

Dominant predators mediate the impact of habitat size on trophic structure in bromeliad invertebrate communities

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Abstract. Local habitat size has been shown to influence colonization and extinction processes of species in patchy environments. However, species differ in body size, mobility, and trophic level, and may not respond in the same way to habitat size. Thus far, we have a limited understanding of how habitat size influences the structure of multitrophic communities and to what extent the effects may be generalizable over a broad geographic range. Here, we used water-filled bromeliads of different sizes as a natural model system to examine the effects of habitat size on the trophic structure of their inhabiting invertebrate communities. We collected composition and biomass data from 651 bromeliad communities from eight sites across Central and South America differing in environmental conditions, species pools, and the presence of large-bodied odonate predators. We found that trophic structure in the communities changed dramatically with changes in habitat (bromeliad) size. Detritivore : resource ratios showed a consistent negative relationship with habitat size across sites. In contrast, changes in predator : detritivore (prey) ratios depended on the presence of odonates as dominant predators in the regional pool. At sites without odonates, predator : detritivore biomass ratios decreased with increasing habitat size. At sites with odonates, we found odonates to be more frequently present in large than in small bromeliads, and predator : detritivore biomass ratios increased with increasing habitat size to the point where some trophic pyramids became inverted. Our results show that the distribution of biomass amongst food-web levels depends strongly on habitat size, largely irrespective of geographic differences in environmental conditions or detritivore species compositions. However, the presence of large-bodied predators in the regional species pool may fundamentally alter this relationship between habitat size and trophic structure. We conclude that taking into account the response and multitrophic effects of dominant, mobile species may be critical when predicting changes in community structure along a habitat-size gradient.

Key words: apex predator; aquatic mesocosms; biomass; body size; food web; insects; metacommunity; multitrophic interaction; Odonata; predation; predator : prey ratio; top-down control.

INTRODUCTION

We have known that the size of a habitat determines the diversity of its ecological community since Robert

MacArthur and Edward Wilson developed the theory of island biogeography (MacArthur and Wilson 1963, 1967). This relationship is driven by effects of habitat size on species colonization and extinction dynamics. These dynamics are especially important in patchy habitats where populations are connected via dispersal to form metapopulations (Levins 1969) and smaller local populations go extinct at higher rates (Hanski and

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Gilpin 1991). More recently, the metapopulation concept has been extended to metacommunities (Wilson 1992, Leibold et al. 2004). This new perspective acknowledges that natural systems consist of many interacting species, organized in multiple trophic levels, whose local and regional persistence may also be influenced by colonization–extinction dynamics to varying degrees (Logue et al. 2011).

Species have unequal colonization and extinction rates (De Bie et al. 2012) and therefore possibly different responses to habitat size. Trophic position in food webs is often positively correlated with body size, rarity, and home-range size (Rooney et al. 2008). These interrelated traits have been associated with higher extinction risks in smaller and more variable habitats due to stochastic events (Ewers and Didham 2006, Laurance et al. 2011) and could be one reason for the more frequent loss of predators from ecosystems, compared with lower trophic levels (Didham et al. 1998, Srivastava et al. 2008, Holt 2009, Hagen et al. 2012). In addition, predators depend on the presence of their prey, and the resulting requirement of prior colonization of habitat patches by lower trophic levels may strengthen area effects on higher trophic levels further, especially for specialist predators (trophic rank hypothesis; Holt et al. 1999). On the other hand, large-bodied species (i.e., often predators) are more mobile (Rooney et al. 2006) and can colonize distant habitat patches more easily.

Species may not only differ in their response to habitat size but also in the roles they play for community functioning. Certain species have been shown to be more important for the maintenance of community structure and stability than others (Power et al. 1996). These strongly interacting species are often dominant or keystone top predators with the potential to control species richness and trophic complexity (Paine 1966). A change in top predator presence or abundance as a response to changes in habitat size may initiate trophic cascades that can dramatically alter food-web structure and ecosystem state (Terborgh et al. 2001, Dobson et al. 2006, Staddon et al. 2010, Estes et al. 2011, Atwood et al. 2013). Such losses in top predators may also interact with more direct effects of habitat size on lower trophic levels, such as changes in resource availability (Post 2002). The differential sensitivity of species or trophic groups to habitat size and related habitat-size-driven differences in food-web structure are especially relevant in a conservation context, where we strive to predict community responses to habitat fragmentation and habitat loss (Terborgh et al. 2001, Estes et al. 2011).

While it has been established that communities in small habitats typically have fewer species in total (MacArthur and Wilson 1963), fewer species within each trophic level (Hart and Horwitz 1991), and often shorter food chains (Spencer and Warren 1996, Post et al. 2000, Post 2002, Takimoto and Post 2013), we still know relatively little about the effect of habitat size on trophic community structure, especially in terms of the

relative biomass of organisms at different trophic levels. However, biomass may be a better indicator of changes in food-web structure and functioning than richness or abundance because rewiring of trophic links is a realistic response to extinctions and may prevent communities from collapsing until insufficient energy is left to be transferred to the next trophic level (Thierry et al. 2011). The effects of habitat size on certain aspects of the structure of multitrophic communities have been investigated on islands (e.g., Wilson and Simberloff 1969, Losos and Ricklefs 2009) and in ponds, lakes (e.g., Post et al. 2000, Chase et al. 2009), and moss patches (e.g., Gilbert et al. 1998, Staddon et al. 2010). More recently, plant-held waters (phytotelmata) have come into the view of metacommunity ecologists (Sota 1996, Kneitel and Miller 2003). Here, we use bromeliad phytotelmata as a model system of naturally discrete aquatic habitat patches of varying sizes to examine the relationship of the trophic structure of their inhabiting invertebrate communities with habitat size.

