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Niche and metabolic principles explain patterns of diversity and distribution: theory and a case study with soil bacterial communities

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The causes of biodiversity patterns are controversial and elusive due to complex environmental variation, covarying changes in communities, and lack of baseline and null theories to differentiate straightforward causes from more complex mechanisms. To address these limitations, we developed general diversity theory integrating metabolic principles with niche-based community assembly. We evaluated this theory by investigating patterns in the diversity and distribution of soil bacteria taxa across four orders of magnitude variation in spatial scale on an Antarctic mountainside in low complexity, highly oligotrophic soils. Our theory predicts that lower temperatures should reduce taxon niche widths along environmental gradients due to decreasing growth rates, and the changing niche widths should lead to contrasting α- and β-diversity patterns. In accord with the predictions, α-diversity, niche widths and occupancies decreased while β-diversity increased with increasing elevation and decreasing temperature. The theory also successfully predicts a hump-shaped relationship between α-diversity and pH and a negative relationship between α-diversity and salinity. Thus, a few simple principles explained systematic microbial diversity variation along multiple gradients. Such general theory can be used to disentangle baseline effects from more complex effects of temperature and other variables on biodiversity patterns in a variety of ecosystems and organisms.

1. Introduction

The complex entanglement of ecological and evolutionary processes hinders the development of a unified understanding of the forces shaping patterns of biodiversity. Yet two fundamental attributes of organisms affect the distribution and diversity of species: their niches and metabolisms. An organism's niche is the set of conditions under which it can survive and reproduce [1]; and an organism must have a sufficiently efficient and high rate of metabolism to survive and reproduce. Thus, an organism's metabolic capabilities must, at least in part, determine its niche, and its niche imposes constraints on its distribution. Furthermore, as different organisms have different niches, only a subset of a regional collection of species can have niches allowing survival and reproduction in the conditions found at a local site. Therefore, the distribution of niches, mediated by metabolic requirements, constrains the size and composition of the subset of organisms with niches matching local conditions, limiting local species richness (α-diversity) and the turnover in species composition between sites (β-diversity).

It is unclear, however, to what degree niche and metabolic constraints shape patterns of diversity along environmental gradients and in different kinds of

organisms. An essential approach for elucidating the role of these constraints on diversity is to empirically and theoretically study ecological systems and suites of environmental gradients characterized by relative simplicity and minimal confounding variables. Indeed, it seems unlikely that ecologists will be able to develop a robust and unifying understanding of more complex ecological systems without first gaining better insight into the ecology and biogeography of simpler counterparts.

Thermal diversity gradients are especially important to ecology due to the fundamental effect of temperature on metabolic and other biological rates [2] and its wide variability across the globe. Two diversity gradients associated with temperature have received a lot of attention, particularly in plants and animals: latitudinal and altitudinal diversity gradients. Although many researchers suggest temperature plays a central role in these gradients [3–7], especially in latitudinal diversity gradients, the precise role of temperature remains controversial, largely because evolutionary histories and other abiotic variables, in addition to temperature, often change along the gradients. Furthermore, little quantitative theory exists that makes baseline predictions of how temperature and other environmental variables should affect taxon niches and how these effects should scale up to affect α- and β-diversity. Such fundamental theory is necessary to disentangle baseline effects from more complex effects of temperature and correlated variables on diversity.

Among microbes, limited and conflicting information exists regarding latitudinal and elevational diversity gradients. A variety of α-diversity patterns have been reported along elevational gradients, including increasing, decreasing, invariant and hump-shaped patterns [8–13]. The limited global-scale studies of latitudinal patterns in microbes have reported either little change in α-diversity or increasing α-diversity with temperature [7,14,15]. Few studies have examined microbial β-diversity along elevational gradients [16]. The variability in α-diversity patterns may be due to substantial changes in macroorganism communities along the gradients with associated changes in organic inputs to soil, plant–microbe mutualisms, microbial niches linked to animal life, or differences in sampling and sequencing depth between studies. Gradients in pH and salinity are also widely studied in microbes [14,17,18], yet understanding of how these physico-chemical variables scale up to affect diversity is also limited. Given that microbes exhibit extraordinary phylogenetic and functional diversity, which underpins biogeochemical cycles, investigation of microbial diversity gradients is crucial for developing unified understanding in ecology and biogeography.

In order to understand the role of interlinked metabolic and niche effects in shaping diversity patterns, we (i) develop baseline theory integrating metabolic and niche principles that predicts how, all else being equal, α- and β-diversity should change along gradients in temperature and other environmental variables and (ii) evaluate these theoretical predictions by investigating the distribution and diversity of bacterial taxa along gradients in pH, salinity and elevation (temperature) in an ecosystem and landscape characterized by its relative simplicity—soil bacteria communities on a mountainside in the McMurdo Dry Valleys, Antarctica. This ecosystem is characterized by low temperatures, strong water and nutrient limitation, extremely low productivity, and no vascular plants and macroorganisms (electronic supplementary material). Our study is one of the first investigations of diversity along the entire elevational gradient of a mountainside in Antarctica.

