Received: 28 February 2019 | Revised: 29 September 2019 | Accepted: 3 October 2019

DOI: 10.1111/geb.13029

RESEARCH PAPER

Global Ecology and Biogeography | A Journal of Macroecology | WILEY

Species niches, not traits, determine abundance and occupancy patterns: A multi-site synthesis

Nicholas A. C. Marino[1,2] | Régis Céréghino[3] | Benjamin Gilbert[4] | Jana S. Petermann[5,6] | Diane S. Srivastava[7] | Paula M. de Omena[8] | Fabiola Ospina Bautista[9,10] | Laura Melissa Guzman[6] | Gustavo Q. Romero[8] | M. Kurtis Trzcinski[11] | Ignacio M. Barberis[12] | Bruno Corbara[13] | Vanderlei J. Debastiani[14] | Olivier Dézerald[15] | Pavel Kratina[16] | Céline Leroy[17,18] | Arthur Andrew M. MacDonald[3,19] | Guillermo Montero[20] | Valério D. Pillar[14] | Barbara A. Richardson[21] | Michael J. Richardson[21] | Stanislas Talaga[22] | Ana Z. Gonçalves[23] | Gustavo C. O. Piccoli[24] | Merlijn Jocqué[25] | Vinicius F. Farjalla[1]

[1]Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil

[2]Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil

[3]ECOLAB, Université de Toulouse, CNRS, Toulouse, France

[4]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada

[5]Berlin-Brandenburg Institute of Advanced Biodiversity Research, Berlin, Germany

[6]Department of Biosciences, University of Salzburg, Salzburg, Austria

[7]Department of Zoology & Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada

[8]Laboratório de Interações Multitróficas e Biodiversidade, Departamento de Biologia Animal, Instutito de Biologia, Universidade Estadual de Campinas (UNICAMP), Campinas, SP, Brazil

[9]Department of Biological Sciences, University of the Andes, Bogotá, Colombia

[10]Departamento de Ciencias Biológicas, Universidad de Caldas, Caldas, Colombia

[11]Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, British Columbia, Canada

[12]Facultad de Ciencias Agrarias, Instituto de Investigaciones en Ciencias Agrarias de Rosario, Universidad Nacional de Rosario, Consejo de Investigaciones Científicas y Técnicas, Zavalla, Argentina

[13]Laboratoire Microorganismes, Génome et Environnement, Université Clermont Auvergne, Aubière, France

[14]Departamento de Ecologia e Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil

[15]UMR ESE, Ecology and Ecosystem Health, INRA, Rennes, France

[16]School of Biological and Chemical Sciences, Queen Mary University of London, London, United Kingdom

[17]AMAP, IRD, CIRAD, CNRS, INRA, Université de Montpellier, Montpellier, France

[18]EcoFoG, AgroParisTech, CIRAD, CNRS, INRA, Université de Guyane, Université des Antilles, Kourou, France

[19]Centre for the Synthesis and Analysis of Biodiversity (CESAB-FRB), Aix-en-Provence, France

[20]Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, Zavalla, Argentina

[21]Luquillo LTER, Institute for Tropical Ecosystem Studies, College of Natural Sciences, University of Puerto Rico at Rio Piedras, San Juan, Puerto Rico

[22]Unité d'Entomologie Médicale, Institut Pasteur de la Guyane, Cayenne, France

[23]Departmento de Botânica, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil

[24]Departmento de Zoologia e Botânica, Universidade Estadual Paulista, São José do Rio Preto, São Paulo, SP, Brazil

[25]Aquatic and Terrestrial Ecology, Royal Belgian Institute of Natural Sciences, Brussels, Belgium

Correspondence
Nicholas A. C. Marino, Avenida Carlos Chagas Filho, 373, Sala A0-008, Bloco A, Sub-Solo, Laboratório de Limnologia, Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil, CEP 21941-599.
Email: nac.marino@gmail.com

Funding information
Royal Society of Edinburgh; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 2016/01209-9 and 2016/09699-5; Universidad Nacional de Rosario, Grant/Award Number: AGR-210 and AGR-290; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 301514/2017-8, 307689/2014-0, 312770/2014-6 and 401345/2014-9; Natural Sciences and Engineering Research Council of Canada; Centre de synthèse et d'analyse sur la biodiversité; Carnegie Trust for the Universities of Scotland; National Science Foundation, Grant/Award Number: DEB-0218039 and DEB-0620910; International Institute of Tropical Forestry; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: 2013/0877 and 2014/04603-4; Agence Nationale de la Recherche, Grant/Award Number: Labex CEBA, ANR-10-LABX-25-01; Saba Conservation Foundation; Royal Society, Grant/Award Number: NAF\R2\180791; Fondation pour la Recherche sur la Biodiversite

Editor: Jonathan Belmaker

Abstract

Aim: Locally abundant species are usually widespread, and this pattern has been related to properties of the niches and traits of species. However, such explanations fail to account for the potential of traits to determine species niches and often overlook statistical artefacts. Here, we examine how trait distinctiveness determines the abilities of species to exploit either common habitats (niche position) or a range of habitats (niche breadth) and how niche position and breadth, in turn, affect abundance and occupancy. We also examine how statistical artefacts moderate these relationships.

Location: Sixteen sites in the Neotropics.

Time period: 1993–2014.

Major taxa studied: Aquatic invertebrates from tank bromeliads.

Methods: We measured the environmental niche position and breadth of each species and calculated its trait distinctiveness as the average trait difference from all other species at each site. Then, we used a combination of structural equation models and a meta-analytical approach to test trait–niche relationships and a null model to control for statistical artefacts.

Results: The trait distinctiveness of each species was unrelated to its niche properties, abundance and occupancy. In contrast, niche position was the main predictor of abundance and occupancy; species that used the most common environmental conditions found across bromeliads were locally abundant and widespread. Contributions of niche breadth to such patterns were attributable to statistical artefacts, indicating that effects of niche breadth might have been overestimated in previous studies.

Main conclusions: Our study reveals the generality of niche position in explaining one of the most common ecological patterns. The robustness of this result is underscored by the geographical extent of our study and our control of statistical artefacts. We call for a similar examination across other systems, which is an essential task to understand the drivers of commonness across the tree of life.

KEYWORDS
abundance, environmental niche, functional distinctiveness, functional traits, metacommunity, niche breadth, niche position, occupancy

1 | INTRODUCTION

Species with high local abundance also tend to be widespread regionally (Brown, 1984; Gaston et al., 2000), a pattern that may arise by several mechanisms (Borregaard & Rahbek, 2010). Among these, most attention has focused on two mechanisms related to how species use available habitat. The "niche breadth hypothesis" (Brown, 1984) asserts that species able to tolerate a broad range of environmental conditions should be both locally abundant and widespread. The "niche position hypothesis" (also called the habitat availability hypothesis; Hanski, 1993; Venier & Fahrig, 1996) asserts that species capable of using the most common environmental conditions found across habitats in a region (i.e., a central niche position) will be both locally abundant and widespread. These two hypotheses have been tested extensively across taxonomic groups, different climatic regions and different ecosystems, both regionally and across the geographical range of species (Martinez-Meyer, Diaz-Porras, Peterson, & Yanez-Arenas, 2013; Yañez-Arenas, Martínez-Meyer, Mandujano, & Rojas-Soto, 2012; for a brief overview of other studies, see Heino & Tolonen, 2018). Nonetheless, support for either hypothesis as the main driver of patterns of abundance and occupancy is inconclusive (Dallas, Decker, & Hastings, 2017; Slatyer, Hirst, & Sexton, 2013; Weber, Stevens, Diniz-Filho, & Grelle, 2017), and it is unclear whether this is attributable to statistical artefacts or to failure to account for the underlying drivers of niche breadth and position, such as species traits.

Species traits are increasingly being used to predict species–environment associations (McGill, Enquist, Weiher, & Westoby, 2006) and, as such, have been proposed as a driver of abundance and occupancy patterns (Heino & Tolonen, 2018). The rationale is

that species traits determine the range of environmental conditions in which each species can occur, and abundances are expected to reach their maximum when traits best match environmental conditions (Lavorel & Garnier, 2002). This suggests that there might be a suite of traits that could predict which species should be dominant and widespread. This prediction is often tested using only one or a few well-resolved traits (e.g., body size, feeding guild) to explain patterns in abundance and occupancy (Heino & Grönroos, 2014; Heino & Tolonen, 2018; Rocha et al., 2018; Tales, Keith, & Oberdorff, 2004). However, studies based on a few traits have only limited capacity to explain abundance and occupancy; instead, such patterns should be best explained by the niche properties of species.

