ECOGRAPHY

Research

Toward a theory for diversity gradients: the abundance–adaptation hypothesis

Michael D. Weiser, Sean T. Michaletz, Vanessa Buzzard, Ye Deng, Zhili He, Lina Shen, Brian J. Enquist, Robert B. Waide, Jizhong Zhou and Michael Kaspari

M. D. Weiser (michael.d.weiser@ou.edu) and M. Kaspari, Dept of Biology, Univ. of Oklahoma, Norman, OK, USA. MK also at: Graduate Program in Ecology and Evolutionary Biology, Univ. of Oklahoma, Norman, OK, USA, and Smithsonian Tropical Research Inst., Balboa, Republic of Panama, and Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, Univ. of Copenhagen, Copenhagen, Denmark. – S. T. Michaletz, V. Buzzard and B. J. Enquist, Dept of Ecology and Evolutionary Biology, Univ. of Arizona, Tucson, AZ, USA. STM also at: Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM, USA. BJE also at: Santa Fe Inst., Santa Fe, NM, USA. – Y. Deng and J. Zhou, CAS Key Laboratory of Environmental Biotechnology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China. JZ also at: School of Environment, Tsinghua Univ., Beijing, China, and Earth Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA. – Z. He, L. Shen and YD, Inst. for Environmental Genomics and Dept of Botany and Microbiology, Univ. of Oklahoma, Norman, OK, USA. – R. B. Waide, Dept of Biology, Univ. of New Mexico, Albuquerque, NM, USA, and Long Term Ecological Research Network Office, Univ. of New Mexico, Albuquerque, NM, USA.

Ecography
41: 255–264, 2018
doi: 10.1111/ecog.02314

Subject Editor: Nate Swenson
Editor-in-Chief: Miguel Araújo
Accepted 30 January 2017

The abundance–adaptation hypothesis argues that taxa with more individuals and faster generation times will have more evolutionary 'experiments' allowing expansion into, and diversification within, novel habitats. Thus, as older taxa have produced more individuals over time, and smaller taxa have higher population sizes and faster generation times, the Latitudinal Diversity Gradients (LDGs) of these clades should show shallower slopes. We describe the LDGs for archaea, bacteria, fungi, invertebrates and trees from six North American forests. For three focal groups – bacteria, ants, and trees – older taxa had shallower LDG slopes than the more recent, terminal taxa. Across 12 orders of magnitude of body mass, LDG slopes were steeper in larger taxa. The slopes of LDGs vary systematically with body size and clade age, underscoring the non-canonical nature of LDGs. The steepest LDG slopes were found for the largest organisms while the smallest, from bacteria to small litter-soil invertebrates, have shallower- to zero-slope LDGs. If tropical niche conservatism is the failure of clades to adapt to, and diversify in temperate habitats, then the steep LDGs of chordates and plants likely arise from the decreased ability of clades with large individuals to adapt to the multiple challenges of extra-tropical life.

Introduction

The current geographical distribution of species diversity is the result of the diversification, movement and extinction of clades on Earth over the last 3.5 billion yr. Over the last 50 yr, data has accumulated for a view of the latitudinal diversity gradient (henceforth LDG) where the taxonomic diversity of a clade is highest near the equator and declines toward the poles (Pianka 1966, Rosenzweig 1995, Brown

NORDIC SOCIETY OIKOS

www.ecography.org

2014). This 'canonical' pattern is so ubiquitous it is often referred to as an ecological law such that exceptions (Janzen 1981, Stevens and Enquist 1998, Kindlmann et al. 2012) are noteworthy.

An ever-growing number of models have been proposed to account for the LDG (Gotelli et al. 2009). This lack of consensus arises for several related reasons. These models seek to explain why the tropics have more species than temperate zones (reviewed by Mittelbach et al. 2007) using a variety of taxonomic concepts for a mix of clades over different geographic extents at spatial grains from m^2 plots to latitude–longitude grid cells (Rosenzweig 1995, Kaspari 2001, Hillebrand 2004, Martiny et al. 2006). Moreover, these surveys typically represent relatively few phyla (Supplementary material Appendix 1 Fig. A1). Here, we instead seek a general explanation for the slope (b) of the LDG ($\text{Log}_{10}S = a + b \times$ Latitude, where S is the number of taxa from a given clade in a fixed area, and a is the estimated number of taxa found at the equator) and test this explanation with a standardized dataset.

On the origin of latitudinal diversity gradients

We make two key assumptions. First, we assume that most deep clades originated and migrated out of the tropics (i.e. the tropics are both a cradle and a museum, Jablonski et al. 2006, Kerkhoff et al. 2014). Second, we assume that if a clade has not occupied extra-tropical latitudes it is because its propagules cannot persist in these environments. Put another way, we assume that over evolutionary time-scales, more of the currently extant species have arisen in the tropics (Schluter 2016), and that tropical propagules are less likely to immigrate into, naturalize and therefore diversify in temperate environments.

The temperate zone consists of disparate novel environments for tropical clades (Supplementary material Appendix 1 Fig. A2). Proponents of niche conservatism highlight the colder temperatures of temperate environments, suggesting that the primary agent limiting the expansion of tropical clades has been the failure of a clade's populations to adapt to freeze-resistance (Wiens and Donoghue 2004). But temperate zone environments can also expose populations to greater diurnal and seasonal variability, to greater extremes of precipitation and biogeochemistry (Walker and Syers 1976, Kaspari 2012) with consequences for growth and performance (Janzen 1967, Orians and Milewski 2007, Angilletta 2009, Kaspari and Yanoviak 2009, Kaspari et al. 2009). Niche conservatism should result from the failure to adapt to multiple stressors (Palumbi 2001). Thus a key way to allow a tropical clade to populate the rest of Earth is to enhance its rate of adaptation.

The abundance–adaptation hypothesis

Each existing clade, back to its origin, has produced a finite number of individuals. Clades vary in age (i.e. the amount of time it has existed), generation time and spatial extent. Older, widespread clades with short generation times have generated more individuals than younger, localized clades with long generation times. Each individual generated by a clade tests its genome against a particular environment. We assume that clades that have generated more individuals – by being older, more widespread, or more prolific – will have a better chance at adapting to novel environments. We call this the abundance–adaptation hypothesis.

