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Functional traits and environmental conditions predict community isotopic niches and energy pathways across spatial scales

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Abstract

1. Despite ongoing research in food web ecology and functional biogeography, the links between food web structure, functional traits and environmental conditions across spatial scales remain poorly understood. Trophic niches, defined as the amount of energy and elemental space occupied by species and food webs, may help bridge this divide.

2. Here, we ask how the functional traits of species, the environmental conditions of habitats and the spatial scale of analysis jointly determine the characteristics of trophic niches. We used isotopic niches as a proxy of trophic niches, and conducted analyses at spatial scales ranging from local food webs and metacommunities to geographically distant sites.

3. We sampled aquatic macroinvertebrates from 104 tank bromeliads distributed across five sites from Central to South America and compiled the macroinvertebrates' functional traits and stable isotope values ($\delta^{15}N$ and $\delta^{13}C$). We assessed how isotopic niches within each bromeliad were influenced by the functional trait composition of their associated invertebrates and environmental conditions (i.e., habitat size, canopy cover [CC] and detrital concentration [DC]). We then evaluated whether the diet of dominant predators and, consequently, energy pathways within food webs reflected functional and environmental changes among bromeliads across sites. At last, we determined the extent to which the isotopic niches of macroinvertebrates within each bromeliad contributed to the metacommunity

isotopic niches within each site and compared these metacommunity-level niches over biogeographic scales.

4. At the bromeliad level, isotopic niches increased with the functional richness of species in the food web and the DC in the bromeliad. The diet of top predators tracked shifts in prey biomass along gradients of CC and DC. Bromeliads that grew under heterogeneous CC displayed less trophic redundancy and therefore combined to form larger metacommunity isotopic niches. At last, the size of metacommunity niches depended on within-site heterogeneity in CC.

5. Our results suggest that the trophic niches occupied by food webs can predictably scale from local food webs to metacommunities to biogeographic regions. This scaling process is determined by both the functional traits of species and heterogeneity in environmental conditions.

1 | INTRODUCTION

Trophic interactions determine how energy and matter flow within food webs, and are thus important drivers of the stability of natural communities in a rapidly changing world (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013). Recent work has shown the important role of various functional traits (the biological, physiological and ecological attributes) of co-occurring species in determining trophic interactions and food web structure (Lefcheck & Duffy, 2015). Further, functional traits provide a mechanistic link between environmental conditions and food web composition, and between food web composition and energy fluxes within food webs (Duffy et al., 2007). In other words, food webs that share similar trait compositions are expected to respond in a similar way to environmental change. Such a trait-based approach could help predict food web structure in spatially distant communities, regardless of taxonomic differences. Despite recent advances in our understanding of the determinants of functional trait compositions, studies have largely been restricted to single trophic levels or a single taxon (reviewed in Gravel, Albouy, & Thuiller, 2016), especially plants (Lamanna et al., 2014; McKane et al., 2002; Violle, Reich, Pacala, Enquist, & Kattge, 2014), and, to a lesser extent, animals like fishes (Jardine, 2014; Kimbro, Byers, Grabowski, Hughes, & Piehler, 2014; Pool et al., 2016).

Trophic interactions within food webs (e.g., basal sources of energy, assimilated diet) can often be efficiently inferred by biochemical traits of species such as their carbon and nitrogen isotopic composition (Layman, Arrington, Montana, & Post, 2007; Newsome, del Rio, Bearhop, & Phillips, 2007; Rigolet, Thiébaut, Brind'Amour, & Dubois, 2015). Hence, the isotopic space, occupied by various members of a food web in a $\delta^{15}N–\delta^{13}C$ biplot (i.e., isotopic niche), is a relevant descriptor of the total resource use of that community (Newsome et al., 2007). Isotopic niches can be further described in terms of energy pathways within food webs, which may be mediated by the environmental conditions that determine the availability and diversity of food resources (Newsome et al., 2007). In summary, the recasting of food web structure in terms of isotopic niche raises two main questions: (a) What determines the key characteristics of isotopic niches (e.g., size, richness, nestedness; Cucherousset & Villéger, 2015; Villéger, Mason, & Mouillot, 2008) at scales ranging from local food webs to entire metacommunities? And (b) are patterns in isotopic niches consistent over broad biogeographic scales?

The macroinvertebrate food webs found within tank bromeliads (Bromeliaceae) represent ideal model systems to tackle these questions. Tank bromeliads are miniature aquatic ecosystems (allowing complete sampling of all macroinvertebrates), are widely distributed throughout the Neotropics and are highly replicated in nature (Sugden & Robins, 1979). Their rosettes collect rainwater and leaf litter and provide a habitat for numerous aquatic organisms (Benzing, 2000; Frank & Lounibos, 2009). Macroinvertebrates constitute the dominant part of animal biomass within bromeliad ecosystems. They display many feeding modes from detritivores and filter feeders to top predators. In particular, important top predators are odonate larvae, which have strong top-down effects on other macroinvertebrates (Petermann et al., 2015). Odonates, however, are mainly restricted to large bromeliads in mainland areas of Central and South America (Petermann et al., 2015). Bromeliad size, estimated by the maximum amount of water they can hold, is a strong predictor of macroinvertebrate composition and trophic dynamics (Dézerald et al., 2013; Petermann et al., 2015). Terrestrial leaf litter constitutes the main source of basal energy for these aquatic food webs, and trophic and species diversity generally increases with the amount of detritus (Dézerald

et al., 2013). However, as incident light increases, algae also become an important resource for macroinvertebrates (Farjalla et al., 2016). Canopy cover (CC) is therefore an important factor influencing the relative importance of leaf litter inputs and algal production to bromeliads (Farjalla et al., 2016). At last, bromeliads within a site act as a metacommunity, as bromeliad food webs have internal dynamics but are also linked by movement of individuals between insect generations (i.e., emergence of winged, terrestrial adults from bromeliad tanks and subsequent oviposition in the tanks of other bromeliads) or, in the case of noninsect invertebrates, by infrequent phoresy.