Although species traits appear less important than their niche properties in contributing to abundance and occupancy, there are a few limitations from previous studies that need to be considered. First, there is no single trait that can fully describe the ecological strategies used by a species (Céréghino et al., 2018; Winemiller, Fitzgerald, Bower, & Pianka, 2015). As such, abundance and occupancy patterns may be driven by combinations of several traits rather than by individual traits (e.g., body size and trophic guild; Pilière et al., 2016), or by how distinct each species is in terms of trait composition when compared with the rest of the community (Saito, Laroche, Siqueira, & Pavoine, 2018). Second, previous studies have failed to recognize that niche properties of species may be governed by their traits (McGill et al., 2006), and to date, studies do not account for this relationship when analysing abundance and occupancy patterns. Consequently, the largest contribution of species traits to such patterns may be through their effect on niche properties (Figure 1, bottom panel), but this possibility has yet to be tested.

Statistical artefacts may also inflate apparent effects of niche position, niche breadth and traits on abundance and occupancy (Borregaard & Rahbek, 2010). Given that habitats have a limit to the number of individuals that they can support, even random placement of individuals in a habitat matrix would result in species with more individuals occupying a greater number of habitat types. In this case, any relationship between niche breadth, niche position, abundance and occupancy could be attributed to a statistical artefact. Nevertheless, attempts to disentangle such artefacts from biological effects when explaining abundance and occupancy patterns are rare (e.g., Rocha et al., 2018; Siqueira, Bini, Cianciaruso, Roque, & Trivinho-Strixino, 2009), leaving the results from many studies difficult to interpret.

Here, we use the aquatic invertebrate communities found within tank bromeliads to understand how species traits and their niche properties contribute to their patterns of abundance and occupancy. Tank bromeliads are plants within the family Bromeliaceae capable of accumulating rainwater and detritus in their leaf axils, forming a habitat for several invertebrate species; most notably, the immature stages of insects and other small invertebrates (Srivastava et al., 2004). Previous studies on this aquatic microecosystem suggest that these invertebrates are unlikely to be dispersal limited and that community composition varies predictably along environmental gradients related to plant size (i.e., diameter, water volume and number of leaves; Dézerald et al., 2013; Farjalla et al., 2012; Marino, Srivastava, & Farjalla, 2013; Petermann et al., 2015; Richardson, 1999). Furthermore, evidence suggests that this species–environment association is unlikely to be explained by spatial autocorrelation in environmental conditions (Marino et al., 2013, 2017), but by differences in species life-history traits (e.g., environmental tolerance and feeding guild; Dézerald, Céréghino, Corbara, Dejean, & Leroy, 2015; Dézerald et al., 2017). Céréghino et al. (2018) recently compiled trait information from 852 bromeliad invertebrate taxa sampled in several sites across the Neotropics and demonstrated that four major axes of trait variation summarize their ecological strategies (i.e., trophic, habitat, defence and life-history niche axes). As such, aquatic invertebrates from tank bromeliads can be used to test the contribution of biological mechanisms and statistical artefacts to abundance and occupancy patterns.

Using environmental and aquatic invertebrate data sampled from tank bromeliads across 16 sites across the Neotropics, we tested the relative strength and importance of species traits and niche properties on abundance and occupancy while accounting for statistical artefacts. Our approach allowed us to quantify the magnitude of these relationships within and across study sites. We hypothesized that the trait differences of species govern their niche properties, and thus are indirectly related to abundance and occupancy patterns (Figure 1, bottom panel). Importantly, there are two opposing hypotheses that link differences in traits to species abundances and distributions.

First, a distinct combination of traits may allow a species to explore a broad range of environmental conditions. This can occur because distinct trait combinations map onto multivariate environmental conditions better than an average of all traits or because distinct traits weaken biotic interactions, such as competition, reducing their negative effects across a range of environments (Bernard-Verdier et al., 2012; Loughnan & Gilbert, 2017). In either case, such functionally distinct species are expected to have broader niche breadths and live in the most common environmental conditions found across habitats (i.e., have a central niche position; Figure 1, P1a). According to the niche breadth and niche position hypotheses, this would lead to high abundances and frequent occurrences of such species (Figure 1, bottom panel, P2). Alternatively, it may be that very distinct trait combinations constrain the range of environmental conditions of a species and represent an ecological strategy suited to a habitat specialist; as such, functionally distinct species would have narrow niche breadths and could occupy either central or marginal habitats (Figure 1, P1b). Through the niche breadth hypothesis, such habitat specialization is expected to lead to low local abundance and infrequent occurrence (Figure 1, bottom panel, P2 and P3). Finally, given the species–environment relationships reported for aquatic invertebrates from tank bromeliads in previous studies, we predict that relationships between niche breadth, niche position, abundance and occupancy are unlikely to be explained solely by statistical artefacts.