Tropical niche conservatism (Wiens and Donoghue 2004, Wiens et al. 2010, Romdal et al. 2013) represents the failure of adaptation, the inability of a clade of tropical origin to evolve traits that allow it to thrive in the temperate zone. The abundance–adaptation hypothesis then predicts two features of a clade that will allow invasion of the temperate zone and reduce the slope of the LDG. The first is clade age; all else equal older clades will have produced more individuals than newer clades and should thus have shallower LDGs. The second is a clade's prolificacy; a clade that produces more individuals per unit time will have higher rates of adaptation, and shallower LDGs.

How do you make a prolific clade?

One formula for a prolific clade, one that maximizes the net diversification, combines the logic of body size scaling (Peters 1983) with the neutral theory of biodiversity (Hubbell 2001). Body size varies over 17 orders of magnitude with profound consequences for the natural history of the individual (Peters 1983, Yodzis and Innes 1992, Brown et al. 2004, Sibly et al. 2012). Assume that clade diversification (D) is constrained by the total number of mutations occurring in a population per unit time. Thus

$$D \propto Jvg \quad (1)$$

where J is the number of individuals an area can support, v is the per-capita mutation rate, and g is the number of generations per unit time (Hubbell 2001). Assuming a fixed resource supply rate and that per-capita resource use scales with an organism's metabolic rate (Yodzis and Innes 1992) then J should scale as the inverse of body mass. Here, we assume that metabolic rate scales as $M^{0.75}$ (Kleiber 1932) so that $J \propto M^{-0.75}$. Multiplying J by g gives the number of genomes produced per unit time. If generation time scales with body mass as $M^{0.25}$ (Peters 1983) then g should scale as $1/M^{0.25}$ or $M^{-0.25}$, giving us $Jg \propto M^{-1.0}$. We have now defined $D \propto vM^{-1.0}$. We assume, for simplicity, that the per capita mutation rate is independent of body size, although Lynch (2010) suggests that eukaryotes may have mutation rates 2 orders of magnitude higher than prokaryotes. This simplified approach focuses on how the number of mutations limits the maximum diversification rate of a clade. As in Hubbell (2001) it does not explicitly consider other processes that also affect adaptive evolution such as recombination, gene flow and barriers to dispersal.

Now consider the extinction rate, E, of this clade. The average probability of population extinction is, roughly, an inverse of the number of individuals in that population

(Lande 1993, Leigh 1999), in this case J. Since, from above, $J \propto M^{-0.75}$ the probability of population extinction is $1/M^{-0.75}$ or $M^{0.75}$ (Fig. 1a).

Thus the clade's net rate of diversification per area, $D - E$, scales with individual body mass:

$$(D - E) \propto vM^{-1.0} - M^{0.75} \quad (2)$$

As the average mass of an individual in our clade increases, $D - E$ of that clade decreases asymptotically (Fig. 1b). It decreases for two reasons: 1) the clade produces fewer individuals/genomes per unit time, with each genome independently subject to mutations that generate diversity; and 2) for a given resource supply rate, a clade with larger individuals has lower population densities at a higher extinction risk (Enquist et al. 2007). To see how this works, compare a bacterium at $1.0E^{-11}$ g with an oribatid mite at $1.0E^{-6}$ g (a little more than one third of the way to the blue whale's $1.0E^{6}$ g). Oribatid mites would have a net diversification rate 5 orders of magnitude slower than Bacteria.

To sum up, in the abundance–adaptation hypothesis, clades that are old and/or prolific are most likely to spread out of the tropics, with a corollary that clades with small individuals are more prolific and thus should have shallower LDG slopes than clades with large individuals. The two clade traits – clade age and average individual size – are likely linked, as there has been a rough increase in individual size over the history of life (Maynard Smith and Szathmary 2000). The abundance–adaptation hypothesis links historical and metabolic approaches to biodiversity through the different ways of increasing the number of individuals generated by a clade over its lifetime.

Here we present data aimed at the quantification of the slopes and intercepts of LDGs for the three domains of life: Bacteria, Archaea as well as three kingdoms of Eukaryota (Fungi, Plants, and Animals). We do so for six North American forests that vary from a lowland Panamanian forest at 9°N to a western, central subalpine, and eastern forest from 40°N to 44°N latitude (Supplementary material Appendix 1 Fig. A3). We use this data to test two central predictions of the abundance–adaptation hypothesis: 1) that LDG slopes will be steeper for more recent taxa (e.g. species) than the slopes of their older, higher taxa (e.g. families, orders); and 2) the LDG slopes for larger taxa, with slower generation times and evolutionary rates, will be steeper than for smaller taxa.

Methods

Surveys

We examined six forests from across North America (Supplementary material Appendix 1 Fig. A3) from three biogeographic regions: Barro Colorado Island, Panama (BCI) and Luquillo LTER, Puerto Rico (LUQ) from the Neotropical rain forests; Coweeta LTER, North Carolina (CWT) and Harvard Forest LTER, Massachusetts (HFR) temperate deciduous forests of eastern North America; and the coniferous forests of western North America at Niwot Ridge LTER (NWT) and Andrews LTER, Oregon (AND). The selected sites provide variation in ecosystem type from subalpine to tropical forest, in average annual temperature from 2.5 to 25.7°C, and a rough gradient of latitude from 9–44°N. Moreover, Luquillo and Barro Colorado Island are two tropical forests, the former in the Caribbean Sea, the other on the Isthmus of Panama. More detail information about this project can be found at <http://macroeco.lternet.edu/>.

