

# Drivers of individual niche variation in coexisting species

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## Abstract

1. Although neglected by classic niche theory, individual variation is now recognized as a prevalent phenomenon in nature with evolutionary and ecological relevance. Recent theory suggests that differences in individual variation across competitors can affect species coexistence and community patterns. However, the degree of individual variation is flexible across wild populations and we still know little about the ecological drivers of this variation across populations of single species and, especially, across coexisting species.
2. Here, we aimed to (a) elucidate the major drivers of individual niche variation in natural communities and (b) to determine how consistent this variation is across coexisting species and communities.
3. We analysed natural patterns of individual-level niche variation in four species of coexisting generalist frogs across a wide range of tropical communities. Specifically, we used gut contents and stable isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) from frog species and their prey to quantify individual niche specialization. Then, we combined data on local community structure, availability of prey, phylogenetic relationships and predator–prey size models to test how this variation is related to four ecological factors which are predicted to be key drivers of individual specialization: intraspecific competition, interspecific competition, ecological opportunity (i.e., diversity of resources) and predation.
4. We found that the degree of individual trophic specialization varied by up to nine-fold across populations within the same species. This sizable variation in trophic specialization across populations was at least partially explained by gradients of density of competitors (both conspecifics and heterospecifics) and intraguild predation. However, the specific relationships between individual specialization and these ecological gradients were strongly species-specific. As consequences, the identity of the species with more individual variation changed among sites and there was typically no spatial correlation in the degree of individual specialization across coexisting species.
5. Our results show that individual niche specialization within and across species can be strongly context-dependent and that hierarchies of individual variation among coexisting species are not necessarily consistent across communities. Recent theory suggests that this pattern could lead to concurrent changes in competitive interactions across sites and thereby could play a key role in species coexistence at the landscape level. Our results suggest that individual variation across and

within coexisting species has the potential to affect not only species coexistence at local communities, but also regional diversity patterns.

#### KEYWORDS

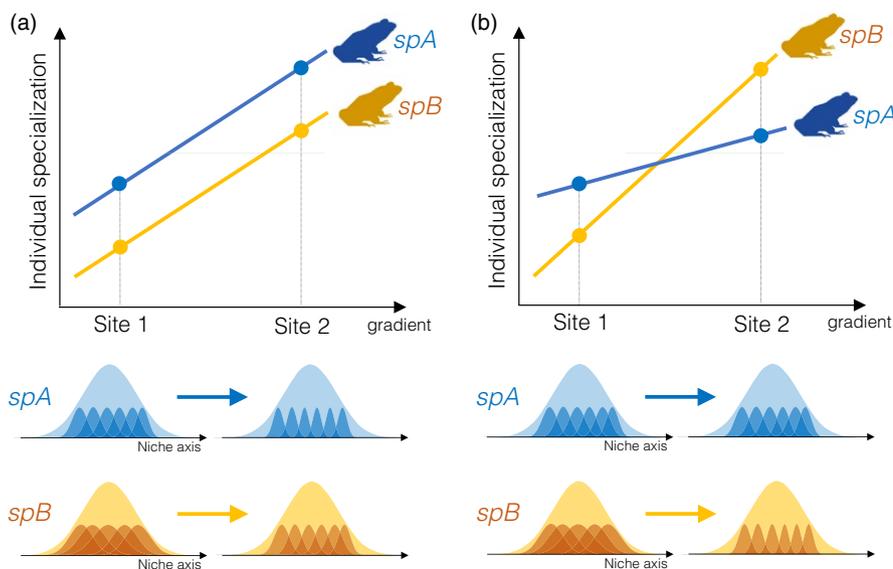
competition, diet, ecological opportunity, intraspecific variation, *Leptodactylus*, species coexistence, stable isotopes, thin-toed frogs

## 1 | INTRODUCTION

Classic niche theory relies on average differences between species to explain diversity patterns in biological communities. Indeed, the assumption of ecological equivalence within species has traditionally underlain niche theory (Chase & Leibold, 2003). However, this long-standing assumption has been challenged in recent years by a boost in the number of studies documenting substantial individual niche variation within populations (Araújo, Bolnick, & Layman, 2011; Bolnick et al., 2003). Furthermore, theory and empirical work indicate that the level of individual variation within populations can have important consequences for population dynamics, species interactions and long-term coexistence (Barabás & D'Andrea, 2016; Bolnick et al., 2011; Forsman & Wennersten, 2016; Hart, Schreiber, & Levine, 2016; Hausch, Vamosi, & Fox, 2018; Pruitt & Modlmeier, 2015; Violle et al., 2012). Despite these recent advances, it is increasingly apparent that the degree of individual niche variation is spatially and temporally flexible in wild populations, responding to shifts in ecological contexts from local to global scales (Araújo & Costa-Pereira, 2013; Araújo et al., 2011). However, we still know little about the extent and drivers of individual niche variation within and across species in natural communities. Yet, this knowledge is essential to develop biologically realistic models and testable quantitative predictions on how individual variation can affect community dynamics (Bolnick et al., 2011; Ingram, Costa-Pereira, & Araújo, 2018; Violle et al., 2012).

Recent theoretical models suggest that the outcome of interspecific competitive interactions (i.e., species coexistence vs. competitive exclusion) strongly depends on how the amount of individual variation differs across competitors (Barabás & D'Andrea, 2016; Hart et al., 2016). For example, considering two coexisting species, it is possible that one of them has consistently higher individual niche variation than the other, which would confer a competitive advantage by reducing mean intraspecific competition, regardless of the ecological context where species are interacting (Barabás & D'Andrea, 2016; Hart et al., 2016) (Figure 1a). Alternatively, if competitors exhibit no consistency in their differences in individual variation, competitive hierarchies can change across ecological contexts (Figure 1b). Thus, it is important to elucidate how coexisting species differ in the degree of individual niche variation across ecological contexts and whether these differences are consistent along environmental gradients. However, the vast majority of previous studies quantified niche specialization within a single target species (Araújo et al., 2011; Bolnick et al., 2003), and little empirical data are available to compare the degree of individual niche variation in populations of co-occurring species (Araújo, Bolnick, Martinelli, Giaretta, & Dos Reis, 2009; Cloyd & Eason, 2016; Faulks, Svanbäck, Ragnarsson-Stabo, Eklöv, & Östman, 2015).