2. Theory

We develop a first-order theory of diversity patterns based on two observations related to organism niches and metabolism: (i) species performance varies along environmental gradients (such as in pH or salinity) so that a given taxon has positive population growth only in a specific part of a gradient (its niche [1]) and (ii) among ectothermic organisms, there is an overall pattern of increasing growth rate with increasing temperature [19].

(a) Prediction 1: higher temperatures promote wider niches both within and among organisms

Consider that the *in situ* performance and growth rate of an organism depends on an environmental condition z, such as pH or salinity. At non-optimal values of z, decreases in growth rate due to physiological effects or altered biotic interactions lead to minimum and maximum values of z at which the organism can maintain positive growth rates necessary to sustain its population. An organism's realized niche thus reflects this growth rate response curve. However, temperature also affects performance, metabolic rate, and growth rate. Owing to its positive effects on biochemical reaction rates, an ectotherm's growth rate and performance increases with temperature for most of its thermal response curve [2,19,20]. Consequently, in this temperature range, the height of an organism's z gradient growth response curve increases with temperature, leading to an increasing range in the values of z that allow positive growth. Thus, increasing temperature should increase a taxon's niche width and consequently its occupancy (derivation in electronic supplementary material). Near the upper limit of an organism's thermal niche, its performance drops off steeply, but the growth rates of other organisms with hotter niches tend to continue to increase with temperature, resulting in an overall interspecific trend of increasing growth rate with increasing temperature from approximately $-40°C$ to $30°C$ or more [2,19,21–24]. Consequently, increasing temperature along a pronounced thermal gradient should also increase the average and maximum niche width and occupancies of taxa comprising communities (figure 1a).

(b) Prediction 2: increasing niche width increases α-diversity but decreases β-diversity

Consider an environmental gradient E, such as temperature, along which niche width changes (figure 1a). Two sites having identical values of E may have different values of an orthogonal environmental variable z. The taxa that can potentially live at a given value of E comprise a source pool with richness S. Different taxa have different niches along the z gradient. Each taxon's niche has a centroid position x and a width w that together dictate whether the niche overlaps with a site's z, thereby constraining the taxon's occurrence. If a taxon has a wider niche, then it can be present at a larger range of conditions. A site's richness thus reflects the proportion of source pool taxa whose niches overlap with local conditions, and increasing niche width increases the proportion of source pool
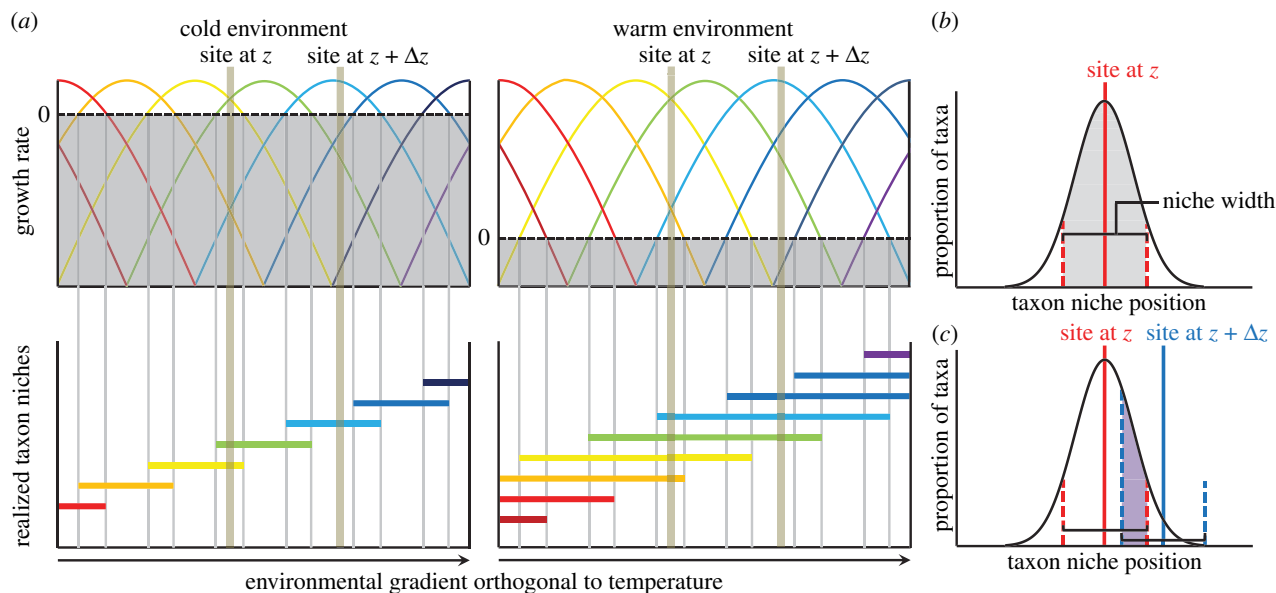
Figure 1. Illustrations of our theory. (*a*) Schematic showing how increasing temperature increases niche width, leading to increasing α-diversity but decreasing β-diversity. Taxa or populations have performance curves along a gradient orthogonal to temperature. Zones of positive growth demarcate their realized niches (matching coloured horizontal bands). Since temperature positively affects growth, growth can be positive across wider ranges of conditions at warmer sites, leading to increased niche widths; consequently, more taxa have niches overlapping with local conditions (thick vertical bars) and more taxa are shared between sites. (*b*) Illustration of how the niche width and source pool's distribution of taxon niche positions along a gradient z orthogonal to temperature affect α-diversity. α-Diversity is proportional to the grey area, the total proportion of source pool taxa having niches overlapping with site conditions. (*c*) Illustration of how niche width affects β-diversity by influencing the number of taxa shared between two sites with different conditions (purple area).

