

## Research



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## Community ecology

# Latitudinal gradients in intraspecific ecological diversity

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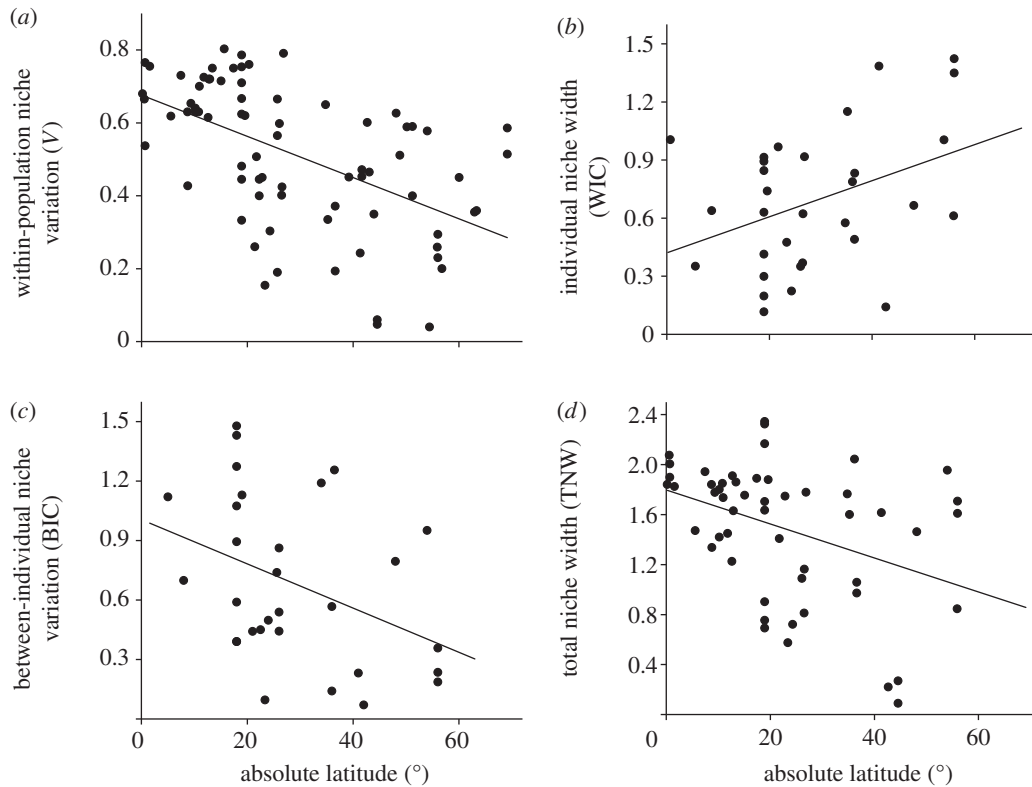
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The increase in the number of species with decreasing latitude is a striking pattern of global biodiversity. An important feature of studies of this pattern up to now has been the focus on species as the fundamental unit of interest, neglecting potential within-species ecological diversity. Here, we took a new perspective on this topic by measuring the degree to which individuals within populations differ in niche attributes across a latitudinal gradient (range: 54.01° S to 69.12° N). We show that 156 populations of 76 species across a wide range of vertebrate and invertebrate animal taxa contain more ecologically diverse assemblages of individuals towards lower latitudes. Our results add a new level of complexity to our understanding of global patterns of biodiversity and suggest the possibility that niche variation is partly responsible for the latitudinal gradients of species diversity.

## 1. Introduction

Individuals can differ substantially in their ecological niches because of phenotypic differences between sexes ('ecological sexual dimorphism'; [1]), age classes ('ontogenetic niche shifts'; [2]) or readily distinguishable discrete morphs that are ecologically divergent ('resource polymorphisms'; [3]). Even after accounting for these sources of variation, individuals can still differ in their niches, a phenomenon called 'individual specialization'—an allusion to the fact that individuals have narrower niches and are, therefore, more specialized than the population as a whole [4]. The latter two forms of intraspecific niche variation are essentially the same phenomenon, representing two ends of a continuum from continuous to discrete niche variation. Importantly, in the last few years, ecologists have come to appreciate that niche variation is widespread [4,5] and can affect the ecological and evolutionary dynamics of populations and communities [6,7].