Assuming that functional feeding traits represent a strong link between the environment, isotopic niches and energy pathways in food webs (Gravel et al., 2016), we predict that any variation in environmental conditions (i.e., CC, detrital concentration [DC] and/or habitat size) that affects the functional trait composition within local communities would also change the attributes of isotopic niches (e.g., richness, evenness; *Prediction 1*, *P1*). For example, food webs fuelled by both allochthonous and autochthonous resources would be expected to have a higher diversity of functional traits related to the processing of coarse and fine organic matter and so may display larger isotopic niches. Similar to that, as odonates are top predators, we predict they will show shifts in dietary composition as the underlying food webs change with environmental conditions (*Prediction 2*, *P2*; Delibes et al., 2015). We also predict that bromeliad food webs subject to different environmental conditions (e.g., changes in CC within a site) may occupy different areas of isotopic space because the basal resources differ, which may broaden the metacommunity-level isotopic niche (i.e., the isotopic niche of all bromeliads within a site; *Prediction 3*, *P3*; Delibes et al., 2015). At last, we expect that metacommunities in different biogeographic regions will have similar isotopic niches in similar environmental conditions. However, if dispersal limits the distribution of species that can exploit certain resources, then metacommunities in different locations could instead occupy distinct portions of the isotopic niche (*Prediction 4*, *P4*). For example, odonates generally do not occur in bromeliads in isolated, cold or high elevation sites, suggesting that the engulfing predator functional niche will be missing from such species pools, reducing the isotopic niche of the community. Partitioning of isotopic niche effects into functional groups vs. environmental effects may help elucidate such patterns. The above predictions, the metrics used in the study and their biological meaning are detailed in Table 1.

2 | MATERIALS AND METHODS

2.1 | Sampling sites and tank bromeliads

Samples were collected at five sites distributed along a latitudinal gradient ranging from 18°N to 25°S (Figure 1). The northernmost site was Puerto Rico, followed by Costa Rica and French Guiana. The vegetation in these sites is dominated by primary and secondary tropical rainforests. The two southernmost sites in Brazil, Macae and Cardoso Island, are in coastal habitats called *restinga*. All samples

were collected within 2 weeks in each site, between January 2011 (Puerto Rico) and September 2012 (Costa Rica). Although different sites were sampled at different times of the year, bromeliad community composition is remarkably stable over the year (Dézerald et al., 2017). Therefore, seasonal effects on food web structure are likely of minor importance. Further descriptions of the sampling sites, including mean monthly temperatures and precipitation, and tank bromeliad characteristics can be found in Petermann et al. (2015) and Farjalla et al. (2016).

Ten to 30 large nonflowering bromeliads with whorls of phytotelmata of similar size were sampled at each site. Whenever possible, bromeliads were collected over a range of CC (i.e., Cardoso Island, French Guiana and, to a lesser extent, Costa Rica). In Puerto Rico, bromeliads were primarily shaded by canopy, whereas in Macae, bromeliads were generally exposed to full sun. The water held by each plant at the time of sampling was collected using either pipettes or by removing the bromeliad and pouring the water into a funnel, and measured. The maximum water volume of each plant, a proxy of habitat size, was quantified by slowly filling the empty bromeliad with a known volume of water until it overflowed. Both the water and detritus contained by the plants were sorted for invertebrates in the laboratory. The fine (150–500 μm) and coarse (>500 μm) dead organic matter from each plant was oven-dried at 40–50°C for 48 hr and weighed. The DC for each plant was calculated as a ratio of (coarse + fine) detritus:water volume. We estimated the amount of CC over each individual bromeliad, as a proxy for the diversity of carbon sources: Low cover allows light for autochthonous algal production and allochthonous inputs of leaf litter, whereas bromeliads under a denser canopy are mainly fed by leaf litter (Farjalla et al., 2016). Canopy cover was estimated using Lemmon spherical densitometer or from photographs according to Farjalla et al. (2016) and Leroy, Corbara, Dejean, and Céréghino (2009). At last, live aquatic macroinvertebrates from water and detritus in the bromeliads were sorted and identified to morphospecies. The taxa were then partitioned into five functional feeding groups (FFGs sensu Cummins, 1974: predators, filter feeders, gatherers, shredders, scrapers) based on gut content analyses (Dézerald et al., 2013) and on the literature (Merritt, Cummins, & Berg, 2008). We used two complementary methods to evaluate the isotopic niches of macroinvertebrates, based either on convex hulls or standard ellipse areas (SEA) (see below), because these methods are differentially sensitive to sample size and to the presence of outliers (Cucherousset & Villéger, 2015; Jackson, Inger, Parnell, & Bearhop, 2011). Overall, one or several isotopic samples were analysed for each taxa in each bromeliad, where the isotopic sample of any given taxa generally consisted of several individuals pooled to obtain sufficient mass for isotopic analysis. Thus, our study should be thought of as representing mean trophic positions of species, rather than accounting for intraspecific variation in feeding behaviour. The procedure used to generate isotopic data is found in Supporting Information Appendix S1, and the taxonomic, functional and isotopic composition of the communities in each site is reported in Supporting Information Table S1.

TABLE 1 Summary of the selected metrics in relation to the predictions tested in this study (P1–P4). Along with each metric name and prediction, the spatial and biological scale of investigation, how these metrics were measured, and their biological meanings are presented

