

Ecological determinism increases with organism size

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Abstract. After much debate, there is an emerging consensus that the composition of many ecological communities is determined both by species traits, as proposed by niche theory, as well as by chance events. A critical question for ecology is, therefore, which attributes of species predict the dominance of deterministic or stochastic processes. We outline two hypotheses by which organism size could determine which processes structure ecological communities, and we test these hypotheses by comparing the community structure in bromeliad phytotelmata of three groups of organisms (bacteria, zooplankton, and macroinvertebrates) that encompass a 10 000-fold gradient in body size, but live in the same habitat. Bacteria had no habitat associations, as would be expected from trait-neutral stochastic processes, but still showed exclusion among species pairs, as would be expected from niche-based processes. Macroinvertebrates had strong habitat and species associations, indicating niche-based processes. Zooplankton, with body size between bacteria and macroinvertebrates, showed intermediate habitat associations. We concluded that a key niche process, habitat filtering, strengthened with organism size, possibly because larger organisms are both less plastic in their fundamental niches and more able to be selective in dispersal. These results suggest that the relative importance of deterministic and stochastic processes may be predictable from organism size.

Key words: *bacteria; bromeliad; competitive exclusion; food web; habitat filtering; macroinvertebrates; niche theory; Restinga de Jurubatiba National Park, Brazil; species co-occurrence; stochasticity; variance partitioning; zooplankton.*

INTRODUCTION

Community structure and species occurrence have often been explained through the niche-based mechanisms of habitat filtering and competitive exclusion (Chase and Leibold 2003). Habitat filtering refers to exclusion of species not adapted to a particular habitat, resulting in positive associations between species with similar fundamental niches. Competition theory predicts that species can competitively exclude each other from suitable habitat, resulting in negative associations between species with similar traits. Habitat filtering and competitive exclusion mechanisms, though leading

to different patterns in co-occurrence, both assume that the occurrence patterns of species are more determined by species' traits than by stochastic aspects of dispersal and demographic drift (Chase and Leibold 2003). However, neutral community models demonstrate that these stochastic processes can generate realistic patterns of species occurrence without requiring trait differences between species (Bell 2001, Hubbell 2001). As neutral models assume demographic equivalence between individuals of different species, communities dominated by neutral processes are not expected to show strong associations of species with either habitats or other species. Neither niche nor neutral models have been able to explain the full range of occurrence patterns observed in ecological data, and some models that integrate niche-based and stochastic dynamics have been proposed

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(Gravel et al. 2006, Adler et al. 2007), but have just begun to be empirically tested (Vergnon et al. 2009).

The adequacy of niche or stochastic processes in explaining community structure may be related to the body size of organisms (Finlay 2002, Cottenie 2005, Beisner et al. 2006, Shurin et al. 2009). Body size is an important integrative attribute of species, and is related to ecological attributes such as total abundance, growth rate, range size, and dispersal capabilities (Allen et al. 2006). Two very different predictions can be made about the influence of body size on the prevalence of niche limitation vs. dispersal limitation. On one hand, microscopic organisms (<2 mm body length; Finlay 2002) have been reported to have higher dispersal capabilities than macroscopic organisms (>2 mm), both because the small size of microscopic organisms allows them to be passively transported on wind or water currents, and because microscopic organisms often have dormant phases that allow them to survive long periods of dispersal before encountering suitable habitat (Finlay 2002, Shurin et al. 2009). Consequently, microscopic species often have global distributions (Finlay 2002) and low compositional turnover over spatial gradients (Hillebrand et al. 2001, Shurin et al. 2009). **This suggests that the occurrence of microscopic species will reflect niche limitation rather than dispersal limitation (popularly paraphrased as “everything is everywhere and the environment selects”), whereas macroscopic organisms will be more dispersal limited** (Cottenie 2005, Beisner et al. 2006, Shurin et al. 2009). **We refer to this as the “size–dispersal” hypothesis.** On the other hand, bacteria are often generalist in their ability to degrade carbon compounds and uptake inorganic nutrients, suggesting that they are overall plastic in abilities (Finlay 2002, Langenheder et al. 2005, despite some highly differentiated exceptions), and so, indistinguishable in niches. For example, Finlay (2002) describes examples of arctic ciliates that can also survive tropical temperatures, or marine bacteria that can also survive in freshwater ecosystems. Although there are also well-known examples of phenotypic plasticity in macroscopic organisms, in general, phenotypic plasticity in macroscopic organisms may be constrained by their longer and more complex developmental pathways. For example, environmental sex determination in fish is generally constrained to an early window in development (Devlin and Nagahama 2002). Even if a morphological trait can be induced later in development, it may be inferior to a fixed trait that has been structurally integrated with other traits during development (the “epiphenotype problem”; DeWitt et al. 1998). **Together, these observations suggest that macroscopic organisms will be more niche-limited than microscopic organisms. We refer to this as the “size–plasticity” hypothesis.**

