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Why Are Predators More Sensitive to Habitat Size than Their Prey? Insights from Bromeliad Insect Food Webs

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abstract: Ecologists have hypothesized that the exponent of species-area power functions (*z* value) should increase with trophic level. The main explanation for this pattern has been that specialist predators require prior colonization of a patch by their prey, resulting in a compounding of the effects of area up trophic levels. We propose two novel explanations, neither of which assumes trophic coupling between species. First, sampling effects can result in different *z* values if the abundances of species differ (in mean or evenness) between trophic levels. Second, when body size increases between trophic levels, effects of body size on *z* values may appear as differences between trophic levels. We test these alternative explanations using invertebrate food webs in 280 bromeliads from three countries. The *z* value of predators was higher than that of prey. Much of the difference in *z* values could be explained by sampling effects but not by body size effects. When damselflies occurred in the species pool, predator *z* values were even higher than predicted, as damselflies avoid small, drought-prone bromeliads. In one habitat, dwarf forests, detrital biomass became decoupled from bromeliad size, which also caused large trophic differences in *z* values. We argue that there are often simpler explanations than trophic coupling to explain differences in *z* values between trophic levels.

Keywords: species-area relationship, trophic rank hypothesis, phytotelmata, incidence functions, predation.

One of the oldest and most general observations in ecology is that larger areas contain more species (Williams 1943; Rosenzweig 1995). Traditionally, ecologists have been interested in the broad similarity of species-area relationships among studies, as this suggests a common mechanism (Connor and McCoy 1979; Rosenzweig 1995). More recently, ecologists have gained insight from the differences among species-area relationships, particularly why patterns differ with evolutionary history (Ricklefs and Bermingham 2004), landscape change (intact vs. fragmented; Gonzalez 2000), human disturbance (fished vs. unfished; Tittensor et al. 2007), and spatial context (nested vs. independent samples; Hoyle 2004; Drakare et al. 2006). In this article, we address a relatively new question: why might species-area relationships differ between trophic levels?

The trophic rank hypothesis (TRH) predicts that the area dependence of species will increase with trophic level because of trophic dependencies between predators and their prey (Holt et al. 1999; Holt and Hoopes 2005). According to the TRH, predators are affected by area in two ways. First, predators and prey are both affected by correlations of patch area with immigration rates, habitat heterogeneity, and demographic stochasticity. However, predators have an additional and indirect constraint of area on their persistence: a predator can persist only in a patch, most likely a large patch, that is already occupied by its prey. Thus, the effects of area multiply up trophic levels. This formulation of the TRH applies primarily to stacked specialist food webs.

More recently, the hypothesis has been expanded to include general effects of prey diversity on predators. Holt and Hoopes (2005) argue that, because larger patches have more diverse prey communities, such patches may provide a greater quantity or reliability of prey biomass for pred-

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ators. Diverse prey communities could also be more nutritionally balanced for predators (DeMott 1998). However, a multitrophic model (Thébault and Loreau 2003) and manipulations of multiple trophic levels (Fox 2004; Gamfeldt et al. 2005) suggest that positive effects of prey diversity on predator consumption rates occur only when all prey species are edible and consumers are specialists. Otherwise, if prey experience a trade-off between growth and resistence to consumption, high-diversity prey communities under predation will likely be dominated by inedible, slow-growing prey species (Leibold 1989; Thébault and Loreau 2003). Predators may also be less efficient at exploiting specific prey in diverse prey communities (Root 1973; evidence reviewed by Duffy et al. [2007]). Indeed, a meta-analysis of algae-herbivore systems shows that grazing is generally reduced at high algal diversities (Hillebrand and Cardinale 2004). Thus, the generalized version of the TRH proposed by Holt and Hoopes (2005) may apply only under certain conditions.

The few empirical studies that have separated species-area relationships by trophic level have found contradictory patterns. Holt et al. (1999) described several data sets that suggest that predators have higher *z* values than their prey, where *z* is the exponent of the power function between species richness (*S*) and area (*A*): $S = cA^z$. Hoyle (2004) examined species-area relationships of microarthropods in moss patches and found carnivorous mites (pooled over several trophic levels) to have higher *z* values than herbivorous and detritivorous mites. By contrast, in a meta-analysis of species-area relationships, Drakare et al. (2006) found no difference in *z* values between trophic levels.