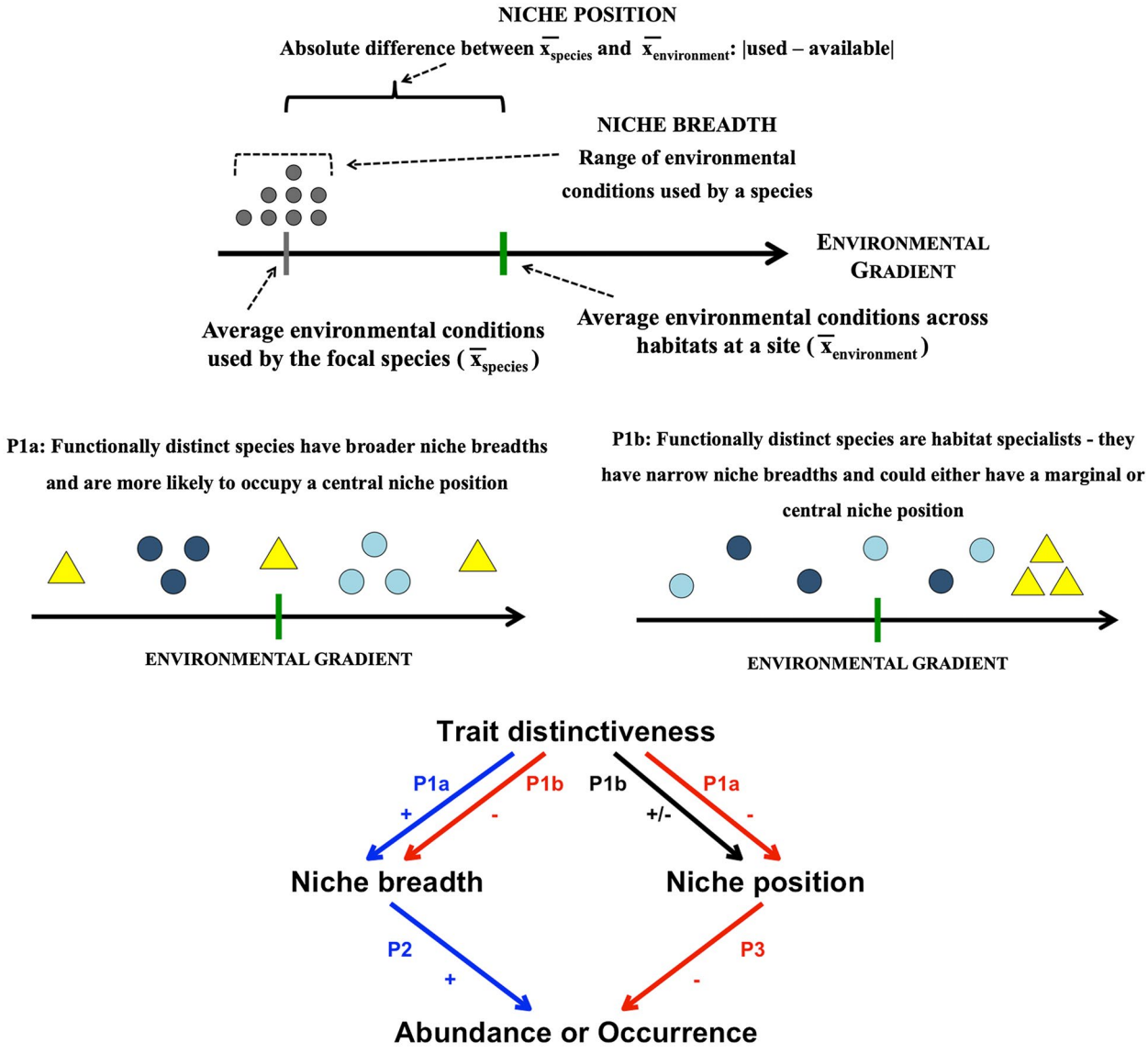


FIGURE 1 Hypothesized relationships between trait distinctiveness, niche breadth, niche position, mean local abundance and occupancy. The top panel represents the distribution of individuals of a given species (grey circles) along an environmental gradient and how such information can be used to estimate the two niche properties of the species : niche breadth and position. Here, its niche breadth is defined as the variance in environmental conditions where a species is found. In contrast, its niche position is estimated as the absolute deviation between the average environmental conditions where this species is found and the average environmental conditions found across available habitats; species with a small deviation (i.e., closer to the green line) have a central niche position, whereas species with larger deviations (i.e., closer to the edges of the environmental gradient) have a marginal niche position. The middle panels represent two alternative hypotheses, through which differences in species traits may be related to those niche properties. In these panels, many species are spread across an environmental gradient, with each species represented by a different colour, and species sharing similar traits represented by the same shape. Following this definition, the species depicted by the yellow triangles is functionally distinct from the others in a metacommunity. We predict that (P1a) if this distinct combination of traits allows such species to explore a broad range of environmental conditions, then we expect it to have broader niche breadth and to have a central niche position (i.e., a positive relationship between trait distinctiveness and niche breadth and a negative relationship between the former and niche position). Alternatively (P1b), if this very distinct trait combination represents an ecological strategy that is suited only to a habitat specialist, we expect such species to have narrow niche breadths and to occupy either central or marginal habitats (i.e., a negative relationship between trait distinctiveness and niche breadth, and no clear relationship between the former and niche position). These two alternative hypotheses are also depicted in the bottom panel, which represents the hypothesized relationships between trait distinctiveness, niche properties and abundance and occupancy patterns tested in the present study. In this path diagram, we also predict that (P2) species with broader niches and (P3) those with a central niche position should be locally abundant and widespread. Blue and red paths depict hypothesized positive and negative relationships, respectively

2 | METHODS

2.1 | Study sites and sampling methods

We recorded the taxonomic composition and abundance for aquatic and semi-aquatic invertebrates from 1,234 tank bromeliads, and the associated environmental conditions, at 16 geographical sites over the Neotropics, from 18.43° N (Kohunlich, Mexico) to 29.43° S (Las Gamas, Argentina) (Figure 2). These data were collected on several occasions from 1993 to 2014, with multiple sampling occasions in different years for some sites (Table 1).

We used similar sampling methods across sites and over time. For each bromeliad, we measured plant diameter as the average of the largest distance between the tips of two leaves on opposite sides of rosettes and counted the number of green leaves forming wells. Next, we removed and measured all water trapped in these wells by syphoning and/or by removing the plant from the substrate and collected its contents in large buckets; these measurements represent the water volume held by the bromeliad. Altogether, these three environmental variables (plant diameter, leaf number and water volume) are key drivers of aquatic invertebrate communities in bromeliads and were used in the calculation of their niche properties (see Section 2.3). These environmental variables do not vary appreciably within the life span of most bromeliad invertebrates (Dézerald et al., 2017).

The invertebrates were sampled directly by dismantling each plant, leaf by leaf, and/or from the water extracted from each bromeliad and were identified using regional taxonomic keys and our reference collections. We found 489 distinct taxonomic units across all tank bromeliads sampled : all individuals were identified to morphospecies belonging to a genus (42%) or family (42%), while a few were identified only to order (9%). This morphospecies approach was a valid method here, because our level of analysis requires only within-site consistency in species identification, given that we focused on abundance and occupancy data collected on each sampling occasion in each site. For simplicity, we will refer to each invertebrate morphospecies as species hereafter.

FIGURE 2 Geographical distribution of the 16 sites included in our study, with sites studied by the same research group sharing the same colours. Sinnamary, Kaw, Petit Saut and Nouragues are all in French Guiana, whereas Ilha do Cardoso, Ilhabela, Maricá, Arraial do Cabo and Macaé are in Brazil

2.2 | Trait distinctiveness

We used data from Céréghino et al. (2018) to extract information on 12 functional traits that represent key life-history, habitat, anti-predator defense and trophic aspects of aquatic invertebrates from bromeliads. These traits were : maximal body size, aquatic developmental stage, reproduction mode, dispersal mode, resistance forms, respiration mode, locomotion mode, food, feeding group, cohort production interval (the time from hatching to emergence), morphological defence and body form. Each trait contained a number of states, which were fuzzy coded on a nominal scale (states cannot be ordered, e.g., feeding group; see Céréghino et al., 2018: Table 1), according to the affinity of each taxon to that state. Scores ranged from zero (no affinity for a given state) to three (high affinity). This technique has been widely used to document the functional traits of the freshwater invertebrates of Europe (Poff et al., 2006; Usseglio-Polatera, Bournaud, Richoux, & Tachet, 2000) and South America (Tomanova & Usseglio-Polatera, 2007). Scores were based on our own observations of live and preserved specimens and on a survey of the literature on bromeliad invertebrates and freshwater invertebrate families/genera in general (e.g., feeding groups were based on the classification of invertebrates into functional feeding groups by Merritt and Cummins (1996). Trait information was coded most often at the genus or family level, as in other studies (Pilière et al., 2016), which is a resolution that is sufficient to capture functional trait diversity of aquatic invertebrates (Poff et al., 2006; Usseglio-Polatera et al., 2000). After removal of species with missing trait information, we extracted trait data for 457 invertebrate species from the 16 sites (*c.* 93% of taxa). Given our extensive sampling effort over space and time, we are confident that we obtained a reliable sample of the species pool of invertebrates found within tank bromeliads in each site.

We used species trait data to calculate the functional trait dissimilarity between each pair of species within each site. Functional trait dissimilarity was quantified using Gower's distance. We then calculated the average functional distance of each species to the other species recorded at that site (i.e., functional distinctiveness *sensu* Grenié, Denelle, Tucker, Munoz, & Violle, 2017), using the function *distinctiveness* from the 'funrar' package (Grenié et al., 2017) available in R v.3.5.1 (R Development Core Team, 2018). This measure describes the degree to which species diverge from the 'average' trait combination found in the species pool; values closer to one represent species that are functionally dissimilar from all other taxa.

TABLE 1 Information on the 16 sites considered in the study and methodological details

Site	Country	Latitude	Longitude	Bromeliad species	Sampling method	Number of sampling visits	Bromeliads sampled	Species pool	Number of species analysed	Water volume (mL)	Plant diameter (cm)	Number of leaves
Kohunlich	Mexico	18.43	−88.8	*Aechmea bracteata*	Dissection	1	40	19	12	217.17 ± 59.31	86.11 ± 5.94	10.07 ± 0.4
El Verde	Puerto Rico	18.32	−65.82	*Guzmania berteroniana*, *Guzmania* sp., *Werauhia* [*Vriesea*] *sintenisii*	Dissection	14	220	62	31	136 ± 7.74	63.95 ± 1.91	39.95 ± 1.02
Saba	The Netherlands Antilles	17.64	−63.23	*Guzmania plumieri*, *Tillandsia utriculata*, *Vriesea antillana*, *Vriesea ringens*	Dissection	4	40	29	17	189.15 ± 24.2	80.29 ± 4.94	54.27 ± 3.46
Dominica	Dominica	15.38	−61.34	*Guzmania megastachya*, *Guzmania plumieri*	Dissection	3	30	27	15	239.83 ± 31.98	78.3 ± 4.9	39.5 ± 2.22
Pitilla	Costa Rica	10.98	−85.43	*Guzmania desautelsii*, *Guzmania* sp., *Vriesea gladioliflora*, *Vriesea kupperiana*, *Vriesea sanguinolenta*, *Vriesea* sp.	Dissection	6	115	60	19	82.13 ± 24.56	55.08 ± 5.86	28.73 ± 2.87
Sinnamary	French Guiana	5.37	−52.95	*Aechmea aquilega*	Pipette	1	39	23	20	638.1 ± 70.06	125.79 ± 5.69	21 ± 0.56
Petit Saut	French Guiana	5.06	−52.07	*Aechmea mertensii*, *Lutheria splendens*.	Pipette	4	199	52	29	78.28 ± 7.39	48.64 ± 2.42	12.61 ± 0.26
Guasca	Colombia	4.77	−74.17	*Tillandsia complanata*, *Tillandsia turneri*	Dissection	1	36	18	12	123.64 ± 24.87	52.27 ± 1.25	52.08 ± 2.2
Kaw	French Guiana	4.51	−52.07	*Aechmea mertensii*	Pipette	1	47	20	11	89.01 ± 11.57	43.17 ± 2.6	13.72 ± 0.47
Nouragues	French Guiana	4.08	−52.68	*Aechmea aquilega*, *Aechmea melinonii*, *Guzmania lingulata*, *Mezobromelia pleiosticha*, *Lutheria splendens*.	Pipette	3	171	57	13	858.06 ± 99.35	57.32 ± 4.78	15.42 ± 0.75
Macaé	Brazil	−22.21	−41.48	*Aechmea lingulata*, *Aechmea nudicaulis*, *Neoregelia cruenta*, *Vriesea neoglutinosa*	Dissection	1	63	44	31	315.02 ± 29.86	41.82 ± 2.78	35.67 ± 2.61
Maricá	Brazil	−22.95	−42.89	*Neoregelia* sp.	Dissection	1	10	24	14	499.4 ± 80.44	52.15 ± 6.35	29.3 ± 1.86
Arraial do Cabo	Brazil	−22.95	−42.04	*Neoregelia* sp.	Pipette	1	10	15	12	662.1 ± 132.86	37.75 ± 2.39	29.4 ± 1.78
Ilha Bella	Brazil	−23.74	−45.29	*Neoregelia* sp.	Dissection	1	10	24	11	655.9 ± 133.9	57.5 ± 5.37	30.3 ± 1.78
Cardoso	Brazil	−25.1	−47.96	*Quesnelia arvensis*	Dissection	3	64	93	16	798.22 ± 158.12	39.5 ± 3.25	55.56 ± 5.09
Las Gamas	Argentina	−29.43	−60.47	*Aechmea distichantha*	Dissection	6	130	34	23	270.76 ± 25.3	67.23 ± 2.63	28.73 ± 0.62

Note: Some sites were sampled in the same country and/or on several occasions. We also present information on the number of tank bromeliads analysed in each site, and estimates of the size of the species pool and the number of species for which we were able to quantify the niche properties (for further details, see Methods section), and the average environmental characteristics observed across sampled bromeliads (*SE* in brackets).