taxa that can be present at a site, leading to increased α-diversity (figure 1*b*). However, because increasing niche width leads to taxa being present across a wider range of sites, the taxonomic composition of two sites differing in z will also share a greater number of taxa, resulting in decreased β-diversity (figure 1*c* and see box 1 for derivations and electronic supplementary material and figure S8 for supporting simulations).

(c) Prediction 3: α-diversity is a monotonic or unimodal function of environmental condition z, depending on the distribution of niche positions along z

In sum, the frequency distribution of niches along a gradient shapes diversity patterns along the gradient. For most unimodal distributions in taxon niche position (x), increasing deviations in a site's z from its mode leads to decreased richness. Even for very odd-shaped distributions, increasing the difference between x's mode and z leads to decreasing richness as the difference becomes large, with multi-modal distributions potentially adding initial bumps to this pattern. As niche width approaches zero, the richness pattern exactly mirrors the x distribution. If the distribution is unimodal and symmetric, then α-diversity is a hump-shaped function of z, with peak richness occurring at mean x. If the distribution instead is monotonically decreasing for all x, such as in exponential distributions, then α-diversity should decrease with increasing z. Unsurprisingly, β-diversity should also increase with increasing difference between two communities' z-values.

Two complimentary approaches can be used to infer the overall shape and central tendency of a niche position distribution. First, the baseline expectation for the overall shape of the distribution may be predicted using fundamental physical and mathematical constraints on the possible values of x in order to infer the most likely and unbiased

distribution given these constraints ([25–27]; see the electronic supplementary material for details). For example, soil conductivity, which provides a measure of salinity, cannot be negative but there is no hard upper bound to large conductivity values. Consequently, the conductivity niche position distribution is expected to be positively skewed (right-tailed), the null expectation being an exponential distribution [25]. As a result, a trend of decreasing richness with increasing conductivity is expected. Since the distribution in pH niche position is fundamentally constrained only by a finite mean and finite variance, its expected distribution is a normal distribution [25], suggesting a hump-shaped relationship between richness and pH.

Consideration of underlying eco-evolutionary mechanisms shaping niche position distributions can be used to further infer distribution attributes. Each taxon's niche evolved as a consequence of some combination of selection pressures and various historical circumstances. The niche position distribution reflects the aggregation of these processes operating within fundamental constraints on potential niche positions. As the processes are mediated by the ecological and biogeographic historical setting, the first-order expectation is that taxon niches are centred on the conditions most common to a locality or region. Therefore, central tendencies of unimodal niche position distributions, such as pH niche positions, should be similar to average conditions.

Our theory can be explicitly extended to multiple environmental variables and corresponding taxon niche positions, quantifying how the distribution of the niche hypervolumes of taxa, *sensu* Hutchinson [1], shapes diversity patterns (see the electronic supplementary material for derivations). Analytical solutions can be obtained for α- and β-diversity as a function of niche width and environmental conditions by assuming particular niche position distributions based on empirical or theoretical information (e.g. see the electronic supplementary material).

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> **Box 1.** Theory on effects of niche width on α- and β-diversity.
>
> Consider the case in which niche width changes along an environmental gradient, E, such as temperature. Two different communities, i and j, have the same value of E but differ along orthogonal environmental variable z by Δz. The taxa that can potentially live at a given E comprise its source pool of richness S. The taxa have niches for z with centroid positions x and a width w that determine their occurrences along z when dispersal is not limiting. For simplicity, we assume here that all taxa at a given E have the same w. In the electronic supplementary material, we present additional theory demonstrating that having w vary between taxa within source pools does not alter our conclusions. Taxon niche positions are distributed according to a density function $f_X(x)$ specifying the proportion of the source pool taxa having niche positions at x. Thus, local richness is proportional to the area under $f_X(x)$ that is centred at a site's z and bounded by niche width (figure 1b):
>
> $$R(z, w) = S \int_{z-w/2}^{z+w/2} f_X(x)\mathrm{d}x. \tag{2.1}$$
>
> The above equation is an increasing function of w that converges on S with increasing w. The null assumption is that S is invariant; however, changes in S can be addressed by substituting in a function for S. Jaccard's β-diversity (β) for two communities is obtained by determining the area under $f_X(x)$ overlapping with both communities (figure 1c), giving
>
> $$\beta = 1 - \frac{C}{R_i + R_j - C}, \tag{2.2}$$
>
> where R_i and R_j are the richness of community i located at z and community j located at $z + \Delta z$, respectively, and C is the number of taxa shared by both communities: $C = 0$ for $w \leq \Delta z$ and $C = S \int_{z+\Delta z-w/2}^{z+w/2} f_X(x)\mathrm{d}x$ for $w > \Delta z$. Equation (2.2) shows that increasing w leads to decreasing β-diversity, with β converging on zero with increasing w and plateauing at one at low w (when $w \leq \Delta z$). Thus, theory predicts that since taxa that reside at lower temperatures should have narrower niches, a lower portion of the taxa adapted to lower temperatures have niches overlapping a given local habitat's conditions, resulting, all else being equal, in lower α-diversity but higher β-diversity.

