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# Competition and resource breadth shape niche variation and overlap in multiple trophic dimensions

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Competition plays a central role in the maintenance of biodiversity. A backbone of classic niche theory is that local coexistence of competitors is favoured by the contraction or divergence of species' niches. However, this effect should depend on the diversity of resources available in the local environment, particularly when resources vary in multiple ecological dimensions. Here, we investigated how available resource breadth (i.e. prey diversity) and competition together shape multidimensional niche variation (between and within individuals) and interspecific niche overlap in 42 populations of congeneric tropical frog species. We modelled realized niches in two key trophic dimensions (prey size and carbon stable isotopes) and sampled available food resources to quantify two-dimensional resource breadth. We found a 14-fold variation in multidimensional population niche width across populations, most of which was accounted for by within-individual diet variation. This striking variation was predicted by an interaction whereby individual niche breadth increased with resource breadth and decreased with the number of congeneric competitors. These ecological gradients also interact to influence the degree of niche overlap between species, which surprisingly decreased with population total niche width, providing novel insights on how similar species can coexist in local communities. Together, our results emphasize that patterns of exploitation of resources in multiple dimensions are driven by both competitive interactions and extrinsic factors such as local resource breadth.

## 1. Introduction

The niche is a foundational concept in ecology that permeates most theories aiming to explain biodiversity patterns. In particular, niche differences between co-occurring species have long been recognized as a fundamental aspect of the assembly of natural communities. Throughout the evolution of niche-based theories of diversity maintenance, from the principle of limiting similarity [1] to the modern coexistence framework [2], the magnitude of overlap in the exploitation of limiting resources between co-occurring species has been key to predicting their stable coexistence or local exclusion [3,4]. Specifically, stabilizing mechanisms associated with niche differences between species should promote negative frequency dependence within species and therefore favour long-term coexistence [2].

Natural communities vary along ecological gradients that create a mosaic of competitive interactions and shape patterns of niche variation. Specifically, classic niche theory predicts that the co-occurrence of competing species leads to niche segregation and/or contraction onto a narrower variety of resources [5,6]. This long-standing hypothesis, though, implicitly assumes that the diversity of available resources is necessarily constrained by the competitors, i.e.

competitive interactions are mediated by strong top-down effects on limiting local resources [7]. However, resource availability (e.g. diversity of prey and microhabitat types) may change strikingly in space and time due not to the direct effects of competitors, but instead to the presence of ecological gradients such as productivity, seasonality, and human impacts [8–11], which may have a marked influence on species' niches and competitive interactions [12–14]. Accordingly, the 'resource diversity hypothesis' predicts that the local variety of available resources favours niche expansion and divergence among species of consumers [15,16]. Therefore, the expected segregating effect of interspecific competition on species' niches should be stronger when there is a greater diversity of available resources, or when resources vary in more ecological dimensions, because there should be more scope for niche partitioning [17,18]. Although this is an intuitive idea, explicit empirical support for the simultaneous and interactive effects of competition and resource diversity on niche breadth and overlap in multiple dimensions is lacking.

A central assumption underlying most of the large body of theoretical and empirical research on niche variation is that niches are properties of populations or species [4,19]. This typological view assumes that conspecific individuals are ecologically equivalent, and overlooks the pervasiveness of intraspecific resource use variation within natural populations [20–22]. As a consequence, the pathways by which variation in individuals' foraging decisions translates into changes in population niche width remain largely unexplored [12]. Specifically, population niche expansion can occur via individuals becoming more generalist (increased within-individual niche variation) and/or individuals diverging in their diets (increased between-individual variation). Importantly, these two non-mutually exclusive paths have distinct ecological and evolutionary implications, including the degree of individual specialization in the population and the potential for frequency-dependent disruptive selection [23–25]. Understanding how both within- and between-individual niche variations respond to ecological gradients will therefore be necessary if we are to predict how niche width and niche overlap influence community-level processes.

Another enduring issue when studying competitive interactions is whether and how to account for the multidimensional nature of niches. Hutchinson's niche concept describes species' niches as multivariate constructs because resources used by organisms inherently vary in multiple dimensions [26,27]. From an empirical perspective, however, ecologists have traditionally investigated variation along niche axes (e.g. food type, prey size, microhabitat use) by analysing each axis separately [22,28]. Importantly, recent studies indicate that considering multiple dimensions of niche variation may affect estimates of interspecific niche overlap [29–31]. Specifically, multidimensional approaches capture the orientation and shape of species' niches, providing a more complete representation of their resource use and partitioning [32] (electronic supplementary material, figure S1). Because of this disconnect between a conceptual multivariate niche versus empirically estimated univariate niche axes, meaningful quantification of niche overlap remains a challenge in ecology and evolution [33–35].