2.3 | Niche properties

We measured the niche properties for each species using the outlying mean index (OMI; Dolédec, Chessel, & Gimaret-Carpentier, 2000). The OMI method measures niche position along the dominant environmental gradient represented by the sites. Specifically, the niche position of a species compares the mean environment experienced by an individual of that species (i.e., the abundance-weighted mean of all sites occupied by that species) with the mean environment that would be experienced by a hypothetical species that occurs in equal abundance at all sites. The OMI method gives a high value when most individuals occur towards one end of the environmental gradient; therefore, a high OMI value is interpreted as a "marginal" niche position. The OMI method also estimates niche breadth as the variance in environmental conditions experienced by different individuals of a species (i.e., the abundance-weighted dispersion in environmental conditions of occupied sites); species with larger values have broader niches. Together, these two measures define the realized environmental niche of each species at each site.

We calculated the niche position and breadth of each species at each site using environmental data on bromeliad water volume at the time of sampling, plant diameter and the number of leaves. We had complete environmental data for 821 plants. Before calculating these niche properties, we standardized all environmental variables and Hellinger-transformed invertebrate abundance data, to down-weight the undue influence of rare species in ordinations such as canonical analysis, which is at the core of the OMI analysis (Legendre & Gallagher, 2001). We also removed invertebrate species that occurred in only one or two bromeliads at each site, following previous studies (e.g., Heino & Grönroos, 2014). Given this constraint on the minimal number of records per species and the number of bromeliads available, we were able to determine the niche properties for 226 distinct bromeliad invertebrate species across all 16 sites, some of which appeared in more than one site (e.g., the damselfly *Leptagrion andromache* in Macae and Ilha do Cardoso; Table 1). We used the functions *niche* and *niche.param* from the 'ade4' package (Dray & Dufour, 2007) in R to run the OMI analysis.

2.4 | Data set compilation

We assembled the final data set used for statistical analyses by collating, for each species, the site-specific trait distinctiveness with the niche position and breadth measures. Although data on trait distinctiveness were available for all invertebrate species initially recorded in each site, this was not the case for their niche properties. Therefore, all analyses were constrained to a set of 712 observations from the 226 species for which we were able to extract information on both measures (Table 1). Following previous studies, for each species recorded on a given sampling occasion in each site, we calculated the mean local abundance across occupied bromeliads and the proportion of bromeliads occupied, as a measure of regional occupancy (Heino & Tolonen, 2018).

2.5 | Data analysis

2.5.1 | Can trait distinctiveness and niche properties explain abundance and occupancy?

Our main hypothesis posits direct and indirect effects of trait distinctiveness and niche properties on the abundance and occupancy patterns of aquatic invertebrates (Figure 1). Given these hypothesized relationships among variables, where variables can be both predictors and responses, a piecewise structural equation model (pSEM; Lefcheck, 2016; Shipley, 2000) would be a useful statistical approach to test our predictions. However, we also aimed to quantify both the overall magnitude and heterogeneity in these relationships within and across sites. A pSEM applied to all data would allow us to quantify the former, but we would be unable to do so for the latter. As such, we applied the pSEM individually to data from each study site and coupled it with a meta-analysis of the results (Gurevitch, 2013).

For the within-site analysis, we used three models to describe the hypothesized paths in pSEM. The first model used the trait distinctiveness of each species as a fixed predictor of their niche breadth (Figure 1, bottom panel, path from trait distinctiveness to niche breadth). The second model used the trait distinctiveness of each species as a fixed predictor of their niche position (Figure 1, bottom panel, path from trait distinctiveness to niche position). The third model used niche breadth and position as predictors of either their mean local abundance or occupancy (i.e., one model fitted to each of these response variables; Figure 1, bottom panel, path from niche properties to abundance or occupancy). We used general linear models (GLMs) to fit the models when sampling was conducted only once at a given site and linear mixed effects model when data on more than one sampling were available (in which case, we added a random intercept term for the sampling occasion). We applied a ln-transformation to mean local abundance, niche position and niche breadth data to improve model fit to the data and verified parametric assumptions by visual inspection of data and model residuals. We decided not to logit-transform occupancy data, as in some previous studies, given that applying such a transformation provided a worst fit of the models to the data [untransformed occupancy : Akaike information criterion (AIC) = 86.25, deviance = 78.25; logit-transformed occupancy : AIC = 2,632.62, deviance = 2,624.62] and a previous meta-analysis suggested that the way in which occupancy is transformed is unlikely to affect the patterns we are studying (Blackburn, Cassey, & Gaston, 2006). Likewise, we chose not to use a binomial distribution to model occupancy data given that it provided a worst fit to the data than a model using a normal distribution (GLM with normal distribution : AIC = 337.14; GLM with a binomial distribution : AIC = 400.32). We evaluated pSEM model fits using Shipley's test of *d*-separation through Fisher's C statistic (Shipley, 2000). We used the 'piecewiseSEM' package to run the pSEM (Lefcheck, 2016).

After fitting the site-specific pSEMs, we extracted the standardized path coefficients and associated standard errors for each of the six hypothesized relationships (trait distinctiveness → niche breadth;

trait distinctiveness → niche position; niche breadth → mean local abundance; niche position → mean local abundance; niche breadth → occupancy; and niche position → occupancy). Then, we used a weighted random-effects meta-analysis model to quantify the overall magnitude of these relationships across sites and the amount of heterogeneity between sites. We fitted a single model to each path, in which we used the standardized path coefficient of each site as the common effect size measure, weighted each observation by the inverse of its sampling variance (SE^2 of the standardized path coefficient; Rosenberg, Rothstein, & Gurevitch, 2013), and quantified two measures of heterogeneity in the estimated overall effect sizes for each path (Higgins & Thompson, 2002): Q_T and I^2. The former represents the total heterogeneity in effect sizes across sites and is used to test the null hypothesis of homogeneity in effect sizes for the analysed path across sites. The latter quantifies the percentage of the total variation in the overall effect size attributed to differences between sites (i.e., between-site heterogeneity : total heterogeneity ratio). We verified the parametric assumptions of each model by visually inspecting the data and residual plots. We used the *rma* function available in the 'metafor' package (Viechtbauer, 2010) in R to fit the weighted random-effects meta-analysis model, estimate overall effect sizes and 95% confidence intervals (CIs), and calculate Q_T and I^2.

2.5.2 | Do statistical artefacts explain the relationships between niche properties, abundance and occupancy patterns?

One way to examine whether statistical artefacts account for the relationship between niche properties and abundance (or occupancy) is to test whether the slope of the relationship between them differs from that expected under a null model where individuals of each species are randomly distributed across the environmental gradient. By performing such null model analyses for each of the sites we studied, we could determine whether observed patterns are more likely to be attributed to statistical artefacts or biological effects. To this end, we used the IT null model from Ulrich and Gotelli (2010), which assigns individuals randomly to habitat patches with probabilities proportional to their relative abundance in the data set. Benchmark tests show that this null model has fairly low type I error rates and good statistical power to test the null no species × environment associations (Ulrich & Gotelli, 2010).