3. Material and methods

(a) Site description, sampling and abiotic data

This study was conducted in bare mineral soils from Mt Voslips, Antarctica, characterized by approximately -18°C mean annual air temperature at its bottom [28], approximately 10 cm per year precipitation [29], and extremely low soil organic carbon and nitrogen contents ([30]; see the electronic supplementary material, appendix and data for details). An elevational transect was established on the peak approximately 1300 m.a.s.l., with perpendicular secondary transects following contour lines separated by 200 m of elevation. Along these secondary transects approximately 200 g samples were collected from 10×10 cm quadrats at 0, 10, 20, 110, 1110 and 11 110 cm by homogenizing with sterilized scoops within the quadrats to 5 cm depths. This logarithmically spaced design was chosen to obtain samples separated by multiple orders of magnitude variation in distance, allowing for more powerful analyses of distance effects.

Samples were sorted in the laboratory under laminar flow hoods to isolate fine soil fractions (less than 2 mm) and then subsampled to create composite samples for each transect to determine average organic matter and nitrogen content (details in the electronic supplementary material). Soil pH, conductivity (a measure of salinity), total nitrogen and organic carbon were determined as described previously [31]. Mean annual air temperature was estimated for each transect using an empirically supported climatic model customized for the region (as described in [32], electronic supplementary material).

(b) DNA sequence analysis

We extracted DNA from the 42 soil samples and sequenced 16S rRNA genes as described previously [33] with universal bacterial primers and protocols used in other McMurdo Dry Valley studies ([31], electronic supplementary material). Forty samples were successfully sequenced. 16S rRNA gene sequences were quality filtered, denoized, screened for PCR errors, chimaera checked, and processed, as described previously ([31]; electronic supplementary material), and assigned to operational taxonomic units ('species') using a 97% genetic similarity cut-off. We used subsampling to normalize for differences in sequencing depth between samples and the Chao1 richness estimator—a robust non-parametric lower bound richness estimator commonly used in ecology—to provide estimates of the number of taxa in communities (α-diversity) that account for sampling effects connected to field collection and DNA extraction and sequencing ([34]; electronic supplementary material). Raw sequence data have been submitted to NCBI Sequence Read Archives, accessible through Bioproject PRJNA232062.

(c) Statistical analysis

Canoco for Windows v. 5.0 was used to estimate relative taxon niche widths and abundance-weighted altitudinal positions. Canonical correspondence analysis (CCA) arranged individual taxa along ordination axes to maximize the distances between samples attributable to differences in environmental variables. Ordination axes were constrained by elevation, log conductivity and pH. As we were interested in the relationship between elevation and niche width, we explored the niche axes orthogonal to elevation. Thus, we included elevation as a covariate to obtain two canonical axes, the first correlated with conductivity and the second with pH. Conductivity and pH niche widths were calculated as standard deviations of the scores of the first and second axis, respectively [35]. Altitudinal niche positions were calculated so that the axes were constrained with altitude only and this first canonical axis thus represented the arrangement of taxa and samples along the elevational gradient. Niche position along this axis was then calculated for each taxon as abundance-weighted means of sample scores.