Theories on optimal foraging provide guidelines on which ecological factors could drive differences in individual variation. Specifically, these theories posit that four main ecological factors should affect the degree of individual niche variation:



**FIGURE 1** Conceptual representation of how the hierarchy of individual specialization across two coexisting species (*spA*, *spB*) may vary along an ecological gradient. (a) *spA* has consistently higher individual niche variation than *spB* (either in Site 1 and Site 2), which would confer a competitive advantage to *spA* by reducing its mean intraspecific competition along the gradient. (b) Competitors exhibit no consistency in their differences in individual variation: in the Site 1, *spA* has higher individual specialization; the scenario is the opposite in Site 2

intraspecific competition, interspecific competition, ecological opportunity and predation (Araújo et al., 2011; but see Toscano, Gownaris, Heerhartz, & Monaco, 2016). Intraspecific competition can increase among-individual niche variation if it constrains the use of a common optimal resource and therefore individuals begin to feed on alternative resources that differ according to individuals' phenotypes (Svanbäck & Bolnick, 2005, 2007). Ecological opportunity (i.e., diversity of available resources) is also expected to increase individual niche variation by expanding individuals' foraging possibilities and then allowing their niches to diverge (Araújo et al., 2011). In turn, predation may decrease niche variation through density-mediated effects or changes in consumer behaviour (Araújo et al., 2011). Interspecific competition may have positive or negative effects on individual specialization depending on how population and individuals' niches respond to heterospecifics (Bolnick et al., 2010; Van Valen, 1965).

While some experimental and observational studies confirm these expectations for the role of intraspecific competition and ecological opportunity, effects of predation and interspecific competition remain underexplored (Araújo et al., 2011). Furthermore, the majority of these studies focused on the specific effect of only one of these four ecological factors (e.g., intraspecific competition, Svanbäck & Persson, 2004; Svanbäck & Bolnick, 2007; Tinker, Bentall, & Estes, 2008). Only recently have observational studies started to provide some insights on how two ecological factors can interact to determine the degree of individual niche variation in populations (Costa-Pereira, Tavares, de Camargo, & Araújo, 2017; Evangelista, Boiche, Lecerf, & Cucherousset, 2014; Newsome et al., 2015). However, under natural conditions, populations are usually facing all four factors simultaneously to varying degrees and the effects of these factors may not be independent. Furthermore, coexisting species that differ in their life-history traits or level of individual specialization may respond differently to gradients of competition, ecological opportunity and predation. Testing existing theory on ecological drivers of individual variation and its consequences for species interactions, therefore, requires an integrative approach to unravel how these factors drive individual niche specialization in populations of coexisting species (Araújo et al., 2011; Bolnick et al., 2011).

Here, we use a large-scale field survey of natural frog communities to identify key ecological drivers of individual trophic specialization across natural populations and communities of coexisting species. Specifically, we asked: (a) How consistent are differences in individual specialization across species and communities? We predict that co-occurring species should present a consistent hierarchy of individual variation across communities (Figure 1a), which would favour their local coexistence (Barabás & D'Andrea, 2016; Hart et al., 2016). (b) What is the relative importance of intraspecific and interspecific competition, predation and ecological opportunity in explaining the variation of individual specialization across populations? (c) Does the relative importance of these ecological factors vary across coexisting species?

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

Thin-toed frogs (*Leptodactylus* spp.) are a species-rich genus of trophic generalist anurans widely distributed across the Neotropics. Commonly, more than one species of thin-toed frogs can be found co-occurring syntopically (e.g., around ponds) in South American lowlands, exhibiting large diet overlap (De-Carvalho et al., 2008; Piatti & Souza, 2011). Thin-toed frogs forage at night on the ground and in low vegetation, consuming a wide taxonomic range of invertebrate prey, but larger individuals can also prey on small vertebrates, including intraguild predation and cannibalism (Costa-Pereira et al., 2015). Most of the species within this clade are medium-sized frogs (3–11 cm), but some species can reach large body sizes (~20 cm). Individuals within populations of *Leptodactylus* spp. can show substantial diet variation (Araújo et al., 2009).

We studied four areas in central Brazil, two of them in the Pantanal wetlands, Fazenda Barranco Alto (central coordinates: 19.559° S, 56.133° W) and Base de Estudos do Pantanal-UFMS (19.494° S, 57.048° W), one in the Bodoquena Plateau (21.384° S, 56.413° W) and one in the Gran Chaco region (21.683° S, 57.72° W), covering a total area of ~40,000 km<sup>2</sup> (Supporting Information Figure S1). In general, these regions are characterized by Savannah and grassland habitats, with numerous lagoons or ponds that harbour a high biomass of amphibian anurans during the rainy season. Despite some differences in species composition and community structure between these areas, *Leptodactylus* species frequently represent the most common (>70% in terms of abundance and biomass) terrestrial anurans around natural or seminatural lentic water bodies. Here, we focus on the four most common species in this geographical region: *Leptodactylus bufonius*, *Leptodactylus chaquensis*, *Leptodactylus fuscus* and *Leptodactylus podicipinus*. Although these species use similar food resources and microhabitats, they differ in average body size (Supporting Information Figure S2) and reproductive mode (Prado, Uetanabaro, & Haddad, 2005).

### 2.2 | Data collection

We sampled 21 frog communities, accounting for 43 populations of four studied species (*L. bufonius*,  $n = 5$  populations; *L. chaquensis*,  $n = 18$ ; *L. fuscus*,  $n = 7$ ; and *L. podicipinus*,  $n = 13$ ) between mid-November 2014 and early January 2015. This period corresponds to the start of the wet season, when *Leptodactylus* spp. are fully active after several months of low activity and metabolic rates. Importantly, it is a key foraging period to these frogs because it is when they accumulate energy to reproduce (Prado et al., 2005). Thin-toed frogs have a strong association with lentic water bodies. Thus, we defined a community as all the anurans found around natural or seminatural lagoons and separated by at least 1.5 km from any other community (Supporting Information Figure S1). Around each lagoon, we established six 10 × 10 m

plots (sampling area = 600 m<sup>2</sup>/community). To sample available food resources to frogs, we installed 12 pitfall traps (20 cm diameter) and two light traps evenly spaced surrounding the plots. We opened pitfall traps and turned on light traps right after the sunset and retrieved prey samples after 12 hr. Two hours after nightfall, we surveyed each plot (standard collection effort of 1 hr/person/100 m<sup>2</sup>) and hand-captured all frogs and toads found, which were kept in humidified plastic bags. After the anuran survey, collected *Leptodactylus* spp. specimens were euthanized with an overdose of analgesic (lidocaine), kept on ice in the field and then transferred to a -20°C freezer on the same night. Frog and prey samples were kept frozen until laboratory processing. Individuals from other species were identified and released on the same night of sampling. Collection and euthanasia were carried out in accordance with Universidade Estadual Paulista guidelines for the care of vertebrate animals (UNESP Animal Care and Use Committee 03120501).