To implement this null model, we first calculated the total number of individuals of all species found in each bromeliad in each site and used this number as an estimate of the carrying capacity of that particular bromeliad. Then, we randomly redistributed individuals from each invertebrate species across these bromeliads in proportion to their abundance in the site's species pool and estimated their niche position and breadth under this null expectation, in addition to their expected mean local abundance and occupancy. We then fitted two GLMs using species niche breadth and position as predictors, but using either the species mean local abundance or the relative occupancy as response variables. We repeated this procedure 1,000 times for each site and calculated the average and the *SD* for those expected slopes across all runs. Using the observed abundance and occupancy data, we fitted similar GLMs for each of these two response variables and determined whether the observed slopes differed from those expected by chance by calculating a standardized difference between them (z_{slope}):

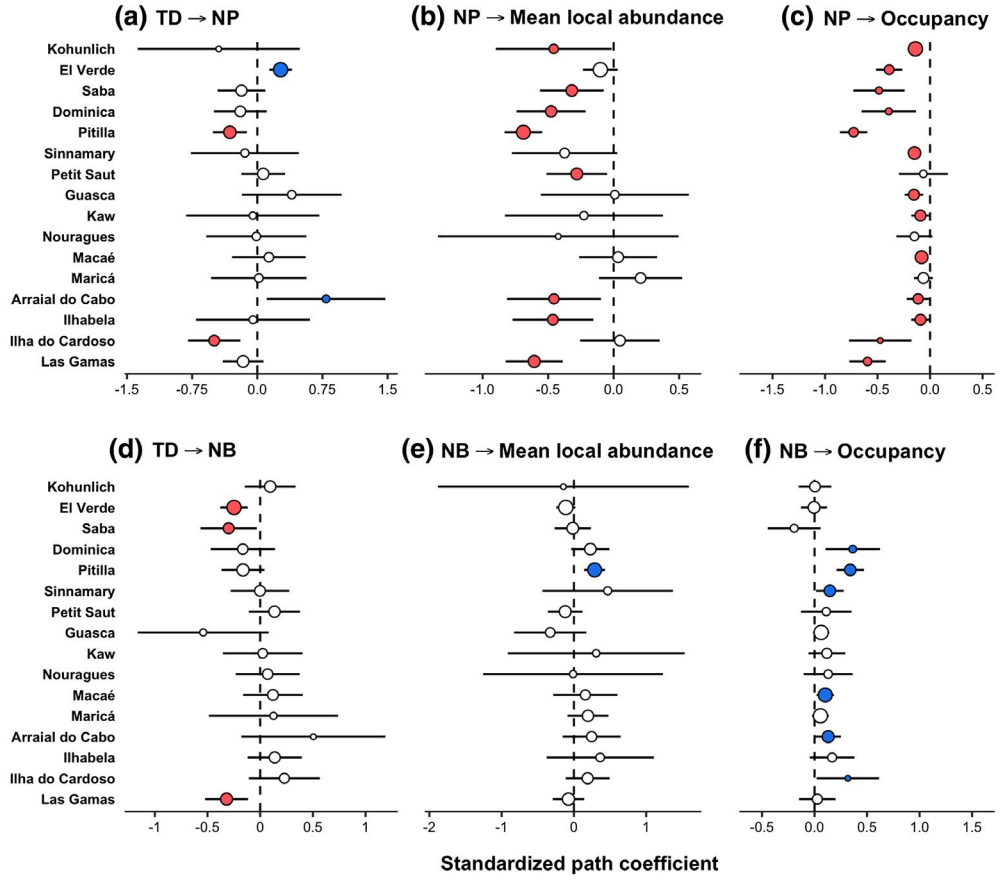
$$z_{slope} = \frac{\beta_{obs} - \bar{\beta}_{exp}}{\sigma_{exp}}$$

where $\beta_{obs\ slope}$ represents the observed slope of the relationship between a species' mean local abundance or occupancy and niche properties (i.e., niche position → mean local abundance, niche breadth → mean local abundance, niche position → occupancy, niche breadth → occupancy), β_{exp} is the average expected slope for such relationship according to the null model, and σ_{exp} is its *SD*. As such, we obtained four estimates for each of the 16 sites we studied, and we considered that the relationships between each predictor and response variable were unlikely to be explained by statistical artefacts when $|z_{slope}| \geq 1.96$ ($\alpha = 0.05$). The R script used to implement the randomization procedure outlined above is available at https://github.com/nacmarino/Scripts/blob/master/randomize.community.abundance.R

3 | RESULTS

3.1 | Trait distinctiveness, niche properties and abundance–occupancy patterns

We found weak support for any relationship between trait distinctiveness and niche position (overall $\beta_{trait\ distinctiveness \rightarrow position} = -0.05$, 95% CI = −0.20 to 0.10; Figure 3a; Appendix S1, Figure S1.1) and with niche breadth across sites (overall $\beta_{trait\ distinctiveness \rightarrow breadth} = -0.05$, 95% CI = −0.15 to 0.06; Figure 3d; Appendix S1, Figure S1.2). This non-significant result held even when we used the original trait axes from Céréghino et al. (2018), rather than trait distinctiveness, as predictors (Appendix S1, Figure S1.3). In contrast, there was a stronger overall negative effect of niche position on occupancy (overall $\beta_{position \rightarrow occupancy} = -0.25$, 95% CI = −0.35 to −0.14; Figure 3c; Appendix S1, Figure S1.4) and on mean local abundance (overall $\beta_{position \rightarrow abundance} = -0.29$, 95% CI = −0.44 to −0.15; Figure 3b; Appendix S1, Figure S1.5), suggesting that the least abundant and least frequent species were those using marginal environmental conditions. In addition, we found an overall positive relationship between niche breadth and occupancy (overall $\beta_{breadth \rightarrow occupancy} = 0.11$, 95% CI = 0.05 to 0.16; Figure 3f; Appendix S1, Figure S1.6), but no clear relationship was evident with mean local abundance (overall $\beta_{breadth \rightarrow abundance} = 0.07$, 95% CI = −0.04 to 0.19; Figure 3e; Appendix S1, Figure S1.7); that is,



Panel	Overall [95% CI]
(a)	-0.05 [-0.20, 0.10]
(b)	-0.29 [-0.44, -0.15]
(c)	-0.25 [-0.35, -0.14]
(d)	-0.05 [-0.15, 0.06]
(e)	0.07 [-0.04, 0.19]
(f)	0.11 [0.05, 0.16]

FIGURE 3 Forest plots showing the variation in the standardized path coefficients (a) from trait distinctiveness (TD) to niche position (NP), (b) from niche position to mean local abundance and (c) occupancy, (d) from trait distinctiveness to niche breadth (NB), and (e) from niche breadth to mean local abundance and (f) occupancy. Each circle represents the standardized path coefficient estimated according to the site-specific piecewise structural equation model, with error bars representing the 95% confidence interval for that estimate (for the exact values, see Appendix S3). The size of each circle is directly related to the inverse of its sampling variance, with larger circles representing more precise estimates. Open circles represent standardized path coefficients whose confidence intervals contain zero, whereas red and blue circles represent standardized path coefficients that are statistically smaller and greater than zero, respectively. The inset table presents the overall standardized path coefficient across sites for each panel, estimated according to a random-effects meta-analysis model; values in square brackets are their 95% confidence intervals (CIs). Observations in each panel are ordered from the northernmost (Kohunlich, Mexico) to the southernmost site (Las Gamas, Argentina)

species with broader niches were widespread within sites but were not necessarily locally abundant.

Differences between sites contributed to some heterogeneity in the overall effect sizes found for each path, as suggested by the Q_T and I^2 metrics (Table 2; see Appendix S2). In general, the relationship between niche properties, abundance and occupancy differed mostly in magnitude, but not in direction, across sites, whereas the relationship between trait distinctiveness and niche properties differed in both direction and magnitude (Figure 3). For example, trait distinctiveness and niche position were positively related in the El Verde site, negatively related in the Pitilla and Ilha do Cardoso sites, but unrelated in most other sites (Figure 3a).

Site-specific pSEMs presented a good fit to the data, especially after the addition of a few missing paths in some models (Appendices S2 and S3). However, the addition of these and other paths was rare across the pSEMs (i.e., a direct path from trait distinctiveness to occupancy only in Saba; see Appendix S2) and is not discussed further.

3.2 | Disentangling statistical artefacts from biological effects

We found that the slope of the relationship between niche position and mean local abundance deviated from that expected with the null model for 14 of the 16 sites, and that with occupancy deviated for eight sites (Table 3). In contrast, most of the observed relationships between niche breadth, mean local abundance and occupancy did not deviate from the null model (number of sites that deviated from the null model : mean local abundance = 3; occupancy = 2; Table 3). These results indicate that most of the niche position effects we found could be attributed to biological mechanisms, whereas those of niche breadth could be attributed to statistical artefacts. In other words, statistical artefacts alone cannot explain all the patterns we found.

TABLE 2 Heterogeneity measures from the random-effects meta-analysis models on each path

Path analysed	Q_T	*p*	I^2 (%)
Trait distinctiveness → niche position	50.66	<.001	63.83
Niche position → mean local abundance	68.51	<.001	74.43
Niche position → occupancy	143.17	<.001	94.76
Trait distinctiveness → niche breadth	34.95	.002	55.20
Niche breadth → mean local abundance	28.07	.021	46.48
Niche breadth → occupancy	32.3	.006	55.69

Note: The Q_T value is the statistic calculated to test the null hypothesis of homogeneity in estimated slopes across sites, and follows a χ^2 distribution with d.f. = $k - 1$ (where k is the number of sites, $n = 16$); a rejection of the null hypothesis ($p \leq .05$) suggests that there is variation in the overall effect size for the path analysed between sites. The I^2 value is an additional measure of heterogeneity, interpreted as the percentage of the total heterogeneity in the overall effect size attributed to differences between sites.