Although there is evidence that the occurrence of most organisms, big and small, is limited to some degree by both their fundamental niches and dispersal abilities; such observations cannot distinguish between the relative

importance of niche and dispersal limitation for differently sized organisms. The clearest tests of the size–dispersal and size–plasticity hypotheses, therefore, require community-level comparisons of different organisms, ranging from microscopic to macroscopic, over the same environmental and spatial gradient (see also Beisner et al. 2006, Shurin et al. 2009). In this paper, we used a data set of bacteria, zooplankton (rotifers and microcrustaceans), and aquatic macroinvertebrates sampled from the same phytotelm bromeliads to demonstrate methods that can be used to distinguish between the size–dispersal and size–plasticity hypotheses. For each organism group, we tested whether species were associated with habitat variables or with other species, both interpreted as evidence of niche-based processes. The size–dispersal hypothesis predicts that the strength of niche-limitation should increase in the order macroinvertebrates < zooplankton < bacteria, whereas the size–plasticity hypothesis predicts the reverse order. Once habitat associations are accounted for, the remainder of variation in community composition can be decomposed into pure effects of space (distance between bromeliads), covariance between environment and space, and an unexplained fraction. **Stochasticity in community structure related to dispersal limitation may be reflected in any of these fractions, depending on the degree of spatial structuring of the dispersal process** (Cottenie 2005, Beisner et al. 2006). If the size–dispersal hypothesis is correct, and dispersal is spatially structured, we would expect the importance of space in explaining community structure to increase in the order bacteria < zooplankton < macroinvertebrates.

MATERIALS AND METHODS

Surveys of bromeliad fauna

This study was conducted at Restinga de Jurubatiba National Park, in Rio de Janeiro State, Brazil. The restinga vegetation at this site consisted of patches of shrubs and trees, surrounded by open areas of sand, all of which contained high densities of bromeliads. We examined the fauna in the four most common bromeliad species at this site: *Aechmea nudicaulis*, *Aechmea lingulata*, *Vriesea neoglutinosa*, and *Neoregelia cruenta*. These bromeliad species differ in both morphology and habitat preferences (e.g., shrub patches vs. open areas), and so represented a broad range of environmental conditions for the fauna inhabiting their water-filled tanks.

We sampled bacteria, zooplankton, and macroinvertebrates (taxa listed in Appendix A) from bromeliads in the morning on four alternate days in January 2008 without precipitation. Sixteen plants of each bromeliad species were randomly chosen from a marked pool of 50 plants per species. All water from each tank in the bromeliad was removed by siphoning and measured.

To sample the zooplankton community, we filtered water samples from each bromeliad with a 50- μ m plankton net and fixed the organisms in 5% buffered formalin.

Zooplankton were identified at the lowest possible taxonomic unit (species in most cases except for bdelloid rotifers and harpacticoid copepods, lumped at the level of class and order, respectively) and subsamples were counted (>100 individuals) under a compound microscope (for rotifers) or a stereomicroscope (for copepods).