Here, we studied the variation of the multidimensional individual- and population-level niche variation in congeneric tropical thin-toed frog species (*Leptodactylus* spp.) across ecological gradients. The focal species overlap in activity period, foraging microhabitat, and prey types, and sometimes but not always co-occur in local communities [36]. Specifically, we investigated how the presence of congeneric competitors and local resource breadth, defined as the diversity of resources available to consumers, interact to determine (i) population niche width, (ii) intraspecific niche variation, and (iii) interspecific niche overlap. We used a recently proposed analytical framework to model species' niches by simultaneously incorporating multiple niche dimensions and individual-level niche variation [29]. We predicted that population niche width would increase with the breadth of available resources (resource diversity hypothesis) and decrease with the number of interspecific competitors. Further, we investigated whether this population niche variation along gradients emerged via individuals specializing and diverging their diets (increased between-individual variation) [5] or becoming more generalist (increased within-individual variation) [24,25]. Finally, we predicted that increased resource breadth would reduce interspecific niche overlap by providing more scope for species to diverge in their diets.

## 2. Material and methods

### (a) Study system

Thin-toed frog species (genus *Leptodactylus*) are a suitable system for studying how competition and resource breadth shape niche variation for several reasons. First, thin-toed frogs have broad but patchy distributions across Neotropical lowlands, and several ecologically similar congeneric species may co-occur syntopically in local communities. Second, they are trophic generalists and exhibit broadly similar diets [36]. Adult thin-toed frogs forage at night on the ground and in low vegetation, consuming a broad variety of invertebrates (e.g. ants, termites, leafhoppers, and micromoths) and, occasionally, small vertebrates [36,37]. Finally, recent evidence suggests that the diet of these congeneric species is flexible and context dependent, responding to natural gradients of competition and prey limitation [36,38]. For more details about our study region see [36,38] and the electronic supplementary material.

### (b) Field sampling and laboratory processing

In the rainy season, between November 2014 and January 2015, we sampled frog communities around the margins of 21 ponds in a grassland area of approximately 40 000 km$^2$ in the Brazilian Pantanal, one of the largest and most pristine tropical wetlands (electronic supplementary material, figures S2 and S3). The rainy season in the Pantanal is an important period to native frogs during which they are fully active and forage extensively to accumulate energy for reproduction [39]. In each sampled site, we surveyed an area of 600 m$^2$ (six 10 × 10 m plots, less than 15% of the area surrounding the target lagoon; sampling effort of 1 h/person/100 m$^2$), hand-capturing all frogs and toads that were found.

Thin-toed frogs accounted for 93.3% of the total biomass of anurans captured, therefore we opted to focus on interspecific competition only among these congeneric species. Communities consisted of one, two, or three coexisting *Leptodactylus* species (seven communities in each scenario), with a total of 42 populations represented across sites. All *Leptodactylus* spp. (*L. bufonius*, *L. chaquensis*, *L. fuscus*, and *L. podicipinus*) specimens ($n_{\text{total}} = 904$, average of approximately 22 individuals/

population, electronic supplementary material, table S2) were euthanized with an overdose of lidocaine and then transferred to a −20°C freezer. In order to sample food resources available to frogs, we used 12 pitfall traps (20 cm diameter, 2 traps/plot) and two light traps evenly spaced in each local community. We opened pitfall traps and turned on light traps right after sunset and retrieved prey samples after 12 h. Collection and euthanasia procedures were carried out in accordance with Universidade Estadual Paulista guidelines for the care of vertebrate animals (UNESP Animal Care and Use Committee 03120501).

We analysed individuals' and species' niches in two key continuous trophic dimensions: prey size and prey carbon stable isotopes ($\delta^{13}$C). Prey size is strongly associated with energetic return, interaction strengths, and attack rates across diverse taxa and ultimately can affect individual fitness [40–42]. $\delta^{13}$C is also widely used as a trophic niche dimension, as it varies among primary producers (e.g. C3 versus C4 photosynthetic pathways in plants) and provides temporally integrated information on prey species' reliance on different food chains [43,44]. Because $\delta^{13}$C is also associated with the taxonomic identity of arthropods in our study system [36,45], this niche dimension also reflects the selection of functionally distinct prey types, which may also have major fitness implications for frogs [46]. We counted, identified (to family level in most cases, electronic supplementary material, table S1 and S2), and measured body size (length) of all prey items found in the gut contents of the frogs ($n = 6172$ cumulative prey items) (electronic supplementary material, table S1 and figure S4). To quantify the available resources to frogs, we carried out the same procedures for all individuals of potential prey species collected in the light and pitfall traps ($n = 9470$ cumulative available prey). We measured carbon stable isotopes ($\delta^{13}$C) of organisms from each prey category in each community. Samples were rinsed in deionized water, oven-dried for 48 h at 60°C, ground and weighed (approx. 0.5 mg) into tin capsules. The abundance of $^{13}$C/$^{12}$C was determined at the Washington State University Stable Isotope Core Laboratory using an Elemental Combustion System 4010 elemental analyser (Costech Analytical, Valencia, CA, USA) and a Delta Plus XP continuous flow isotope ratio mass spectrometer (Thermofinnigan, Bremen, Germany), then converted to conventional delta units, referenced against the international standard Pee Dee belemnite (PDB). The standard deviation of replicates of the internal reference material (Nylon) was 0.03‰.