	Metric name	Scale of investigation	Measurement	Biological meaning
P1.	Communities that contain a diversity of feeding modes (high FRich) will collectively be able to exploit a greater variety of resources (high IRich of consumers); thus, FRich and IRich will be correlated. Similar to that, communities with high functional evenness (FEve) will be more efficient at exploiting the available range of resources, and this will be reflected in high isotopic evenness (IEve) of the consumers. At last, we predict that isotopic niches will not only be affected by the functional traits of the consumers, but also by the environment: The greatest IRich and IEve values are expected under low canopy, when both algae and detritus are basal resources. Under high canopy cover (CC), low light limits algal growth			
	Isotopic (IRich) and functional (FRich) richness	Community within a bromeliad	Volume of the minimum convex hull that includes all species in isotopic (scaled $\delta^{15}N$-$\delta^{13}C$) and functional (biomass and functional feeding groups [FFGs]) space (Laliberté & Legendre, 2010)	Diversity of resource use and feeding modes, respectively
	Isotopic (IEve) and functional (FEve) evenness	Community within a bromeliad	Regularity in the distribution of species in the isotopic (scaled $\delta^{15}N$-$\delta^{13}C$) and functional (biomass and FFGs) space (Laliberté & Legendre, 2010)	Equitability in resource use or feeding modes, respectively
P2.	If the relative composition of invertebrate feeding groups changes over environmental gradients (detrital concentration, water volume or CC), then odonate predators are predicted to also shift their dietary composition			
	Energy pathways	Individual odonate larvae within a bromeliad	Relative contribution of each feeding group to odonate diets using mixing models (Parnell et al., 2010)	Main energy pathways within food webs
P3.	Bromeliad food webs that occur in different environmental conditions are predicted to also be different in their isotopic niche (high Metacommunity standard ellipse areas [SEAc]/Bromeliad SEAc ratio, low isotopic nestedness)			
	Metacommunity SEAc/ Bromeliad SEAc	Community within a bromeliad	Ratio between metacommunity SEAc (SEA corrected for sample sizes) and bromeliad-level SEAc (Jackson et al., 2011)	Difference between bromeliads in occupancy of isotopic space
	Isotopic nestedness	Communities among bromeliads	Ratio between area shared and the area of the smallest convex hull (Cucherousset & Villéger, 2015)	Degree to which bromeliads occupy subsets of other bromeliads' isotopic space
P4.	If P3 is true, then metacommunity isotopic niches may be larger (in terms of SEAc, carbon range [CR], nitrogen range [NR]) in environmentally heterogeneous sites. At the scale of biogeographic regions, metacommunity isotopic niches may be nested when sites have similar environmental conditions but not when sites have distinct environmental conditions			
	SEAc	Metacommunity defined by a site	Areas of isotopic space encapsulated by a metacommunity, corrected for sample size (Jackson et al., 2011)	Trophic space exploited by a metacommunity
	CR	Metacommunity defined by a site	Distance between the most and least ^{13}C-depleted species (Jackson et al., 2011)	Diversity of basal resources within the metacommunity
	NR	Metacommunity defined by a site	Distance between the most and least ^{15}N-depleted species (Jackson et al., 2011)	Length of the metacommunity-level food chain
	Isotopic nestedness	Regional, comparing metacommunities (sites)	Ratio between the isotopic area shared between two metacommunities and the area of the smallest convex hull (Cucherousset & Villéger, 2015)	Complementarity or redundancy in resource use

2.2 | Influence of functional trait composition and environmental conditions on bromeliad-level isotopic niches

The isotopic niche of macroinvertebrates was quantified as a convex hull encompassing the average isotopic values of each species within each bromeliad. Because differences between sites and bromeliads in the range of $\delta^{15}N$ and $\delta^{13}C$ values of consumer taxa can influence the characteristics of isotopic niches, such as richness and evenness, we scaled the relative position of each taxon within the isotopic biplot space containing all taxa from all sites (Cucherousset & Villéger, 2015). The scaling procedure is applied on each stable isotope separately and does not affect the distribution of the values. Instead, in the scaled isotopic space, both axes ($\delta^{15}N$ and $\delta^{13}C$) have similar ranges (from 0 to 1) and thus contribute equally to the computation of isotopic niches (more details about the equation can be found in Cucherousset & Villéger, 2015). Hereafter, we refer to these new coordinates as "scaled $\delta^{15}N$" and "scaled $\delta^{13}C$." We focused on

FIGURE 1 Geographic distribution of study sites

two characteristics of isotopic niches: isotopic richness and isotopic evenness (Table 1). Isotopic richness is a diversity metric that represents the amount of isotopic space occupied by all species in the community or metacommunity, while isotopic evenness evaluates the regularity in the distribution of all species within the same isotopic space (Cucherousset & Villéger, 2015; Villéger et al., 2008).

As potential drivers of isotopic niches, we focused on the functional trait composition of macroinvertebrate communities (functional richness and evenness) and important environmental conditions (maximum water volume, DC and CC). Functional richness and evenness were calculated as for the isotopic niche, but here, the biplot space is formed by two trophic-related traits: the FFGs and invertebrate biomass. As FFGs and invertebrate biomass are commonly measured traits for aquatic invertebrates, we considered how functional metrics based on such traits related to those based on isotopic niches. For this analysis, we used the *FD* package in R (Laliberté & Legendre, 2010), as it can handle both categorical (FFGs) and continuous data (invertebrate biomass, scaled $\delta^{15}N$ and scaled $\delta^{13}C$). The average per capita dry mass of each invertebrate morphospecies was retrieved from different survey datasets published in a recent study (from some of the same sites but at different years or periods of the year; Petermann et al., 2015). The invertebrate biomass was then obtained by multiplying the average per capita dry mass by the mean density of each morphospecies (i.e., abundance divided by maximum water volume and averaged across all bromeliads from a given site). Details regarding the calculation and biological meaning of these metrics are presented in Table 1 and Supporting Information Appendix S2.

To assess whether the isotopic niche of communities can be predicted from environmental characteristics and functional trait composition, we used linear and generalized linear mixed-effect models. Here, per bromeliad metrics of isotopic niche were used

as response variables while functional diversity metrics, environmental characteristics and their interaction constituted the independent predictors. As we found correlations among environmental variables, we used as pure estimates of each variable the residuals of each variable regressed against all other environmental variables. Because we were not interested in the influence of site-specific processes in this scale of analysis, we included "Site" as a random effect. Models were fitted with a Gaussian and beta distribution for isotopic richness and evenness, respectively, as these distributions provided the best fit to the data and met all statistical assumptions (*nlme*-package and *glmmADMB*-package in R). The significance of each parameter in the full model was evaluated using either type II or III ANOVA (*car*-package in R), depending on whether interactions were nonsignificant or significant, respectively. We present final models containing only significant variables. The significance of the final model was compared to the reduced model containing only the random effect using likelihood ratio tests. Adherences to model assumptions were graphically assessed, the normality of model residuals was evaluated via Shapiro tests, and the conditional and marginal R^2 were estimated. Marginal and conditional R^2 values could not be estimated for models fitted with a beta distribution.