However, even if *z* values did consistently increase with trophic level, this is not proof of the TRH if other mechanisms also predict this pattern. In this article, we first present a null model of how sampling a community can lead to higher *z* values for predators than for prey, and then we discuss how body size can lead to similar patterns. We then use insect food webs to empirically distinguish between these hypotheses.

Sampling Effects

We propose a null model for differences in *z* values between trophic levels on the basis of sampling effects. Suppose patch colonization can be approximated by a random draw from a regional pool of individuals. We show that, in this case, any differences between trophic levels in either the mean or the distribution of the regional abundances of species will likely result in differences in *z* values, even in the absence of interactions between species. This explanation serves as a null model for the TRH because it assumes that the occurrence of a predator species is completely independent of the occurrence of its prey.

In our model, random colonization of patch *i* occurs until the patch is saturated with individuals. Like most species-area models, we assume that the saturated number of individuals in the patch, n_i, is proportional to the area of patch, a_i. If the regional abundance of individuals is much larger than the number found in any patch, then the composition of any patch can be approximated by sampling with replacement from the regional distribution of individuals. The probability of selecting an individual from trophic level *x* is then simply equal to the proportion of individuals in the regional pool belonging to that same trophic level. The latter quantity is related to the number of species in the regional pool of trophic level *x* (S_x) and the mean regional abundance of those species ($\overline{N}_x$). Thus, after random colonization of the patch, the total number of individuals in patch *i* from trophic level *x*, n_{xi}, is expected to be

$$n_{xi} = \frac{s_x \overline{N}_x}{\sum_{j=1}^{t} s_j \overline{N}_j} a_i k, \qquad (1)$$

where *t* trophic levels are represented in the regional pool and *k* is a constant reflecting the maximum number of individuals per unit area. The number of species of trophic level *x* in patch *i*, s_{xi}, is determined by both n_{xi} and the species accumulation function $g(n_x)$ for each trophic level (i.e., a function that predicts the number of species of trophic level *x* represented by n_x individuals of that trophic level who are randomly sampled from the regional pool):

$$s_{xi} = g(n_{xi}). \qquad (2)$$

The precise form of $g(n_x)$ will depend on the exact regional species abundance distribution for trophic level *x* (Preston 1960; May 1975), but in general it will approach an asymptote (equal to S_x) at a rate determined by the evenness of abundances for that trophic level (Olszewski 2004).

Thus, s_{xi} is ultimately determined by the combination of equations (1) and (2). Because both equations are affected by at least some components of regional species abundance distributions for each trophic level (mean species abundance, number of species, and evenness of abundances), any difference between trophic levels in these components is likely to result in differences in how s_{xi} scales with patch area and, hence, different *z* values for species-area relationships. We illustrate this point by simulating colonization of patches by two groups of species, with the ranked abundance of species in each regional pool following a geometric distribution. Groups with either lower