## (c) Modelling multidimensional niches and interspecific overlap

To represent species' niche widths in a multidimensional space, we used a recently proposed framework for modelling the between- and within-individual components (BIC and WIC, respectively) of the population niche as a set of variance–covariance matrices [29]. WIC represents the variation in prey size and $\delta^{13}$C of the resources used by each individual in the population; while BIC represents the variation among individuals in average resource use [23]. These niche components were inferred using multiple response generalized linear mixed models (MGLMM) employing Bayesian Markov Chain Monte Carlo analysis in the R package MCMCglmm [47].

We first standardized the data to ensure that the niche component matrices would be readily interpretable [29]. Because prey size and $\delta^{13}$C values are measured on different scales (prey size ranged from 1 to 64 mm; prey $\delta^{13}$C from −34.1 to −10.9 ‰) (electronic supplementary material, table S2 and figure S5), estimates of bi-dimensional niche components would be skewed toward the dominant axis [29]. Therefore, within each sampling site, we scaled available prey size (log-transformed) and $\delta^{13}$C to vary between 0 (minimum prey size or $\delta^{13}$C observed in the environment) and 1 (maximum values) and then calculated the corresponding scores for the consumed prey (see details in the electronic supplementary material). Importantly, this rescaling procedure did not affect the relative position of prey in bivariate niche space (electronic supplementary material, figure S6). Then, for each population, individual identity was modelled as a random effect to obtain the variances and covariances between individuals in the prey size and prey carbon stable isotope dimensions (G-structure, BIC). The residual variances and covariances (R-structure) corresponded to the average within-individual variation (WIC). The multivariate matrices BIC and WIC were estimated using the posterior means of each variance and covariance, then summed to estimate the total niche width (TNW) (see details in [29]). Each MCMC ran for 43 000 iterations (thinning interval = 50, burn-in = 3000), and convergence was assessed using the Gelman–Rubin diagnostic based on five independent runs. A similar model without the random effect of individual identity was fitted using samples from the pitfall and light traps to estimate the two-dimensional breadth of available resources in each community.

Our study framework is illustrated in figure 1. For each species in a community, the variance–covariance matrices representing between- and within-individual niche components and TNW are represented as standard ellipses expected to contain approximately 40% of the data regardless of sample size [48]. Standard ellipses are often used in ecological studies because their projection on either niche axis corresponds to a standard interval (1 s.d.), $\bar{X}_1 \pm 1s_{X1}$ and $\bar{X}_2 \pm 1s_{X2}$ [49], therefore representing 'core' niche areas that should be most relevant for competitive interactions. To quantify resource breadth (i.e. the degree to which available prey are spread in this two-dimensional niche space), we calculated the area of the resource standard ellipse. Importantly, the number of coexisting *Leptodactylus* spp. was not correlated with resource breadth across sites ($r = -0.17$, d.f. = 19, $p = 0.44$), suggesting that these gradients are independent in our study system.

To quantify the amount of multidimensional niche overlap between each pair of coexisting species, we computed the overlapping area between TNW standard ellipses in each community in the R package spatstat [50]. As a more intuitive relative measure of niche overlap experienced by each population, we calculated the proportion of its TNW standard ellipse that overlapped with the TNW standard ellipse of at least one heterospecific population. Finally, we calculated the degree of individual specialization as the size (i.e. sum of the eigenvalues) of the WIC matrix divided by the size of the TNW matrix (see details in [29]). This ratio assumes lower values as individual specialization increases, because BIC is a larger proportion of TNW [51]. To explore the relationship between uni- versus multidimensional niche overlap, we calculated analogous unidimensional overlap based on the intersection between species' standard intervals for prey size or $\delta^{13}$C (see details in the electronic supplementary material).

## (d) Statistical analyses

To investigate the drivers of variation in the size of each multidimensional niche component (TNW, WIC, and BIC) across populations, we constructed linear mixed models in the package lme4 [52]. We modelled each of these niche components as a function of resource breadth, the number of coexisting *Leptodactylus* spp. (one-, two-, or three-species sites), and their interaction. We included species identity nested within site (community) as a random effect, as we did not have specific predictions about the effects of particular species. Each sampled population used in the analyses consisted of more than 10 individuals and an average of more than three prey items per individual.