2.3 | Energy pathways for odonates in relation to prey biomass and environmental conditions

Energy pathways from prey to predators were analysed via stable isotope mixing models using the *siar*-package in R (Stable Isotope Analysis in R; Parnell, Inger, Bearhop, & Jackson, 2010). We constrained our analyses to the diet of odonate larvae, because: (a) these top predators are broadly distributed across all study locations (except Puerto Rico); (b) odonates display a generalist predatory behaviour and so are likely to integrate multiple channels in the food web; and (c) they exert a strong top-down control on whole invertebrate communities (Petermann et al., 2015). We evaluated the relative proportion of four FFGs (i.e., filter feeders, gatherers, scrapers and shredders) to the diet of odonate larvae ($n = 103$). Individual prey taxa within a given FFG displayed substantial isotopic variability (Supporting Information Table S1), suggesting that those taxa may not be suitable for inclusion as a single prey source in the form of a given FFG (Phillips, Newsome, & Gregg, 2005). Therefore, within each bromeliad ($n = 57$), stable isotope data of the most abundant invertebrate prey per FFG were averaged (i.e., all individuals from a single prey taxa per FFG) and model input data were entered as means and standard deviations. Here, the relative abundances of invertebrate prey per FFG were evaluated at the site level. When no standard deviations could be provided because only one isotopic sample was available in a given bromeliad, we assigned a value of 1 to the missing *SD* of both stable isotopes (76% of the sources). This value of 1 was estimated from our dataset, and was based on the average variability of all sources in all bromeliads for which several isotopic samples were available (mean $SD^{13}C \pm SE = 0.96 \pm 0.1$; mean $SD^{15}N \pm SE = 0.75 \pm 0.1$; $n = 87$).

As lipids have more negative $\delta^{13}C$ values relative to other biochemical compounds due to kinetic isotope effects, the use of bulk carbon and nitrogen stable isotopes can bias interpretations of dietary habits in consumers when organisms differ in their lipid content (Kiljunen et al., 2006; Logan et al., 2008). Similar to that, the chitin of arthropods has a lower $\delta^{15}N$ value relative to proteins, resulting in potential $\delta^{15}N$ biases of C:N ratios. We assessed the magnitude of these potential biases by evaluating the variability in elemental composition of organisms (C:N ratios; Logan et al., 2008). We found a C:N ratio of 4.98 ± 0.04 (mean ± *SE*; *n* = 697), while other studies have found values from 3.3 to 4.8 for lipid-corrected C:N ratios using the whole body of freshwater macroinvertebrates as in our study (*n* < 100, Kiljunen et al., 2006; Logan et al., 2008). Our averaged uncorrected C:N ratio is thus within <0.2 of the lipid-corrected C:N ratios found in those studies, suggesting that the macroinvertebrates (mostly dipteran larvae) found in bromeliads have relatively low lipid content (or they store energy in the form of glycogen, a C-poorer molecule; e.g., chironomid larvae). The C:N ratios are also remarkably consistent among taxa, with 95% of the almost 700 samples falling within 3.73 and 7.81. In addition, there was a weak but significant negative correlation between $\delta^{15}N$ values and C:N ratios of all organisms ($\tau = -0.15$, *p* = <0.0001; Supporting Information Figure S1) whereas the overall relationship between $\delta^{13}C$ values and C:N ratios was not significant ($\tau = 0.06$, *p* = 0.1; Supporting Information Figure S1). Any biases related to elemental composition are therefore limited in our dataset but potentially greater for nitrogen than carbon stable isotopes. Because C:N ratios are often poor predictors of variation in $\delta^{13}C$ of macroinvertebrates (Kiljunen et al., 2006; Logan et al., 2008), we did not apply any corrections on bulk carbon and nitrogen stable isotope data.

To test the robustness of model outputs to variation in discrimination values, we used discrimination factor values obtained from (a) a broad range of invertebrates from the literature ($\delta^{13}C$: 0.5 ± 0.5‰; $\delta^{15}N$: 2.5 ± 1.0‰; Caut, Angulo, & Courchamp, 2009) and (b) our own data using published equations between invertebrate consumer tissues and diet isotope ratios (diet-dependent discrimination factor [DDDF]; $\delta^{13}C$: 0.95 ± 0.5‰; $\delta^{15}N$: 3.7 ± 0.7‰; Caut et al., 2009). As no qualitative or quantitative changes were observed when using the two discrimination factors, and because the DDDF was directly estimated from our data (Caut et al., 2009; Gorokhova, 2017), we presented only the results using the DDDF. To assess how changes in the relative contribution of the different FFGs to the diet of odonates were influenced by variations in the relative biomass of each prey group and environmental conditions, we performed generalized linear mixed-effect models for each FFG separately, fitted with a beta distribution. Model specifications and selection procedures were similar to previous models.

2.4 | Contribution of individual tank bromeliads to the metacommunity isotopic niches

We refer to the metacommunity isotopic niche as the total isotopic space of all invertebrates living in bromeliads within a given site (i.e., SEA encompassing the average isotopic values of each species within each site regardless of bromeliad identity). To assess the contribution of invertebrate communities found in each tank bromeliad to the metacommunity isotopic niche within a given site, we estimated the SEA (Table 1) for each individual bromeliad within a site and for each metacommunity using the *siar*-package in R (Jackson et al., 2011). Here, we used median values for each bromeliad and metacommunity corrected SEA (SEAc). All SEA were standardized for the number of morphospecies within a given bromeliad (bromeliad SEAc) and within a given site (metacommunity SEAc). We standardized both bromeliad and metacommunity SEAc to keep the two metrics independent (Kraft et al., 2011). Unlike isotopic richness and evenness, both bromeliad SEAc and metacommunity SEAc were estimated within the isotopic biplot space (unscaled $\delta^{15}N$ and $\delta^{13}C$; Jackson et al., 2011). We then used the ratio of each metacommunity SEAc from a given site divided by each bromeliad SEAc of that same site and compared variations in these values among sites using multiple comparison tests (based on Kruskal–Wallis test; *pgirmess*-package in R).