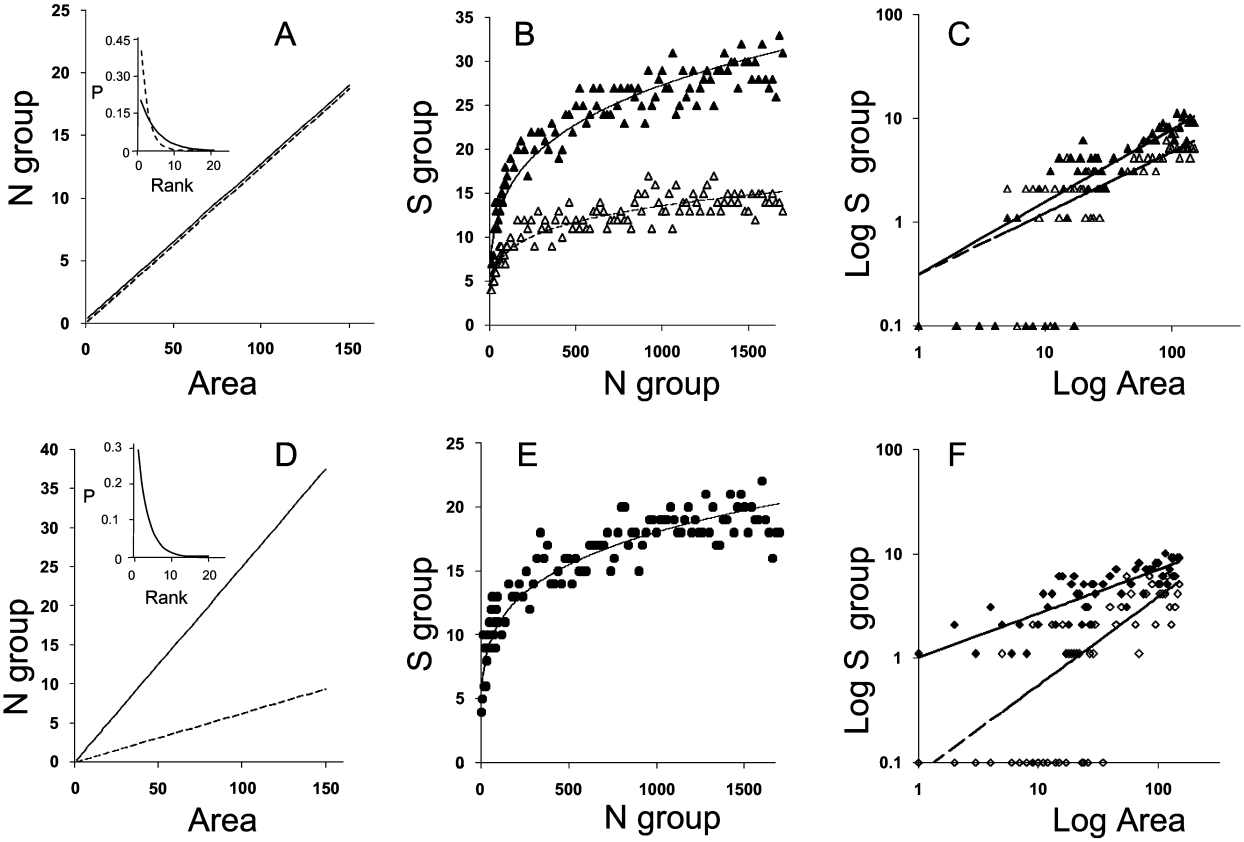

Figure 1: Relationship between species abundance, species accumulation functions, and species-area functions for two groups of species (e.g., predators and prey). Groups with the same regional species abundances (*A*) but different species accumulation curves (*B*) have different species-area slopes but similar intercepts (*C*). Groups with different abundances (*D*) but similar species accumulation curves (*E*) have different species-area slopes and intercepts (*F*). The species accumulation curves in *B* and *E* are power functions fitted to random draws from the inset rank-abundance curves, which follow a geometric distribution, $P(\text{rank}) = p(1-p)^{(\text{rank}-1)}$, where P is the abundance of a species as a proportion of total abundance (*A–C*, *solid line*, $P = .2$; *dashed line*, $P = .4$; *D–F*, $P = .3$). Both groups have a species pool of 50 species. Data for the species-area relationships were simulated by assuming that the number of individuals for a given area is a Poisson-distributed random variable and by randomly drawing each individual from the appropriate rank-abundance curve.

regional abundance or greater evenness have higher z values (fig. 1).

Body Size Effects

In many systems, predators are larger bodied than their prey and body size may itself affect z values. A recent meta-analysis found higher z values for communities composed of larger organisms in several types of species-area relationships (Drakare et al. 2006), a trend the authors attributed to the lower dispersal rates of large organisms. Similar differences in z values are reported for birds and mammals on islands (Matter et al. 2002). The authors attributed this pattern to smaller species being more sensitive to environmental fluctuations. Thus, differences in z values between predators and prey may ultimately be the result of differences in body size. This explanation is mechanistically incomplete in that it does not explain why predators are larger than their prey. Nonetheless, it is distinct from the TRH, as it requires no trophic coupling between particular predator and prey species.

Bromeliad Insect Food Webs

We examine trophic level differences in local species-area relationships using 280 bromeliad insect food webs collected in different forest types within three Caribbean countries. Bromeliads are Neotropical plants composed of a rosette of elongate leaves. We studied species where the leaf axils collect both rainwater and fallen detritus. The detritus forms the basal resource for an aquatic food web consisting of detritivorous and predatory invertebrates (mainly insect larvae but also annelids, ostracods, and mites; Richardson 1999; Armbruster et al. 2002; Srivastava 2006). In the forest bromeliads described here, algal production is negligible. Although there is some intraguild predation, the diet of all predators is dominated by detritivores, leading to an aquatic invertebrate food chain of essentially two trophic levels (D. Srivastava, unpublished stable isotope analysis). We use data from bromeliads varying by four orders of magnitude in size to examine differences in z values between trophic levels. By examining large numbers of similar food webs obtained with identical methodology, we are able to conduct powerful tests for effects of trophic levels on species-area relationships in this particular habitat.