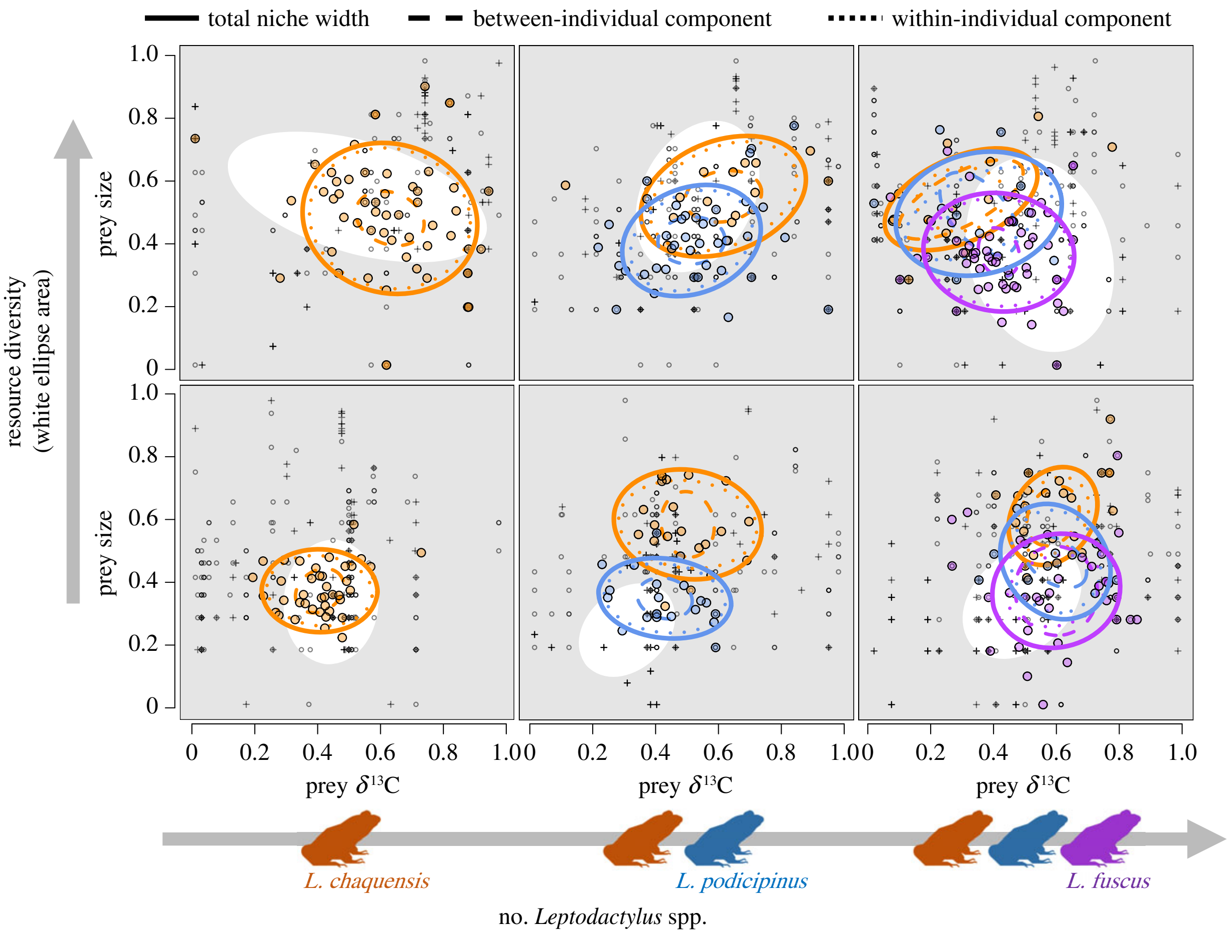

**Figure 1.** Representation of available and realized individual-level trophic interactions for tropical frog species (*Leptodactylus* spp.) in six of the 21 studied sites (different panels) across gradients of resource breadth and number of congeneric competitors. Available prey items at each sampling site along body size and $\delta^{13}$C niche axes are represented with '+' and local prey breadth is represented by the white-filled ellipse. Realized trophic interactions (i.e. each prey item found in gut contents) are shown as unfilled grey circles and individual frogs' means of prey size and $\delta^{13}$C are the same plot indicated by filled circles. Niche axes were scaled to vary between 0 (min prey size or $\delta^{13}$C observed in the environment) and 1 (max value observed in the environment). Finally, the variance–covariance matrices corresponding to between- and within-individual niche components (WIC and BIC) and the corresponding total niche width (TNW) for each frog population are represented by dashed, dotted, and continuous coloured lines, respectively. We present a map and this graphical representation for all 21 studied sites in the electronic supplementary material, figure S1.

We also constructed two separate generalized linear mixed models with beta distributions in the package glmmTMB [53] to elucidate the ecological drivers of variation in niche overlap and individual specialization across populations. We included resource breadth, number of coexisting *Leptodactylus* spp., their interaction, and TNW as additive predictors and species identity nested within site (community) as a random effect. *p*-values were obtained using likelihood ratio tests. All data analyses were performed in R v. 3.4.1 [54].

## 3. Results

### (a) Variation of population and individual niches

The size of the multidimensional TNW on the prey size and $\delta^{13}$C axes varied 14-fold across populations (electronic supplementary material, figure S7). This variation was explained by differences in the number of coexisting *Leptodactylus* species and available niche area in the environment, which varied 10-fold across sites (table 1, figures 1 and 2). Frog populations in sites with greater resource breadth had larger TNW, but the presence of competitors seemed to prevent TNW from reaching the largest values observed in one-species sites (figure 2*a*). Interestingly, we found a significant interaction between these two predictors (table 1), indicating that the rate of increase of TNW as a function of the available niche was steeper in sites with one or two *Leptodactylus* species when compared to communities with three congeneric coexisting species (figure 2*b*).