Aquatic macroinvertebrates were collected from both the siphoned water, as well as any water and detritus still trapped by the bromeliad upon dissection. Macroinvertebrates were identified by taxonomists to species, where possible, and morphospecies otherwise.

The bacterial community composition profile was determined using denaturing gradient gel electrophoresis (DGGE; Muyzer et al. 1993). Water samples were pre-filtered through 3.0- μm pore-size nitrocellulose filters, and bacteria were collected on 0.2- μm pore-size nitrocellulose filters. Filters were stored at -20°C . The same procedure was performed for a water sample of nearby Cabiúnas Lagoon, which was used as a control in the analyses. Bacterial DNA was extracted from the filters using the FastDNA SPIN Kit for soil (MP Biomedicals, Solon, Ohio, USA), and polymerase chain reaction (PCR) amplifications (following Haridoim et al. 2009) were performed using a thermal cycler. DGGE was carried out using a Dcode Universal Mutation Detection System. The 6% polyacrylamide gels were made with a denaturing gradient from 40% to 70%. After electrophoresis, gels were stained with SYBR Green I nucleic acid gel stain (Molecular Probes, Eugene, Oregon, USA) and visualized by the STORM image capture system. This image capture system is capable of identifying different DNA bands in a sample and among samples in a gel by their final position and in relation to a control sample, capturing bacterial operational taxonomic units (OTUs) that jointly determine >95% of total abundance. Only presence-absence data of the bacterial community were used in further analysis due to uncertainty in the ability of PCR to generate unbiased estimates of abundance. Although there is some variance in taxonomic resolution within and between groups (OTU for bacteria, and species or morphospecies for most macroinvertebrates and zooplankton), for simplicity, we describe associations and interactions between taxa as “species associations” and “species interactions,” respectively. We consider how variation in taxonomic resolution may affect our results in the *Discussion*.

Environmental conditions within bromeliads

Prior to sampling each bromeliad for fauna, we measured maximum water temperature (between 13:00 and 15:00 hours in full sun), distance to shrubs, plant diameter, and number of water-filled tanks (central tank plus axils containing water). We characterized the chemical profile of the bromeliad water by measuring: chlorophyll *a* and water turbidity (both with a portable fluorometer), pH (pH meter), dissolved inorganic phosphorus (spectrophotometrically determined

through formation of phosphorus molybdate), dissolved inorganic nitrogen as the sum of ammonium (blue indophenol colorimetric method) and nitrate (flow injection analyzer), dissolved organic carbon (total carbon analyzer), and water color (inverse of the absorbance coefficient at 430 nm). Water subsamples were filtered through 0.8- μm filters prior to measurements of nutrient concentration. Further details of water chemistry analyses are in a previous publication (Haubrich et al. 2009).

Statistical analyses

The goals of the analyses were to determine if the strength of (1) species associations, (2) habitat associations, or (3) spatial associations differed between the three organism types. Both species and habitat associations are consistent with niche-limitation, whereas spatial associations may reflect dispersal limitation when dispersal is spatially structured.

Patterns of species co-occurrence (goal 1) were examined using the computer program EcoSim (Gotelli 2000) and the *C*-score index, which measures the average number of “checkerboard units” (mutually exclusive presence) between all possible pairs of species. The *C* score of each community is the average of all possible checkerboard pairs, calculated for species that occur at least once in the community matrix. The community *C* score is then compared with 5000 other *C* scores generated by 5000 statistical randomizations of the original species occurrence data, keeping row and column totals constant. We tested the patterns of species co-occurrence for each community using the complete data set (all bromeliads pooled together) and each bromeliad species separately. If a community is structured by deterministic forces such as competitive exclusion or habitat filtering, the community *C* score should be greater than expected by chance. Particularly, if the community *C* score is greater than expected by chance for the complete data set but not for the within-bromeliad species data sets, we would suspect that differences between fauna in their associations with bromeliad species (i.e., habitat filtering) accounted for a substantial portion of the *C*-score result in the complete data set.