TABLE 3 Results of the null model approach comparing the observed and expected slopes for the relationship between species' mean local abundance (or occupancy), niche position and breadth

Location	$z_{NP \rightarrow Abund}$	$z_{NB \rightarrow Abund}$	$z_{NP \rightarrow Occup}$	$z_{NB \rightarrow Occup}$
Kohunlich	**2.49**	−0.67	−0.23	−0.45
El Verde	**15.43**	0.03	1.51	0.01
Saba	**23.09**	**−3.24**	**7.16**	−0.42
Dominica	**4.04**	−0.67	**2.44**	1.03
Pitilla	**2.48**	0.7	−0.87	0.78
Sinnamary	**8.68**	−0.83	0.28	0.61
Petit Saut	**8.68**	−0.68	**4.98**	−0.42
Guasca	**4.62**	**−3.4**	0.39	0.56
Kaw	**5.15**	0.13	**1.97**	0.83
Nouragues	0.42	**2.06**	**−5.4**	**5.49**
Macaé	**12.99**	−0.72	**5.36**	1.8
Maricá	**5.1**	0.79	**2.74**	1.01
Arraial do Cabo	1.87	1.86	1.28	**2.07**
Ilhabela	**2.35**	0.64	**2.81**	0.37
Ilha do Cardoso	**5.47**	0.71	1.81	0.99
Las Gamas	**1.97**	−1.08	1.63	−0.69

Note: We determined whether the observed slopes differed from those expected by chance by calculating a standardized difference between them (z_{slope}), with a value of $|z_{slope}| \geq 1.96$ indicative of such differences. Significant differences in z_{slope} are highlighted in bold.
Abbreviations: Abund = mean local abundance; NB = niche breadth; NP = niche position; Occup = occupancy.

4 | DISCUSSION

Understanding whether and how species traits and their niche properties are related to species abundance and occupancy patterns has been a central focus of several studies over the past decade (reviewed by Heino & Tolonen, 2018). However, a broad-scale analysis of the drivers of such patterns and relationships has been lacking (Borregaard & Rahbek, 2010). Our results fill this gap across metacommunities composed of species inhabiting the same type of habitat over a large geographical area. We found that trait distinctiveness among species was unrelated to abundance and occupancy patterns, but that both niche properties (i.e., niche position and breadth) explained the variation in local abundance and regional occupancy across species. Before we corrected for statistical artefacts, this appeared to be driven by species that occupy central niches and, to a lesser extent, by species possessing wider niche breadths being more abundant. However, after accounting for statistical artefacts, the niche breadth effects were mostly attributed to sampling artefacts, but those of niche position were not. This suggests that the ability of species to exploit the most available habitats is the key driver of their abundance and occupancy patterns in our study system. Nevertheless, several questions remain and could be tackled in future studies, such as what contributes to the between-site variation in the magnitude of the relationships we examined, and why trait distinctiveness was related to niche properties in only a few sites.

In our study, we found that niche position (i.e., ability to exploit the most available habitat) was the key driver of abundance and occupancy patterns, which we expected based on the species–environment association often reported for aquatic invertebrates from tank bromeliads (Dézerald et al., 2013; Marino et al., 2013; Petermann et al., 2015; Richardson, 1999). A new finding, however, is that statistical artefacts can have a large influence on the relative contribution of niche position and breadth to abundance and occupancy patterns. This suggests that previous studies that overlooked such artefacts are likely to have underestimated the importance of niche position and overestimated that of niche breadth in explaining abundance and occupancy patterns across species. To a similar end, a few previous studies used a resampling technique and partitioned the data into independent subsets to calculate the niche properties and the abundance and occupancy of each species (Rocha et al., 2018; Siqueira et al., 2009). Although this method avoids the use of the same data to estimate a species' niche properties, abundance and occupancy, it still does not directly address statistical artefacts attributable to numerical effects (i.e., species with more individuals occupying a greater number of habitat types simply as a result of random placement). Given the potential for statistical artefacts to account for some of the observed relationships between abundance, occupancy and niche properties (in particular, niche breadth), we recommend that appropriate null models be selected in future studies.

Species traits are expected to be related to the environmental conditions where species are found and also to determine how abundant they can be in those conditions (Lavorel & Garnier, 2002; McGill et al., 2006). Nonetheless, we found little evidence that species

traits were related to niche properties and explained abundance and occupancy patterns across all sites. This result was consistent even after we used the trait axes from Céréghino et al. (2018) instead of average trait distinctiveness, indicating that this was not caused by the method we chose to represent species traits. Previous studies have also reported that species traits either fail or are weakly related to abundance and occupancy (Heino & Grönroos, 2014; Heino & Tolonen, 2018; Rocha et al., 2018; Tales et al., 2004). These studies often attribute this lack of predictive capacity to a poor choice of the traits used in analyses, in addition to their inadequate coding and the selection of the wrong environmental gradients. However, we chose traits that are strongly correlated with aquatic invertebrate distributions (Poff et al., 2006) and that describe the main ecological strategies predicted by the life-history and habitat template theories (Céréghino et al., 2018; Winemiller et al., 2015). Likewise, we measured the niche properties of each species based on the main environmental gradients known to structure ecological communities and food webs in our study system. Therefore, we are confident that methodological limitations cannot explain why species traits were unrelated to niche properties and abundance–occupancy patterns across all sites.

Although the meta-analyses provided weak support for traits to be related to niche properties in general, they did not indicate that traits are irrelevant in structuring biological diversity in our study system, but rather that their relevance might differ between metacommunities. Indeed, our results indicated that species traits might be related to their niche properties in some sites, but the significance and even direction of this relationship varied among sites (Figure 3). This suggests that there may be considerable variation in the contribution of the hypothesized drivers to observed abundance–occupancy patterns, even when the same broad taxonomic group is considered in a similar type of habitat. The reasons for this large heterogeneity among the sites we examined are still unclear, and exploring them is beyond the scope of this manuscript. However, we offer a few insights that might be addressed by future studies, as follows.

First, the niche properties of each species were measured in multivariate space; each of the three bromeliad size variables (i.e., plant diameter, water volume and number of leaves) may be related to species traits in different ways, resulting in no net relationship between the traits and the combined environmental gradient. This has been shown in plant species, where some traits may converge along an abiotic or biotic gradient but diverge along other gradients (Loughnan & Gilbert, 2017). Second, it has been hypothesized that there may be many multivariate trait optima for a given environment, and standard statistical approaches may be unable to distinguish multiple optima from statistical noise (Marks & Lechowicz, 2006). Third, the OMI method measures the realized niche of each species, not the fundamental niche. As such, it might also be that other unmeasured factors related to bromeliad size could have changed how species traits are expressed along this gradient. For example, previous studies of bromeliad aquatic invertebrates show that both predation and facilitation can alter the survivorship and abundance of aquatic invertebrates (Hammill, Atwood, Corvalan, & Srivastava, 2015; Marino, Srivastava, & Farjalla, 2016; Starzomski, Suen, & Srivastava, 2010) and that top-down effects are dependent on habitat size (Petermann et al., 2015). Nevertheless, it is hard to include species interactions explicitly when measuring niche properties, owing to the difficulty in characterizing species interaction networks and whether these networks are sensitive to species abundances or other environmental contexts (Poisot, Stouffer, & Gravel, 2015). In addition, we do not expect spatial effects within sites to contribute to the patterns we found, given that previous studies suggest that these invertebrates are not dispersal limited, and bromeliads growing close together may show a large difference in environmental conditions (Farjalla et al., 2012; Marino et al., 2013, 2016, 2017). Despite these concerns, we still expect realized niche properties to be related to abundance and occupancy, given that both are the end products of species interactions and other processes acting on ecological communities. Fourth, we did not consider the role of phylogenetic non-independence in driving associations among traits, abundances and occupancy (Borregaard & Rahbek, 2010), given that a phylogeny of bromeliad invertebrates is still lacking. Future work on trait–environment relationships could examine how species traits change along environmental gradients within and across sites, what determines the biogeographical distribution of these traits, whether trait matching between predators and prey predicts their occupancy patterns, and the role of phylogeny in such associations. Furthermore, we analysed species abundance and occupancy separately, as in previous studies (reviewed by Heino & Tolonen, 2018). However, it would be interesting to determine in future studies how species niches and traits influence the abundance–occupancy relationship per se, because any factor that influences both abundance and occupancy might not influence the relationship between them. This could be done, for example, by building null models for the slopes to test how the addition of different mechanisms changes the relationship.