Bromeliads are Neotropical plants that in many species are epiphytic and form tanks within their leaf axils, in which rainwater and dead organic matter accumulate (Benzing 2000). Microorganisms, algae, and detritivorous and predatory invertebrates subsequently colonize these tanks and form multitrophic communities that use the detrital organic matter as a basal resource (Richardson et al. 2000, Srivastava and Bell 2009, Starzomski et al. 2010). Bromeliad communities are naturally organized as metacommunity systems with local habitats (individual bromeliads) connected by the dispersal of invertebrates. These systems are relatively simple in their trophic structure and species pool, and their local communities can be censused in their entirety, yielding “taxonomically unrestricted” samples (Cotgreave et al. 1993, Armbruster et al. 2002). Tank-forming bromeliads occur over a wide geographic area, from southern Florida, USA to northern Argentina, allowing the generality of ecological patterns over space to be assessed. Bromeliads differ in size over several orders of magnitude, holding from a few milliliters up to 20 liters of water. This large difference in the size of their habitat influences detritivore density and species richness (Richardson 1999, Srivastava 2006, Jocque and Field 2014), algal biomass (Marino et al. 2011), predator:prey richness ratios, and subsequently, topological properties of connectance webs (Dézerald et al. 2013), as well as the presence of odonate larvae (Srivastava 2006). Odonate larvae are large, dominant generalist predators in tropical phytotelmata (Fincke et al. 1997, Yanoviak 2001, Srivastava 2006, Srivastava and Bell 2009). However, odonates only occur in bromeliads over part of the geographic range of Bromeliaceae, from Mexico in the north to Argentina in the south (Kitching 2000). They have not been recorded from bromeliads on smaller Caribbean islands. In those areas that lack odonates, smaller-sized invertebrate species make up the

TABLE 1. Detailed characteristics of the study sites, including latitude and longitude, range of elevations of the locations of data collection (in meters above sea level; a.s.l.), the presence of odonates in the regional pool at the site, the bromeliad genera that were sampled, and the number of bromeliads that were sampled in total at each site (*N*).

Site location	Site description	Latitude and longitude
Costa Rica	Estación Biológica Pitilla, Área de Conservación Guanacaste, primary and secondary forest, pasture. Mean monthly temperature 25.8–29.4°C. Mean monthly rainfall 2–452 mm/month.	10.98° N, 85.43° W
Dominica	Morne Trois Pitons, Boeri Lake, and Morne Diablotins, subtropical wet (Tabonuco) forest, montane thicket, cloud forest. Mean monthly temperature ~24–29°C. Mean monthly rainfall ~40–300 mm/month.	15.41° N, 61.35° W
Puerto Rico, USA	Luquillo Experimental Forest (LEF) El Verde, LEF Trade Winds Trail, and LEF Pico Del Este subtropical wet (Tabonuco) forest, lower montane wet (Palo Colorado) forest, and dwarf forest. Mean monthly temperature 18–25°C. Mean monthly rainfall 150–600 mm/month.	18.30° N, 65.79° W
Saba, Netherlands	Sandy Cruz, lower and upper Mt. Scenery, moist secondary tropical forest, cloud forest. Mean monthly temperature ~22–26°C. Mean monthly rainfall ~120–300 mm/month.	17.63° N, 63.24° W
Honduras	Cusuco National Park, cloud forest, primary and secondary forest. Mean monthly temperature 22.2–28.0°C. Mean monthly rainfall 17–658 mm/month.	15.54° N, 88.26° W
Brazil		
Cardoso	Parque Estadual da Ilha do Cardoso (PEIC). 22 500-ha Atlantic island located on the south coast of São Paulo state, southeastern Brazil. Mean monthly temperature 16.9–23.1°C. Mean monthly rainfall 27–292 mm/month.	25.07° S, 47.92° W
Macae	Parque Nacional da Restinga de Jurubatiba (PNRJ), located in the northeast of Rio de Janeiro State, southeastern Brazil. Wet tropical climate with mean monthly temperature 21.7–26.9°C. Mean monthly rainfall 22–123 mm/month.	22.38° S, 41.75° W
Picinguaba	Parque Estadual da Serra do Mar (PESM), Núcleo Picinguaba. Wet tropical Atlantic rain forest <i>restinga</i> with no well-defined wet and dry seasons. Poor sandy soils, trees ~15 m height, dense understorey. Mean annual temperature 22.6°C. Annual rainfall up to 2600 mm/year.	23.35° S, 44.83° W

apex-predator level of bromeliad food webs. So far, we know relative little about how the shape of biomass pyramids changes with habitat size in bromeliad communities and other systems, and especially how general any effect of habitat size may be across broad geographic areas with different species compositions and predator types.

Here, we analyze biomass data from more than 600 bromeliad food webs collected at different sites in Central and South America to examine the effect of habitat size (bromeliad volume) on the trophic structure of these communities. We hypothesize that trophic structure in terms of the ratios of standing-stock biomass between trophic levels changes along the habitat-size gradient. Specifically, we expect habitat size to primarily affect large-bodied predator species, leading to increases in predator : prey (i.e., predator : detritivore) biomass ratios with increasing habitat size. Detritivore : resource biomass ratios are expected to show the opposite pattern in relation to habitat size, for example as a top-down response to changes at the predator level. We further hypothesize that these changes in community structure are universal across sites and detritivore species compositions. If predator traits are important in determining the strength of top-down effects, we expect the differential occurrence of large-bodied odonate predators at different sites to modulate changes in biomass ratios along the habitat-size gradient.