The SEAc metric focuses on the core of isotopic niches but does not provide any information on extreme values and, perhaps more importantly, on the extent to which isotopic niches overlap between bromeliads. Therefore, we also estimated the isotopic nestedness between any pairs of bromeliads (Table 1) within a given site as the percentage of isotopic overlap between overlapping convex hulls, expressed relative to the smallest convex hull (Cucherousset & Villéger, 2015). Isotopic nestedness is a special case of niche overlap in which the isotopic niche space of some bromeliads is a subset of the isotopic niche space of other bromeliads and can vary from 0 (no nestedness) to 1 (complete nestedness). We compared variations in the average values of overlap among sites using multiple comparison tests based on Kruskal–Wallis tests.

2.5 | Differences between sites in metacommunity-level isotopic niches

To evaluate the consistency in metacommunity isotopic niches among sites (e.g., all morphospecies from all bromeliads within a given site), we compared estimates of several isotopic metrics. For the metacommunity in each site, we estimated the ranges of $\delta^{15}N$ and $\delta^{13}C$ values (nitrogen range [NR], and carbon range [CR], respectively) and the SEAc using the *siar*-package in R (Jackson et al., 2011). Variation in SEAc among sites was then compared using a multiple comparison test (see above). Because extremely large sample sizes can bias the significance of the test (Lin, Lucas, & Shmueli, 2013), a random subsample of SEAc (*n* = 30) from the 10,000 posterior draws of the Bayesian output (i.e., output generated by *siar*) for each site was used as a response variable, and the site identity was used as a predictor. At last, we also calculated "isotopic nestedness," which estimates, in this case, the extent of overlap between the isotopic niches of any given two

metacommunities (Table 1). Similar to the estimates of bromeliad-level niche overlap, "isotopic nestedness" is based on convex hulls, which capture extreme values better than standardized ellipses. All statistical analyses were conducted using the R statistical language V. 3.2.1 (R Core Team, 2015) and evaluated under a 95% confident interval.

3 | RESULTS

3.1 | Influence of functional trait composition and environmental conditions on bromeliad-level isotopic niches

At the level of individual bromeliads, we found a significant positive effect of functional richness on isotopic richness (Estimate ± SE = 6.71 ± 1.13, χ^2 = 36.19, p = <0.0001). In addition, isotopic richness increased with DC (Estimate ± SE = 0.01 ± 0.004, χ^2 = 9.51, p = 0.002). None of the remaining environmental variables had a significant effect on isotopic richness (log-likelihood final/reduced model = −132.2/−113.4, p = <0.0001; marginal R^2 = 0.34; conditional R^2 = 0.34). On the other hand, we found no relationships between isotopic evenness and any of these variables (i.e., functional evenness and environmental variables; log-likelihood final/reduced model = 77.5/72.6, p = 0.24).

3.2 | Energy pathways for odonates in relation to prey biomass and environmental conditions

Depending on the study location and bromeliad, any given FFG contributed from 9% to 74% to the diet of odonates (minimum and maximum estimates from SIAR output, respectively; Supporting Information Table S2). The relative biomass of different FFGs, either alone or in interaction with environmental conditions, was a strong predictor of consumption patterns by odonates in all models (Table 2). Patterns of FFG consumption were not significantly influenced by the bromeliad sizes (i.e., maximum water volume). The consumption of filter feeders increased with their biomass in bromeliads only when DC was high (significant PB:DC interaction; p = 0.004; Table 2). The consumption of gatherers significantly increased with their biomass. The proportion of shredder biomass in the diet of odonates was positively correlated with their biomass and with increasing CC (PB:CC; p = 0.03). In contrast, the consumption of scrapers decreased as CC increased and increased with both their biomass in the bromeliad and the DC (Table 2).

3.3 | Contribution of individual tank bromeliads to the metacommunity isotopic niche

The contribution of each bromeliad to the metacommunity isotopic niche was dependent on both the isotopic space occupied by the average bromeliad (as estimated by SEAc) and the degree to which any bromeliad isotopic niche overlaps that of other bromeliads in

TABLE 2 Effects of environmental and community variables on the relative contribution of each functional feeding group to the diet of odonate larvae as determined by generalized mixed-effect models

	Estimate ± SE	df	χ^2	p
Filter feeders (N = 36)				
Intercept	−0.51 ± 0.15	1	11.8	0.0006
PB	−0.07 ± 0.35	1	0.04	0.84
DC	−0.01 ± 0.004	1	7.6	0.006
PB:DC	0.07 ± 0.03	1	8.3	0.004
Random effect = 0.06; log-likelihood (34.5/39.4); p = 0.02				
Gatherer (N = 42)				
Intercept	−0.65 ± 0.11			
PB	0.63 ± 0.18	1	11.9	0.0005
Random effect = 1.3e-7; log-likelihood (27.3/32.5); p = 0.001				
Scraper (N = 33)				
Intercept	−0.57 ± 0.18			
PB	0.74 ± 0.31	1	5.9	0.02
DC	0.006 ± 0.002	1	5.2	0.02
CC	−0.009 ± 0.002	1	13.0	0.0003
Random effect = 1.3e-7; log-likelihood (29.9/36.1); p = 0.006				
Shredder (N = 41)				
Intercept	−0.18 ± 0.21		0.7	0.4
PB	−0.18 ± 0.4	1	0.2	0.6
CC	−0.01 ± 0.004	1	12.9	0.0003
PB:CC	0.02 ± 0.007	1	4.7	0.03
Random effect = 1.1e-7; log-likelihood (31.1/39.2); p = 0.001				

Notes. The log-likelihood values of the reduced and final models (reduced/final) and associated significance (p) are displayed. Note that nonsignificant variables and interactions are not shown (in particular, maximum water content). Random effect: site (variance in final model); PB: percentage of a given functional group biomass; DC: detrital concentration; CC: canopy cover (%); N: number of bromeliads; df: degrees of freedom.