In summary, the ability of species to exploit common habitats is the main driver of species abundance and occupancy patterns in aquatic invertebrates of tank bromeliads. The consistency of this result across sites suggests that this pattern is robust despite differences in evolutionary, climatic and other structuring forces acting on these communities over the broad geographical gradient that we examined. Our study also found a limited ability of species traits to explain such patterns directly or indirectly and a relatively large role of statistical artefacts in accounting for the effects of niche breadth on the patterns we examined. Given the interest in understanding the contribution of different drivers to abundance and occupancy patterns, these results highlight the need for future studies to address statistical artefacts and, more importantly, to examine whether the contribution of different drivers is consistent over broad geographical scales for species inhabiting similar types of habitats (e.g., stream invertebrates). Such information would be essential to our understanding of the causes of commonness across the tree of life.

ACKNOWLEDGMENTS

This is a publication of the Bromeliad Working Group. This paper was produced with the support of Centre for the Synthesis and Analysis of Biodiversity-Foundation for Research on Biodiversity (CESAB-FRB) as part of the activities of the Functional Webs Working Group. We acknowledge support for field surveys provided by the Agence Nationale de la Recherche through an Investissement d'Avenir grant (Labex CEBA, ANR-10-LABX-25-01) to C.L. and R.C., by a Bolsa de Pesquisa no Exterior-Fundação de Amparo à Pesquisa do Estado de São Paulo (BPE-FAPESP) grant #2016/01209-9 to G.Q.R., by a Royal Society grant (NAF\R2\180791) to P.K. and G.Q.R., by Conselho Nacional de Pesquisa (CNPq)-Brazil research grants to G.Q.R. (#301514/2017-8), V.D.P. (#307689/2014-0) and V.F.F. (#312770/2014-6), by Natural Science and Engineering Research Council (NSERC) Discovery and E.W.R. Steacie grants to D.S.S., and by grants from the Royal Society of Edinburgh, the Carnegie Trust for the Universities of Scotland, the US National Science Foundation (NSF) (DEB-0218039 and DEB-0620910), International Institute of Tropical Forestry-United States Department of Agriculture (USDA IITF) (#01-1G11120101-001) and the Saba Conservation Foundation to B.A.R. and M.J.R., and by Universidad Nacional de Rosario grants (AGR-210 and AGR-290) to I.M.B. and G.A.M. We acknowledge postdoctoral fellowship support from a Programa Nacional de Pós-Doutorado-Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (PNPD-CAPES) grant #2014/04603-4 to P.M.O., a PNPD/CAPES grant #2013/0877 to N.A.C.M., a FAPESP grant #2016/09699-5 to A.Z.G., doctoral support from NSERC and University of British Columbia (UBC) to L.M.G., and a CNPq grant (#401345/2014-9) under the Ciências sem Fronteiras program to V.J.D. We thank Jonathan Lui and Alathea Letaw for helping to build the Bromeliad Working Group database with A.A.M.M. and D.S.S., and Georgia Medeiros, L.M.G., Sarah Amundrud and others for helping to populate it. We thank B. Starzomski for contributing data, and Jonathan Belmaker and two anonymous reviewers, whose comments and suggestions helped to improve the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

N.A.C.M. conceived the ideas, analysed the data and wrote the first draft of the manuscript. R.C., D.S.S., V.F.F., P.M.O., F.O.B. and L.M.G. discussed and contributed ideas for the data analysis. A.A.M.M. built the R package *fwdata*, which we used to extract all data from the Bromeliad Working Group database. R.C., D.S.S. and P.K. built the trait database, with input from F.O.B. and P.M.O. All authors except V.D.P. and V.J.D. collected the data. All authors reviewed and contributed to early drafts of this manuscript and gave final approval for publication.

ORCID

Nicholas A. C. Marino https://orcid.org/0000-0002-5702-5466
Benjamin Gilbert https://orcid.org/0000-0002-4947-6822
Ana Z. Gonçalves https://orcid.org/0000-0002-9036-8831

DATA AVAILABILITY STATEMENT

All the raw data we used in this manuscript are available in the R package *fwdata*. Instructions for downloading the package and data can be found at https://github.com/SrivastavaLab/fwdata. The processed data used to perform all analyses has been deposited at the Dryad Digital Repository, and can be accessed at https://doi.org/10.5061/dryad.4mw6m906g; any other query related to additional data should be submitted directly to the corresponding author.

REFERENCES

Bernard-Verdier, M., Navas, M. L., Vellend, M., Violle, C., Fayolle, A., & Garnier, E. (2012). Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. *Journal of Ecology*, *100*, 1422–1433. https://doi.org/10.1111/1365-2745.12003

Blackburn, T. M., Cassey, P., & Gaston, K. J. (2006). Variations on a theme: Sources of heterogeneity in the form of the interspecific relationship between abundance and distribution. *Journal of Animal Ecology*, *75*, 1426–1439. https://doi.org/10.1111/j.1365-2656.2006.01167.x

Borregaard, M. K., & Rahbek, C. (2010). Causality of the relationship between geographic distribution and species abundance. *The Quarterly Review of Biology*, *85*, 3–25. https://doi.org/10.1086/650265

Brown, J. H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist*, *124*, 255–279. https://doi.org/10.1086/284267

Céréghino, R., Pillar, V. D., Srivastava, D. S., de Omena, P. M., MacDonald, A. A. M., Barberis, I. M., … Montero, G. (2018). Constraints on the functional trait space of aquatic invertebrates in bromeliads. *Functional Ecology*, *32*, 2435–2447. https://doi.org/10.1111/1365-2435.13141

Dallas, T., Decker, R. R., & Hastings, A. (2017). Species are not most abundant in the centre of their geographic range or climatic niche. *Ecology Letters*, *20*, 1526–1533. https://doi.org/10.1111/ele.12860

Dézerald, O., Céréghino, R., Corbara, B., Dejean, A., & Leroy, C. (2015). Functional trait responses of aquatic macroinvertebrates to simulated drought in a Neotropical bromeliad ecosystem. *Freshwater Biology*, *60*, 1917–1929. https://doi.org/10.1111/fwb.12621

Dézerald, O., Leroy, C., Corbara, B., Dejean, A., Talaga, S., & Céréghino, R. (2017). Environmental drivers of invertebrate population dynamics in Neotropical tank bromeliads. *Freshwater Biology*, *62*, 229–242. https://doi.org/10.1111/fwb.12862

Dézerald, O., Talaga, S., Leroy, C., Carrias, J.-F., Corbara, B., Dejean, A., & Céréghino, R. (2013). Environmental determinants of macroinvertebrate diversity in small water bodies: Insights from tank-bromeliads. *Hydrobiologia*, *723*, 77–86. https://doi.org/10.1007/s10750-013-1464-2

Dolédec, S., Chessel, D., & Gimaret-Carpentier, C. (2000). Niche separation in community analysis: A new method. *Ecology*, *81*, 2914–2927. https://doi.org/10.1890/0012-9658(2000)081[2914:NSICA]2.0.CO;2

Dray, S., & Dufour, A.-B. (2007). The ade4 package: Implementing the duality diagram for ecologists. *Journal of Statistical Software*, *22*, 1–20.

Farjalla, V. F., Srivastava, D. S., Marino, N. A. C., Azevedo, F. D., Dib, V., Lopes, P. M., … Esteves, F. A. (2012). Ecological determinism increases with organism size. *Ecology*, *93*, 1752–1759. https://doi.org/10.1890/11-1144.1

Gaston, K. J., Blackburn, T. M., Greenwood, J. J. D., Gregory, R. D., Quinn, R. M., & Lawton, J. H. (2000). Abundance–occupancy relationships. *Journal of Applied Ecology*, *37*, 39–59. https://doi.org/10.1046/j.1365-2664.2000.00485.x

Grenié, M., Denelle, P., Tucker, C. M., Munoz, F., & Violle, C. (2017). funrar: An R package to characterize functional rarity. *Diversity and Distributions*, *23*, 1365–1371. https://doi.org/10.1111/ddi.12629

Gurevitch, J. (2013). Meta-analysis of results from multisite studies. In J. Koricheva, J. Gurevitch, & K. Mengersen (Eds.), *Handbook of meta-analysis in ecology and evolution* (pp. 313–320). Princeton, NJ: Princeton University Press.

Hammill, E. D. D., Atwood, T. B., Corvalan, P., & Srivastava, D. S. (2015). Behavioural responses to predation may explain shifts in community structure. *Freshwater Biology*, *60*, 125–135. https://doi.org/10.1111/fwb.12475

Hanski, I. (1993). Three explanations of the positive relationship between distribution and abundance of species. In R. E. Ricklefs & D. Schluter (Eds.), *Species diversity in ecological communities: Historical and geographical perspectives* (pp. 108–116). Chicago, IL: University of Chicago Press.