METHODS

Study sites and bromeliads

We recorded taxonomic composition, abundance, and biomass of aquatic organisms from 651 bromeliads at eight geographical sites spanning several thousand kilometers in distance and varying in elevation, climate, bromeliad species, and the occurrence of odonate predators (Table 1). We collected the data between 1993 and 2011 with multiple years of data collection at many of the sites. All data sets were collected using consistent census methods, facilitating a joint analysis across sites.

The macroscopic invertebrate species compositions at these sites vary, but typically include detritivorous larvae of Diptera such as Chironomidae, Culicidae, Syrphidae, and Tipulidae, and Coleoptera such as Scirtidae. Odonata (in our data set exclusively Zygoptera) occur in bromeliads at some sites only and are the dominant invertebrate predators there. The sites in our data set that contain odonates in the regional species pool are Costa Rica and the three Brazilian sites: Cardoso, Macae, and Picinguaba. Odonates are absent from regional species pools at Dominica, Saba, Netherlands, Puerto Rico, USA, and the field site in Honduras. Further predatory invertebrates include Ceratopogonidae, Chironomidae, Corethrellidae, Culicidae, and Tabanidae (Diptera), and Dytiscidae and Hydrophilidae (Coleoptera).

TABLE 1. Extended.

Elevation (m a.s.l.)	Years sampled	Odonates	Bromeliad genera	<i>N</i>
527–786	1997, 2000, 2002, 2004, 2010	present	<i>Guzmania</i> Ruiz and Pavón, <i>Werauhia</i> J.R. Grant	117
775–1160	2002	absent	<i>Guzmania</i> , <i>Werauhia</i>	30
295–980	1993, 1994, 1996, 1997, 2010	absent	<i>Guzmania</i> , <i>Werauhia</i>	200
530–845	2009	absent	<i>Guzmania</i> , <i>Werauhia</i>	30
1347–2084	2006, 2007	absent	<i>Tillandsia</i> L.	157
9	2008, 2011	present	<i>Quesnelia</i> Gaudich.	41
10	2008	present	<i>Vriesea</i> Lindl., <i>Aechmea</i> Ruiz and Pavón, <i>Neoregelia</i> L.B. Sm.	63
8	2009	present	<i>Aechmea</i>	13

The sampled bromeliad species differed among sites. In many cases, the actual bromeliad species identities could not be determined without floral structures. Generally, the morphology of the bromeliad (i.e., the local habitat structure for the inhabiting communities) seems to be important for invertebrate community composition, and bromeliad taxonomic identity might only be integrating over several morphological characteristics or microhabitat affinities (Marino et al. 2013). There is no evidence of species-specific associations between particular bromeliad species and their faunas once morphological and habitat covariates are accounted for (Benzing 1990).

Habitat size was measured as the maximum water-holding capacity of the bromeliad (volume in mL) by filling the plant to the point of overflowing, or estimated using allometric equations based on the number of leaves and the basal leaf width (adjusted $R^2 = 0.94$, $n = 129$ bromeliads), and in the case of Honduras on the number of leaves and their biomass (adjusted $R^2 = 0.92$, $n = 17$ bromeliads). The inclusion of a weighting parameter for data quality (measured vs. estimated) did not change the results of initial analyses and was omitted from final analyses.

Resource biomass

The detritus in the bromeliad, which is the basal resource for the invertebrate community, was collected and separated from bromeliad water using sieves and

filter paper. It was subsequently dried and weighed. In some cases, detritus with a diameter of smaller than 150 μm or larger than 2 cm was not measured and was instead estimated from allometric equations using data from measured size classes of detritus (adjusted $R^2 = 0.90$, $n = 25$ bromeliads for detritus smaller than 150 μm , adjusted $R^2 = 0.78$, $n = 62$ bromeliads for detritus larger than 2 cm). The inclusion of a weighting parameter for data quality (measurement of dry or wet mass of all size classes vs. estimation of at least one size class) did not change the results of initial analyses and was omitted from further analyses.

Invertebrate communities

Bromeliad plants were dissected leaf by leaf or washed out using strong water pressure from a hose to extract the organisms that can retreat to the small gaps between interlocking leaves. All macroscopic aquatic and semi-aquatic organisms larger than ~ 0.5 mm were identified to species or morphospecies level and counted (Appendix: Table A1). Ostracoda, Acari, and Branchiopoda were observed, but not collected or counted because of their small size. Note that microscopic organisms contribute to decomposition processes and constitute prey for larger organisms, but potentially to a smaller extent than macroscopic organisms. For example, invertebrate shredders have been shown to constitute a large proportion of the biomass and contribute most of the ecosystem function in the form of decomposition in

a stream ecosystem (Hieber and Gessner 2002) and in bromeliads (LeCraw 2014).

We assigned all organisms to a trophic position based on information from the literature and personal observations. Predators were defined as those organisms that feed on other macroscopic invertebrates, including engulfer predators as well as piercers. Although there is some intraguild predation in bromeliad invertebrate food webs (Dézerald et al. 2013), this is usually incidental to the main prey of detritivorous invertebrates, so we felt justified in simplifying the food webs in our study and considering all predators as a single trophic level. All other taxa were classified as detritivores. Similarly, this term summarizes a range of different detritivorous feeding groups such as deposit feeders, gatherers, scrapers, shredders, and filter feeders whose common food resource is detritus.