Interspecific patterns in niche width were examined using LOESS regression, quadratic regression and quantile regression. A description and results of the quantile regressions can be found in
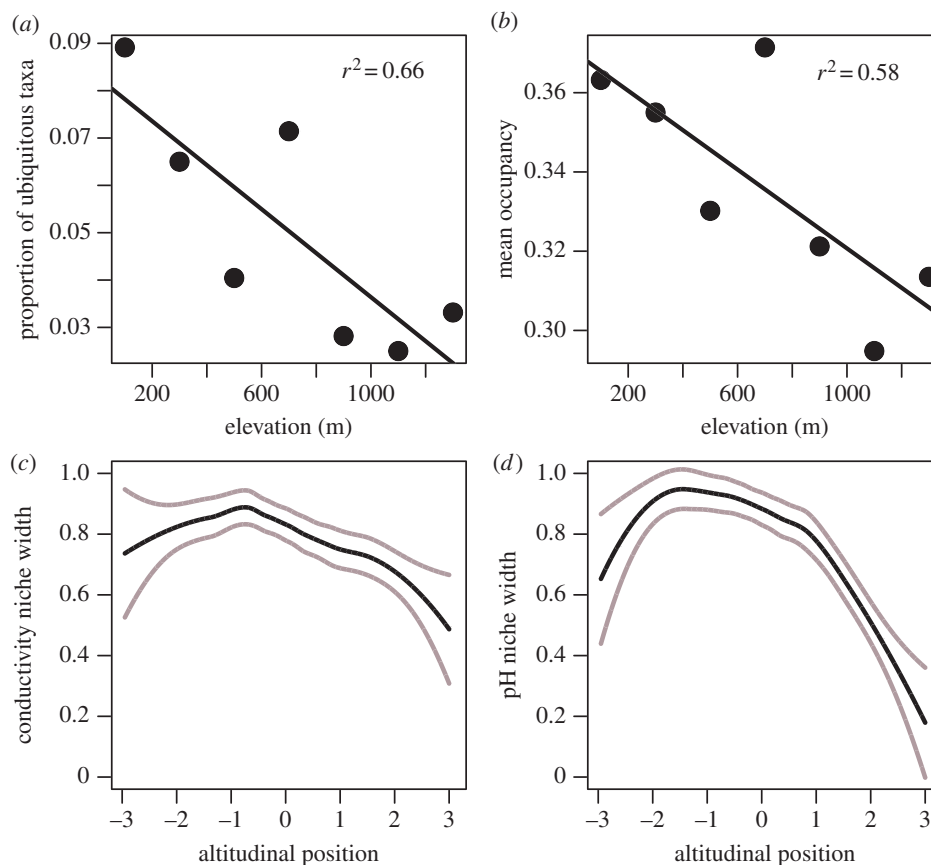
Figure 2. Complimentary measures showing that taxon niche widths tend to decrease with elevation. The proportion of taxa ubiquitously distributed within a transect (a) and the mean occupancy of taxa (b) decrease with increasing elevation. Smoothing local regression of conductivity niche widths (c) and pH niche widths (d) versus taxon altitudinal position shows that the niche widths are highest at low elevations and lowest at high elevations. Altitudinal position is abundance-weighted, normalized altitudinal position of a taxon on the mountainside. Grey lines indicate 95% confidence intervals. Note that since taxa with very wide niches cannot simultaneously have extreme niche positions, 'edge effects' necessarily lead to the lowest and highest altitudes having smaller niche widths, resulting in the hump-shapes; however, the right-skew of the hump-shapes indicates an overall pattern of decreasing niche widths with increasing elevation. (Online version in colour.)

the electronic supplementary material. LOESS regression was performed in R [36]. For the LOESS regression, we excluded single-occurrence taxa because these taxa were numerous, representing 51% of all taxa and their distribution did not exhibit a pattern with respect to elevation (electronic supplementary material, figure S6). Consequently, their inclusion in LOESS regression would obfuscate any pattern in niche width exhibited by the other taxa.

Ordinary and multiple linear regression were used to reveal relationships between richness and temperature, elevation, soil N content, soil organic matter content, log conductivity and pH. The best performing multiple linear regression model was determined using a backward selection procedure to remove the non-significant predictors according to the Akaike information criterion (AIC) in R using the function 'lm' from the package 'stats' (see the electronic supplementary material, tables S1 and S2 for complete results). The subsampled Chao1 richness and raw number of taxa were highly correlated ($r^2 = 0.67$) and the nature and statistical significance of the α-diversity analyses were the same for the two richness estimates. Thus, we report only results for Chao1 richness.

4. Results

(a) Niche widths and occupancies

In agreement with Prediction 1, the proportion of taxa ubiquitously distributed along a transect decreased with elevation (figure 2a; $r^2 = 0.66$, $p = 0.027$). Similarly, the mean proportion of sites occupied by taxa within a transect (occupancy) decreased with elevation (figure 2b; $r^2 = 0.58$, $p = 0.046$).

Using CCA to quantify each taxon's abundance-weighted relative niche width and altitudinal position [36], a smoothing local regression (LOESS) of taxon pH and conductivity niche widths versus altitudinal position shows that lower elevations have the largest widths (figure 2c,d, smoothing parameter (α) = 0.7; electronic supplementary material). Regressions of quadratic functions for both pH and conductivity niche widths were also significant, with peaks in mean niche width (maxima of quadratic functions) located towards the bottom-half of the mountain (all $p < 0.01$, see the electronic supplementary material and figure S2). We also performed linear regression on the effects of elevation on within-transect conductivity and pH niche widths of the taxa observed at all transects, quantifying niche widths by the ranges in conditions occupied by a taxon within a transect. Slopes of these intraspecific relationships between niche width and elevation were significantly less than zero, indicating that a taxon's realized niche tends to be narrower at higher elevations (one-sided, one-sample T-tests on slopes, all $p < 0.001$; see the electronic supplementary material, figures S3 and S4). Thus, both intraspecific and interspecific variation in niche width was predictably related to temperature and underpinned the observed occupancy and niche width gradient.