Sampling in the six forests

In 2011–2012, tree species were surveyed using modified Gentry plots. Five 0.1 ha Gentry plots were established within the 25 ha plot at each site (Supplementary material Appendix 1 Fig. A3). Each Gentry plot consisted of five 100 × 2 m transects separated by a distance of 8 m,

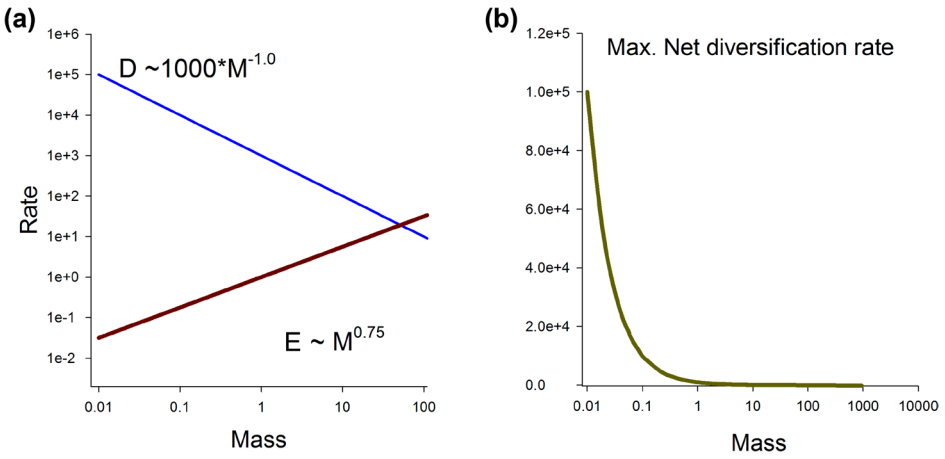

Figure 1. A model of diversity based on the scaling of diversification and extinction rates to mass. (a) Rates of diversification D and extinction E scale in opposite ways with body mass (scalar of 1000 used just to fit lines on same graph). (b) The maximum net diversification rate, D – E, decreases with mass as a consequence.

so that each Gentry plot was located within a 42 × 100 m area (<http://macroeco.lternet.edu/?q=node/13>). All plant stems greater than 1 cm basal diameter rooted within transects were identified to species. While we refer to the plants surveyed as 'trees', and the vast majority were trees, shrubs and herbaceous plants were included using the 1 cm basal diameter determinant. For plants that extended outside of the transect boundaries, inclusion criteria varied by growth form; trees were censused if the center of their stem base fell within the transect bounds, lianas were censused if rooted within the transect, and hemiepiphytes were censused if any part of the aerial root of rhizome fell within the transect. Stems were tallied as separate individuals if they were not connected above-ground or below-ground within approximately 10 cm of the soil surface.

In 2012, we sampled soil bacteria, archaea, fungi, and invertebrates, using a nested sampling design. Twenty-one $1m^2$ plots were arranged in a cross (Fig. 3) with plots at 1, 10, 50, 100 and 200 m in each cardinal direction from a central plot. We first sampled 9 cores through the litter and ca 10 cm in the soil (Oakfield Apparatus Company model HA). Soils were kept on ice in the field, then at –20°C (LUQ, CWT, AND, NWT) or –80°C (BCI, HFR) until shipped overnight on dry ice to the Inst. for Environmental Genomics at the Univ. of Oklahoma.

After placing soil samples in the cooler, we sifted litter and ca 0.5 cm of mineral soil in each plot through 1 cm mesh screens, bagged the siftate, and extracted it for two days in Tulgren funnels with 25 W bulbs (Bestelmeyer et al. 2000). Tulgren funnels use a heat gradient to drive soil invertebrates downward, where they are collected in 95% EtOH.

Quantifying diversity

The 16S rDNA sequencing detected 6 104 785 reads of 255 402 distinct bacterial OTUs and 17 931 reads of 436 Archaea OTUs. The ITS sequencing detected 4 569 225 reads of 29 740 (putatively) fungal OTUs. Of the 53 591 arthropods collected, we found 33 635 oribatid mites, 1828 ants, and 409 spiders. The tree sampling found 17 253 stems from 443 species. See Supplementary material Appendix 1 for more detailed methods on estimating taxonomic diversity.

Testing the abundance–adaptation hypothesis

All measures of taxonomic diversity (species, family, OTU, etc.) were transformed to base-10 logarithm ($Log_{10}S$) so that a unit change in diversity equals 1 order of magnitude change in linear diversity counts. Thus, for example, 'doubling' of any taxon across the latitudinal gradient examined will show the same slope, regardless of the diversity of those taxa.

We used LSM regression in the form of $Log_{10}S = a + b \times$ Latitude, and interpreted the resulting '*a*' as the estimated richness at the equator, and '*b*' as the slope of the LDG. We tested the prediction of a flatter LDG with clade age for three of the focal taxa with well-resolved phylogenies: the bacteria, the ants, and the trees (which is actually a paraphyletic functional group, but one widely used in diversity studies). As an ordinal proxy for clade age of the macrobes, we used higher taxonomic levels: genus and subfamily for ants; genus, family, order and APG clade for trees. Assuming a phylogenetically robust taxonomy, higher taxonomic divisions cannot be older than lower taxonomic levels within them (i.e. a species cannot be older than the genus to which it belongs). For the bacteria, we generated data sets that used sequence similarity values from 80 to 99% to distinguish among OTUs, and used the above protocol to generate an estimate of *b*. Specifically, we test the prediction that b approaches 0 as we tallied the diversity of OTUs defined by decreasing sequence similarity (i.e. as we effectively tallied the distribution of older and older taxa with latitude). We did the same for the ants and trees, but using traditional taxonomic criteria for ants and trees.

It was a greater challenge to evaluate the prediction that as average individual body size decreased, the *b* of the LDG would approach 0. This was primarily due to the difficulty in assigning individual mean body size to the wide variety of taxa on earth, particularly the microbes.

For two microbial kingdoms – the Archaea and Fungi – we were not confident in our ability to recognize phyla (Kõljalg et al. 2013). The bacteria, in contrast yielded 30 phyla (plus 1 category 'unrecognized'). When calculating LDGs for bacteria phyla, we removed six that were recorded from only one forest (Aquificae, Deferribacteres, Lentisphaerae, Thermotogae) and two (Synergistetes, SR1) that were recorded from only three forests. The remaining 80%, found at 5 or 6 forests, were used to generate LDGs using their respective OTUs at 97% sequence similarity.

For our invertebrate clades, we quantified diversity at the m^2 grain for three Hexapoda of different mean size (Collembola, non-ant insects and ants), the Myriapoda, and two Arachnida of different mean size (Araneae and Acari). We estimated their average mass (i.e. total mass of n dried individuals/n) using individuals extracted from soil and litter of a Panama rainforest in 2006. Litter was collected from 72: 0.25 m^2 plots and shaken through 1 cm mesh. This sifted litter was placed in Berlese funnels, which warm the litter with a light and catches the invertebrates in a jar of ethanol below. These samples were sorted under a dissecting microscope, identified, and sized along their long axis. These lengths were converted to estimates of dry mass (mg) using the scaling equations in (Kaspari and Weiser 2007). As ants are colonial insects, the appropriate measure of mass of is that of the ant colony. We used (Kaspari and Weiser 2011) summary of colony mass estimates for 664 ant populations from 49 localities, with an average mass of ca 0.01 g.