The same person (RCP) measured the snout-vent length of each specimen using a digital caliper (0.01 mm) and dissected frogs to obtain gut contents (both stomach and intestine) under stereomicroscope. Individuals were sexed by the examination of gonads. Specimens without developed gonads were considered juveniles. We quantified individual diets by counting and identifying to the lowest taxonomic level possible (family level in most cases) all prey items found in gut contents. To quantify the available resources to frogs, we also counted and identified (family level) all potential prey that we collected using light and pitfall traps ( $n = 9,470$  cumulative prey items over all traps).

Complementary to gut content analysis, we measured stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) of the frogs ( $n = 974$  individuals) and their prey. Stable isotopes have been used as a measure of long-term feeding history in trophic studies, allowing inferences on individual temporal consistency in diet (Layman et al., 2012). We removed a piece (1 × 1 cm) of liver from each frog individual, which incorporates isotope values of consumers' diets for several weeks (Dalerum & Angerbjörn, 2005). Liver and prey samples (retrieved from pitfall and light traps or gut contents) were rinsed in deionized water, oven-dried for 48 hr at constant 60°C, grounded and weighed (~0.5 mg) into tin capsules. Because C:N ratios were overall low (<4), we did not extract lipids from our samples or mathematically correct them to account for lipid content (Post et al., 2007). The abundances of <sup>13</sup>C/<sup>12</sup>C and <sup>15</sup>N/<sup>14</sup>N were 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 (Thermo Finnigan, Bremen, Germany). We report isotope compositions using conventional delta notation, showing differences between the observed concentration and that of Pee Dee Belemnite for carbon and atmospheric N<sub>2</sub> for nitrogen. The standard deviation of replicates of the internal reference material (Nylon) was 0.03% for  $\delta^{13}\text{C}$  and 0.06% for  $\delta^{15}\text{N}$ .

### 2.3 | Proxies to ecological mechanisms

It was not possible to directly measure the magnitude of the four ecological factors believed to affect individual specialization in wild populations. We therefore followed previous studies (Cloyd & Eason, 2016; Evangelista et al., 2014; Newsome et al., 2015) and used proxies to represent their magnitudes in each population. We measured intraspecific competition and ecological opportunity using the density of conspecifics and the Shannon Index of diversity of available resources as proxies, respectively. The effects of the density of conspecifics (and heterospecifics) on the degree of individual specialization should also depend on the amount of available food resources. Therefore, we also quantified the total biomass of prey in the environment for each community.

We used a metric that combines both the local structure of communities and the phylogenetic relationships between coexisting species to quantify the strength of interspecific competition. Specifically, we calculated a measure of effective density of heterospecifics ( $N_z$ ) experienced by each population in each community based on the quantitative genetic competition model proposed by Doebeli (1996):

$$N_z = \int \rho(z')\alpha(z, z')dz$$

In this model, the effective population density corresponds to the proportion of each alternative phenotype  $z'$  (or, in our case, species  $z'$ ), represented by  $\rho(z')$ , weighted by its competitive effect on the focal phenotype  $z$  (species  $z$ ). The competitive effect,  $\alpha(z, z')$ , represents the per capita decrease in the population growth of the species  $z$  for each individual of the species  $z'$  added to the community, which can be modelled as:

$$\alpha(z, z') = \exp\left(-\frac{(z-z')^2}{2\sigma_\alpha^2}\right)$$

Here, we considered the difference between phenotypes ( $z, z'$ ) as the phylogenetic distance between two given species. Using the R package picante (Kembel et al., 2010), we calculated the phylogenetic distance between all pairs of coexisting species from a cladogram based on the time-calibrated tree proposed by Pyron and Wiens (2011) (Supporting Information Figure S2). The constant  $\sigma_\alpha^2$  determines how sharply the competition decays with the increase in the divergence between phenotypes. As an empirical value to this constant is not available in the literature, we determined  $\sigma_\alpha^2 = 0.05$ , which was the best value to approximate the competitive function based on our data to a Gaussian function (Doebeli, 1996). Using smaller or larger values ( $\sigma_\alpha^2 = 0.25$  and  $\sigma_\alpha^2 = 0.75$ ) did not qualitatively change the results. In summary, our metric of effective density of heterospecifics for a given population increases when co-occurring species are closely related and abundant. We acknowledge this approach implicitly assumes that closely related species are ecologically more similar and therefore compete more strongly for

food resources, which is not always true in biological communities (Cadotte, Jonathan Davies, & Peres-Neto, 2017; Godoy, Kraft, & Levine, 2014). However, considering that species diet and reproductive modes are associated with evolutionary proximity in our system (Uetanabaro, Prado, Rodrigues, Gordo, & Campos, 2008), we believe that phylogenetic relationships can be a good representation of the similarity of trophic niches between frog species.

As a proxy for predation pressure, we quantified the median likelihood of intraguild predation for a given population. During fieldwork and gut content analyses, we observed many events of intraguild predation and cannibalism in our studied system. We acknowledge that intraguild predation is not the only type of predation pressure that thin-toed frogs experience, as predation by birds and snakes have been reported in this system (Costa-Pereira, Ingram, Souza, & Araújo, 2016). However, numeric and biomass domination of *Leptodactylus* spp. (>90% of the total biomass of anurans, see Results) in the studied communities suggest that intraguild predation and cannibalism should account for a substantial portion of predation in our system. As predation is strongly size-structured in frogs, we used an approach that combines predator-prey size relationships with the observed local size structure of communities. Specifically, using only the anuran prey consumed by thin-toed frogs ( $n = 33$ , gut contents analyses), we regressed the log-transformed predator ( $y$ -axis) and prey ( $x$ -axis) body sizes (snout-vent length) and obtained a 95% quantile regression model (intercept = 1.133,  $\beta = 0.447$ ), which allowed us to establish the upper boundary of the feeding range (Costa-Pereira, Lucas, et al., 2018; Gravel, Poisot, Albouy, Velez, & Mouillot, 2013). Using this predator-prey body size model, we estimated for each individual the minimum size of a potential intraguild predator. Therefore, we used this critical size value to quantify the number of potential intraguild predators that co-occurred with each individual in the studied communities. Finally, we calculated the median value of the distribution of estimated number of potential intraguild predators to represent the likelihood of intraguild predation pressure for each studied frog population.