We tested habitat associations (goal 2) in two different ways, each with complementary strengths. First, we examined whether species occurrence differed between the four species of bromeliads, since bromeliad species differed (MANOVA $F_{3,63} = 8.92$, $P < 0.0001$) in most measured environmental variables (univariate ANOVAs; turbidity, dissolved inorganic phosphorus, and nitrate not significant, but eight other measures, $F_{3,63} > 3.1$, $P < 0.05$) and presumably also in other unmeasured variables. Second, in case the prior analysis lost explanatory power either by defining habitat by categories rather than continuous environmental variables or by not explicitly factoring out space, we also used multivariate methods to

examine species associations with environmental variables, while controlling for spatial location. For the categorical approach, we measured the amount of faunal species differentiation between bromeliad species using the β Raup-Crick dissimilarity index (Chase et al. 2011), which measures the deviation of pairwise comparisons of community dissimilarity from the null expectation under random assembly. The null expectation was generated using 1000 randomizations (see Chase et al. 2011 for details). This procedure allowed us to compare the β diversity of organism types, independent of organismal differences in α diversity (bacteria $\alpha >$ zooplankton or macroinvertebrate α , repeated-measures ANOVA, $F_{3,59} = 87.5$, $P < 0.05$). In other approaches, covariance between α and β diversity can confound results (Chase et al. 2011). We then tested if, within an organism type, communities were influenced by bromeliad species. **If bromeliad species identity affects community composition, pairwise dissimilarity indexes between communities in different bromeliad species should be greater than those in the same bromeliad species.** As pairwise indices are not independent of each other, we tested the significance of this comparison using a randomization procedure (using the ANOSIM routine in package *vegan* in R; R Development Core Team 2009). Specifically, the ANOSIM statistic R was calculated as the scaled difference between vs. within bromeliad species in the mean ranks of pairwise dissimilarity values. An R statistic of 0 indicates no effect of bromeliad species on community composition, whereas $R = 1$ indicates the maximum possible effect of bromeliad species on community composition. The significance of the R statistic is assessed by 1000 random permutations of the bromeliad species vector.

For the continuous habitat association test, we used a partial redundancy analysis (p RDA) to quantify the amount of variability in each community composition that can be attributed to pure environmental factors (E , the spatial component of environment removed), pure spatial predictor (S , the environmental component of space removed), and the covariance between environmental variables and the spatial predictor ($E + S$) (Peres-Neto et al. 2006). This analysis allowed us to simultaneously examine the importance of environment (goal 2) and space (goal 3) in determining community structure. We used presence-absence data to compose each biological matrix (bacteria, zooplankton, aquatic macroinvertebrates). To avoid overfitting our model by including too many explanatory variables, we removed variables that were unimportant or collinear with other variables using a forward selection procedure. The final environmental matrix was composed of: water temperature, pH, water color, concentrations of chlorophyll a , suspended material (turbidity), inorganic nitrogen, inorganic phosphorus, and the volume, diameter, and number of water-containing tanks of each bromeliad. We represented space using eigenvector-based filters selected using Moran's I . We also

characterized space using trend surface analysis (Gittins 1968) because of reports that different representations of space can result in different conclusions (Gilbert and Bennett 2010). However, both spatial characterizations gave us quantitatively similar results, so we reported the former. The remaining variation that was not explained by environmental or spatial predictors was considered as the unexplained variation. The percentages of the total variation in each community attributed to each component of variation were based on the adjusted (unbiased) fractions, which consider in each analysis the total number of predictors and the sample size. The significance of each fraction was tested by permutation tests using 999 randomizations (Peres-Neto et al. 2006). To provide unbiased estimates of the variation partitioning based on RDA, biological data were Hellinger-transformed prior to all analyses. As results were similar with and without rare species, all analyses were done with the complete data set. Partial RDA analyses were performed with the statistical language R version 2.10.0 (R Development Core Team 2009) using the package "vegan".