Finally, we supplemented our dataset with two other clades for which species lists existed for each of our sites (Supplementary material Appendix 1 Table A6): birds and bats. Estimates of average species mass came from (Thibault et al. 2011) and (Smith et al. 2003), respectively.

Statistics

We used an ANCOVA (SAS 2006) on $\log_{10}$ Chao 1 (Chao 1987) diversity estimates to compare the slopes of the LDG for the six focal taxa, and followed up the simple least squares regressions to calculate the 6 LDGs. To quantify the LDG at the m^2 grain (for microbes and invertebrates) and 200 m^2 grain (trees), we used plotted observed log10S of the 126 plots against the six latitudes from which they came, using LSM regression. To test the prediction of decreasing LDG slope with decreased taxonomic or phylogenetic resolution, we plotted LSM derived slopes of observed diversity from 99 to 80% sequence similarity (for bacteria) in 1% increments and taxonomic group (for trees and ants), and analyzed the resulting slopes with least squares regression.

To test the prediction of a decreased LDG slope with decreasing body size, we used the m^2 observed diversity of clades, or partial clades that could be characterized by an average individual mass as described above. The LDG slope was calculated using all 126 plots, and these slopes were plotted against the estimated average body mass. For the microbes, there was insufficient taxonomic resolution to analyze phyla of Fungi or Archaea separately, but such phyla level resolution did exist for bacteria – 24 of which were found at 5 or more sites and hence included.

Quantifying latitudinal diversity gradients

We transposed the dataset to identify plots with no records for each phylum, filled those with 0s, then retransposed back into list format. The number of taxa per each m^2 plot was tallied, and the LSM from regressing $\log_{10}S$ versus latitude for the 21 plots per site were used to calculate the slope b (the regression coefficient) and intercept.

Results

Across the six sites, the slopes and intercepts of the LDG varied across our six focal taxa (Table 1, Fig. 2). As expected, latitude accounted for considerable variation in estimated $\log_{10}$OTU site richness (ANCOVA Latitude $F_{1,24} = 18.6$, $p = 0.0002$). The estimated OTU richness at the equator (i.e. the intercept of the LDG) varied over 4 orders of magnitude from 79 oribatid species to over 250 000 bacteria OTUs (Table 1; ANCOVA taxa effect $F_{5,24} = 16.8$, $p < 0.0001$, Fig. 2). However, the intercept may underestimate diversity for most taxa – particularly for Bacteria and Fungi – given the failure of diversity estimates to stabilize over the sample plots (Supplementary material Appendix 1 Fig. A4). The slope of the LDG, b, varied from 0 for Oribatida and Archaea to Fungi to –0.037 for trees (Table 1, Latitude × Taxon $F_{5,24} = 2.6$, $p = 0.051$).

Table 1. Linear models of Log_{10} site Chao diversity versus latitude for six taxa across six forests. Coefficient values shown when $p < 0.05$, otherwise 'ns'.

Taxon	Log_{10} S at Equator (intercept)	Slope	r^2
Archaea	2.6	ns	ns
Bacteria	5.4	–0.009	0.57
Fungi	4.2	–0.009	0.87
Oribatida	1.8	ns	ns
Formicidae	2.2	–0.035	0.48
Trees	2.8	–0.037	0.62

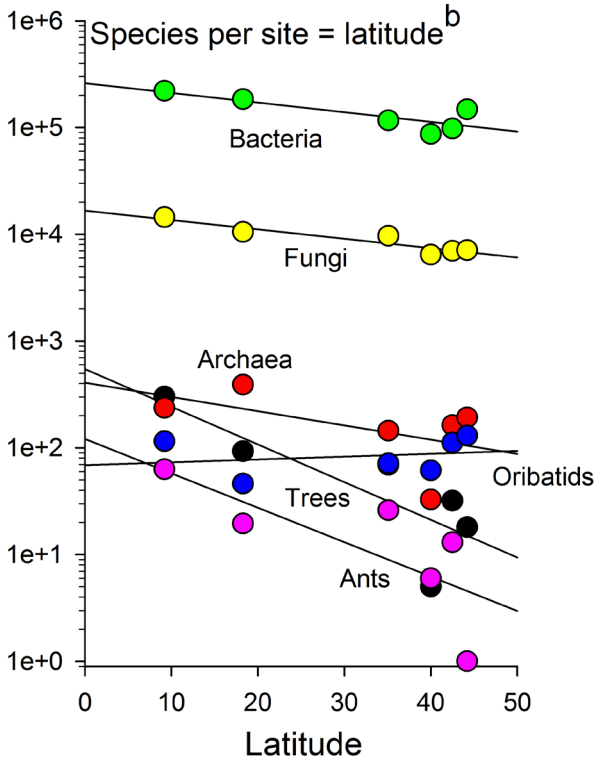

Figure 2. Diversity of our six focal clades across six forests, from Panama to Massachusetts by latitude with latitudinal diversity gradients fit by LSM regression (see Table 1 for statistics).

Diversity among forests and among sample plots

Across the soil plots and tree plots, diversity varied widely, with latitude accounting for widely different fractions of the variation (Fig. 3). Tree plot diversity per 200 m^2 varied 47-fold, from 3 species in a single subalpine forest plot to 142 species in a lowland tropical forest plot. The plots within a given forest yielded similar numbers of species and latitude accounted for 80% of this pooled plot variation (Fig. 3).

Soil microbes and invertebrates showed a different pattern of latitudinal and within-site distribution of diversity. Among the soil microbes (Bacteria + Archaea + Fungi), m^2 plot diversity varied 5-fold, but latitude accounted for only 25% of the diversity at the m^2 scale. Almost all the 17-fold variability in invertebrate plot diversity could be found within most of the sites thus latitude accounted for only 3% of plot diversity. In sum, most of the diversity signal among the trees was biogeographic; most of the diversity signal among the invertebrates, and to a smaller extent, the microbes, was local.

