted slopes between species richness and speciation rate are highly significant for all three taxonomic groups ($P < 0.01$), consistent with the dispersal–assembly hypothesis.

note. First, the speciation-rate estimates for all three groups have non-overlapping 95% CI (horizontal lines), indicating significant variation in speciation rates among equal area latitudinal bands. Second, speciation rates are consistently highest in the tropics (denoted by filled triangles in Fig. 3) for the foraminifera, but generally higher outside the tropics (denoted by open triangles) for the radiolaria. The nannoplankton represents an intermediate case. Finally, third, despite these differences among taxonomic groups with respect to geographical variation in speciation rates, species richness consistently shows a positive relationship with the speciation rate, as predicted by the dispersal–assembly hypothesis. Furthermore, the fitted slopes all differ significantly from 0 ($P < 0.01$). These positive correlations are not a statistical artefact because plot area and sampling effort have both been explicitly controlled for (Table 1), and because the data used to estimate speciation rates have specifically been excluded from the calculations of species richness (see Methods).

DISCUSSION

The results in Fig. 3 provide strong support for the hypothesis that geographical gradients in biodiversity are maintained in part due to spatial variation in speciation rates, as predicted by dispersal–assembly theory (Hubbell 2001). For the foraminifera, we found that species richness and speciation rates both peak near the equator, in agreement with other foraminifera studies conducted using contemporary (Rutherford *et al.* 1999) and fossil data (Wei & Kennett 1986; Allen *et al.* 2006). These results are also consistent with paleontological studies of other taxa that report equatorial peaks in speciation rates (Stehli *et al.* 1969; Durazzi & Stehli 1972; Hecht & Agan 1972; Jablonski 1993; Flessa & Jablonski 1996). By contrast, speciation rates for the other two groups we analysed provide only partial support (nannoplankton) or no support (radiolaria) for the hypothesis that the general trend of increasing biodiversity from the poles to the equator is maintained by a concomitant trend in speciation rates. In particular, speciation rates clearly peak at extreme southern latitudes for the radiolaria (Figs 2 and 3). When assessing the generality of our findings, it is important to recognize that, in contrast to most major taxa, biodiversity is known to peak outside the tropics for many groups of ocean plankton (McGowan & Walker 1993). Nevertheless, if dispersal–assembly mechanisms are primary determinants of broad-scale biodiversity gradients, in general, we would expect species richness to peak outside the tropics for those groups that also have peaks in speciation rates outside the tropics. The results in Fig. 3 support this prediction.

Our analysis explicitly accounts for the pronounced increase in ocean coverage towards the equator (Fig. 1), and therefore represents the first explicit test of Rosenzweig's (1995) hypothesis that biodiversity peaks in the tropics due to the effects of habitat area on speciation rates. In partial conflict with this hypothesis, we found that speciation rates for planktonic foraminifera exhibit a tropical peak even after controlling for habitat area (Fig. 3). Area normalized rates of speciation vary significantly with latitude for the two other taxonomic groups as well, albeit in a more complicated manner. Nevertheless, when the latitudinal distributions of FO events for the three groups (Fig. 2) are viewed in light of the pronounced increase in ocean coverage towards tropical latitudes (Fig. 1), one must conclude that area is a primary driver of latitudinal variation in speciation rates, just not the sole variable of importance.

These findings raise questions about what other factors, besides habitat area, contribute to latitudinal gradients in biodiversity and macroevolutionary dynamics. Speciation occurs as a consequence of genetic divergence among evolutionary lineages from a common ancestor, resulting in reproductive isolation (Coyne & Orr 2004). Building on population genetics theory, Allen *et al.* (2006) have recently published a model that links latitudinal variation in speciation rates to two variables – environmental temperature and total community abundance – through their combined effects on total rates of genetic divergence in communities. Using molecular, fossil, and community abundance data for planktonic foraminifera, Allen *et al.* (2006) demonstrate that the rates of DNA evolution and *per capita* speciation (species individual^{-1} Myr^{-1}) both increase exponentially with ocean temperature in the same way as metabolic rate (i.e. *c.* 15-fold from 0 to 30 °C, Gillooly *et al.* 2001). They attribute the observed exponential increase in per capita speciation rates to the effects of temperature on the individual-level variables that govern rates of genetic divergence (i.e. generation times and mutation rates). The model and results of Allen *et al.* (2006) provide the first theoretical and empirical support for the 'evolutionary speed' hypothesis of Rohde (1978).

The model of Allen *et al.* (2006) yields two predictions of relevance here. First, it predicts temperature-induced enhancement of per capita speciation rates, and thereby explains why the overall speciation rate per unit area increases towards the tropics for planktonic foraminifera (Allen *et al.* 2006), as shown here in Fig. 3. Second, the model predicts that the total rate of speciation in a community should increase linearly with area and with total community abundance per unit area. These predictions follow directly from the model assumption of Allen *et al.* (2006) that the sizes of genetically diverging populations that give rise to new species are independent of total community abundance. This model assumption, in turn, justifies expressing speciation on a per capita basis, as is also

performed in the neutral biodiversity theory of Hubbell (2001). This assumption argues against expression speciation on a per species basis (species species^{-1} Myr^{-1}), as is the convention among evolutionary biologists (Coyne & Orr 2004), because speciation occurs at the level of populations (Coyne & Orr 2004; Allen *et al.* 2006), and because the per capita speciation rate controls the number of species maintained in a dispersal–assembled community (Hubbell 2001).

Given the central importance of total community abundance in determining speciation rates, the ecological factors that control community abundance should be primary determinants of macroevolutionary dynamics (Allen *et al.* 2006) and thus biodiversity (Allen *et al.* 2002). Silicaceous plankton, including radiolaria, tend to be most abundant in eutrophic waters, particularly subpolar waters (Leinen *et al.* 1986), whereas calcareous plankton (foraminifera and nannoplankton) tend to be relatively more abundant in oligotrophic waters. These fundamental differences in the ecological controls on community abundance may explain why the latitudinal distributions of FO events are so different for silicaceous vs. calcareous plankton (Fig. 2). Since biodiversity is ultimately an integrated measure of speciation–extinction dynamics in dispersal–assembled communities (Hubbell 2001), these same ecological factors may also explain pronounced differences in the spatial distributions of biodiversity among taxonomic groups (Fig. 3).

In conclusion, we note that by arguing for direct causal relationships between contemporary ecological variables (i.e. temperature, nutrient availability and community abundance), macroevolutionary dynamics, and biodiversity, we rely heavily on 'niche conservatism', which 'is the tendency of species to retain ancestral ecological characteristics' (Wiens & Graham 2005). Species of ocean plankton often have well-defined physiological tolerances with respect to variables such as temperature and salinity (e.g. Bijma *et al.* 1990), which help determine the boundaries of their geographical distributions in the open ocean (Hemleben *et al.* 1989). In the absence of niche conservatism, biodiversity gradients will tend to become decoupled from macroevolutionary dynamics by the movement of species to areas outside their regions of origin (Goldberg *et al.* 2005). The potential for such geographical decoupling is particularly high for ocean plankton because of their capacity for global-scale passive dispersal (Darling *et al.* 2000). The strong positive correlations we report between species richness and speciation rates for three distinct groups of ocean plankton (Fig. 3), therefore, not only support the importance of dispersal–assembly mechanisms in generating biodiversity gradients, but also support the importance of niche–conservatism mechanisms in maintaining them.

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