Heino, J., & Grönroos, M. (2014). Untangling the relationships among regional occupancy, species traits, and niche characteristics in stream invertebrates. *Ecology and Evolution*, *4*, 1931–1942. https://doi.org/10.1002/ece3.1076

Heino, J., & Tolonen, K. T. (2018). Ecological niche features override biological traits and taxonomic relatedness as predictors of occupancy and abundance in lake littoral macroinvertebrates. *Ecography*, *41*, 2092–2103. https://doi.org/10.1111/ecog.03968

Higgins, J. P. T. T., & Thompson, S. G. (2002). Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine*, *21*, 1539–1558. https://doi.org/10.1002/sim.1186

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, *16*, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579.

Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*, 271–280. https://doi.org/10.1007/s004420100716

Loughnan, D., & Gilbert, B. (2017). Trait-mediated community assembly: Distinguishing the signatures of biotic and abiotic filters. *Oikos*, *126*, 1112–1122. https://doi.org/10.1111/oik.03945

Marino, N. A. C., Srivastava, D. S., & Farjalla, V. F. (2013). Aquatic macroinvertebrate community composition in tank-bromeliads is determined by bromeliad species and its constrained characteristics. *Insect Conservation and Diversity*, *6*, 372–380. https://doi.org/10.1111/j.1752-4598.2012.00224.x

Marino, N. A. C., Srivastava, D. S., & Farjalla, V. F. (2016). Predator kairomones change food web structure and function, regardless of cues from consumed prey. *Oikos*, *125*, 1017–1026. https://doi.org/10.1111/oik.02664

Marino, N. A. C., Srivastava, D. S., MacDonald, A. A. M., Leal, J. S., Campos, A. B. A., & Farjalla, V. F. (2017). Rainfall and hydrological stability alter the impact of top predators on food web structure and function. *Global Change Biology*, *23*, 673–685. https://doi.org/10.1111/gcb.13399

Marks, C. O., & Lechowicz, M. J. (2006). Alternative designs and the evolution of functional diversity. *The American Naturalist*, *167*, 55–66. https://doi.org/10.1086/498276

Martinez-Meyer, E., Diaz-Porras, D., Peterson, A. T., & Yanez-Arenas, C. (2013). Ecological niche structure and rangewide abundance patterns of species. *Biology Letters*, *9*, 20120637. https://doi.org/10.1098/rsbl.2012.0637

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, *21*, 178–185. https://doi.org/10.1016/j.tree.2006.02.002

Merritt, R. W., & Cummins, K. W. (1996). *An introduction to the aquatic insects of North America* (3rd ed.). Dubuque, IA: Kendall/Hunt Publishing Company.

Petermann, J. S., Farjalla, V. F., Jocque, M., Kratina, P., MacDonald, A. A. M., Marino, N. A. C., … Srivastava, D. S. (2015). Dominant predators mediate the impact of habitat size on trophic structure in bromeliad invertebrate communities. *Ecology*, *96*, 428–439. https://doi.org/10.1890/14-0304.1

Pilière, A. F. H., Verberk, W. C. E. P., Gräwe, M., Breure, A. M., Dyer, S. D., Posthuma, L., … Schipper, A. M. (2016). On the importance of trait interrelationships for understanding environmental responses of stream macroinvertebrates. *Freshwater Biology*, *61*, 181–194. https://doi.org/10.1111/fwb.12690

Poff, N. L., Olden, J. D., Vieira, N. K. M., Finn, D. S., Simmons, M. P., & Kondratieff, B. C. (2006). Functional trait niches of North American lotic insects: Traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, *25*, 730–755. https://doi.org/10.1899/0887-3593(2006)025[0730:FTNONA]2.0.CO;2

Poisot, T., Stouffer, D. B., & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary through space and time. *Oikos*, *124*, 243–251. https://doi.org/10.1111/oik.01719

R Development Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Richardson, B. A. (1999). The bromeliad microcosm and the assessment of faunal diversity in a Neotropical forest. *Biotropica*, *31*, 321–336.

Rocha, M. P., Bini, L. M., Siqueira, T., Hjort, J., Grönroos, M., Lindholm, M., … Heino, J. (2018). Predicting occupancy and abundance by niche position, niche breadth and body size in stream organisms. *Oecologia*, *186*, 205–216. https://doi.org/10.1007/s00442-017-3988-z

Rosenberg, M. S., Rothstein, H. S., & Gurevitch, J. (2013). Effect sizes: Conventional choices and calculations. In J. Koricheva, J. Gurevitch, & K. Mengersen (Eds.), *Handbook of meta-analysis in ecology and evolution* (pp. 61–71). Princeton, NJ: Princeton University Press.

Saito, V. S., Laroche, F., Siqueira, T., & Pavoine, S. (2018). Ecological versatility and the assembly of multiple competitors: Cautionary notes for assembly inferences. *Ecology*, *99*, 1173–1183. https://doi.org/10.1002/ecy.2197

Shipley, B. (2000). A new inferential test for path models based on directed acyclic graphs. *Structural Equation Modeling: A Multidisciplinary Journal*, *7*, 206–218. https://doi.org/10.1207/S15328007SEM0702_4

Siqueira, T., Bini, L. M., Cianciaruso, M. V., Roque, F. O., & Trivinho-Strixino, S. (2009). The role of niche measures in explaining the abundance–distribution relationship in tropical lotic chironomids. *Hydrobiologia*, *636*, 163–172. https://doi.org/10.1007/s10750-009-9945-z

Slatyer, R. A., Hirst, M., & Sexton, J. P. (2013). Niche breadth predicts geographical range size: A general ecological pattern. *Ecology Letters*, *16*, 1104–1114. https://doi.org/10.1111/ele.12140

Srivastava, D. S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S. P., Miller, T. E., … Trzcinski, M. K. (2004). Are natural microcosms useful model systems for ecology? *Trends in Ecology and Evolution*, *19*, 379–384. https://doi.org/10.1016/j.tree.2004.04.010

Starzomski, B. M., Suen, D., & Srivastava, D. S. (2010). Predation and facilitation determine chironomid emergence in a bromeliad-insect food web. *Ecological Entomology*, *35*, 53–60. https://doi.org/10.1111/j.1365-2311.2009.01155.x

Tales, E., Keith, P., & Oberdorff, T. (2004). Density-range size relationships in French riverine fishes. *Oecologia*, *138*, 360–370. https://doi.org/10.1007/s00442-003-1430-1

Tomanova, S., & Usseglio-Polatera, P. (2007). Patterns of benthic community traits in Neotropical streams: Relationship to mesoscale spatial variability. *Fundamental and Applied Limnology*, *170*, 243–255. https://doi.org/10.1127/1863-9135/2007/0170-0243

Ulrich, W., & Gotelli, N. J. (2010). Null model analysis of species associations using abundance data. *Ecology*, *91*, 3384–3397. https://doi.org/10.1890/09-2157.1

Usseglio-Polatera, P., Bournaud, M., Richoux, P., & Tachet, H. (2000). Biological and ecological traits of benthic freshwater macroinvertebrates: Relationships and definition of groups with similar traits. *Freshwater Biology*, *43*, 175–205. https://doi.org/10.1046/j.1365-2427.2000.00535.x

Venier, L. A., & Fahrig, L. (1996). Habitat availability causes the species abundance–distribution relationship. *Oikos*, *76*, 564–570. https://doi.org/10.2307/3546349

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, *36*, 1–48.

Weber, M. M., Stevens, R. D., Diniz-Filho, J. A. F., & Grelle, C. E. V. (2017). Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. *Ecography*, *40*, 817–828. https://doi.org/10.1111/ecog.02125

Winemiller, K. O., Fitzgerald, D. B., Bower, L. M., & Pianka, E. R. (2015). Functional traits, convergent evolution, and periodic tables of niches. *Ecology Letters*, *18*, 737–751. https://doi.org/10.1111/ele.12462

Yañez-Arenas, C., Martínez-Meyer, E., Mandujano, S., & Rojas-Soto, O. (2012). Modelling geographic patterns of population density of the white-tailed deer in central Mexico by implementing ecological niche theory. *Oikos*, *121*, 2081–2089. https://doi.org/10.1111/j.1600-0706.2012.20350.x

BIOSKETCH

The Bromeliad Working Group is an international network of researchers studying the faunal food web inhabiting water-filled bromeliads. Our objective is to use this system, naturally replicated from Florida to Argentina, to develop a synthesis of community ecology, biogeography and phylogeny. To realize this aim, we have developed a large database of survey data and have conducted replicated experiments over both hemispheres.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Marino NAC, Céréghino R, Gilbert B, et al. Species niches, not traits, determine abundance and occupancy patterns: A multi-site synthesis. *Global Ecol Biogeogr.* 2019;00:1–14. https://doi.org/10.1111/geb.13029