## 2.4 | Measures of individual niche specialization

To quantify the degree of individual specialization, we used two complementary sources of trophic niche information at the individual scale, gut contents and stable isotope data. Stable isotopes allowed us to infer temporal consistency in the diets of individuals because they reflect nutrients assimilated over many feeding events. Gut contents allow us to accurately determine the diet (e.g., high taxonomic resolution) and infer how coexisting species and individuals are partitioning specific resources within a given period of time (Araújo et al., 2011). Gut contents of thin-toed frogs commonly contain a high number of prey items during the rainy season (mean of 7 prey/individual, max of 110 prey/individual).

For gut contents data, we first calculated the proportional similarity index (PS<sub>*i*</sub>) for each individual  $i$ , which measures the overlap between individual  $i$ 's niche and the population niche. The average of PS<sub>*i*</sub> values corresponds to the IS individual specialization index,

which is the average overlap between individuals' niches and the population niche (Bolnick, Yang, Fordyce, Davis, & Svanbäck, 2002). To obtain a more intuitive measure of individual specialization, we subtracted the observed IS index of each population from 1, resulting in the  $V$  index (Bolnick, Svanbäck, Araújo, & Persson, 2007). When all individuals' niches overlap totally with the population niche, the  $V$  index is 0 and assumes higher values as the amount of individual specialization increases. We tested whether each observed  $V$  value could be generated if individuals sample prey stochastically from the population diet distribution (i.e., the significance of  $V$  indexes) using Monte Carlo bootstrap simulations (1,000 replicates) (Zaccarelli, Bolnick, & Mancinelli, 2013). As measures of individual specialization based on gut contents can also be influenced by the degree of taxonomic resolution (Newsome et al., 2015), we calculated the  $V$  index using both Order and Family level identifications separately. As we found a high correlation between these indexes ( $r = 0.84$ ,  $p < 0.001$ ), we only used family-level data in the analyses.

Gut contents do not necessarily reflect individuals' long-term feeding preferences. Thus, we also obtained a measure of  $V$  calculated from stable isotopes of carbon and nitrogen.  $\delta^{13}\text{C}$  provides information on how individuals' feeding preferences differ in terms of types of foods consumed (e.g., C3 vs. C4 food chains), while  $\delta^{15}\text{N}$  indicates differences in trophic level of consumed prey over time (Fry, 2007). We used empirically observed parameters (population diet distribution, number of individuals sampled, isotope values [ $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ ] of all prey and their dry masses) to simulate populations with varying degrees of diet variation and isotopic variance among individuals (see details in Araújo, Bolnick, Machado, Giaretta, & dos Reis, 2007). For each sampled frog population, we simulated 5,700 virtual populations and then generated an expected relationship between the  $V$  index and isotope variance specific for that population. Finally, we used this relationship to convert empirically observed isotope variances into estimates of  $V_{\delta^{13}\text{C}}$  and  $V_{\delta^{15}\text{N}}$  which can be compared to  $V$  values calculated from gut content data. Importantly, as simulations account for local prey's isotopic distributions,  $V$  values are comparable among populations even when there are differences in isotopic baselines across sites. We ran simulations in the program VARIso 1.0 (Araújo et al., 2007).

## 2.5 | Statistical analyses

We performed all statistical analyses in R 3.4.1. To test whether differences in the degree of individual specialization between coexisting species are consistent across communities, we first subtracted the calculated  $V$  indexes ( $V$ ,  $V_{\delta^{13}\text{C}}$  or  $V_{\delta^{15}\text{N}}$ ) between each pair of coexisting populations. In this case, if two locally coexisting species have exactly the same degree of individual specialization, the difference between them is zero. To test whether there is a directional trend of difference, that is, consistently higher or lower individual variation for a given species in relation to other species across communities, we performed a one-sample  $t$  test comparing the values of the difference in individual specialization for each pair of species with zero. Additionally, we correlated

(Pearson) the calculated values of individual specialization between each pair of species across communities. If the degree of two given species varies consistently across communities, we would observe a positive correlation, indicating that individual specialization in both species is driven by similar mechanisms. For these and the following analyses, we only used populations with more than seven individuals and with significant  $V$  index values (Monte Carlo simulations).

To determine which ecological factors help explain variations in the degree of individual specialization across populations and their relative importance, we constructed linear mixed models in the package `LME4` (Bates, Maechler, Bolker, & Walker, 2014) with  $V$ ,  $V_{\delta^{13}\text{C}}$  or  $V_{\delta^{15}\text{N}}$  as response variables and density of conspecifics, effective density of heterospecifics, intraguild predation likelihood, resource diversity and biomass of available prey as additive predictors. These predictors are not correlated (pairwise Pearson correlation, all  $p$ -values > 0.13) and we centred and scaled them before the analysis to facilitate comparisons of the resulting coefficients. We included the interaction of species identity with each of these factors (except biomass of prey, which was used only to control the effect of different resource abundances on the densities of conspecifics and heterospecifics) to determine whether effects of predictors vary across species. We also included site (community) nested within the geographical area as random effect. Although prior studies assumed a linear relationship between the degree of individual specialization and ecological gradients, recent studies have found quadratic patterns (Evangelista et al., 2014; Jones & Post, 2013; Mateus, Ortega, Mendes, & Penha, 2016). We therefore compared the fit of a linear vs. a quadratic model using corrected Akaike's information criteria ( $AIC_c$ ). We excluded *L. bufonius* from these analyses because of small sample size ( $n = 5$  populations). Visual inspection of residual plots did not reveal any clear deviations from normality or homoscedasticity.  $p$ -Values were obtained using Type II Wald chi-square tests in