The latitudinal gradient of species diversity, in which the number of species increases towards the equator, is one of the most conspicuous ecological patterns [8,9]. An important feature of studies of this pattern up to now has been the focus on species as the fundamental unit of interest (but see [10,11]), neglecting potential within-species ecological diversity. Here, we took a new perspective on this topic by testing for the existence of a latitudinal gradient of within-species niche variation. If, as predicted by theory, niche variation decreases with the number of interspecific competitors [12], we should expect a gradient of increasing niche variation in the species-poor communities towards higher latitudes. In fact, some of the most striking examples of niche variation in natural populations result from competitive release in depauperate communities [13–15], suggesting that niche variation will tend to be stronger in less diverse communities. On the other hand, the potentially higher diversity of resources at lower latitudes—mainly driven by higher species diversity—should provide more ecological opportunity, which is expected to promote higher niche variation [16–19].



**Figure 1.** Relationship between latitude and niche variation. Dots represent species averaged across 1–15 populations. (a) The  $V$  index of within-population niche variation; higher values indicate that populations contain more ecologically diverse assemblages of individuals. (b) The within-individual component (WIC) of niche width representing the average niche width of individuals within populations, (c) the between-individual component (BIC) measuring the variation among individuals' niche positions and (d) the TNW of the population;  $TNW = WIC + BIC$ .

## 2. Material and methods

We reviewed the literature, searching for examples in which niche differences among individuals within-populations were quantified. We found 156 populations belonging to 76 animal species—71 of which measured individual variation in prey taxa consumed, one in microhabitat use, three in foraging behaviour and one in both prey taxa and microhabitat use—spanning a latitudinal gradient from 54.01° S to 69.12° N (electronic supplementary material, table S1). Measures of niche variation were directly collected from publications or calculated by us whenever raw ecological data were available. Geographical coordinates were directly taken from publications or, whenever they were not reported, we estimated them using the locality names provided in publications. We did not include data from experimental manipulations in our analysis, focusing on natural populations. Measures of niche variation were calculated at the population level. In order to avoid pseudo-replication, whenever two or more populations of the same species were analysed (or one single population was surveyed repeatedly across seasons or years), we calculated, for each species, a mean degree of niche variation across populations (or points in time) and estimated a geographical range centroid as the average of coordinates of reported localities (see electronic supplementary material, figure S1). It is possible that some of the populations assigned to a given species may actually be cryptic species [20], in which case our 'species-level' average would contain two or more closely related species. However, because we measured variation within populations and not between populations, our estimates of intraspecific variation should not be artificially inflated by interspecific variation.

We used the  $V$  index of within-population niche variation, which varies from 0 to 1 and assumes higher decimal values as individuals become more heterogeneous [21] (see the electronic

supplementary material for details). We also used Roughgarden's [22] total niche width (TNW) to quantify the niche width of populations, which is the Shannon index of diversity applied to the population's distribution of resource use. TNW can be partitioned into a within-individual component (WIC) of niche width—the average individual niche width—and a between-individual component (BIC) of niche width—the variation between-individuals' niche positions—so that  $TNW = WIC + BIC$ . Niche variation can also be measured by the ratio  $WIC/TNW$  [12,22]. In 12 cases in which this measure was reported and we had no raw data with which we could calculate the  $V$  index, we built a function to convert  $WIC/TNW$  into  $V$  (see the electronic supplementary material for details). We separately regressed  $V$ , TNW, WIC and BIC on absolute latitude. In the case of  $V$ , we ran an additional model including TNW as a covariate to account for the fact that  $V$  measures will tend to be higher as population diet breadth increases (see the electronic supplementary material for details). Because we sampled a wide range of taxa (see electronic supplementary material, table S1), we also ran mixed-effects models, including 'taxon' as a random effect to account for any taxonomic structure in our data. Measures of niche variation were calculated in the program *INDSPEC* v. 1.0 [23] and regressions were performed in *SYSTAT13*.

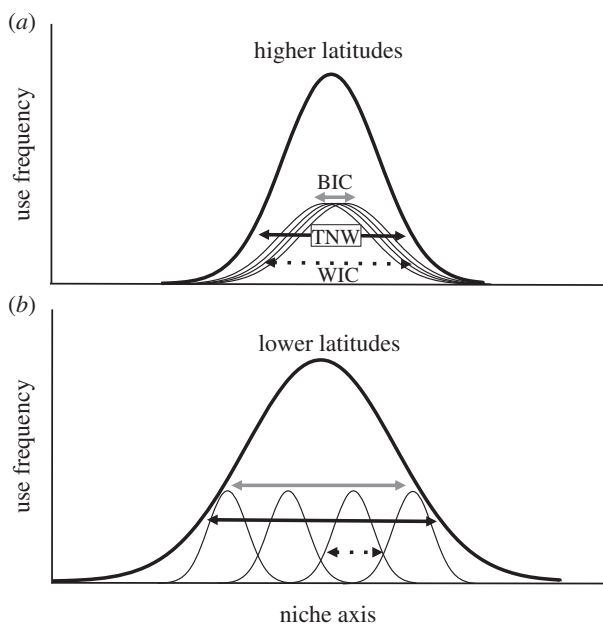
## 3. Results

We found a negative relationship between the degree of within-population niche variation and latitude (figure 1a)—the model including TNW as a covariate yielded qualitatively similar results (table 1). We found that individual niches became increasingly narrower towards lower latitudes (figure 1b). This decrease in absolute individual niche width was offset