Organisms at all life-history stages were included in our analysis (larvae, pupae, and adults). Only in one case do we have evidence that the trophic level of a species that was found as larva and adult in our study changes with life-history stage (Coleoptera.48, see Appendix: Table A1). The other predators might feed on smaller prey items in their younger stages but, as far as we are aware, do not shift trophic position. Pupae were assigned the same feeding group as larvae even though they do not feed, because the duration of the pupal period is generally much shorter than the duration of the larval period. Thus, pupal biomass represents very recent larval feeding that we wished to capture in our analysis. Pupae made up a low proportion of the biomass compared with larvae and adults and their inclusion did not influence the results.

Invertebrate biomass

Invertebrate dry mass was measured directly for some data sets (Dominica, Puerto Rico, Saba, and partly for Cardoso and Costa Rica). Where only wet mass was available, it was converted to dry mass using a simple conversion factor c . We derived c from data with measurements of both wet and dry mass, using data that were as specific to each taxonomic group as possible. These wet-to-dry conversion factors ranged from $c = 0.07$ (Chironomidae) to $c = 0.32$ (Coleoptera). In some cases, only the length of individuals was measured and dry mass was estimated according to allometric equations specific to each taxonomic group. Where no individual measurements were available, average mass for species or higher-level taxonomic groups was used. A weighting parameter for data quality was used in the analyses. Data were classified into: (1) high data quality, a measurement of dry or wet mass or length measurement at individual level or a classification of the individuals into specific size classes, (2) intermediate data quality, a mean value for the species or higher taxonomic group originating from the same data set, and (3) low data quality, a mean value for the species or higher taxonomic group originating from a different

data set. As the weighted analysis using this parameter produced the same results, the weighting parameter was omitted from final analyses.

Statistical data analysis

We summed up the biomass of all organisms at the main food-web levels per bromeliad: predators, detritivores (prey), and resources (detritus). Predator:detritivore biomass ratios and detritivore:resource biomass ratios were calculated for each bromeliad and \log_{10} -transformed to achieve normality. Bromeliads that did not contain any predators were excluded from the analysis of predator:detritivore ratios (107 out of 651 bromeliads). This exclusion constitutes a conservative approach. The inclusion of these data points by using a small value as predator biomass before \log_{10} transformation of the ratio did not qualitatively change the results but led to stronger effects. We furthermore analyzed the abundance (number of individuals) of predators and detritivores (square-root-transformed), their per capita biomass (\log_{10} -transformed), the absolute total biomass at each trophic level (\log_{10} -transformed), and the presence of odonates in individual bromeliads at sites where odonates are part of the regional species pool.

We used mixed-effects models in order to determine the main drivers of biomass food-web structure at two spatial scales (Pinheiro and Bates 2000). The explanatory variables at site level were the latitudinal location and the presence of odonate predators in the regional pool of each site as a binary variable (presence-absence). The explanatory variable at the bromeliad level was the \log_{10} -transformed bromeliad volume that expresses habitat size for the inhabiting communities. Since the aim of the analysis was to identify generalities across sites, we used site as a random effect instead of testing site as an explanatory variable (fixed effect) in the model. We did not use additional between-site or within-site abiotic explanatory variables (e.g., climate data), since these were not available at comparable scales for all sites. The fixed effect latitude and the random effect site include the additional variation that is, for example, due to between-site climatic differences. We conducted all statistical analyses in R version 3.0.1 (R Core Team 2013). We carried out linear mixed-effects models using the lme function of the package nlme and analyzed odonate presence in each bromeliad with a generalized linear mixed-effects model (function glmer in package lme4, family set as binomial, link set as logit; Bolker et al. 2008).

RESULTS

We found a strong and consistent decrease in detritivore:resource biomass ratios with increasing habitat size at all sites and countries, independent of the presence of odonates in the regional species pool (Fig. 1A, Table 2). This change in the detritivore:resource ratios resulted from detritivore biomass increas-