RESULTS

All communities, regardless of organism size, showed much stronger patterns of species co-occurrence than expected by chance (Table 1). Such patterns could be due to competitive exclusion and other species interactions, because of covariance among species in their responses to habitat conditions, or spatial covariance of dispersal-limited species (Ulrich 2004, Bell 2005). When we examined species co-occurrence patterns within particular bromeliad species, we found bacteria to still exhibit nonrandom co-occurrence ($P = 0.007$ to 0.046). However, zooplankton and macroinvertebrates had essentially random species occurrences within bromeliad species ($P > 0.2$), except for a marginally significant C score for macroinvertebrates in *A. nudicaulis* ($P = 0.049$). This suggests that habitat filtering between bromeliad species played a larger role in determining species co-occurrence within zooplankton and macroinvertebrates than within bacteria.

Habitat conditions varied in their influence on different organism types. The composition of bacterial communities was highly variable and unaffected by either bromeliad species (ANOSIM $R = -0.042$, $P = 0.89$; Fig. 1) or specific environmental variables ($<1\%$ of total variation once spatial variables accounted for; Fig. 2). **By contrast, the composition of macroinvertebrate communities differed between bromeliad species (ANOSIM $R = 0.143$, $P < 0.001$; Fig. 1) and was strongly influenced by environmental variables (29% of total variation once space accounted for; Fig. 2).** Zooplankton communities showed habitat associations that were intermediate between bacteria and macroinvertebrate communities (bromeliad species ANOSIM $R = 0.492$, $P < 0.001$, environmental variables explained 17% of total variation after accounting for space; Figs. 1 and 2). Once

TABLE 1. The prevalence of mutually exclusive species pairs in ecological communities, as estimated by *C* scores.

Organism type	Observed <i>C</i> -score index	Simulated <i>C</i> -score index		<i>P</i>
		Median	Variance	
All bromeliads				
Bacteria	102.97	102.29	0.03	0.000
Zooplankton	30.98	29.60	0.30	0.011
Macroinvertebrates	144.93	137.40	0.98	0.000
Within bromeliad species				
<i>Vriesea neoglutinosa</i>				
Bacteria	6.756	6.679	0.001	0.007
Zooplankton	2.981	2.861	0.015	0.204
Macroinvertebrates	3.156	3.000	0.048	0.205
<i>Neoregelia cruenta</i>				
Bacteria	8.242	8.205	0.001	0.046
Zooplankton	2.679	2.646	0.018	0.351
Macroinvertebrates	6.733	6.616	0.043	0.272
<i>Aechmea lingulata</i>				
Bacteria	5.231	5.179	0.001	0.042
Zooplankton	4.397	4.331	0.014	0.268
Macroinvertebrates	5.978	6.018	0.047	0.559
<i>Aechmea nudicaulis</i>				
Bacteria	7.576	7.510	0.001	0.019
Zooplankton	1.593	1.493	0.030	0.209
Macroinvertebrates	5.833	5.371	0.062	0.049

Notes: Significance (*P* value) was assessed by comparing the *C* score in the observed species–bromeliad matrix to the distribution of *C* scores generated by 5000 randomizations of the original matrix. The *C*-score index measures the average number of “checkerboard units” (mutually exclusive presence) between all possible pairs of species. The *C* score of each community is the average of all possible checkerboard pairs, calculated for species that occur at least once in the community matrix. Analyses were conducted for three different organismal types (bacteria, zooplankton, macroinvertebrates), either for all bromeliads regardless of species or within each bromeliad species. Significant *P* values (*P* < 0.05) are indicated by boldface type.