the same metacommunity (isotopic nestedness). The SEAc of each bromeliad contributed significantly more to the metacommunity SEAc in French Guiana, Costa Rica and Puerto Rico (average ratios: 0.8 ± 0.1, 0.4 ± 0.04 and 0.5 ± 0.09, respectively) than in Cardoso Island and Macae (average ratios of metacommunity SEAc/bromeliad SEAc: 2.0 ± 0.2, and 1.7 ± 0.2, respectively; Kruskal–Wallis χ^2 = 55.1; df = 4; p < 0.0001; Figure 2a). Note that the average size of bromeliad SEAc was not significantly different among most study locations, except between Cardoso Island and Macae (Kruskal–Wallis χ^2 = 13.5; df = 4; p < 0.0082), suggesting that the size of metacommunities is driving the observed pattern (see next section). The isotopic nestedness among individual bromeliads was significantly higher in Puerto Rico and Macae (0.52 ± 0.03 and 0.4 ± 0.02, respectively) compared to French Guiana, Costa Rica and Cardoso Island (0.24 ± 0.02%, 0.15 ± 0.02% and 0.25 ± 0.02%, respectively; Kruskal–Wallis χ^2 = 117.5; df = 4; p < 0.0001; Figures 2b and 3a,b).
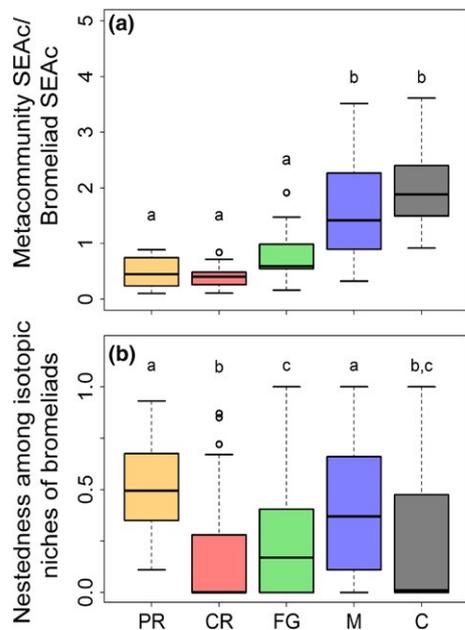
FIGURE 2 Contribution of bromeliad-level isotopic niches to metacommunity isotopic niches. (a) Distribution of ratios of bromeliad-level SEAc to metacommunity-level SEAc. (b) Distribution of overlap values between the convex hulls of each pair of bromeliads within any given site. Note that values in (a) may be >1.0 as greater uncertainty is attributed to bromeliad-level SEAc (small sample sizes) compared to metacommunity SEAc (larger sample sizes). Sites are ordered from northernmost (left) to southernmost (right) sites. PR: Puerto Rico; CR: Costa Rica; FG: French Guiana; M: Macae (Brazil); C: Cardoso Island (Brazil)

3.4 | Differences between sites in metacommunity-level isotopic niches

The study sites displayed contrasting species pools in terms of morphospecies composition and richness, with Cardoso Island (Brazil) being the most speciose site and Puerto Rico being the most depauperate site (Supporting Information Table S1). The size of the metacommunity isotopic niche (SEAc) also showed a strong geographic pattern of increase from the northernmost (Puerto Rico) to the southernmost (Cardoso Island) site (Figure 3c,d). The size of the metacommunity isotopic niche was influenced by the natural range of nitrogen and carbon stable isotopes in each site, but the importance of each element was dependent on the sampling site. The size of the metacommunity isotopic niche was mainly determined by the range of carbon isotope values in Cardoso Island and Macae, by nitrogen isotope values in Costa Rica, and equally by carbon and nitrogen isotopes in French Guiana and Puerto Rico (Figure 3c).

The five metacommunity isotopic niches segregated into two groups with very low isotopic niche overlap between them (nestedness = 6%). The first group was composed by the northernmost sites based in rainforests, Puerto Rico, Costa Rica and French Guiana, while the second group was composed by the southernmost sites based in coastal *restingas*, Cardoso Island and Macae. Nestedness in the first group varied from 14% to 92%, while in the second group it was 64% (Table 3; Figure 3a,b).

4 | DISCUSSION

In this study, we used the food webs contained in 104 bromeliads from five sites in Central and South America to evaluate which factors determined the key characteristics of isotopic niches at increasingly large spatial scales, from individual bromeliads to local metacommunities and from metacommunities to the biogeographic region. We found that: (a) regardless of geographic location, the isotopic space occupied by all species (isotopic richness) within individual bromeliads could be predicted from the functional composition of invertebrates in combination with the DC within bromeliads; (b) within sites, predatory larvae of odonates consumed prey FFGs relative to their local availability and biomass in the system, but their diet was also influenced by gradients of DC and CC. These results support our predictions that invertebrate functional traits and environmental gradients would influence the characteristics of isotopic niches at the bromeliad level (*P1*) and the dietary composition of top predators (*P2*); (c) individual tank bromeliads that differed in environmental conditions also contained trophically dissimilar communities (e.g., low nestedness among individual isotopic niches) which broadened the metacommunity isotopic niche (e.g., Cardoso Island vs. Puerto Rico); and (d) metacommunity isotopic niches increased in size from northernmost, rainforest sites (Puerto Rico, Costa Rica, French Guiana) to southernmost, *restinga* sites (Macae and Cardoso Island, both in Brazil) and displayed low nestedness between northern and southern sites. These findings also support our predictions that bromeliad food webs that occur in heterogeneous environmental conditions have different isotopic niches (*P3*) and form larger metacommunity isotopic niches at the site level (*P4*).