In general, the within-individual component of niche variation (WIC, variation in prey size, and $\delta^{13}$C of the resources used by each individual in the population) contributed more to the total population niche than the between-individual component of niche variation (BIC, variation among individuals in average resource use), resulting in a relatively low average degree of individual specialization (median WIC/TNW = 0.72). WIC and BIC responded differently to the studied gradients. As the area of the available niche increased across communities, individuals became more generalist (increase in WIC), particularly in one- and two-*Leptodactylus* species sites. On the other hand, niche divergence among individuals (BIC) did not respond to gradients of niche availability and competition (table 1, figure 3). As a result, the degree of individual niche variation tended to decrease as population niche expanded, meaning that more generalist populations (large TNW) had relatively lower diet specialization among individuals (i.e. larger WIC/TNW) because individual niche width expanded faster than population niche width.

**Table 1.** Effects of the presence of congeneric competitors and local resource breadth on multidimensional niche components (total niche width, within- and between-individual components [23]), individual niche specialization, and interspecific niche overlap in thin-toed frogs (*Leptodactylus* spp.).

| | | resource breadth | | | number of *Leptodactylus* spp. | | | interaction | | | total niche width (TNW) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **response variable** | **intercept** | **estimate** | $\chi^2$ | *p*-value | **estimate** | $\chi^2$ | *p*-value | **estimate** | $\chi^2$ | *p*-value | **estimate** | $\chi^2$ | *p*-value |
| total niche width (TNW) | 0.034 | 0.78 | 13.88 | <0.001 | 0.007 | 6.71 | 0.03 | −0.19 | 3.64 | 0.05 | | | |
| within-individual component (WIC) | 0.016 | 0.69 | 14.62 | <0.001 | 0.007 | 8.49 | 0.01 | −0.18 | 4.13 | 0.04 | | | |
| between-individual component (BIC) | 0.017 | 0.08 | 2.66 | 0.26 | 0.0006 | 0.04 | 0.98 | −0.009 | 0.04 | 0.85 | | | |
| | **intercept** | **estimate** | *z* | *p* | **estimate** | *z* | *p* | **estimate** | *z* | *p* | **estimate** | *z* | *p* |
| proportion of overlapping niche | −6.547 | 94.17 | 3.27 | 0.001 | 3.18 | 4.05 | <0.001 | −30.49 | −3.09 | 0.002 | −26.51 | −3.93 | <0.001 |
| individual specialization (WIC/TNW) | 0.045 | −1.33 | −0.18 | 0.86 | −0.003 | −0.007 | 0.99 | 0.06 | 0.008 | 0.99 | 11.09 | 1.845 | 0.06 |

### (b) Variation in trophic overlap across coexisting species

The proportion of niche overlap across coexisting *Leptodactylus* populations was highly variable. As expected, unidimensional niche overlap was usually higher than multidimensional overlap (figure 4), ranging from 21 to 100% for prey size and from 46 to 100% for prey $\delta^{13}$C. Considering the overlap calculated from our multidimensional approach, in two-species site populations showed between 11 and 76% niche overlap with the other species, while in three-species sites, this percentage varied from 40 to 100% (figure 5*a*). This observed decrease in overlap is due to a combination of multidimensionality *per se* and the specific orientation and shape of the niches (figure 4).

The striking ninefold variation in multidimensional niche overlap was significantly explained by the focal population's TNW and the interaction between the number of coexisting congeneric species and the available resource breadth (table 1). Increments in resource breadth led to higher niche overlap in two-species sites, but not in three-species sites (electronic supplementary material, figure S8). Surprisingly, populations with larger niche area (larger TNW) experienced relatively lower niche overlap (figure 5), suggesting that a decrease in multidimensional niche breadth does not necessarily reduce overlap across species as predicted by niche theory.

## 4. Discussion

Ecologists have long been fascinated by patterns of variation in resource use between and within coexisting species. The multidimensionality of niches has been acknowledged for some time, while heterogeneity among individuals within populations has become increasingly apparent in recent years. However, few if any studies have considered both niche dimensionality and individual-level niche variation simultaneously to address the drivers of niche width and niche overlap in coexisting species. By modelling the trophic niches of congeneric tropical frogs in two key dietary dimensions, we showed that the variation in population niche width across communities was mostly accounted for by within-individual diet variation. In line with predictions from classic niche theory, this multidimensional niche variation can be predicted by gradients of resource breadth and species richness across natural communities. These gradients affected not only single species' niches but also the degree of trophic niche overlap across ecologically similar species. Together, these results emphasize that patterns of multidimensional resource use and differentiation among consumers are highly flexible across ecological contexts, depending strongly on local resource breadth.

### (a) Population and individual niche variation

We found the influence of putative interspecific interactions on multidimensional niche breadth to be largely dependent on locally available resources. This context-dependent effect of competition on niche breadth arises because diversity in available prey sizes and $\delta^{13}$C may enhance the scope for consumer niche expansion [13,55]. Indeed, our results indicate that the diversifying effects of available prey diversity (available niches) on dietary niche width are stronger than the constraining effects of the number of coexisting competitors.