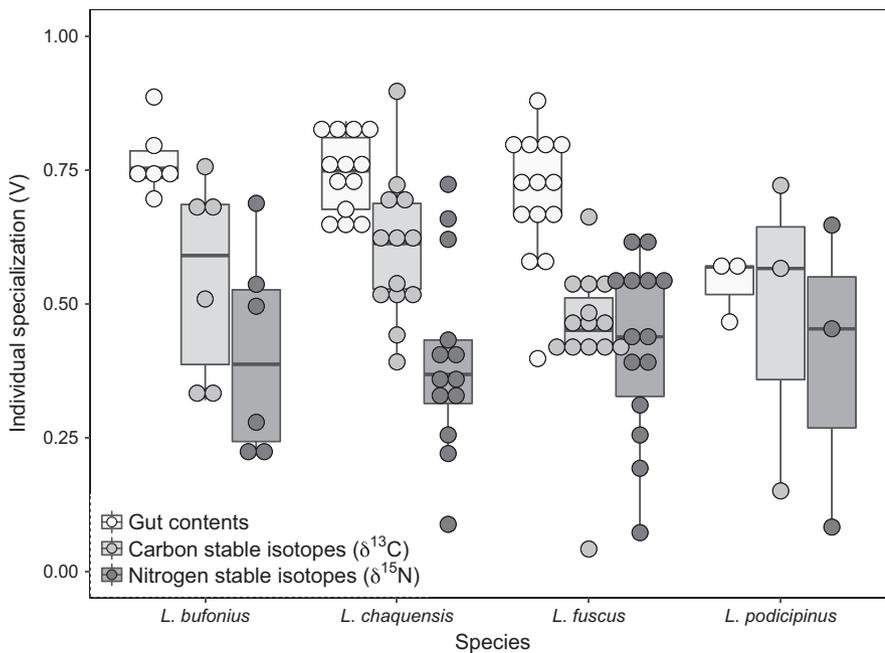
the package “`CAR`” (Fox et al., 2016). Data underlying the analyses are deposited in the Dyad Digital Repository: <https://doi.org/10.5061/dryad.mq2h237> (Costa-Pereira, Rudolf, Souza, & Araújo, 2018).

### 3 | RESULTS

Across the 21 sites, thin-toed frogs (*Leptodactylus* spp.) were the dominant species accounting for 68.23% of the captured individuals and 93.34% of the total biomass of anurans. In most of the sampled communities, we found three thin-toed frog species coexisting, and in four communities only one *Leptodactylus* species was sampled. *Leptodactylus chaquensis* was the most abundant and frequent species ( $n = 493$  individuals, 18 communities), followed by *L. podicipinus* ( $n = 337$ , 16), *L. fuscus* ( $n = 95$ , 13) and *L. bufonius* ( $n = 49$ , 5). These last three species presented similar body size distributions (between 25 and ~50 mm), while *L. chaquensis* reached up to 90 mm (Supporting Information Figure S3). We identified 6,172 prey items from gut contents. Thin-toed frogs had a broad diet, consuming 85 prey types. Termites (24.8%), ants (19.91%), leafhoppers (4.41%) and micromoths (4.25%) were the most common prey types, corresponding to more than half of all food items (Supporting Information Table S1). Thin-toed frogs also exhibited a wide range of isotope values, which can be related to the large spatial extent of our study area.  $\delta^{13}\text{C}$  ranged from  $-27.57\text{‰}$  to  $-12.16\text{‰}$  (mean =  $-21.14\text{‰}$ ,  $SD = \pm 2.85$ ) and  $\delta^{15}\text{N}$  from  $-2.88\text{‰}$  to  $14.14\text{‰}$  (mean =  $7.92\text{‰}$ ,  $SD = \pm 1.89$ ).

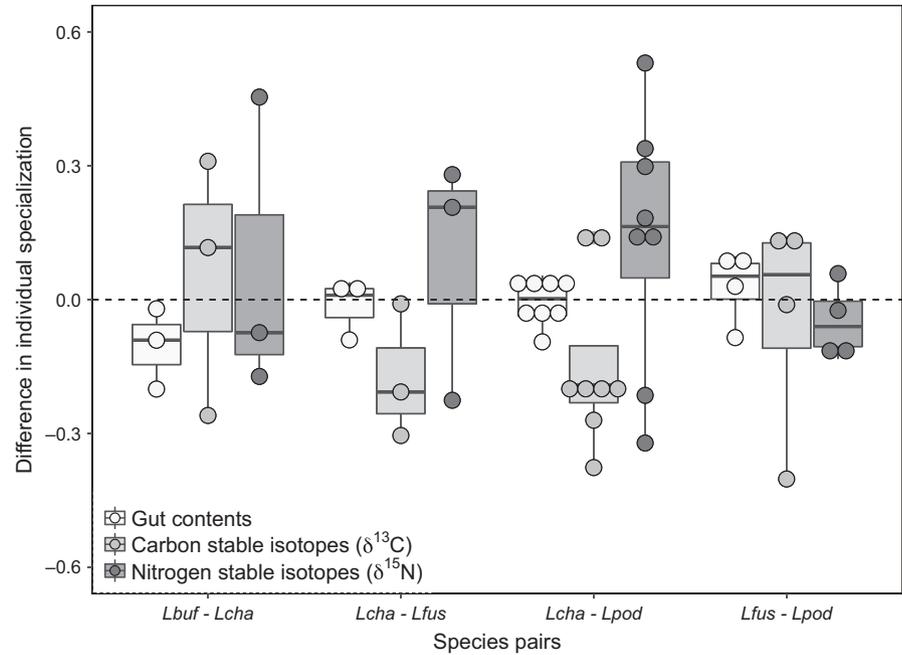
#### 3.1 | Variation in individual specialization across populations

Individual diet specialization based on dietary data ( $V$ -values) and stable isotopes (either  $V_{\delta^{13}\text{C}}$  or  $V_{\delta^{15}\text{N}}$ ) were positively correlated, and  $V$ -values were generally larger than  $V_{\delta^{13}\text{C}}$  and  $V_{\delta^{15}\text{N}}$  (Figure 2, Supporting



**FIGURE 2** Values of individual trophic specialization from populations of four species of thin-toed frogs calculated from gut contents ( $V$ ) or stable isotopes ( $V_{\delta^{13}\text{C}}$  and  $V_{\delta^{15}\text{N}}$ ). Higher values of  $V$  indexes (max = 1) indicate larger trophic divergence among individuals. Each dot represents a single frog population

**FIGURE 3** Differences in individual trophic specialization across pairs of coexisting thin-toed frog species. Each point corresponds to the magnitude of difference in individual specialization calculated gut contents ( $V$ ) or stable isotopes ( $V_{\delta^{13}\text{C}}$  and  $V_{\delta^{15}\text{N}}$ ) across two populations of different species that co-occur in a given community. Each dot represents the magnitude of the difference in individual specialization across two coexisting frog populations (not all potential pairwise species combinations occurred). The dashed line represents a scenario where coexisting species have exactly the same degree of individual specialization (i.e., difference in the strength of individual specialization equal to zero)