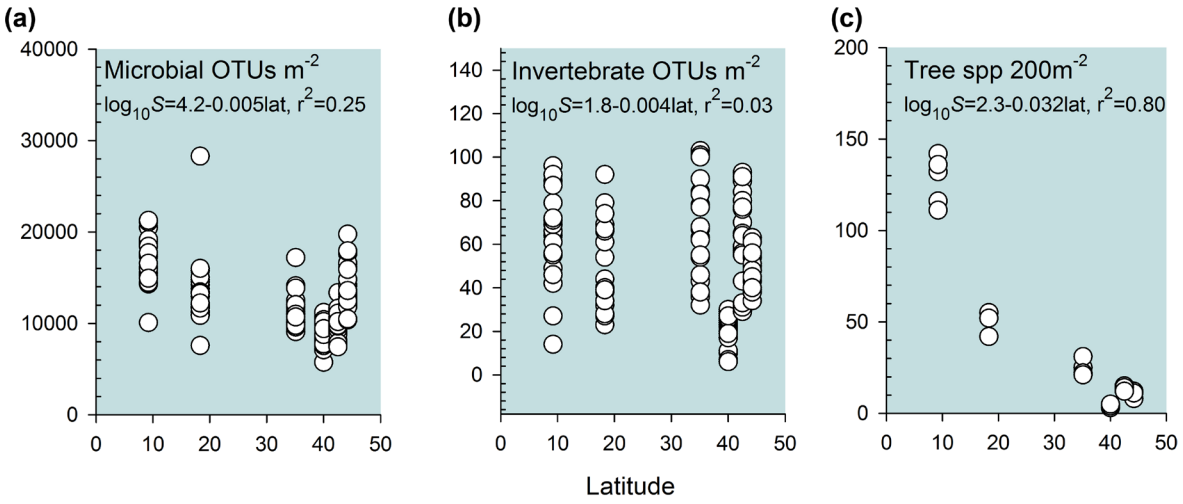

Figure 3. The number of OTUs found in each of the sample plots at the six sites. (a) Microbial OTUs (Archaea, Eubacteria, and Fungi) found in each of the 126 1 m^2 plots (21 per site); (b) arthropod morphospecies found in each of the 126 1 m^2 plots; and (c) tree species found in each of the 30 200 1 m^2 plots (5 per site).

Tests of the abundance–adaptation hypothesis

As predicted, the slope of the LDG decreased with taxonomic scope, a proxy for clade age (Fig. 4). For Bacteria, older clades were assumed to arise from higher sequence similarity criteria: the slope of the bacterial LDG dropped ca 0.004 for every 1% increase in sequence similarity (LSM regression $y = 0.03 - 0.0004 \times \text{similarity}$, $r^2 = 0.99$). The slope of the Bacteria LDG decreased (i.e. became steeper) from –0.0016 at 80% sequence similarity to ca –0.007 from 93–98% sequence similarity. At 99% sequence similarity, the LDG slope increased to ca –0.006 (i.e. became flatter), possibly due to OTUs not being lumped due to very few base-pair differences. For trees and ants, we used the taxonomic hierarchy to contrast LDGs of older and younger taxa. For trees, the slope of the LDG at the scale of Angiosperm Phylogeny Group clades was 44% more shallow than the LDG at the scale of plant species. The slope for ant subfamilies was 47% more shallow than the slope for ant species.

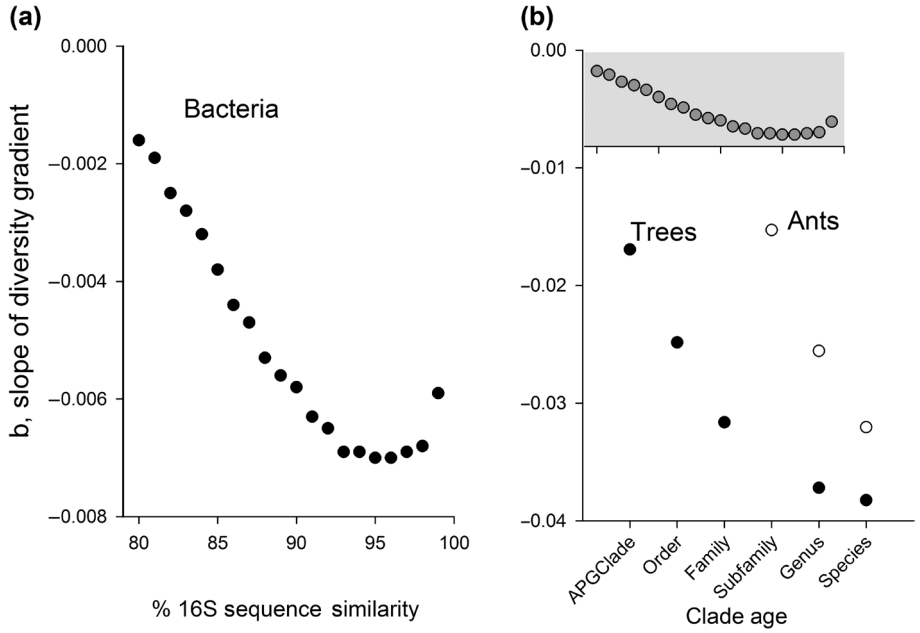

Figure 4. The slope of the latitudinal gradient for three clades as a function of the phylogenetic or taxonomic resolution (to proxy clade age) of its OTUs. (a) Varies the percent similarity definition used to delimit bacteria OTUs compared to slope of regression ($\log_{10}$OTU richness = a + b × Latitude). (b) Does the same for trees and ants using traditional taxonomic categories. The inset at the top of (b) represents the data for bacteria from (a) on the same scale as the ants and trees.

A second prediction of the abundance–adaptation hypothesis is that clades with smaller individual body masses will show flatter LDG slopes (Fig. 5). Such mass estimates, at least in the first approximation, are available for 8 animal clades (and one paraphyletic functional plant group, the trees). The slope decreased 24 fold from Collembola to trees, over a mass range of 11 o.m., (LSM regression, $b = -0.02 - 0.0035 \times \log_{10}\text{Mass}$, $p < 0.0001$, $n = 9$). A similar, if slightly steeper decrease, is found for the invertebrate clades alone (LSM regression, $b = -0.03 - 0.0052 \times \log_{10}\text{Mass}$, $p < 0.038$, $n = 6$).