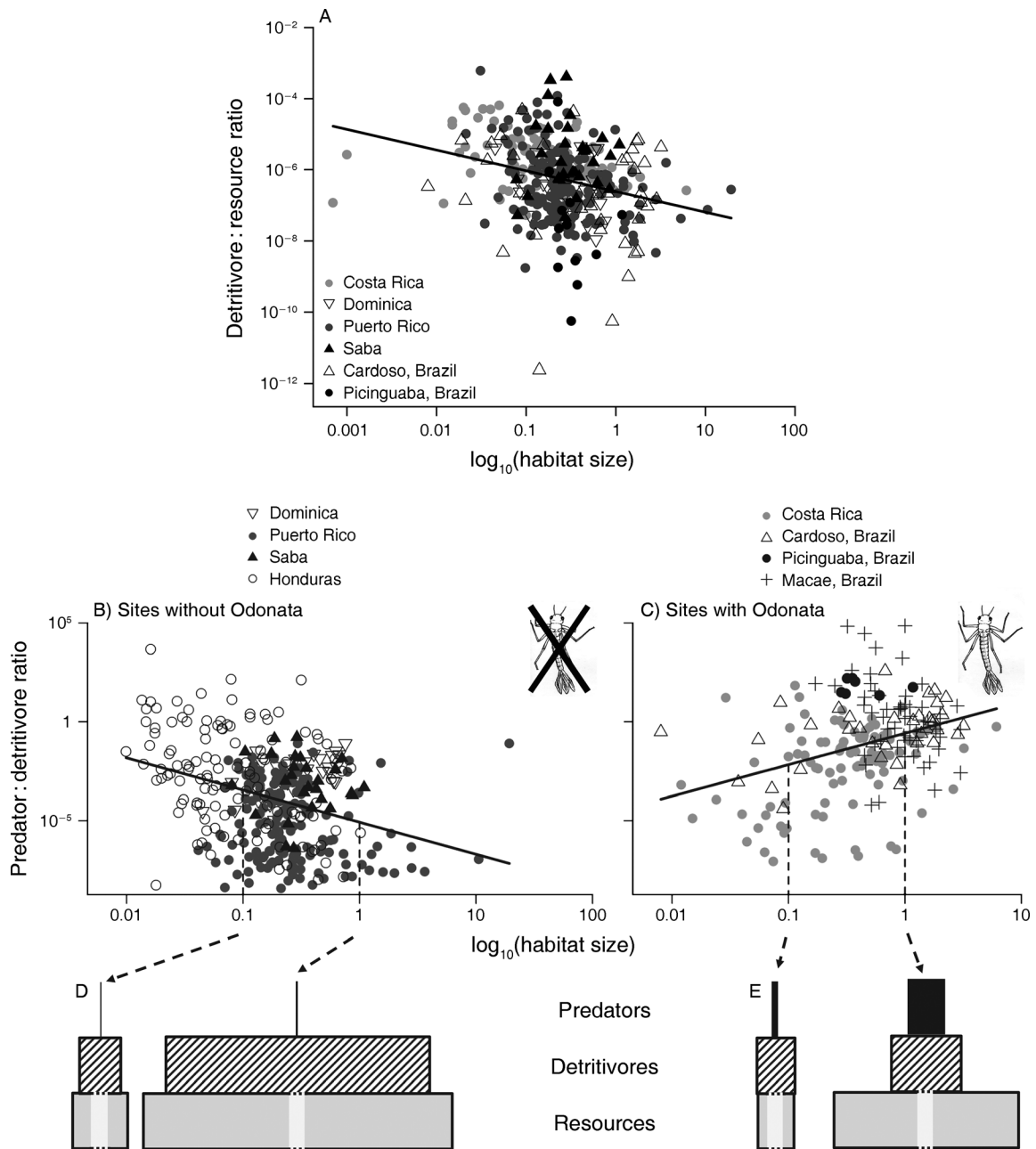


FIG. 1. Food-web structure changes along the habitat-size gradient (where habitat size is \log_{10} -transformed bromeliad volume, originally measured in L), including (A) detritivore : resource biomass ratio (slope = -0.58 ± 0.11 ; all means \pm SE; resource data were only available for six sites), (B) predator : detritivore biomass ratio for sites without odonates (slope = -1.62 ± 0.25), and (C) with odonates (slope = 1.59 ± 0.31) in the regional species pool. These changes in trophic structure can be visualized as trophic pyramids (predators, shown in black, detritivores, shown in hatching, and resources, shown in gray) for two selected sizes of bromeliad (0.1 L and 1 L) for (D) sites without odonates and (E) sites with odonates. Panels (D) and (E) show back-transformed biomass estimates from the fitted model (Appendix: Table A2) for the different food-web levels on a relative scale, with predator and detritivore biomass on the same scale but resource biomass scaled by division by an arbitrary value of 500 for visual clarity (indicated by the dashed line and light gray patch in the resource biomass bar).

ing less strongly than resource biomass along the habitat-size gradient (Appendix: Fig. A1 and Table A2).

Predator : detritivore biomass ratios changed with latitude (Table 2, Appendix: Fig. A2), and there was a significant interactive effect between the presence of

odonates in the regional species pool and habitat size. Predator : detritivore ratios decreased with increasing habitat size for sites without odonates in the regional pool (Dominica, Saba, Puerto Rico, and Honduras; Fig. 1B). This change in predator : detritivore ratios was due

TABLE 2. Results of the linear mixed-effects model analysis testing main effects and two-way interactions on biomass ratios (\log_{10} -transformed) with site as a random effect.

Effect	Detritivore:resource ratio			Predator:detritivore ratio		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Latitude	1, 3	4.37	0.1278	1, 5	22.35	0.0052
Odonate presence	1, 3	1.01	0.3895	1, 5	0.21	0.6689
Habitat size	1, 350	19.86	<0.0001	1, 529	3.24	0.0724
Latitude × habitat size	1, 350	0.82	0.3671	1, 529	3.26	0.0716
Odonate presence × habitat size	1, 350	1.45	0.2293	1, 529	23.95	<0.0001

Note: Habitat size is \log_{10} -transformed bromeliad volume (originally measured in mL) and *P* values <0.05 shown in bold.

to predator biomass increasing less strongly than detritivore biomass along the habitat-size gradient (Appendix: Fig. A1). By contrast, for the sites with odonates in the regional pool (Costa Rica, Cardoso, Macae, and Pinguaba), predator:detritivore ratios increased strongly with increasing habitat size (Fig. 1C). This increase in predator:detritivore ratios resulted from strong increases of predator biomass along the habitat-size gradient and only weak increases of detritivore biomass (Appendix: Fig. A1). The frequency of odonate presence in individual bromeliads at sites with odonates showed a positive relationship with habitat size (Appendix: Fig. A3, $P < 0.001$). Where present, odonates were the dominant predators in terms of relative biomass per bromeliad (Appendix: Fig. A4), and Tabanidae, Ceratopogonidae, and Chironomidae were among the next-most dominant species. At sites from which odonates were absent, Chironomidae, Syrphidae, and Corethrellidae showed the highest relative biomass. We also tested the effect of the presence of Tabanidae in the regional pool, since they were another large-bodied, dominant predator only present in bromeliads at some sites (Costa Rica,

Cardoso, Pinguaba, Macae, and Honduras). However, there was no effect of tabanid presence on detritivore:resource biomass ratios or predator:detritivore biomass ratios (Appendix: Table A3).