Information Figure S4).  $V_{\delta^{13}\text{C}}$  and  $V_{\delta^{15}\text{N}}$  were not correlated (Supporting Information Figure S4), indicating that these two tracers are capturing different aspects of the frogs' trophic ecology. Trophic specialization within populations varied by twofold for dietary data, 10-fold for  $\delta^{13}\text{C}$ , and almost 20-fold for  $\delta^{15}\text{N}$  (Figure 2). For all indexes, species presented relatively high individual specialization (mean values:  $V = 0.71$ ;  $V_{\delta^{13}\text{C}} = 0.52$ ;  $V_{\delta^{15}\text{N}} = 0.41$ ), indicating that individuals within thin-toed frogs commonly show sizable diet divergence. However, these mean values are not useful to represent the amount of individual specialization in a given species because we found a high variability across populations of each species (Figure 2). For example, we observed some populations of *L. chaquensis* composed by generalist individuals (e.g.,  $V = 0.39$ ;  $V_{\delta^{13}\text{C}} = 0.04$ ;  $V_{\delta^{15}\text{N}} = 0.07$ ) and others by individuals with highly specialized diets ( $V = 0.87$ ;  $V_{\delta^{13}\text{C}} = 0.66$ ;  $V_{\delta^{15}\text{N}} = 0.62$ ).

### 3.2 | Spatial synchrony of individual specialization across coexisting species

We found no consistent directional differences in individual specialization across species. The distribution of the magnitudes of difference in individual specialization between pairs of coexisting species was not different from zero for any pair of species and any metric (Figure 3, Supporting Information Table S2). Overall, we also observed no correlation in the degrees of trophic variation of coexisting species across communities. We only found a significant correlation of individual specialization (gut contents) for *L. chaquensis* and *L. podicipinus* ( $r = 0.71$ ,  $p = 0.05$ ) (Supporting Information Table S3).

### 3.3 | Ecological drivers of individual trophic variation

For dietary and stable isotope-based metrics of individual specialization, models including fixed effects as quadratic terms presented

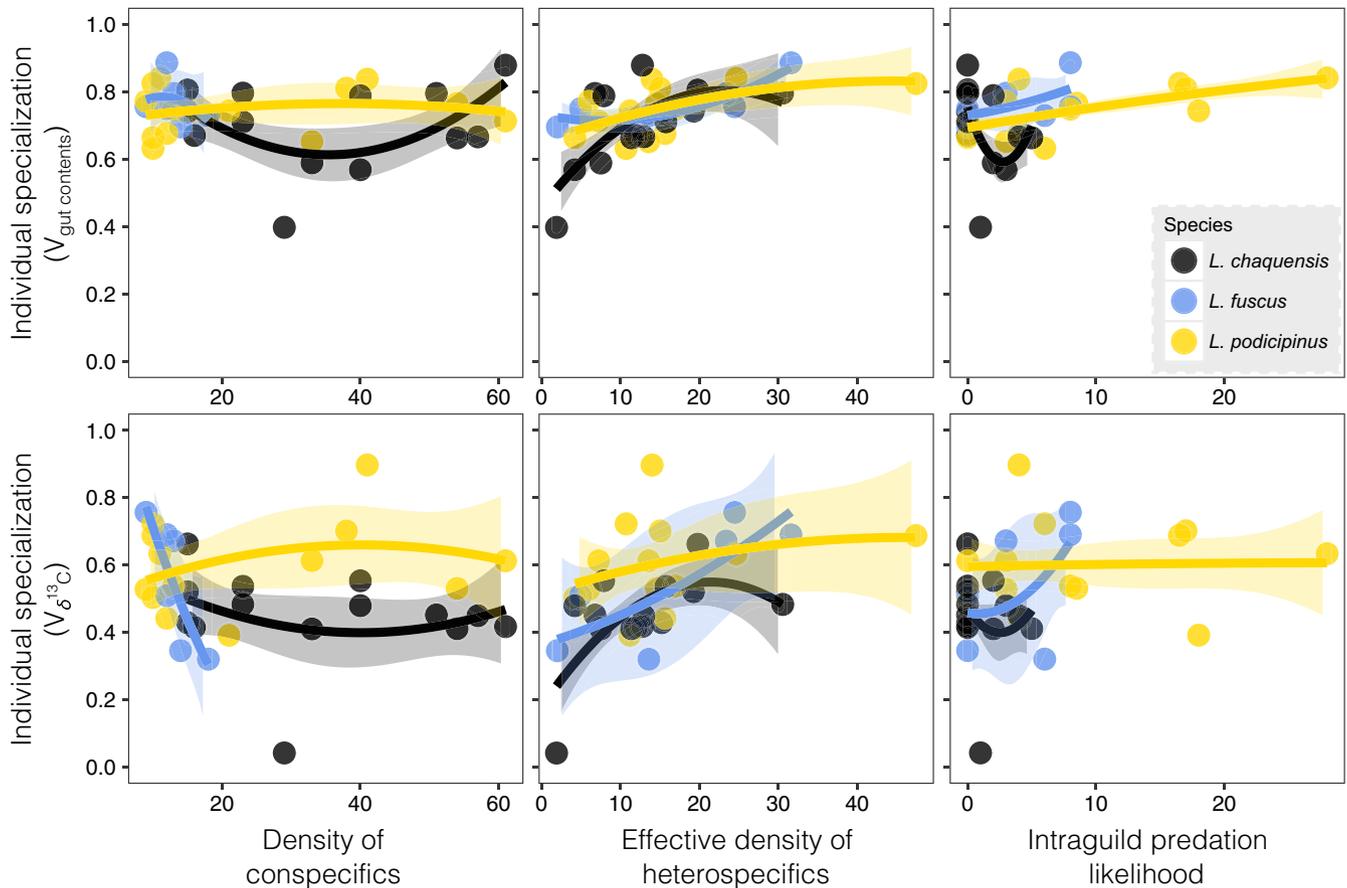
substantially lower  $\text{AIC}_c$  values when compared to models with linear terms ( $V = -58.52$  vs.  $-336.74$ ;  $V_{\delta^{13}\text{C}} = -21.67$  vs.  $-267.49$ ;  $V_{\delta^{15}\text{N}} = -8.42$  vs.  $-47.95$ ), so our inferences are based on quadratic models. Density of conspecifics was a major factor explaining the trophic variation across populations (Table 1). Consistent with theory, intraguild predation and effective density of heterospecifics also significantly contributed to explain variation in individual specialization, but diversity of resources had no significant explanatory power (Table 1, Supporting Information Table S4). Importantly, we observed significant interaction terms of our predictors with species identity, indicating that the effects of these ecological drivers on the degree of individual specialization differ across species (Table 1, Figure 4, Supporting Information Figure S5). Generally, responses of individual specialization to the four gradients were similar across metrics for each species (Figure 4, Supporting Information Figure S5). Overall, results were robust and did not change when we removed extreme points or one species to make sure all species had similar ranges of values for the predictors (Supporting Information Table S5).