Variations in the attributes of trophic niches in space and/or time are often evaluated in isolation from the abiotic environment (Pool et al., 2016), potentially resulting in a poor comprehension of the combined effects of biotic and abiotic drivers on food web structure. Using food webs that are a few metres to several thousand kilometres away from each other, we confirmed our expectations that the isotopic niche size of a given community is positively correlated with both functional richness and the quantity of basal resources in the system (i.e., DC). First, a large variability in the values or modalities of a few functional traits, namely FFGs and per capita biomass, may favour the coexistence of species via a better partitioning of food and habitat resources (Adam, Kelley, Ruttenberg, & Burkepile, 2015), especially in small and contained habitats (Azevedo, Kraenkel, & Pamplona da Silva, 2012). We expected isotopic diversity to correlate with functional diversity, because species that differ substantially in their feeding traits and relative biomasses are likely to also differ in their position within food webs. We also expected invertebrate functional and isotopic diversity to be positively correlated with DC as higher amount of energy at the base of food webs is likely to stimulate productivity, and therefore diversity at higher levels (Gambi, Pusceddu, Benedetti-Cecchi, & Danovaro, 2014; Mindel, Neat, Trueman, Webb, & Blanchard, 2016).

Our findings also indicate that bromeliad food webs with an even distribution of biomass among FFGs did not necessarily have

FIGURE 3 Variations in isotopic niches among the different sites: PR: Puerto Rico, CR: Costa Rica, FG: French Guiana, M: Macae (Brazil), C: Cardoso Island (Brazil). (a) Convex hulls of the total areas of metacommunity isotopic niches are plotted in the scaled biplot space. (b) Convex hulls of the total areas of isotopic niches within individual bromeliads are plotted in the scaled biplot space. Unfilled polygons depict the convex hulls of metacommunity isotopic niches. (c) The standard ellipse areas of metacommunities (metacommunity SEAc) are plotted in the isotopic biplot space with a 95% confidence interval. The coloured bars indicate the range of variation in δ^{15}N and δ^{13}C on each study site. (d) Ranges of variation of metacommunity SEAc sorted along a north–south gradient (northernmost and southernmost sites on the left and right, respectively). Shared letters indicate nonsignificant differences
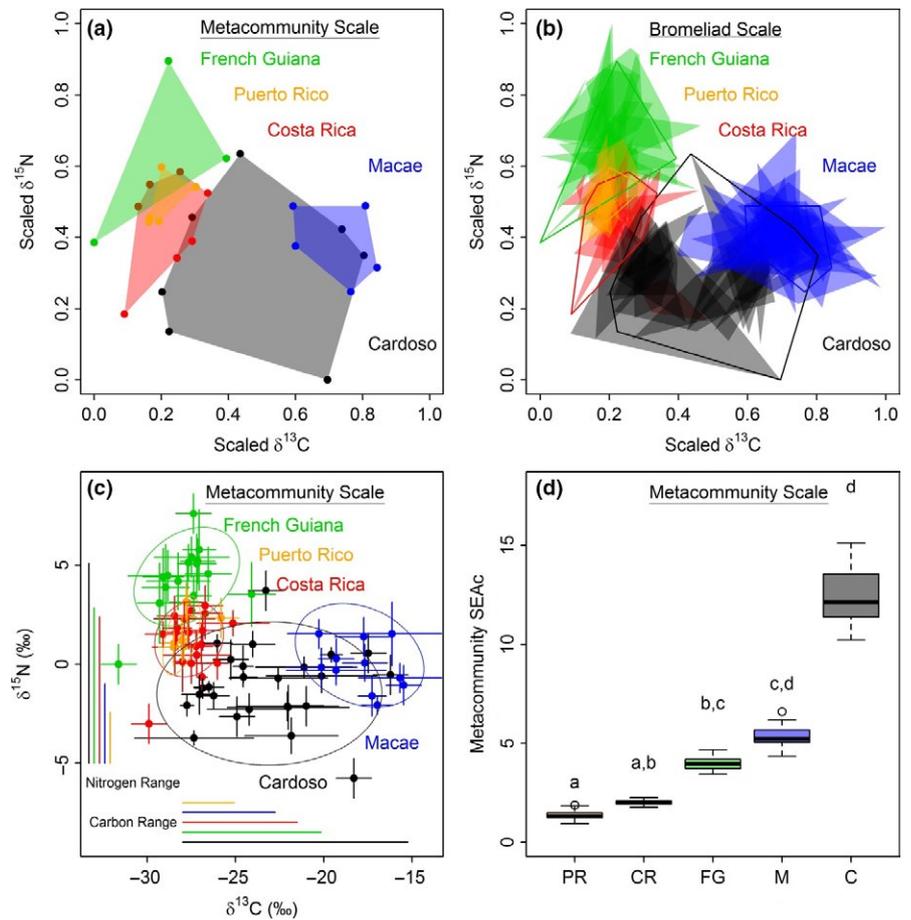
TABLE 3 Pairwise comparisons of isotopic niche characteristics among sites using the isotopic nestedness metric (in %). This metric was calculated within the scaled isotopic biplot space (see also Figure 3a,b)

	Isotopic nestedness				
	Puerto Rico	**Costa Rica**	**French Guiana**	**Macae**	**Cardoso Island**
Puerto Rico	–	92	47	0	0
Costa Rica		–	14	0	6
French Guiana			–	0	0
Macae				–	64
Cardoso Island					–

an even distribution of species in the isotopic niche space (see also Hoeinghaus & Zeug, 2008; Pool et al., 2016; Schleuter, Daufresne, Massol, & Argillier, 2010). One source of confusion when interpreting variations in isotopic niches is the use of weighted or unweighted diversity metrics that, respectively, do or do not account for species biomasses (Rigolet et al., 2015). Traditional weighted functional indices usually take into account how a given functional space is filled (e.g., richness, dispersion, evenness) but also the distribution of biomass among species. It is, however, impossible to discriminate between variations in a given index per se and communities with very unbalanced species distribution (i.e., communities dominated by invasive species or large-bodied predators). In our study, the distribution of invertebrate biomass was explicitly included as a distinct functional trait or predictor of isotopic niches. We found that isotopic evenness was unrelated to functional evenness. A likely explanation

is that the biomass distribution of FFGs varied along gradients of environmental conditions, disrupting the predicted relationship.