Given the paucity of microbial size data, we present them in Fig. 5 as simply smaller than Collembola. The abundance–adaptation hypothesis predicts that clades with smaller individuals will have LDG slopes that approach 0. The 24 bacteria phyla show a broad range of slopes, with b's that average –0.0067. The five most species rich phyla, representing 89% of OTUs in a m^2 plot, have an average b of –0.0054 (Supplementary material Appendix 1 Fig. A5). This slope is similar to that for Fungi, –0.0054, which in turn is similar to that for Collembola and spiders. The Archaea yield an LDG slope between Myriapoda and ants.

Discussion

The tropical niche conservatism hypothesis posits that most clades originate in the tropics (Kerkhoff et al. 2014) and that 'the adaptations necessary to invade and persist in regions that experience freezing temperatures have evolved only in some' (Wiens and Donoghue 2004). Here we use the logic of neutral and scaling theories to ask why some clades have shallower LDGs. We conclude that older clades and those with smaller individuals are more likely to generate subclades that leave the tropics (and hence temper latitudinal gradients of diversity). Both features increase the number of genomes that are then tested in new environments. Clades with small individuals, in particular, should benefit from higher diversification rates and lower extinction rates (Fig. 1), resulting in higher net diversification rates that play out over the Earth's 17 orders of magnitude range of body mass. We reframe niche conservatism as a special case of lack of evolutionary potential, one most likely to limit large taxa that evolve more slowly.

A tenet of tropical niche conservatism is that extratropical clades are more likely to be of more recent origin. This is consistent with our observation that deeper clades (i.e. higher taxonomic levels and less restrictive OTU definitions) have shallower LDGs: taxonomic orders are more likely than families to include sub-clades that have left the tropics. For example, Treseder and colleagues (2014) posit that two relatively recent Divisions – Ascomycetes and Basidiomycetes – have hardier spores that have allowed them to expand into the drier and more variable temperate zones. Given that we use ordinal proxies of clade age (i.e. taxonomic ranks for trees and ants and sequence similarity for microbes) we cannot reject that using actual clade ages may give different results.

The abundance–adaptation hypothesis posits that prolific clades – those that produce more individuals – should diversify more quickly as a result. In a recent analysis of terrestrial vertebrate diversity, Jetz and Fine (2012) argue that taxa in a given bioregion will diversify with 1) increasing time that the region has existed, 2) the region's area, and 3) it's productivity. We note that decreasing the body size of individuals in a clade increases 1) apparent time (through shorter generation time), 2) apparent area (through higher abundance), and 3) apparent productivity (through decreased per capita energy use). Likewise, Hillebrand's (2004) meta-analysis found that clades of predators yielded steeper LDGs. Predators tend to

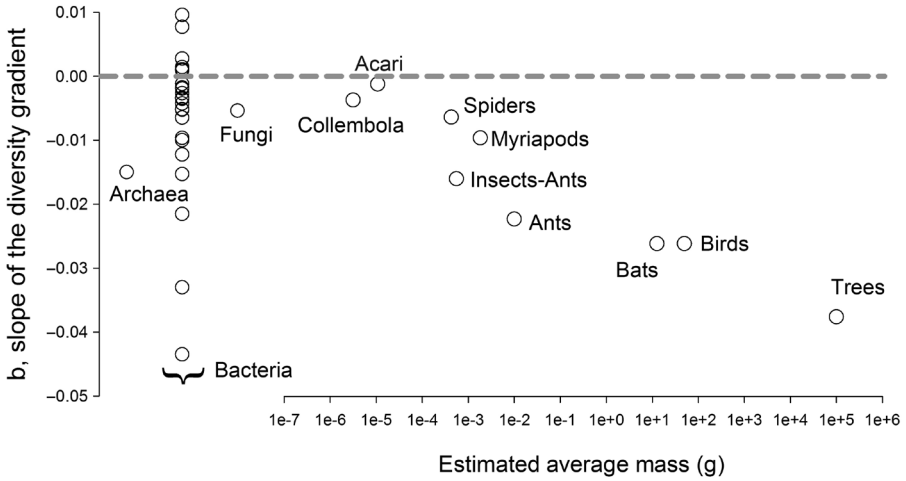

Figure 5. The slope of the latitudinal diversity gradient for clades versus their estimated size; grey dashed line represents no latitudinal gradient. The slope of regression, b, ($\log_{10}$OTU richness = a + b × Latitude) decreases for the animals and plants, for which first approximations of average individual size are possible. The fungi and archaea (which cannot be accurately resolved into subgroups) and bacteria (which yielded 24 widely-distributed phyla), are arranged at the low end of the average mass spectrum, but cannot reliably be assigned an average size. For slopes and body size, see Supplementary material Appendix 1 Table A3.

be larger than their prey and exist at lower abundances (Colinvaux 1979). Body size has the potential for synthesizing a large fraction of the biodiversity datasets.

We present a pattern where tropical niche conservatism appears to be relaxed in the clades with the smallest taxa (see also Hillebrand 2004). More datasets that combine body mass, spatial patterns of diversity, and a well-resolved phylogeny are needed to evaluate this result's generality. Exceptions likely exist, pointing to other mechanisms underlying LDGs (Buckley et al. 2010).

The role of size in microbial diversification is a particular challenge. A thorough study of size distribution in microbes is untenable, as most bacterial OTUs can't be cultured. Existing data, which has focused on documenting the extremes, have shown that fungi vary in size from one-celled yeasts to hectare-covering Basidiomycetes (Smith et al. 1992), bacterial mega-phylum Proteobacteria can vary 10 o.m. and Cyanobacteria, 4 o.m. (Shuter et al. 1983, Schulz and Jørgensen 2001). A second known unknown arises when we consider that the logic of the abundance–adaptation's scaling component is built largely from studies of plants (photoautotrophs) and animals (chemoheterotrophs). It remains to be seen if our scaling logic applies to metabolically divergent microbial chemoautotrophs and photoheterotrophs.

Local vs regional gradients of diversity and the body mass perspective

Much of what we know about LDGs involves taxa for which data can be compiled in lat–long grids (Gotelli et al. 2009, Jetz and Fine 2012). We instead explore the LDG of communities (1 m^2 plots for soil organisms, 200 m^2 plots for trees). To some extent, we make a virtue of necessity: the sheer number of taxa, and incomplete taxonomy of soil organisms force us to focus at this modest spatial scale. However, the abundance and diversity of microbes and invertebrates in our 21 1m^2 plots compare favorably to that of birds, mammals, or trees in areas the size of watersheds, bioregions, and continents. One m^2 plots are large areas to the bacteria, fungi, and mites that live in them.