We begin our analysis of mechanisms by noting that bromeliad insects do not conform to the stacked specialist food webs required in the original formulation of the TRH (Holt et al. 1999). Predators in phytotelm insect food webs are almost always facultatively generalist (Kitching 2000), as supported by our own observations of bromeliad insects. In this article, we ask whether observed differences in z values between trophic levels can be explained by either sampling effects or body size effects.

Methods

Data Collection

We completely censused insects in 280 bromeliads from forests in Costa Rica (60 bromeliads), Puerto Rico (190 bromeliads), and Dominica (30 bromeliads). In Costa Rica, bromeliads were collected from a premontane tropical moist forest near Estación Biológica Pitilla in the Área de Conservación Guanacaste (10°59′N, 85°26′W; 700 m elevation). This forest contains both primary forest, with large trees and dense canopy cover, and regenerating secondary forest (recent to ~80 years old), with more light and smaller trees (see Srivastava et al. 2005 for details). Bromeliads were collected in 1997 in both primary and secondary forest ($n = 22$), in 2000 in primary forest ($n = 20$), and in 2002 in secondary forest ($n = 18$).

In Puerto Rico, bromeliads were collected from three forest types in the Luquillo Experimental Forest (18°20′N 60°50′W) over an elevational gradient: tabonuco forest (TF; a lower montane rain forest; <600 m elevation), palo colorado forest (PC; montane rain forest; 600–900 m elevation), and dwarf forest (DF; 900–1070 m elevation). Bromeliads were collected in 1993 ($n = 20$ per habitat), 1994 ($n = 20$ per habitat), and 1996 ($n = 20$ for TF and DF; $n = 10$ for PC). In 1997, bromeliads were collected only in TF ($n = 10$) and PC ($n = 10$; for further details, see Richardson 1999; Richardson et al. 2000).

In Dominica, bromeliads were collected in 2002 from three habitats ($n = 10$ per habitat): TF on Morne Trois Pitons (15°24′N, 61°18′W; 775–850 m elevation), mid-elevational montane thicket at Boeri Lake (15°24′N, 61°18′W; 800–850 m elevation), and DF on Morne Diablotins (15°30′N, 61°24′W; 1100–1160 m elevation).

We standardized our field methods between sites. In all cases, we carefully dissected each bromeliad leaf by leaf and washed the detritus into white trays. Bromeliad water and detritus were searched thoroughly for insects and other invertebrates (e.g., large mites and annelids) that were visible to the naked eye. We restricted our analysis to insects found exclusively in the aquatic or semiaquatic (moist detritus) regions of the bromeliad, as terrestrial insects probably have limited interactions with aquatic insects in bromeliads. Insects were identified to the species or morphospecies level, and abundance was recorded. We separated insects into trophic levels, using published literature about various groups and our own field observations. We considered detritivores to be the lowest trophic level and their predators to be the second trophic level.

Bromeliads provide three-dimensional, rather than two-dimensional, habitats for insects. Therefore, bromeliad size was estimated not as an area but as a volume (the maximum water-holding capacity of the plant in mL); in addition, we estimated the total mass of contained detritus (g dry mass). Detrital mass is often considered to be an estimate of total energy in phytotelm studies (e.g., in treeholes; Srivastava and Lawton 1998), but in bromeliads, the distinction between total energy and habitat size is often trivial: the amount of detritus is generally proportional to volume (power function exponent ± SE = 1.01 ± 0.16, where 1 represents perfect proportionality, $r = 0.83$, $n = 20$ Costa Rican bromeliads). Detritus creates a structural habitat for insects by providing refuges from predation and interference competition, so it is arguably a measure of habitat size as much as it is of productivity (see also Richardson 1999). We did not have measurements for both volume and detrital mass for all bromeliads from all sites, but we estimated the missing data from other size-related data. Specifically, in Costa Rica, we converted some measurements of mass of detritus >150 μm into total detrital mass (calibration regression $r^2 = 0.98$, $n = 25$ Costa Rican bromeliads), and in Puerto Rico we converted measurements of bromeliad width and leaf number into volume ($r^2 = 0.75$, $n = 10$).