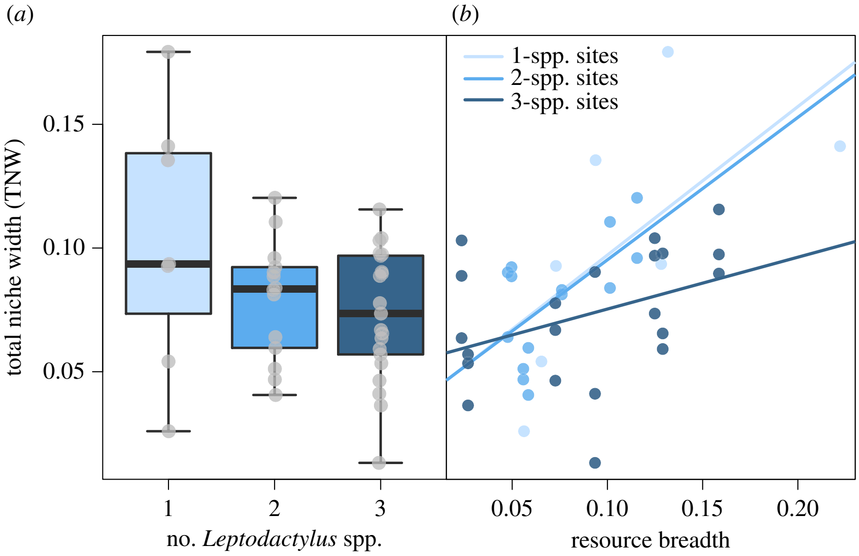

**Figure 2.** (*a*,*b*) Effect of the number of coexisting congeneric species and breadth of available resources on the total niche width (TNW) of 42 populations of tropical frog species (*Leptodactylus* spp.) in the Pantanal wetlands, Brazil. (Online version in colour.)

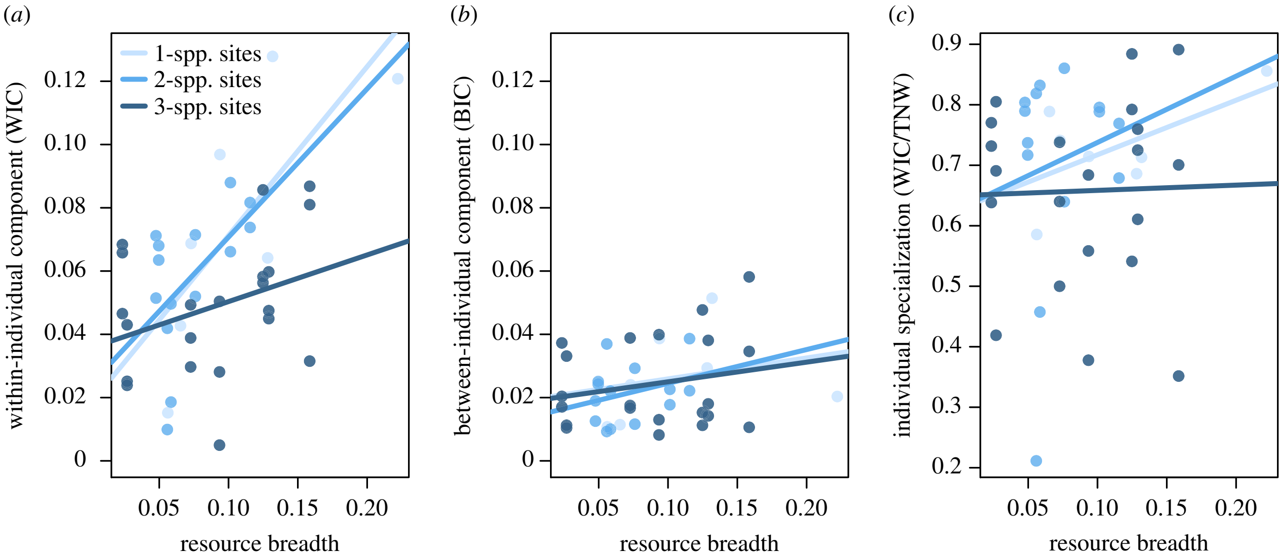

**Figure 3.** (*a–c*) Effect of the number of coexisting congeneric species and breadth of available resources on the three niche components of 42 populations of tropical frog species (*Leptodactylus* spp.): within-individual variation (WIC), between-individual variation (BIC), and total niche width (TNW). (Online version in colour.)

While we did not investigate the role of competitor identity in this study, future investigations could focus on specific species with divergent functional traits to gain a more complete understanding of how community composition as well as richness influence niche variation. Historically, competition has been invoked as the major driver of niche variation in nature, but our findings support the idea that available resource diversity is an important yet neglected force structuring the exploitation of resources in multiple dimensions.

As expected by the Optimal Foraging Theory (OFT) [5,23], we found that multidimensional population niche width (TNW) expansion occurs predominantly via increased within-individual niche diversity (WIC). In other words, the absence of competitors and increased resource breadth lead individuals to increase their own niche width by adding new resources to their diets (e.g. larger or smaller prey), becoming more generalist. Bolnick *et al.* [24] refer to this scenario as 'parallel release' because individual and population niche widths expand accordingly. This finding contradicts the long-standing niche variation hypothesis [5], which posits that competitive release leads to an expansion in TNW via greater between-individual variation (BIC) while individual niche widths remain constant. This prediction has received recent empirical support [56–58] and is expected when functional trade-offs constrain individuals' ability to incorporate additional prey types, limiting WIC expansion [59]. Therefore, contradicting previous one-dimensional empirical evidence [36,60], our results suggest that the trophic niches of *Leptodactylus* species are not strongly limited by functional trade-offs (e.g. morphological, physiological, or cognitive constraints) but instead that individuals possess substantial behavioural plasticity to explore alternative resources [61].