Our focus on replicated plots at a limited number of forests allows us to contrast the relative role of latitude and local conditions (and, of course, sampling error) in generating between-plot variation (Fig. 3). In modified Gentry plots of 200 m^2, latitude accounted for 80% of observed variation in tree diversity. In m^2 soil plots that averaged 260 oribatids and likely tens of millions of bacteria, latitude accounted for 3 and 25% of variation in invertebrate and microbial m^2 diversity. For all soil organisms combined, latitude accounted for 25% of variation in the diversity at the m^2 scale – 25–90% of the total m^2 variation in soil diversity could be found at a given site. In marked contrast to trees, the diversity of soil organisms appears largely determined at scales of hundreds of meters, not thousands of kilometers.

That said, while the effect of latitude on diversity diminishes with decreasing body size, it rarely disappears (i.e. the average diversity of bacteria in a m^2 plot is 50% higher in lowland rainforest than in the alpine forest). Temperature remains the strongest abiotic correlate of site level diversity tested for Bacteria, Archaea, and Fungi (Zhou et al. 2016) consistent with a variety of meta-analyses highlighting temperature as a main correlate of diversity at geographic scales (Currie 1991, Rohde 1992, O'Brien 1998, Hawkins et al. 2003, Šímová et al. 2011). Temperature has been linked to diversification rates (Rohde 1992, Allen et al. 2002) and extinction rates (e.g. through niche conservatism) but a host of other drivers and abiotic conditions, including primary productivity, likely combine to limit the carrying capacity and diversity of a m^2 of soil (Kaspari 2001, Hurlbert and Stegen 2014).

Conclusion

To sum up, our goal here is to recast niche conservatism as the failure to adapt to novel environments and provide an initial test with a novel data set. We trust the abundance–adaptation hypothesis will see further rigorous tests as further studies of the biogeography of diversity are wed with even more resolved phylogenies. Moreover, other features of a clade – beyond its age and body size – should shape its cumulative genomic diversity and thus its ability to adapt to novel environments: sexual vs asexual reproduction, the presence of lateral gene transfer, and, of course mutation rates.

Here we suggest that clade age and body size are key covariates for understanding the distribution of LDG slopes across the diversity of life. Much of the noise in existing meta-analyses (Hillebrand 2004) may arise from the idiosyncratic collection of biodiversity datasets, one that is heavily skewed toward (relatively large) animals and plants. Chordates and trees are biogeography's model organisms; their steep LDGs have been influential in our view of the biogeography of diversity. But sequencing technologies are revealing that the biogeography of (old and tiny) microbes often differ in substantial ways from taxa with larger individuals (Fierer and Jackson 2006, Martiny et al. 2006). If we are correct, this is not due to 'microbial exceptionalism' (even given their metabolic diversity and capacity for lateral gene transfer). Instead, microbes appear qualitatively unique because they are quantitatively smaller – 13 orders of magnitude on average smaller than birds. The same processes that allow small organisms to rapidly fill niches in laboratories and anthropogenic habitats (Rainey and Travisano 1998, Palumbi 2001, Elena and Lenski 2003) should allow them to rapidly colonize and populate the earth. Moreover, our data suggests that another group of small organisms – soil invertebrates – 7 to 10 orders of magnitude smaller than the average bird – show LDG slopes more similar to microbes than to birds and trees (see also evidence for flat LDGs in nematodes and phytoplankton, Stomp et al. 2011, Nielsen et al. 2014). LDGs are variable, not canonical; body size and clade age can be important tools for describing and understanding the distribution of LDGs across the diversity of life.

Acknowledgements – Morgan Ernst and Ethan White pointed to body size data for birds and bats. We thank the administration and staff of the field stations/research areas: Barro Colorado Island (STRI) and Coweeta, H. J. Andrews, Harvard Forest, Luquillo and Niwot Ridge (LTER).
Funding – This work was supported by NSF EF-1065844, with J. H. Brown as the senior PI. MK thanks the Danish National Research Foundation and the Center for Macroecology, Evolution and Climate for support during the writing and analysis stage of this paper.