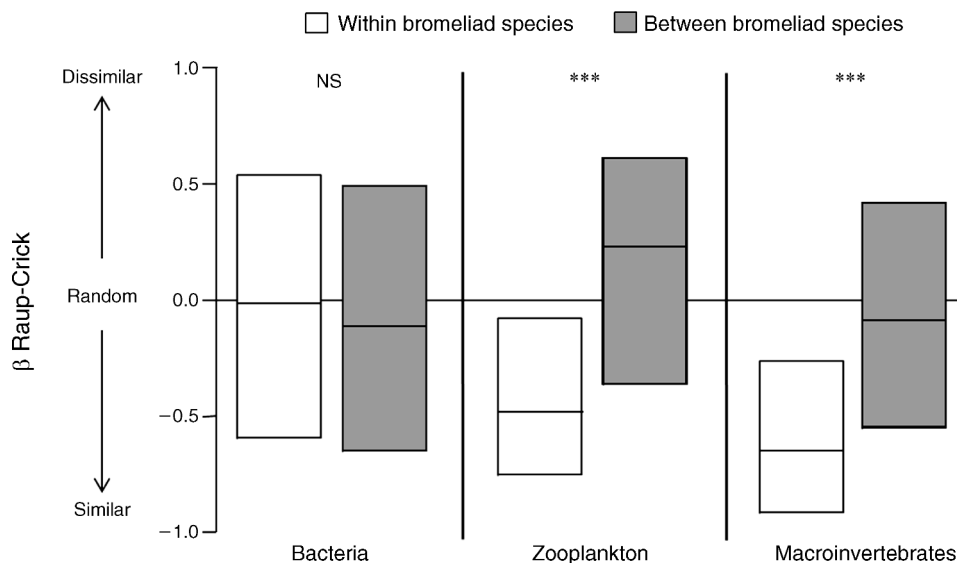


FIG. 1. Community dissimilarity within and between bromeliad species. Pairwise dissimilarity indexes of fauna were calculated within (open) and between (gray) bromeliad species. In the boxplots, the line is the median, and the boxes show 95% confidence intervals. The β Raup-Crick dissimilarity metric standardizes dissimilarity values, with +1 representing maximum dissimilarity and –1 representing maximum similarity. If a boxplot includes the value zero, similarity is not significantly different from a random-assembly null model. Comparisons of within- and between-bromeliad species used a randomization test of pairwise dissimilarity values.

*** *P* < 0.001; NS, not significant.

we controlled for environmental variables, the distance between bromeliads (ranging from centimeters to 120 m) had a significant but minor influence on bacterial communities (explained 2% of total variation) and no influence on the composition of either zooplankton or macroinvertebrate communities (Fig. 2). In all analyses, a portion of the variance could not be attributed purely to space or environment (the environment and space covariance term in Fig. 2), but our results are robust even if this portion of the variance was entirely due to spatial factors or entirely due to environmental factors.

DISCUSSION

All organism groups showed the nonrandom species associations that are expected from niche-based processes when multiple bromeliad species were considered. However, when we controlled for bromeliad species, these nonrandom species associations largely disappeared for zooplankton and macroinvertebrates, but not bacteria. One interpretation of these results is that bromeliad species are important habitat filters for zooplankton and macroinvertebrates, but not bacteria. This is in agreement with our analyses of community structure, which showed that the strength of environmental determinism increased with organism size, from negligible for bacteria, to medium for zooplankton, to strong for macroinvertebrates. This pattern in habitat filtering is consistent with the size–plasticity hypothesis and contrary to the size–dispersal hypothesis. Space was largely unimportant in explaining community structure, suggesting that dispersal processes are either not spatially structured or not important at the scale of our study.