### (b) Context dependence of niche overlap

Although the concept of limiting similarity among coexisting species is the backbone of classic niche theory [1], we found that the studied syntopic, congeneric frog species exhibit variable and often high (or even complete) trophic niche overlap.

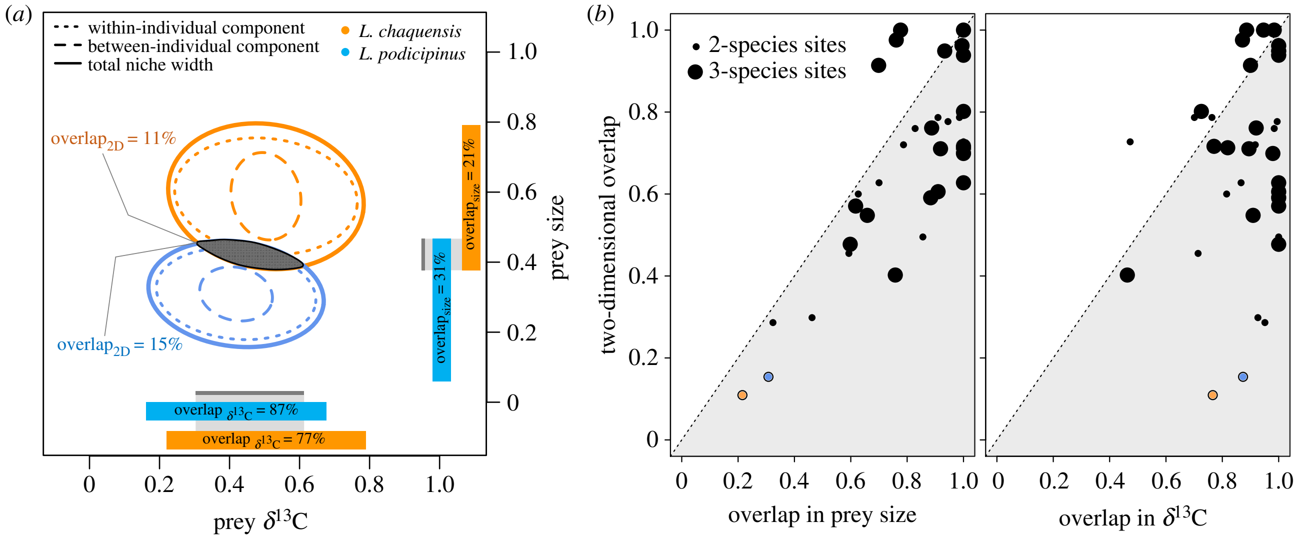

**Figure 4.** (*a*) An example (site LEP08) of how perceived niche overlap between coexisting populations of thin-toed frogs (*Leptodactylus chaquensis* and *L. podicipinus*) may be considerably distinct when one or two trophic dimensions are considered at a time. When niche axes are analysed separately (blue and orange bars), frog populations appear to overlap substantially in prey $\delta^{13}$C (77 and 87% of the overlapping area) and moderately in prey size (21 and 31%). However, given the specific orientation and shape of the bidimensional niche ellipse, the amount of perceived overlap is lower than the observed for individual dimensions. (*b*) Relationship between multidimensional (*y*-axis) versus unidimensional (*x*-axes; (*a*) prey size, (*b*) prey $\delta^{13}$C) estimates of the percentage of overlapping population niche. Dashed line corresponds to the 1 : 1 relationship. Populations in the grey area had higher unidimensional niche overlap than multidimensional. Orange and blue points indicate the populations of *Leptodatylus chaquensis* and *L. podicipinus* showed in (*a*). (Online version in colour.)