The differential shifts in biomass at different trophic levels with habitat size resulted in different trophic pyramids in small and large bromeliads for sites without and with odonates (Fig. 1D, E). In most sites without odonates, trophic pyramids were Eltonian in shape (bottom-heavy), in that each higher food-web level had less biomass than that below it. The only exceptions were some small bromeliads in Honduras (positive \log_{10} -transformed predator:detritivore ratios in Fig. 1B). By contrast, trophic levels were more equitable in biomass in sites with odonates, with inverted (top-heavy) trophic pyramids regularly found in the largest bromeliads (positive \log_{10} -transformed predator:detritivore ratios in Fig. 1C).

Changes in organism abundance (number of individuals per bromeliad) along the habitat-size gradient also differed between trophic levels. Detritivore abundance increased strongly with habitat size at odonate-free sites (Fig. 2A, Table 3), but not at sites with odonates (Fig.

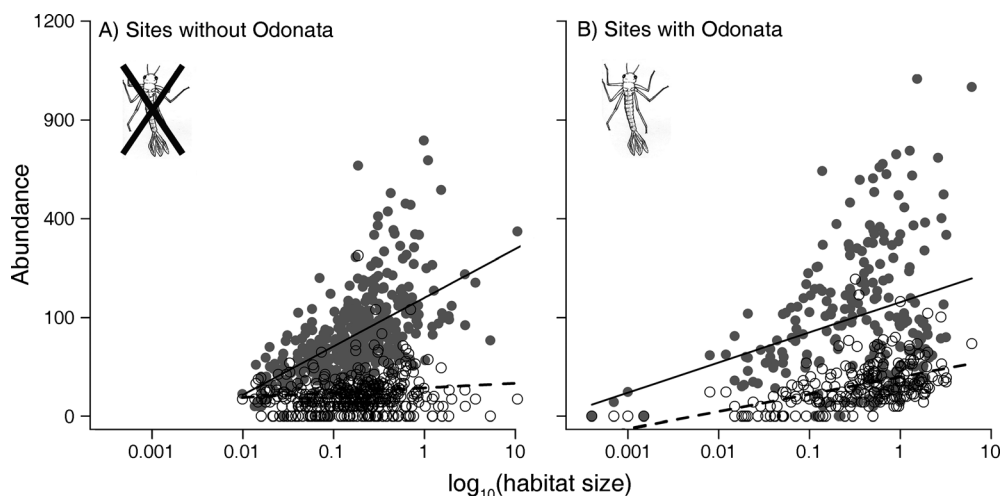


FIG. 2. Abundance (number of individuals, square-root-transformed) of predators and detritivores along the habitat-size gradient (\log_{10} -transformed bromeliad volume, originally measured in L) for (A) sites without and (B) sites with odonates in the regional species pool. Predator biomass is depicted by open symbols and dashed lines (slopes = 0.45 ± 0.18 and 1.77 ± 0.20 for sites without and with odonates, respectively), detritivore biomass by filled gray symbols and thick solid lines (slopes = 4.98 ± 0.34 and 3.05 ± 0.63). Abundance data were not available for the Pinguaba site in Brazil.

TABLE 3. Results of the linear mixed-effects model analysis testing main effects and two-way interactions on the abundance of detritivores and predators in each bromeliad (both square-root-transformed) with site as a random effect.

Effect	Detritivore abundance			Predator abundance		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Latitude	1, 4	2.67	0.1776	1, 4	0.75	0.4332
Odonate presence	1, 4	2.36	0.1995	1, 4	0.01	0.9442
Habitat size	1, 620	274.20	<0.0001	1, 527	13.15	0.0003
Latitude × habitat size	1, 620	4.87	0.0276	1, 527	0.07	0.7975
Odonate presence × habitat size	1, 620	46.02	<0.0001	1, 527	12.46	0.0005

Notes: Cases where no detritivores ($n = 3$ cases) or no predators ($n = 57$ cases) were found were excluded to be comparable with \log_{10} -transformed response variables (biomass ratios and per capita mass). Habitat-size transformation is as in Table 2. *P* values <0.05 shown in bold.

2B). In contrast, predator abundance was constant along the habitat-size gradient at odonate-free sites (Fig. 2A), but increased at sites with odonates present (Fig. 2B).

These shifts in abundance (Fig. 2) and in absolute total biomass at each trophic level (Appendix: Fig. A1) are reflected in differential changes in average per capita biomass of detritivores and predators. Per capita biomass of detritivores increased strongly with habitat size at those sites without odonates (Fig. 3A, Table 4), but did not change along the habitat-size gradient at sites with odonates in the regional pool (Fig. 3B). In contrast, predator per capita biomass did not change with habitat size at sites where odonates do not occur (Fig. 3A), but increased strongly with increasing habitat size at sites with odonates (Fig. 3B).

DISCUSSION

We found a strong and general decrease in detritivore:resource ratios with increasing habitat size. In contrast, the effect of habitat size on predator:detritivore ratios was modified by the presence of odonates in the regional species pool. At sites with odonates, the

average per capita and total biomass of predators increased strongly along the habitat-size gradient because odonates predominately occurred in large bromeliads. This shift in biomass ratios between trophic levels led to markedly different trophic structures in large vs. small bromeliads.