At first, it may seem surprising that habitat associations were stronger for macroinvertebrates than bacteria, given previous evidence that suggests larger organisms are less effective dispersers, limiting their ability to track environmental heterogeneity (Beisner et al. 2006, Shurin et al. 2009). However, considerations of dispersal mode may explain this apparent paradox. Except for a single oligochaete species, all of our macroinvertebrate species were insects. Although bromeliads likely receive fewer insect eggs than they receive founding individuals of bacteria or zooplankton species, this is countered by the fact that adult insects oviposit eggs in suitable habitat (Ellis et al. 2006). Thus, it is not surprising that insects (with active dispersal) show stronger habitat associations than organisms with passive dispersal, like zooplankton or bacteria (see also Frank and Lounibos 1987). In many systems, macroorganisms can actively select appropriate habitat for dispersal. The exception that proves the rule is fish in lakes, whose dispersal is more constrained by waterways than that of aquatic micro-organisms, and consequently, show the inverse pattern to that shown here: Fish are more spatially structured and less environmentally determined than micro-organisms (Beisner et al. 2006, Shurin et al. 2009). The deterministic patterns we found

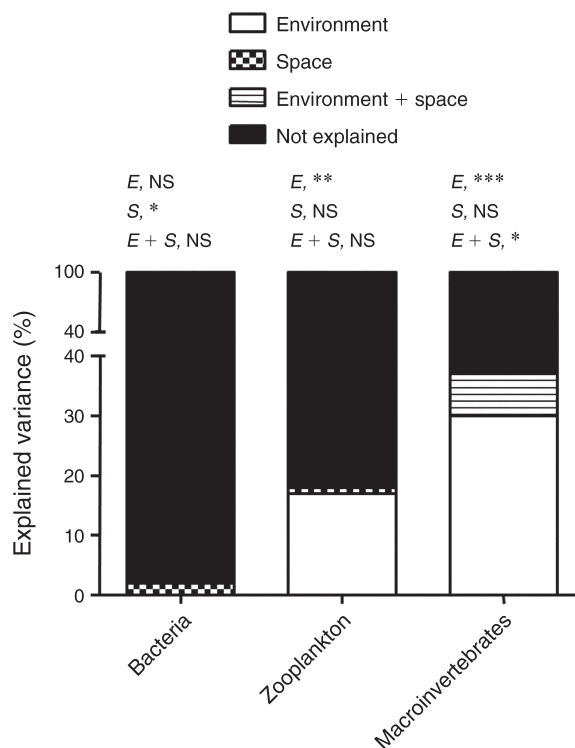


FIG. 2. Results of variation partitioning in the partial redundancy analysis (*p*RDA) for all communities, using presence–absence data to compose the biological matrix, direct linear distances between bromeliads to compose the spatial matrix, and limnological and structural characteristics of each bromeliad to compose the environmental matrix. *E* (environment) is the pure effect of environmental factors, *S* (spatial) is the pure effect of spatial predictor, and *E* + *S* is the covariance between environmental and spatial predictors. The explained variance of *E*, *S*, and *E* + *S* is based on the adjusted R^2 .

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant.

for macroinvertebrates are in accordance with previous studies of bromeliad insects that show strong patterns in both species co-occurrence (Gilbert et al. 2008) and habitat associations (Ngai et al. 2008).

The negligible associations between bacterial species and habitat conditions in bromeliads confirms results from other habitats (Langenheder and Ragnarsson 2007) and suggests that many bacteria may have similar fundamental niches (Finlay 2002, Langenheder et al. 2005, Östman et al. 2010), but do not occur everywhere because of limited dispersal (Lindström et al. 2006, Östman et al. 2010). Our results also agree with a recent study in Swedish lakes (Östman et al. 2010) that found bacterial communities to more closely follow neutral predictions than phytoplankton, but are in contrast with a study on Canadian lakes (Beisner et al. 2006). However, even though bacteria were indistinguishable in habitat associations, we still found evidence of nonrandom associations between bacterial species (Table 1). There are three potential explanations for this pattern. First,