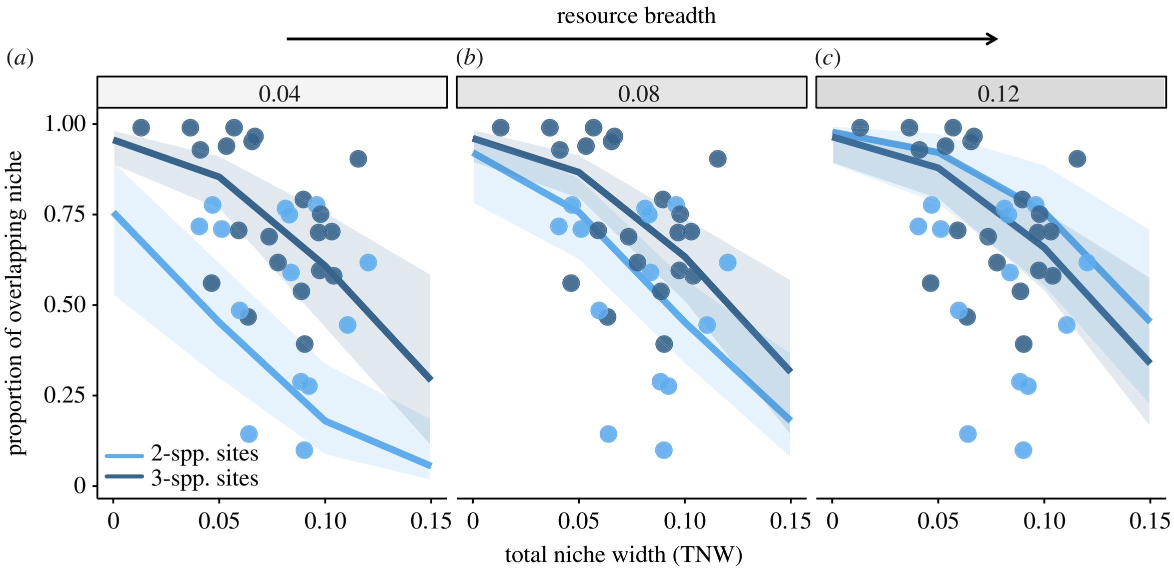

**Figure 5.** (*a–c*) Interactive effect of number of coexisting species and total niche width (TNW) on the proportion of overlapping niche in 35 populations of tropical frog species (*Leptodactylus* spp.) in the Pantanal wetlands, Brazil. (*a–c*) Shows how the predicted responses derived from the model vary across different levels of resource breadth. (Online version in colour.)

Our multidimensional metric of niche overlap allowed us to overcome some limitations of classic one-dimensional approaches. We simultaneously considered foraging decisions based on two widely studied trophic niche dimensions, prey size and $\delta^{13}$C (which is related to prey taxonomic identity and reliance on different primary producers). Our approach accounts for variances and covariances between these trophic axes associated with both between- and within-individual variation, allowing a more meaningful measure of niche overlap [29]. As expected, niche overlap was usually higher when calculated from the single axis in isolation (prey size or carbon stable isotopes) than when obtained from two axes simultaneously, corroborating the enduring idea that niche multidimensionality provides more scope for partitioning between competitors [26,62,63]. Unidimensional niche overlap was particularly high when only $\delta^{13}$C was considered, suggesting that thin-toed frogs tend to partition the trophic niche based mainly on prey size, which may be more directly associated with frog species traits such as body size and gape width [38].

In a multidimensional perspective, thin-toed frogs varied substantially in their degree of niche overlap across communities. This sizable variation was predicted ’by the TNW of the population and the interactive effect between the number of coexisting congeneric species and resource breadth. Unexpectedly, increments in resource breadth across two-species sites lead to higher interspecific niche overlap, but in three-species sites, niche overlap did not respond to resource breadth (electronic supplementary material, figure S8). These findings contradict the classic view that diversity of potential resources results in niche partitioning among consumers [26], suggesting that in low resource diversity scenarios, species tend to diminish their multidimensional niche overlap when the number of coexisting species allows it to happen. Together, these results indicate the need to consider not only the composition of competitors but also the trophic environment in which species are interacting to understand their niche complementarity across gradients.

Importantly, the total population niche breadth also affected proportional niche overlap, but the direction of this effect was opposite to what was predicted by niche theory. Niche packing (i.e. narrower niche widths) is traditionally proposed as a key process to decrease interspecific trophic overlap in species-rich communities [16,17,64]. In this view, reductions in niche breadth tend to decrease interspecific overlap and therefore favour coexistence. However, our results show that populations with large-sized niches exhibit relatively smaller niche overlap with coexisting species. This counterintuitive result suggests that trophic generalism may constitute a strategy to decrease relative overlap within trophic guilds if niche expansion occurs toward regions of unoccupied multidimensional niche space, increasing TNW and niche segregation in trophic space simultaneously. This hypothesis deserves further investigation, likely in experimental systems, and may contribute to the enduring debate on how numerous generalist species can coexist within a trophic guild, particularly in hyperdiverse tropical ecosystems [65–67].

### (c) Implications

Our findings bring new insights to the long-standing debate on how similar species can coexist in a local community. First, our dataset including multiple foraging observations per individual allowed us to infer that within-individual variation plays an important role in the dynamics of niche expansion, as is suggested by niche models [68,69] but rarely empirically evaluated. Further, instead of treating niche area and interspecific overlap as unidimensional properties, we modelled niches in a two-dimensional trophic space, revealing that niche multidimensionality reduces interspecific overlap. Simultaneous consideration of multiple niche dimensions can directly impact the perceived functional role of species in ecosystems [70] and the estimation of stabilizing forces in empirical studies [35]. Finally, our results emphasize how strongly species interactions can depend on extrinsic variables such as local resource breadth, which links classic niche theory with recent attempts to understand how environmental change, such as climate change and habitat conversion, affects species interactions.

Data accessibility. Data available from the Dryad Digital Repository at: https://doi.org/10.5061/dryad.bj7rn5t [71].

Authors' contributions. R.C.-P., M.S.A., and T.I. conceived the ideas; R.C.-P., M.S.A., and F.L.S. designed methodology; R.C.-P. and F.L.S. conducted fieldwork; R.C.-P. processed samples; R.C.-P. and T.I. analysed the data; R.C.-P. led the writing of the manuscript; all authors contributed to revisions.

Competing interests. We declare we have no competing interests.

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