(b) Elevational diversity gradient

As predicted, α-diversity decreased with elevation (figure 3a; $r^2 = 0.34$, $p < 0.001$), and in contrast the mean Jaccard β-diversity (a.k.a. Jaccard distance) of all pairwise comparisons

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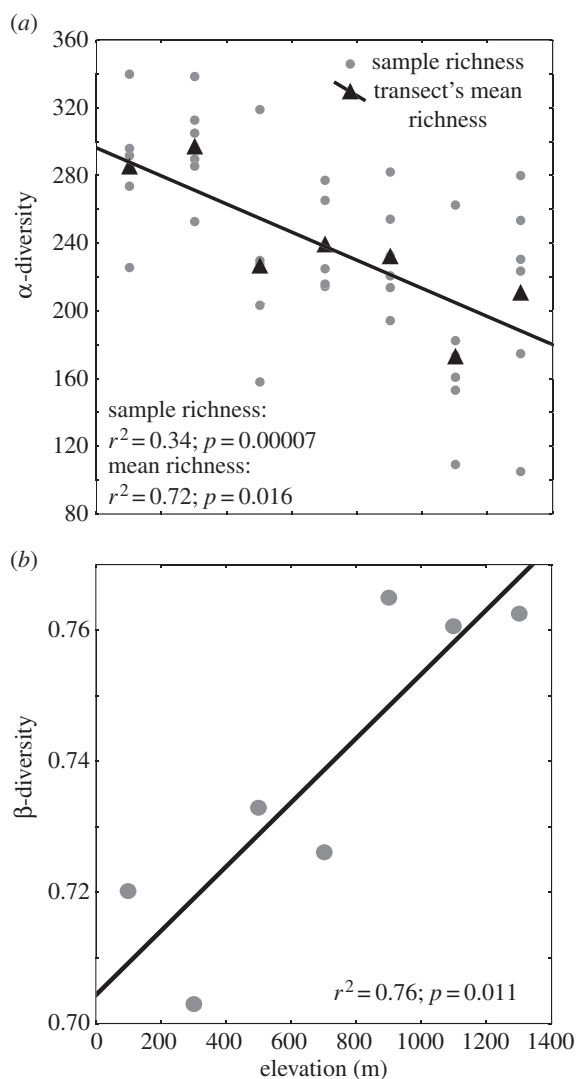rspb.royalsocietypublishing.org Proc. R. Soc. B 282: 20142630

Figure 3. Changes in (a) α-diversity and (b,c) β-diversity with elevation. In (b), β-diversity is the mean Jaccard distance for all pairwise comparisons of communities within a transect.

Figure 4. Relationship between local taxonomic richness and abiotic variables. (a) Richness increases with increasing mean annual air temperature and (b) decreases with increasing soil nitrogen content. Thick lines show the overall relationships. Note that soil nitrogen content was only determined for a composite sample of the entire transect rather than individual samples.

within a transect increased with elevation (figure 3b; $r^2 = 0.76$, $p = 0.011$). Also, taxonomic spatial turnover, another measure of β-diversity quantified by the slope of log Jaccard β-diversity versus log distance between pairwise comparisons (the distance decay of similarity), increased with elevation from 100 to 1100 m ($r^2 = 0.91$, $p = 0.003$; electronic supplementary material, figure S7). Since increasing elevation in the McMurdo Dry Valleys is characterized by decreasing air temperature and increasing soil nitrogen content, α-diversity increased with air temperature and decreased with soil nitrogen (figure 4a,b). However, soil organic carbon, which is strongly correlated with microbial biomass in the Dry Valleys [26], was not significantly correlated with elevation ($p = 0.113$). The negative richness-nitrogen relationship is of interest as nitrogen deposition in the region is correlated with precipitation [37], which increases with altitude. This suggests that the negative effect of decreasing temperature on diversity may dominate in spite of increased nutrient and water availability, which is noteworthy since nitrogen and water can be limiting resources in these soils.