Our analysis of odonate diet provides a concrete example of how one particular energy pathway is influenced by functional diversity. As predicted, the relative contribution of FFGs to the diet of predatory damselflies was influenced by variation in the biomass of these functional groups along gradients in environmental conditions. In addition, environmental conditions influenced odonate diet, likely through a direct influence on macroinvertebrate taxonomic composition. Environmental gradients resulted in the unequal distribution of FFGs among bromeliads within sites, resulting in idiosyncratic patterns of trophic interactions that tracked prey availability. For example, an increase in CC may increase the production of shredder biomass (i.e., organisms such as tipulids that feed upon coarse organic matter or dead leaves) and subsequently lead to high consumption of shredders

by odonate larvae (significant interaction between DC and shredder biomass; Table 2). On the other hand, some functional groups may be under-represented in the diet of predators with respect to their availability; for example, some filter feeders (e.g., *Culex* spp., Culicidae) display antipredator behavioural traits that prevent their consumption by odonate larvae (Hammill, Atwood, Corvalan, & Srivastava, 2015). Altogether, these results underscore the importance of predators' generalist behaviour in dampening variations in prey resources driven by varying environmental conditions and/or antipredator behavioural or morphological traits in prey species (Rooney & McCann, 2012).

The isotopic niche size of the metacommunity increased significantly from the northernmost site in Puerto Rico down to Cardoso Island on the coast of Brazil. This pattern may reflect the higher diversity of basal resources in the southernmost *restinga* sites. In bromeliad ecosystems (Brouard et al., 2011; Farjalla et al., 2016), as well as in many lotic and lentic ecosystems (Takamura & Nakagawa, 2016; Wallace & Eggert, 2009), canopy cover, by altering incident radiation, generally determines the availability and relative importance of allochthonous (litter fall) vs. autochthonous (algae) resources at the base of the food webs. Allochthonous and autochthonous energy sources differ widely in their isotopic and nutritional values, with terrestrial (allochthonous) subsidies being more depleted in ^{13}C and potentially less nutritious for invertebrate growth than algal sources (autochthonous; Taipale et al., 2014). As shown by previous studies, wider gradients of CC in *restinga* sites, especially Cardoso, compared to northern, rainforest sites (e.g., Puerto Rico, French Guiana and Costa Rica) resulted in a greater variety of energy sources for macroinvertebrates (Farjalla et al., 2016). Because the average sizes of bromeliad-level isotopic niches were not significantly different among sites (except between Cardoso Island and Macae), differences between bromeliads in their basal carbon sources must drive site differences in the metacommunity isotopic niche.

More general, variation between bromeliads in their isotopic niches can play a key role in explaining metacommunity isotopic niches. We found that the relative contribution of bromeliad-level isotopic niches to metacommunity isotopic niches was smaller in Cardoso Island than in Puerto Rico, and isotopic niches were less nested in the former than in the latter site. The influence of site-specific light exposure, therefore, provides a persuasive explanation for the shifts in isotopic niches across geographically distant sites. Note that this result is independent of differences between metacommunities in species richness as ellipses were corrected for differences in sample sizes (i.e., in the number of species per site or per bromeliad).

4.1 | Caveats and concluding remarks

Growing evidence indicates that changes in the isotopic niche characteristics of species and communities do not necessarily pinpoint the expected underlying processes, such as modifications in feeding habits between consumers and resources (Gorokhova, 2017; Jabot, Giraldo, Lefebvre, & Dubois 2017; Pool et al., 2016). For instance, the structure of food webs (e.g., species richness, connectance) may affect the accuracy of isotopic metrics (e.g., Rao, mean nearest

neighbour distance) in describing trophic relationships (Jabot et al., 2017). In particular, isotopic metrics poorly described food webs with high species richness, low connectance, long food chains and a dominance of omnivores. Although we used different isotopic metrics and the aquatic food webs found in tank bromeliads have opposite characteristics (i.e., low species richness, high connectance, short food chains; Dézerald et al., 2013), explicitly integrating the food web structures in our analyses may strengthen our interpretations of changes in isotopic niches.

In addition, we focused on the isotopic niche characteristics from small to large spatial scales, but another important scale not addressed in our study was from individuals to species. Intraspecific variation in species traits (e.g., elemental composition, life-history traits, behaviour) has long been recognized as an influence on the dynamics of ecological interactions (see review in Bolnick et al., 2011). For example, intraspecific variability in the physiological status of Baltic mysids influences isotopic niche characteristics (using Layman's metrics; Gorokhova, 2017). Although our study involved a substantial sampling effort (700 isotopic values, 104 tank bromeliads), the replication within taxa was low, that is from one to five isotopic samples that often pooled several individuals per taxa (Supporting Information Appendix S1) in each tank bromeliad. This low replication prevented us from fully addressing intraspecific variability in isotopic values. Although we did not compare intraspecific to interspecific variability in isotopic or functional trait values in this study, this additional information could help refine our predictions of the relationship between trophic niches, energy pathways, functional composition and environmental conditions (Bolnick et al., 2011). High intraspecific variation in trophic niches could result in a substantial contribution of the niches of individual species to metacommunity niches (Araújo, Bolnick, & Layman, 2011), a possibility that could be tackled in future research.

Our study suggests that isotopic niches and energy pathways are predictable across broad biogeographic scales, as long as species functional traits and important environmental drivers are carefully selected and evaluated interactively. In a specific manner, we found that we could understand the isotopic niche space occupied by bromeliad food webs at a regional scale by considering metacommunity and bromeliad-level patterns in, respectively, environmental heterogeneity and functional composition. This approach suggests a new way forward in food web ecology that integrates insights from both trait-based and metacommunity ecology.

AUTHOR'S CONTRIBUTIONS

O.D. wrote the manuscript; O.D. and A.L.G. designed and conceived the study; A.L.G., B.A.R., B.C., C.L., D.S.S., G.C.O.P., G.Q.R., J.-F.C., M.J.R., N.A.C.M., R.C. and V.F.F. conducted the fieldwork; and O.D. analysed the data. All authors made substantial contributions to the development of the ideas presented here, commented critically on drafts of the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

Data are deposited in the Dryad Digital Repository (Provisional DOI: https://doi.org/10.5061/dryad.bn5155f) (Dézerald et al. 2018).

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SUPPORTING INFORMATION

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