**Table 1.** Model results of regression analysis relating niche components and latitude.

| dependent variable | factor   | slope  | s.e.  | t      | p      | F      | d.f. | r <sup>2</sup> | p      |
|--------------------|----------|--------|-------|--------|--------|--------|------|----------------|--------|
| V                  | latitude | −0.006 | 0.001 | −5.390 | <0.001 | 29.051 | 1,73 | 0.29           | <0.001 |
| V <sup>a</sup>     | latitude | −0.005 | 0.001 | −4.086 | <0.001 | 42.742 | 2,48 | 0.64           | <0.001 |
|                    | TNW      | 0.207  | 0.035 | 5.834  | <0.001 |        |      |                |        |
| WIC                | latitude | 0.009  | 0.004 | 2.222  | 0.034  | 4.938  | 1,29 | 0.15           | 0.034  |
| BIC                | latitude | −0.011 | 0.005 | −2.387 | 0.024  | 5.696  | 1,29 | 0.16           | 0.024  |
| TNW                | latitude | −0.014 | 0.005 | −3.009 | 0.004  | 9.055  | 1,50 | 0.15           | 0.004  |

<sup>a</sup>The interaction term latitude × TNW was not significant ( $p = 0.774$ ) and was removed from the model; V, WIC, BIC and TNW as in figure 1.



**Figure 2.** Conceptual representation showing the increase in niche variation from (a) higher to (b) lower latitudes. Curves represent the population (thick curves) and individual (thin curves) use frequency along an arbitrary niche axis. As we move from higher to lower latitudes, individual niches become narrower (smaller WIC) and more disparate (higher BIC). The decrease in WIC is offset by the increase in BIC, so that there is an expansion of the population niche, TNW (WIC, BIC and TNW as in figure 1).

by higher levels of interindividual niche variation (figure 1c), leading to the broadening of population niches (figure 1d). An analysis focusing on the subset of case studies measuring individual variation in prey taxa yielded essentially the same results (see electronic supplementary material, table S2). The models including ‘taxon’ as a random effect showed qualitatively similar results (see electronic supplementary material, table S3), but the relationship between WIC and latitude was no longer significant. This was probably a result of low power owing to the relatively small sample size and the inclusion of the random ‘taxon’ term.

## 4. Discussion

Our results can be summarized as follows: the degree of within-population niche variation increases towards lower latitudes because individual niches become increasingly

narrower and more disparate, with a concomitant expansion of the population niche (figure 2). If we assume that there is no gradient in WIC (see electronic supplementary material, table S3), latitudinal gradients in niche variation are primarily driven by changes in BIC. Regardless of the mechanism underlying changes in the degree of niche variation (both changes in WIC and BIC or only the latter), this pattern indicates that not only are there more species at lower latitudes, but also their populations contain more ecologically diverse assemblages of individuals. Our results suggest that the high diversity of resources (ecological opportunity; [5]) in the tropical region promotes higher intraspecific niche variation. Importantly, this effect is apparently more important than interspecific competition—which should increase with species diversity and constrain niche variation [12]—in determining the levels of intraspecific niche variation at a global scale.

The patterns described here are in stark contrast with predictions from classic ‘niche packing’ theories [24,25], according to which species should have narrower niches in species-rich communities. Moreover, our results suggest that within-species niche variation may actually be a driver of species diversity. First, within-population niche variation is predicted to facilitate speciation [26–28]. In line with this prediction, clades of amphibians and fishes in which resource polymorphisms have evolved are consistently more diverse than clades showing no such niche variation [29]. Second, within-species niche and life-history variation can increase population persistence and act as a buffer against extinction, as suggested by recent studies on insects, amphibians, lizards, snakes and mammals [30–33]. Finally, recent ‘individual variation’ theory has highlighted the importance of individual variation in allowing species coexistence, and therefore promoting species diversity [34,35]. This theory has been proposed as an alternative to ‘niche’ and ‘neutral’ theories of biodiversity [36] and predicts a positive relationship between niche variation and species diversity, as reported here. Our results, therefore, suggest the possibility that niche variation is partly responsible for the latitudinal gradients of species diversity.

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