References

Allen, A. P. et al. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. – Science 297: 1545–1548.
Angilletta, M. J. 2009. Thermal adaptation: a theoretical and empirical synthesis. – Oxford Univ. Press.
Bestelmeyer, B. T. et al. 2000. Field techniques for the study of ground dwelling ants – an overview, description, and evaluation. – In: Agosti, D. et al. (eds), Ants: standard methods for measuring and monitoring biodiversity. Smithsonian, pp. 122–144.
Brown, J. H. 2014. Why are there so many species in the tropics? – J. Biogeogr. 41: 8–22.
Brown, J. H. et al. 2004. Toward a metabolic theory of ecology. – Ecology 85: 1771–1789.
Buckley, L. B. et al. 2010. Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. – Proc. R. Soc. B 277: 2131–2138.
Chao, A. 1987. Estimating the population size for capture–recapture data with unequal catchability. – Biometrics 43: 783–791.
Colinvaux, P. A. 1979. Why big fierce animals are rare: an ecologist's perspective. – Princeton Univ. Press.
Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. – Am. Nat. 137: 27–49.
Elena, S. F. and Lenski, R. E. 2003. Evolution experiments with microorganisms: the dynamics and genetic bases of adaptation. – Nat. Rev. Genet. 4: 457–469.
Enquist, B. J. et al. 2007. Metabolic scaling and the evolutionary dynamics of plant size, form, and diversity: toward a synthesis of ecology, evolution, and paleontology. – Int. J. Plant Sci. 168: 729–749.
Fierer, N. and Jackson, R. B. 2006. The diversity and biogeography of soil bacterial communities. – Proc. Natl Acad. Sci. USA 103: 626–631.
Gotelli, N. J. et al. 2009. Patterns and causes of species richness: a general simulation model for macroecology. – Ecol. Lett. 12: 873–886.
Hawkins, B. A. et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. – Ecology 84: 3105–3117.
Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. – Am. Nat. 163: 192–211.
Hubbell, S. 2001. The unified neutral theory of biodiversity and biogeography. – Princeton Univ. Press.
Hurlbert, A. H. and Stegen, J. C. 2014. When should species richness be energy limited, and how would we know? – Ecol. Lett. 17: 401–413.
Jablonski, D. et al. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. – Science 314: 102–106.
Janzen, D. H. 1967. Why mountain passes are higher in the tropics. – Am. Nat. 101: 233–249.
Janzen, D. H. 1981. The peak in North American ichneumonid species richness lies between 38 degrees and 42 degrees N. – Ecology 62: 532–537.
Jetz, W. and Fine, P. V. 2012. Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. – PLoS Biol. 10: e1001292.
Kaspari, M. 2001. Taxonomic level, trophic biology, and the regulation of local abundance. – Global Ecol. Biogeogr. 10: 229–244.
Kaspari, M. 2012. Stoichiometry. – In: Sibly, R. M. et al. (eds), Metabolic ecology: a scaling approach. Oxford Univ. Press, pp. 34–48.
Kaspari, M. and Weiser, M. 2007. The size-grain hypothesis: do macroarthropods see a fractal world? – Ecol. Entomol. 32: 279–282.
Kaspari, M. and Yanoviak, S. P. 2009. Biogeochemistry and the structure of tropical brown food webs. – Ecology 90: 3342–3351.
Kaspari, M. and Weiser, M. 2011. Energy, taxonomic aggregation, and the geography of ant abundance. – Ecography 35: 65–72.
Kaspari, M. et al. 2009. Sodium shortage as a constraint on the carbon cycle in an inland tropical forest. – Proc. Natl Acad. Sci. USA 106: 19405–19409.
Kerkhoff, A. J. et al. 2014. The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. – Proc. Natl Acad. Sci. USA 111: 8125–8130.
Kindlmann, P. et al. 2012. Inverse latitudinal gradients in species diversity. – In: Storch, D. et al. (eds), Scaling biodiversity. Cambridge Univ. Press, pp. 246–257.
Kleiber, M. 1932. Body size and metabolism. – Hilgardia 6: 315–353.
Kõljalg, U. et al. 2013. Towards a unified paradigm for sequence – based identification of fungi. – Mol. Ecol. 22: 5271–5277.
Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. – Am. Nat. 142: 911–927.
Leigh, E. G. J. 1999. Tropical forest ecology: a view from Barro Colorado Island. – Oxford Univ. Press.
Lynch, M. 2010. Evolution of the mutation rate. – Trends Genet. 26: 345–352.
Martiny, J. et al. 2006. Microbial biogeography: putting microorganisms on the map. – Nat. Rev. Microbiol. 4: 102–112.
Maynard Smith, J. and Szathmary, E. 2000. The origins of life: from the birth of life to the origin of language. – Oxford Univ. Press.
Mittelbach, G. G. et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. – Ecol. Lett. 10: 315–331.
Nielsen, U. N. et al. 2014. Global-scale patterns of assemblage structure of soil nematodes in relation to climate and ecosystem properties. – Global Ecol. Biogeogr. 23: 968–978.
O'Brien, E. M. 1998. Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. – J. Biogeogr. 25: 379–398.
Orians, G. H. and Milewski, A. V. 2007. Ecology of Australia: the effects of nutrient-poor soils and intense fires. – Biol. Rev. 82: 393–423.
Palumbi, S. R. 2001. Humans as the world's greatest evolutionary force. – Science 293: 1786–1790.
Peters, R. H. 1983. The ecological implications of body size. – Cambridge Univ. Press.

Pianka, E. 1966. Latitudinal gradients in species diversity: a review of the concepts. – Am. Nat. 100: 33–46.
Rainey, P. and Travisano, M. 1998. Adaptive radiation in a heterogeneous environment. – Nature 394: 69–72.
Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. – Oikos 65: 514–527.
Romdal, T. S. et al. 2013. Life on a tropical planet: niche conservatism and the global diversity gradient. – Global Ecol. Biogeogr. 22: 344–350.
Rosenzweig, M. L. 1995. Species diversity in space and time. – Cambridge Univ. Press.
SAS 2006. SAS/STAT user's guide, version 9.1. – Sas Inst.
Schluter, D. 2016. Speciation, ecological opportunity, and latitude. – Am. Nat. 187: 1–18.
Schulz, H. N. and Jørgensen, B. B. 2001. Big bacteria. – Annu. Rev. Microbiol. 55: 105–137.
Shuter, B. J. et al. 1983. Phenotypic correlates of genomic DNA content in unicellular eukaryotes and other cells. – Am. Nat. 122: 26–44.
Sibly, R. M. et al. 2012. Metabolic ecology: a scaling approach. – John Wiley and Sons.
Šímová, I., et al. 2011. Global species–energy relationship in forest plots: role of abundance, temperature and species climatic tolerances. – Global Ecol. Biogeogr. 20: 842–856.
Smith, F. A. et al. 2003. Body mass of Late Quaternary mammals: Ecological Archives E084-094. – Ecology 84: 3403–3403.
Smith, M. L. et al. 1992. The fungus *Armillaria bulbosa* is among the largest and oldest living organisms. – Nature 356: 428–431.
Stevens, G. C. and Enquist, B. J. 1998. Macroecological limits to the abundance and distribution of *Pinus*. – In: Richardson, D. M. (ed.), Ecology and biogeography of the genus *Pinus*. Cambridge Univ. Press, pp. 183–190.
Stomp, M. et al. 2011. Large-scale biodiversity patterns in freshwater phytoplankton. – Ecology 92: 2096–2107.
Thibault, K. M. et al. 2011. Multimodality in the individual size distributions of bird communities. – Global Ecol. Biogeogr. 20: 145–153.
Treseder, K. K. et al. 2014. Evolutionary histories of soil fungi are reflected in their large-scale biogeography. – Ecol. Lett. 17: 1086–1893.
Walker, T. W. and Syers, J. K. 1976. The fate of phosphorus during pedogenesis. – Geoderma 15: 1–19.
Wiens, J. J. and Donoghue, M. J. 2004. Historical biogeography, ecology and species richness. – Trends Ecol. Evol. 19: 639–644.
Wiens, J. J. et al. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. – Ecol. Lett. 13: 1310–1324.
Yodzis, P. and Innes, S. 1992. Body size and consumer–resource dynamics. – Am. Nat. 139: 1151–1175.
Zhou, J. et al. 2016. Temperature mediates continental-scale diversity of microbes in forest soils. – Nat. Commun. 7: 12083.

Supplementary material (Appendix ECOG-02314 at <www.ecography.org/appendix/ecog-02314>). Appendix 1.