Although the elevational diversity patterns support our Prediction 2, the β-diversity pattern could also be driven by elevational changes in the spatial heterogeneity of soil characteristics. Under niche-based mechanisms of
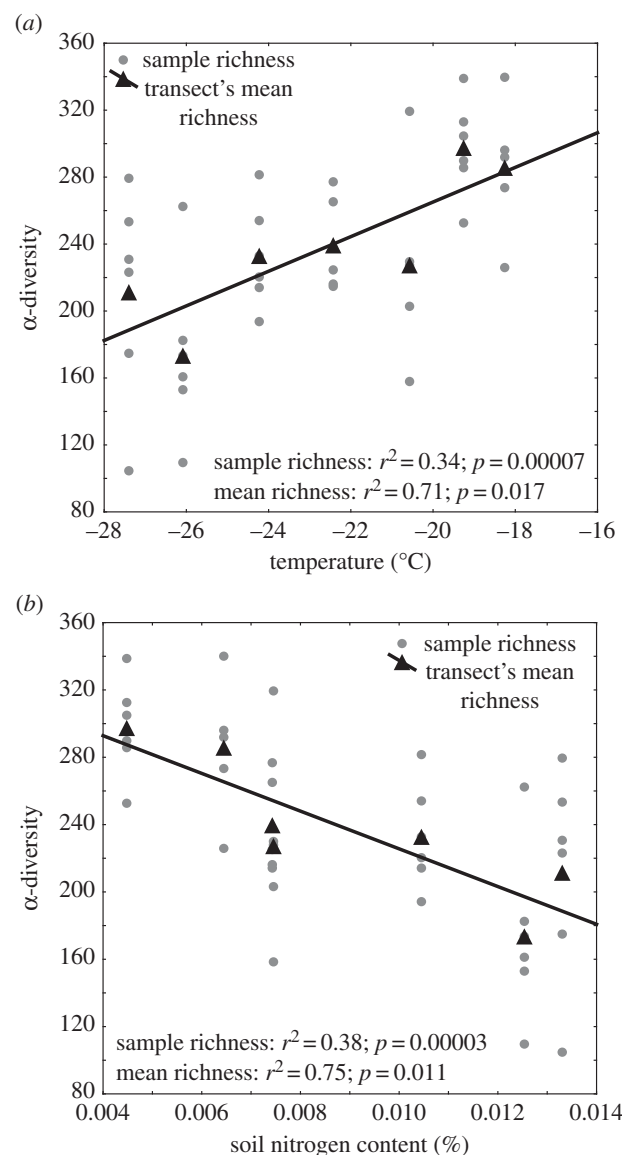
community assembly, greater environmental heterogeneity at higher elevations would lead to increased spatial turnover in community composition. We did not find support for this explanation: relationships between variance in standard soil physico-chemical variables and elevation or β-diversity were not significant (all $p > 0.36$, all $r^2 < 0.18$).

(c) pH and salinity diversity gradients

The distribution of conductivity niche positions was highly skewed with a long right tail, whereas pH niche positions exhibited a symmetric, unimodal distribution (electronic supplementary material, figure S5). In agreement with our Prediction 3, α-diversity exhibited a monotonic decrease with conductivity and a hump-shaped pattern with pH (figure 5). The hump-shaped richness–pH relationship reached its maximum at pH 9.09, close to our samples' mean pH of 8.91 (see also electronic supplementary material, figure S9). Within-transect pH and conductivity trends followed the across-transect trends. The best performing regression model
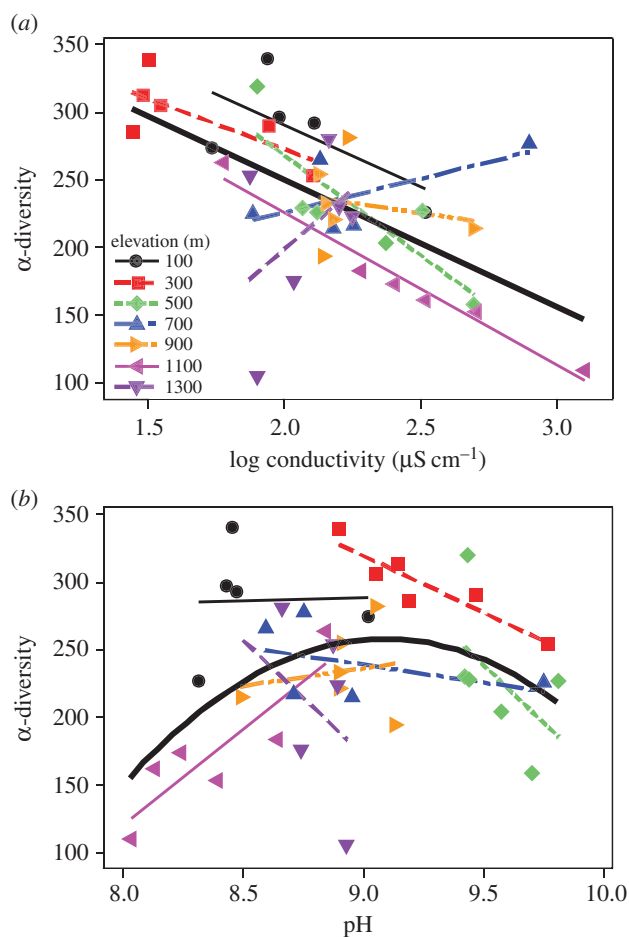
Figure 5. Relationship between taxonomic richness and abiotic variables, both within and across transects. (*a*) Richness decreases with increasing conductivity, which provides a measure of salinity. (*b*) Across transects, richness exhibits a hump-shaped, quadratic relationship with pH and linear regressions within transects generally follow this trend, with a greater number of positive slopes occurring at low pH and negative occurring at high pH. In (*a*,*b*), bold black lines are across-transect fits and thinner lines are within-transect fits.

included only temperature, conductivity and the quadratic effect of pH as predictors of α-diversity (total $R^2 = 0.62$, electronic supplementary material, tables S1 and S2).