## 4 | DISCUSSION

One of the tenets of ecological theory is that niche variation in ecological systems is primarily associated with differences between species. Recent studies have challenged this principle by demonstrating substantial variation within species (Bolnick et al., 2003; Rudolf, Rasmussen, Dibble, & Van Allen, 2014; Siefert et al., 2015), but the primary sources of this variation and its ecological consequences are still unclear. Here, we show that individual specialization varied up to ninefold across populations within the same species. This sizable variation in trophic specialization across populations was at least partially explained by density gradients of competitors (both conspecifics and heterospecifics) and intraguild predation. However,

**TABLE 1** Results of mixed-effects linear models investigating how ecological drivers of niche variation (effective density of heterospecifics, density of conspecifics, intraguild predation likelihood, prey diversity and prey biomass) affect individual specialization ( $V$  indexes) in thin-toed frogs (*Leptodactylus* spp.)

Ecological factor	$V$ (gut contents)			$V_{\delta^{13}\text{C}}$ (stable isotopes)			$V_{\delta^{15}\text{N}}$ (stable isotopes)		
	$\chi^2$	$df$	$p$	$\chi^2$	$df$	$p$	$\chi^2$	$df$	$p$
Polynomial models [ $\text{poly}(x,2)$ ]									
Effective density of heterospecifics	27.18	2	<0.01	20.989	2	<0.01	7.46	2	0.02
Density of conspecifics	4,191.47	2	<0.01	6,507.3	2	<0.01	300.18	2	<0.01
Intraguild predation likelihood	25.57	2	<0.01	239.52	2	<0.01	68.84	2	<0.01
Prey diversity	5.15	2	0.07	0.5661	2	0.75	4.30	2	0.12
Prey biomass	9.08	2	0.01	6.3533	2	0.04	1.74	2	0.42
Species	62,244.7	2	<0.01	3,011.50	2	<0.01	2,539.02	2	<0.01
Interactions									
Effective density of heterospecifics $\times$ spp.	39.82	3	<0.01	37.362	3	<0.01	1.48	3	0.25
Density of conspecifics $\times$ spp.	45.97	4	<0.01	7.1326	4	0.13	4.62	4	0.33
Intraguild predation likelihood $\times$ spp.	22.35	4	<0.01	14.185	4	<0.01	5.58	4	0.23
Prey diversity $\times$ spp.	170.31	2	<0.01	94.76	2	<0.01	63.62	2	<0.01



**FIGURE 4** Relationships between three significant drivers of individual niche variation and the observed strength of individual diet specialization calculated from dietary data ( $V_{\text{gut contents}}$ ) and carbon stable isotopes data ( $V_{\delta^{13}\text{C}}$ ) across populations and species (represented by different colours) of thin-toed frog species

these responses to ecological gradients were highly species-specific. As a consequence, there was typically no correlation in the degree of individual specialization (either calculated from gut contents or stable isotopes) across coexisting species. Our results indicate that individual niche specialization is strongly context-dependent (i.e., flexible along ecological gradients) and that there is no consistent hierarchy of individual variation across species in our system. These results emphasize the need to account for differences in individual variation across competing species along ecological contexts to understand how this phenomenon affects species coexistence.

#### 4.1 | Ecological drivers of individual trophic variation

Theory suggests that the magnitude of individual trophic variation should depend on the level of intra- and interspecific competition, ecological opportunity and predation (Araújo et al., 2011). Our study system allowed us to measure proxies of all these ecological factors and test their simultaneous effects on the degree of individual specialization in coexisting frog species. We found that these factors, particularly intraspecific competition, helped to explain differences in the degree of individual diet specialization across populations in the short (gut contents) and longer terms (stable isotopes). However, our results show that the responses of individual specialization to competition and predation are not the same across coexisting species, the sign of which (positive or negative) depending on species identity. Despite these idiosyncrasies, the observed effects of the four ecological factors on the degree of diet variation partially matched theoretical predictions and previous experimental evidence.

Intraspecific competition has been indicated as a major driver of interindividual niche differences (Araújo et al., 2011). Consistent with this prediction, we found that density of conspecifics was a significant and the most important predictor of short- and long-term individual specialization. However, in contrast to previous evidence suggesting that intraspecific competition generally favours individual niche variation (Svanbäck & Bolnick, 2007; Svanbäck & Persson, 2004), we found that it may either increase or decrease individual specialization. These distinct responses can arise from species-specific mechanisms that govern how prey rank preferences differ among individuals (Svanbäck & Bolnick, 2005). For example, if individuals within a population differ in their top-ranked prey (e.g., because of foraging trade-offs), low population density results in stronger individual specialization ("distinct preferences model"; Svanbäck & Bolnick, 2005), such as the pattern observed for *L. fuscus* (Figure 4, Supporting Information Figure S5). Alternatively, if consumers share their top-ranked prey, but rank less preferred resources differently, diet variation should increase with intraspecific competition ("refuge model"; Svanbäck & Bolnick, 2005). Overall, our results suggest that the nature of the effect of intraspecific competition on the degree of individual specialization in natural populations may be less obvious than commonly assumed (Araújo et al., 2011).

Surprisingly, the diversity of available resources did not explain variations in the degree of individual specialization. This contrasts with previous studies revealing an overall positive effect of ecological opportunity on diet variation because higher prey diversity creates more opportunity for individual diet variation by expanding individuals' foraging options (Costa-Pereira et al., 2017; Evangelista et al., 2014; Newsome et al., 2015). This discrepancy may simply arise because thin-toed frogs are generalists which consume a wide variety of species. As communities always harboured a large richness of prey types in our system (>14 invertebrate families), it is very likely that ecological opportunity was never constrained enough to refrain individual diets from diverging. Systems where consumers experience a clearer gradient of prey diversity may still show a positive relationship with prey diversity, but our results suggest that ecological opportunity may not be biologically important in generalist species in diverse communities. However, because our proxy for ecological opportunity is a "snapshot" of the diversity of available prey for frogs, we acknowledge that the lack of a relationship between individual variation and diversity of resources might also be driven by fluctuations in diversity of available resources over time that were not captured by our sampling method.