species can show negative covariances in homogeneous environments when trade-offs between competitive abilities and dispersal abilities create patch dynamics (Cotterill 2005). There have been few investigations of such trade-offs in bacteria, but we note that bacteria differ in their ability to encyst following drying (Jones and Lennon 2010), which may affect rates of dispersal to new locations. Second, weak species associations can occur in neutral models simply through spatially structured dispersal, as individuals of species that randomly co-occur will, through dispersal, create neighborhoods of co-occurrence (Ulrich 2004, Bell 2005). This explanation is consistent with the weak but significant spatial structure in bacterial composition (Fig. 2). Finally, we cannot exclude the possibility that habitat affects bacteria at smaller spatial or taxonomic scales than used in our study, or that stochasticity in top-down effects overwhelms the environmental signal. We do note, however, that we measured exactly the same hydrological parameters that determine bacterial productivity in bromeliads (Haubrich et al. 2009) and bacterial composition in nearby larger water bodies (Laque et al. 2010). We characterized bacterial diversity by using DNA-based operational taxonomic units, which may separate bacteria at higher taxonomic levels than the species-level generally used for macroinvertebrates and zooplankton. However, it has frequently been argued that habitat filtering is expected to appear even stronger at higher taxonomic levels, given the phylogenetic conservatism of habitat-related traits (e.g., Diamond 1986).

In this study we present correlative evidence supporting the size-plasticity hypothesis, but there are several shortcomings of this approach. First, we considered only three categories of organism size, limiting the power of our analysis. Second, we are unable to discount the possibility that differences other than body size and plasticity are responsible for the differences in the strength of habitat filtering between bacteria, zooplankton and macroinvertebrates; certainly these taxa differ in many other ways, including generation time, reproductive mode, and trophic level. At first glance it may seem that both issues could be addressed if we also considered body size variation within organism types. However, we have argued that the greater importance of habitat filtering for macroinvertebrates is due in part to the active selection of dispersal sites, whereas zooplankton and bacteria are passive dispersers. There is virtually no variation in dispersal mode within our organism types, so it is perhaps not surprising that, although larger organisms have stronger habitat filtering when multiple organism groups are considered, this result is not also seen within organism groups; if anything, the body size effect is slightly reversed (Appendix B).

Other researchers attempting to test the size-dispersal and size-plasticity hypotheses will probably grapple with these same issues. How then could these hypotheses be further tested? First, we hope that by formally outlining these hypotheses we will inspire other

researchers to use our methodology for a wide variety of organism types, which collectively will increase the power of the observational analysis. Second, the assumptions underlying the hypotheses could be experimentally tested. The size-plasticity hypothesis assumes that macroscopic organisms have narrower fundamental niches than microscopic organisms; this could be experimentally tested by monitoring survival of organisms introduced to sites spanning a broad environmental gradient. The size-dispersal hypothesis assumes that small-bodied organisms disperse faster to suitable habitat than larger organisms; this could be tested by providing new, suitable habitat and monitoring colonization rates (for an example of this approach see Shulman and Chase 2007).

In summary, our study shows that the niche process of habitat filtering strengthens from bacteria to zooplankton to macroinvertebrates, consistent with the size-plasticity hypothesis. Ecological theory is moving beyond simplistic contrasts of ecological determination of community structure with trait-neutral effects of stochasticity, by recognizing that community structure can be explained by both sets of processes (Gravel et al. 2006, Adler et al. 2007). Recent research has shown that the relative importance of ecological determinism varies with ecosystem conditions such as productivity (e.g., Chase et al. 2010). This study shows that another aspect of ecological context also matters: Organisms of different size also differ in the relative importance of ecological determinism. Thus, although food webs as a whole may be influenced by both deterministic and stochastic processes (e.g., Thompson and Townsend 2006, Chase et al. 2010), the relative importance of these processes may change substantially between component organisms.

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SUPPLEMENTAL MATERIAL

Appendix A

A list of faunal taxa (excluding bacteria) recorded in four different species of bromeliads at Macaé, RJ, Brazil (*Ecological Archives* E093-152-A1).

Appendix B

An analysis of the effects of body size and dispersal mode within organism groups (*Ecological Archives* E093-152-A2).