Effects of habitat size at sites without odonates

The trophic structure of bromeliad-inhabiting invertebrate communities at sites without odonates showed a signature of bottom-up control (Heath et al. 2013), with all trophic levels increasing in absolute biomass with increasing habitat size. However, the slope of these relationships was smaller at higher trophic levels, resulting in decreasing biomass ratios between adjacent trophic levels, both for detritivore:resource and predator:detritivore ratios. Energy loss between trophic levels is inherent to most food webs (Lindeman 1942, Brown et al. 2004, Reuman et al. 2009). A possible reason for the change in the magnitude of this loss with bromeliad size could be shifts in resource-encounter rates, either due to changing habitat complexity (see Appendix: Fig. A5 for this data set and Srivastava

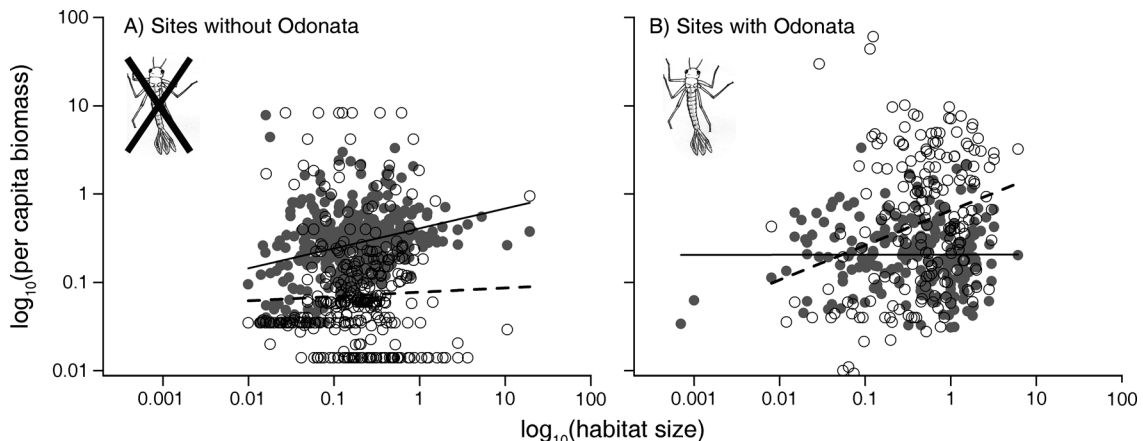


FIG. 3. Mean per capita biomass (\log_{10} -transformed, originally measured in mg) of predators and detritivores in bromeliads of different sizes (\log_{10} -transformed volume, originally measured in L) for (A) sites without and (B) sites with odonates in the regional species pool. Mean predator per capita biomass is depicted by open symbols and dashed lines (slopes = 0.11 ± 0.16 and 0.84 ± 0.25 for sites without and with odonates, respectively), mean detritivore per capita biomass by filled gray symbols and solid lines (slopes = 0.52 ± 0.08 and 0.003 ± 0.096). Per capita biomass was not available for the Pinguaba site in Brazil.

TABLE 4. Results of the linear mixed-effects model analysis testing main effects and two-way interactions on mean per capita biomass of detritivores and predators in each bromeliad (both \log_{10} -transformed) with site as a random effect.

Effect	Per capita mass detritivores			Per capita mass predators		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Latitude	1, 4	1.58	0.277	1, 4	2.50	0.1892
Odonate presence	1, 4	0.07	0.8095	1, 4	2.29	0.2044
Habitat size	1, 620	70.90	< 0.0001	1, 527	50.08	< 0.0001
Latitude × habitat size	1, 620	1.04	0.3076	1, 527	3.46	0.0635
Odonate presence × habitat size	1, 620	15.01	0.0001	1, 527	7.15	0.0077

Note: Habitat size transformation is as in Table 2, *P* values <0.05 shown in bold.

[2006]) or due to the decreasing resource densities along the habitat-size gradient (abundance/volume and biomass/volume, results not shown).

Small predators are often limited in their prey size range, and their prey may grow into a size refuge, exceeding small predators' gape-widths or piercing abilities (Woodward and Hildrew 2002). Small predators might track the biomass of their prey (donor- or bottom-up-controlled interaction) rather than control it top-down. This is supported by our finding that detritivore per capita biomass increased along the habitat-size gradient at sites without odonates, where most of the predators were smaller-bodied species such as ceratopogonids or chironomids. In bromeliads, predatory chironomids and ceratopogonids only prey on a subset of the detritivore food web, unlike odonates (Dézerald et al. 2013), and have insignificant effects on detritivore abundances (Starzomski et al. 2010, LeCraw 2014). These size-class shifts are a typical response to changes in predation pressure, as, for example, shown for the response of macroinvertebrates to fish predation in pond ecosystems (Crowder and Cooper 1982). A greater abundance and diversity of large prey or non-prey could further reduce feeding rates even on small edible prey via interaction modification (Kratina et al. 2007).

Effects of habitat size at sites with odonates

Our results suggest that bromeliad-inhabiting invertebrate communities were more strongly controlled top-down at sites where odonates are present in the regional species pool. There was a strong effect of habitat size on odonate presence in individual bromeliads at these sites. Those highly mobile large predators are not expected to experience dispersal limitation at the spatial scales in our study (Córdoba-Aguilar 2008) and hence, were probably not influenced by habitat size per se in the colonization process. Instead, it is likely that a higher risk of drought or other external factors that cause harsher, more variable conditions in smaller bromeliads make them an unsuitable habitat for odonates, which have very long larval periods. These conditions might negatively affect oviposition decisions or survival beyond early life-history stages (top-down forcing sensu Heath et al. [2013]). Pimm and Kitching (1987) showed for artificial tree holes that

disturbance rather than resources controlled food chain length, i.e., the presence of predators.