The observed species-specific effects of intraguild predation on the strength of individual specialization might be explained by its complex effects on population and individual niches. Predation can affect diet specialization indirectly via density-mediated effects and/or directly by altering prey foraging activity. A number of studies show that predators can drastically reduce foraging activity and habitat use on prey populations (Lima, 1998; Werner, Gilliam, Hall, & Mittelbach, 1983). Importantly, these nonlethal predation effects can differ across coexisting species (Pearl, Adams, Schuytema, & Nebeker, 2003; Walls, Taylor, & Wilson, 2002). Thus, predation might constrain, to a higher or lower degree, individuals to forage in restricted areas, affecting the strength of individual specialization if resources are patchy on the landscape (Araújo et al., 2011). For example, conspecific individuals vary in their boldness (i.e., propensity to forage in the presence of risk) in a diverse range of taxa (Toscano et al., 2016). Similar behavioural variation could promote individual diet variation in the presence of predation in our system. In this case, shy individuals should forage in safer refuges while bold individuals in more risky areas, potentially increasing diet divergence (Araújo et al., 2011). The relation between individual-level variations in animal personality and diet is a promising subject to future studies aiming to understand the causes and consequences of individual niche variation within wild populations and across coexisting species (Pruitt & Modlmeier, 2015; Toscano et al., 2016).

The effect of interspecific competition on individual specialization remains controversial both in the theoretical and empirical literature (Araújo et al., 2011; Bolnick et al., 2010; Cloyd & Eason, 2016). In general, we found that increases in the effective population sizes of heterospecifics led to an increase in the degree of individual trophic differences, but to varying degrees across frog

species (Figure 4). This pattern is opposite to predictions of the long-standing niche variation hypothesis (Van Valen, 1965). According to this hypothesis, higher interspecific competition tends to deprive populations of certain resources, constraining individual variation (Bolnick et al., 2007). In this case, release from interspecific competition increases population (but not individual) niche widths via increased among-individual variation. We tested a posteriori this hypothesis by modelling the population total niche width (TNW, Roughgarden, 1972) as a function of the effective density of heterospecifics and species identity (fixed effects, site included as a random effect), but we found no significant relationship (GLMM,  $\chi^2 = 0.08$ ,  $p = 0.76$ ). However, we did detect a significant reduction in the within-individual niche component (WIC) as the effective density of conspecifics increased (GLMM,  $\chi^2 = 3.74$ ,  $p = 0.05$ ) (parallel release, Bolnick et al., 2010). Altogether, these results suggest that interspecific competition does not necessarily lead to population niche packing as assumed by classic niche theory (Taper & Case, 1985; Van Valen, 1965), but can actually result in individual niche contraction. This mismatch between population and individual niche responses indicates that release from interspecific competition might not lead to the inclusion of novel prey in a population's diet, but can cause individuals to become more specialized in their diets, decreasing niche overlap with other conspecifics (Bolnick et al., 2010).

#### 4.2 | Magnitude of individual variation in coexisting species

Theory indicates that differences in the amount of individual variation across coexisting species can determine the outcome of competitive interactions. Specifically, it predicts that individual variation makes species coexistence less feasible in most cases because it usually reinforces competitive hierarchies. However, under the specific case of higher variation within the weak competitor, coexistence can be favoured (Barabás & D'Andrea, 2016; Hart et al., 2016). Thus, differences in individual specialization between coexisting species should play a key role in determining the outcome of species interactions and long-term coexistence. Our results show that individual trophic specialization inferred from different temporal scales (hours for gut contents; weeks for liver stable isotopes) and functional dimensions (prey types for dietary and  $\delta^{13}\text{C}$  data; trophic level for  $\delta^{15}\text{N}$ ) can differ considerably even between closely related and ecologically similar co-occurring species in natural communities. However, we also found that the degree of trophic specialization was highly variable across wild populations of the same species (for both gut content and stable isotope-based metrics), and this variation was typically not correlated across species across sites. As a consequence, differences in individual specialization between coexisting species were context-dependent and varied across communities. As a consequence, the identity of the species with more individual variation changed among sites for various species pairs. For example, in some communities, *L. chaquensis*

presented a substantially higher degree of diet variation than *L. podicipinus*, but in other communities the scenario was the opposite.

This pattern could at least partially be explained by the observed species-specific responses to how intraspecific variation scales with different ecological gradients. For instance, our results suggest that long-term individual specialization in *L. fuscus* has a strong negative response to density of conspecifics across populations, while the strength of individual variation in *L. chaquensis* is more driven by the density of heterospecifics (Figure 4). Thus, different combinations of these ecological drivers across communities could lead to shifts in relative individual specialization between coexisting species. These idiosyncratic responses might affect, ultimately, how species interact across communities. For example, if individual niche variation increases more sharply in weaker than in stronger competitors along an ecological gradient, the chance of coexistence might increase as well along this gradient. Thus, the high context-dependency of individual variation across populations and species has the potential to impact stabilizing niche differences and competitive asymmetries.

Regardless of the specific underlying mechanisms, our results indicate that species differ in their degree of individual specialization across different ecological contexts. This pattern has several important implications. First, it indicates that we cannot assume a constant amount of individual variation within competing species in natural communities. Second, it suggests that this pattern might play an important role in species coexistence at the landscape level because it creates a mosaic of diverse competitive interactions across sites, in which species might be superior competitors in some areas but inferior competitors in others. This mechanism is not considered in current metacommunity models but could potentially provide a novel and unexplored mechanism that favours or inhibits species coexistence. New empirical and theoretical models that measure and implement this variation could provide insight into how variation within populations is linked to regional community patterns.

## 5 | CONCLUSIONS

Resolving the causes and consequences of individual niche variation in natural communities is of key importance for understanding the structure and dynamics of populations and communities and ultimately the maintenance of biological diversity (Barabás & D'Andrea, 2016; Bolnick et al., 2011; Hart et al., 2016). Our study elucidates important aspects of individual variation in similar coexisting species that can contribute to more realistic models. While our results support some predictions of current theory, they also provide novel insights into how individual variation differs across and within coexisting species. Our findings indicate that individual variation in natural communities could play an important role not only in species coexistence at local communities, as assumed by current theory, but also in the organization of regional diversity patterns.

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## AUTHOR'S CONTRIBUTIONS

R.C.-P., M.S.A. and V.H.W.R. 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 and analysed the data; R.C.-P. led the writing of the manuscript with substantial contributions of M.S.A. and V.H.W.R. All authors edited the manuscript.

## DATA ACCESSIBILITY

Data supporting results are archived in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mq2h237> (Costa-Pereira, Rudolf et al., 2018).

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#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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