5. Discussion

Other studies along elevational and latitudinal gradients in plants, animals, phytoplankton and planktonic bacteria have also observed positive richness–temperature relationships [4,7,15,38], but our study is one of the first to demonstrate that geographical positive richness–temperature relationships extend to such low temperatures. One proposed explanation is the 'more individuals' hypothesis: productive environments in the tropics and at low-to-mid elevations should support more individuals within a community, which in turn allows more species to maintain population densities sufficient for persistence [39,40]. However, our results suggest resource availability is not responsible for the observed α-diversity pattern, in agreement with literature identifying temperature, separate from factors such as ecosystem productivity and community abundance, as key in controlling many elevational and latitudinal diversity patterns [5,6,15]. By contrast, our β-diversity results were markedly different from most literature (e.g. [41]), showing a decrease with increasing

temperature. Unlike latitudinal gradients typically characterized by smaller range sizes [42] and higher α- and β-diversity at lower latitudes (e.g. [38]), our theory and analyses show that the favourable effect of temperature on growth rate can lead to broader realized niches, which in turn can increase α-diversity but reduce β-diversity.

Our theory also explains α-diversity patterns along pH and conductivity (salinity) gradients, predicting the overall shapes of the distributions in conductivity and pH niche positions and how they shape diversity patterns. The observed hump-shaped trend of α-diversity with pH has been reported in other ecosystems. In our data, however, the optimum pH is 9.09. This value is substantially higher than in a global soil analysis [18] but close to the most common pH for the region (mean pH = 8.91), as predicted and seen in other systems [43]. Therefore, pH effects on richness seem to be mediated by the interaction of niche evolution with regional conditions rather than purely physico-chemical effects.

Our theory and analyses do not preclude other mechanisms of community assembly. Indeed, geographical distance between samples was a significant predictor of community dissimilarity between pairwise comparisons, even after accounting for the effects of differences between samples in pH, conductivity and elevation ($p < 0.01$ from multiple regression on matrices; electronic supplementary material), and the multi-predictor regression model's total R^2 was only 0.28. This indicates there are other important factors controlling microbial distribution on the mountainside, which could include unmeasured environmental variables, historical legacies [44] and/or neutral effects of distance on rates of dispersal [45], gene flow, drift or speciation. Additionally, the distributions of niche positions and widths may be affected by interspecific interactions and their effects on growth rates (and hence realized niches). Although our theory does not explicitly include these effects, it does not preclude them but rather assumes that the strength of such effects is not changing in an opposing manner with respect to temperature (or pH and salinity in the case of Prediction 3). Our theory thus provides a robust first-order approach for predicting diversity patterns, and its application to Antarctic soil bacteria suggests the interaction of niche-based assembly with metabolic effects plays an important role in governing their distribution and diversity along multiple gradients.

It is worth considering our theory's implications for other organisms, gradients and ecosystems. The degree to which our theory explains other gradients depends on the degree to which other forces governing diversity and assembly counterbalance the baseline niche and metabolic effects. For example, along many thermal gradients, rates of predation by ectotherms may increase with temperature [46], which could counter temperature's positive effect on growth in prey and thereby lead to no change in prey niche width or even a decrease in niche width with temperature. Nevertheless, even under these circumstances, the direct physiological effects of temperature on niches must be incorporated in order to develop predictive models of organism niches—and our theory provides a framework for accomplishing this. Likewise, even when there is a niche width gradient, niche width could have a negligible impact on α- and β-diversity if changes in other factors affecting diversity, such as dispersal limitation or source pool richness, offset the effects of changing niche width. It is important to recognize, however, that a lack of observation of predicted patterns does not imply that the

niche and metabolic effects are unimportant in community assembly, but rather that other factors impose stronger constraints on niche width or α- and β-diversity.

Although contrasting α- and β-diversity patterns have not commonly been reported, it is unclear whether this meaningfully suggests that such contrasting diversity patterns are actually rare rather than that relatively few studies have simultaneously investigated α- and β-diversity along appropriate gradients. A contrasting α- and β-diversity pattern has been observed in birds along precipitation-driven productivity gradient spanning hundreds of kilometres [47], suggesting the possibility that our theory may explain diversity patterns in a variety of other organisms, spatial scales and gradients.

6. Concluding remarks

Our results demonstrate that a niche-based mechanism of community assembly, mediated by the metabolic effects of temperature, probably underpins many diversity patterns, at least in microbes. The generalized niche theory predicts diversity patterns along environmental gradients without the need to invoke changes in the richness of source pools or explicitly account for species interactions and effects of ecosystem productivity. It represents a parsimonious and baseline quantitative theory of assembly and diversity gradients that builds on foundational niche concepts (e.g. [1,48]). This characteristic of the theory has the advantage that it implicitly incorporates

numerous eco-evolutionary effects of biotic interactions, which are all encapsulated by the distributions of niche positions and widths. It also explicitly incorporates the effect of temperature on metabolic and growth rates, which is a keystone of current ecological theory [2]. The theory thus integrates processes across a broad range of scales, from individual metabolic rates to geographical patterns. Our study highlights the usefulness of studying natural gradients in extreme environments, which allow for the mitigation of confounding factors and the extension of ecological understanding to the globe's full range in environmental parameters from the tropics to polar regions.

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