Odonates have large per capita biomass and contribute a major proportion of the total predator biomass in bromeliads. Thus they play an important role simply by dominating the predator level. Their high energy requirements lead to a strong top-down pressure, dramatically affecting detritivore abundance, via a dominance rather than a strict keystone effect (Power et al. 1996). Odonates are generalist feeders and as such depend less on the presence of specific prey species (Schowalter 2006). Thus, they could be more tolerant to changes in habitat size in terms of feeding requirements. They do, however, show a certain preference for larger organisms (Fincke et al. 1997, Yanoviak 2001), which are expected to occur more frequently in larger habitats. Per capita biomass of detritivores does not increase along the habitat-size gradient at the sites with odonates, likely because there is no effective size refuge from odonate predation. The sit-and-wait hunting mode of odonates makes them relatively independent of habitat complexity changes per se (as shown, e.g., by Srivastava 2006). However, in contrast with other predators in bromeliads, they show a more amphibious lifestyle (Lounibos et al. 1987) and can move across compartment boundaries within bromeliads. This ability and a potential effect of detritivore mobility could have resulted in the benefit of lower complexity in large bromeliads.

What can we learn from bromeliads?

The strong response of odonates to habitat size is likely driven by habitat-size-dependent colonization as well as extinction processes. However, comparable to other large, mobile-species-coupling communities in patchy systems (Rooney et al. 2008) this habitat-size effect on their occurrence is strongly influenced by movement decisions (in this case oviposition decisions by the adult) in anticipation of habitat suitability. This process is different from mere random habitat-size-related colonization events as envisioned by MacArthur and Wilson (1963, 1967), however, it may result in the same pattern. Examples of comparable naturally patchy, temporal systems that are connected by the dispersal of highly mobile species are other phytotelmata such as mosquito-inhabited water-filled tree holes (Yee et al. 2007) or

Sarracenia plants (Kneitel and Miller 2003) and related artificial container systems (Kneitel and Chase 2004), temporary ponds with odonates (Urban 2004), and mushrooms that are colonized by flies and their staphylinid predators (Stahls et al. 1989). Highly topical evidence regarding the relationship of habitat size and extinction risk comes from anthropogenically fragmented habitats, from which predators are often the first species to disappear, a process that is additionally accelerated by overexploitation (Strong and Frank 2010). As a result, trophic cascades and other structural changes are possible, which have, for example, been described for tropical forest fragments (Laurance et al. 2011), man-made islands (Terborgh et al. 2001), and patchy agricultural landscapes (Kruess and Tschardt 1994).

Where large, mobile predators with small productivity:biomass ratios couple with patchy habitats, they may exert disproportionately strong top-down effects on other parts of the food web and change trophic structure along the habitat-size gradient to the point where biomass pyramids become inverted, as in our case. These types of trophic pyramids have also been reported from coral reefs. Here, the large biomass of sharks as the top predators can likely be explained by their use of multiple habitats and resources (Trebilco et al. 2013). Other top-heavy pyramids have been associated with low habitat heterogeneity (Tunney et al. 2012) and experimental warming (Shurin et al. 2012). Systems that are heavily subsidized with allochthonous material such as plankton communities in lakes have also been reported to be characterized by inverted trophic relationships, at least at lower trophic levels (del Giorgio and Gasol 1995). However, a likely explanation is that the subsidies were not included in estimates of autotroph biomass (del Giorgio and Gasol 1995, Trebilco et al. 2013). In contrast, in our study, we only considered detrital (allochthonous) resources but not autochthonous ones such as algal production, possibly inflating our detritivore:resource ratios. The higher nutrient content of algae as compared to detritus may in fact support insect consumers that grow and emerge quickly. For bromeliads in sun-exposed habitats, high turnover rates of mosquitoes as prey species have been suggested as an explanation for inverted pyramids (Omena 2014). Food-web models indicate that top-heavy trophic pyramids are inherently unstable because energy flows through the trophic levels more rapidly, increasing the variability in population dynamics (Rip and McCann 2011). Further studies are needed to experimentally test the relationship between trophic structure and stability in bromeliad and other systems.

Recent work has emphasized the important role of odonates for ecosystem processes and functions in bromeliads, for example, for decomposition rates (LeCraw 2014) and carbon (Atwood et al. 2013, 2014) and nitrogen dynamics (Ngai and Srivastava 2006). Evidence is also accumulating from other aquatic systems that far-reaching consequences of predator loss for whole-system element cycling may occur (Wilmers et

al. 2012, Jabiol et al. 2013). Furthermore, Staddon et al. (2010) showed for a fragmented moss system that predators could not persist in small fragments, and their loss caused carbon and nitrogen dynamics to change as a consequence of trophic cascades.

By analyzing the trophic structure of 651 natural bromeliad communities from eight sites across Central and South America, we demonstrate that habitat size has strong and pervasive effects on detritivore:resource biomass ratios. However, the presence of a dominant, mobile, large-bodied predator species in the regional pool is critical in mediating the direction and strength of the effect of habitat size on predator:detritivore biomass ratios. Our results show that species with certain traits have the potential to fundamentally alter responses of communities to habitat size in patchy environments, suggesting that we need to consider species identity and trophic structure to grasp the full impact of habitat modifications on communities and their functions (Dobson et al. 2006, Tylianakis et al. 2007).

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SUPPLEMENTAL MATERIAL

Ecological Archives

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