Patterns in Species-Area Relationships

We first examined whether species-area relationships differed between trophic levels. We used a generalized linear mixed model (GLMM) to determine the effects of bromeliad size and trophic level on species richness in bromeliads located in nine habitats in three countries. Observations of richness (y_{ijk}) were assumed to follow a Poisson distribution:

$$y_{ijk} \sim \text{Poisson}(\mu_{ijk}).$$

Our model of linear predictors was

$$\eta_{ijk} = \beta_0 + \beta_1 \text{TL} + \beta_2 \log(\text{size}) + \beta_3 \text{TL} \times \log(\text{size}) + b_{j(i)} + b_i,$$

where $i = 1$–3 countries, $j = 1$–3 habitats, $k = 1$–n plants; where TL = trophic level and size = bromeliad size measured as volume or detrital mass; and where the function $\log(\mu_{jik}) \sim n_{ijk}$ links the model to the data. All logarithms are base *e*. We viewed both habitat and country as random effects, because both were rather arbitrarily (as far as this analysis is concerned) selected from a larger pool of possible habitats and countries. The values $b_{j(i)}$ and b_i are assumed to be independent random variables with $N(0, \sigma^2_{j(i)})$ and $N(0, \sigma^2_i)$. For simplicity, we refer to this as a species-area relationship, although it is more accurately described as a species–habitat size relationship. A significant interaction term between trophic level and bromeliad size indicates a change in the species-area relationship with trophic level.

Because only the Puerto Rico data set examined the same habitat over multiple years, we could not directly include year in the mixed model; instead, we removed year effects from the Puerto Rico data by adjusting all data to correspond to year 1993. Specifically, we modeled log species richness for each habitat as a function of log size, year, and the log size × year interaction. For all habitats, the log size × year interaction was nonsignificant, which allowed us to adjust log species richness in each year to 1993 values by simply subtracting the difference between the intercepts for that year and those for 1993.

Tests for Sampling Effects

We first examined whether predator species were different from prey species in either mean or evenness of their regional abundances. We tested for differences in regional abundance between predator and prey species using a GLMM (log link, Poisson errors) with trophic rank as a fixed factor and country as a random factor. The regional abundance of each species was estimated by summing its abundance over all bromeliads collected within each country (all habitats) and was log transformed before analysis. Evenness was estimated using Pielou's *J*, bootstrapped to obtain 95% confidence intervals (CIs; Pielou 1975).

We used the null model presented above to simulate species colonization as a random process (i.e., species occur independently of each other) that is dependent only on the regional abundance of species (regionally abundant species are more likely to colonize a bromeliad than are rare species) and the size of the bromeliad (large bromeliads experience more colonization events). The regional abundance of each insect species was calculated by pooling all individuals found in bromeliads in each habitat of each country. We assumed that the probability of a species colonizing a bromeliad was proportional to its regional abundance. Each bromeliad was randomly repopulated with individuals from the regional pool until the original total number of individuals was reached. Previous research shows that the total number of individuals in a bromeliad is determined largely by bromeliad structure and size (e.g., Richardson 1999; Srivastava 2006), and thus we view it as a fixed property of the bromeliad. For each run of the simulation, species richness in all bromeliads was plotted against bromeliad size as estimated by either volume or total detrital mass, and differences in predator and prey *z* values were determined. The simulation was repeated 1,000 times with replacement. We then compared predicted differences in *z* values between predators and prey as generated by the null model with observed differences to determine whether random colonization was sufficient to explain the observed patterns.

Our null model can be visualized as a matrix of species (rows) × bromeliads (columns), with cells consisting of the abundance of species *i* in bromeliad *j*. We randomized this matrix, keeping both the row totals (regional abundance of *i*) and the column totals (total number of individuals in *j*) constant. A very similar type of matrix, with presence rather than abundance data, has been widely used to test for species co-occurrence patterns (Connor and Simberloff 1979; Gotelli and Graves 1996). For co-occurrence patterns at least, Gotelli (2000) recommends the use of this type of model for data from variably sized islands, as he found it to be the most resistant to Type I error. Bromeliads are essentially aquatic islands that vary in size.

Tests for Body Size Effects on Incidence

To examine effects of body size on *z* values, we could have categorized species as large-bodied or small-bodied taxa. However, because body size is a continuous variable, such a division would be arbitrary and would reduce the power of the analysis. Instead, we examined correlations between body size and parameters of species' incidence functions that are known to be mathematically linked to *z* values. The incidence function of a species can be characterized by two parameters originating from a logistic regression of incidence on habitat size (nomenclature follows Cook and Hanski 1995): A^* is the habitat size with 50% likelihood of occurrence and x_i is the sensitivity of occurrence

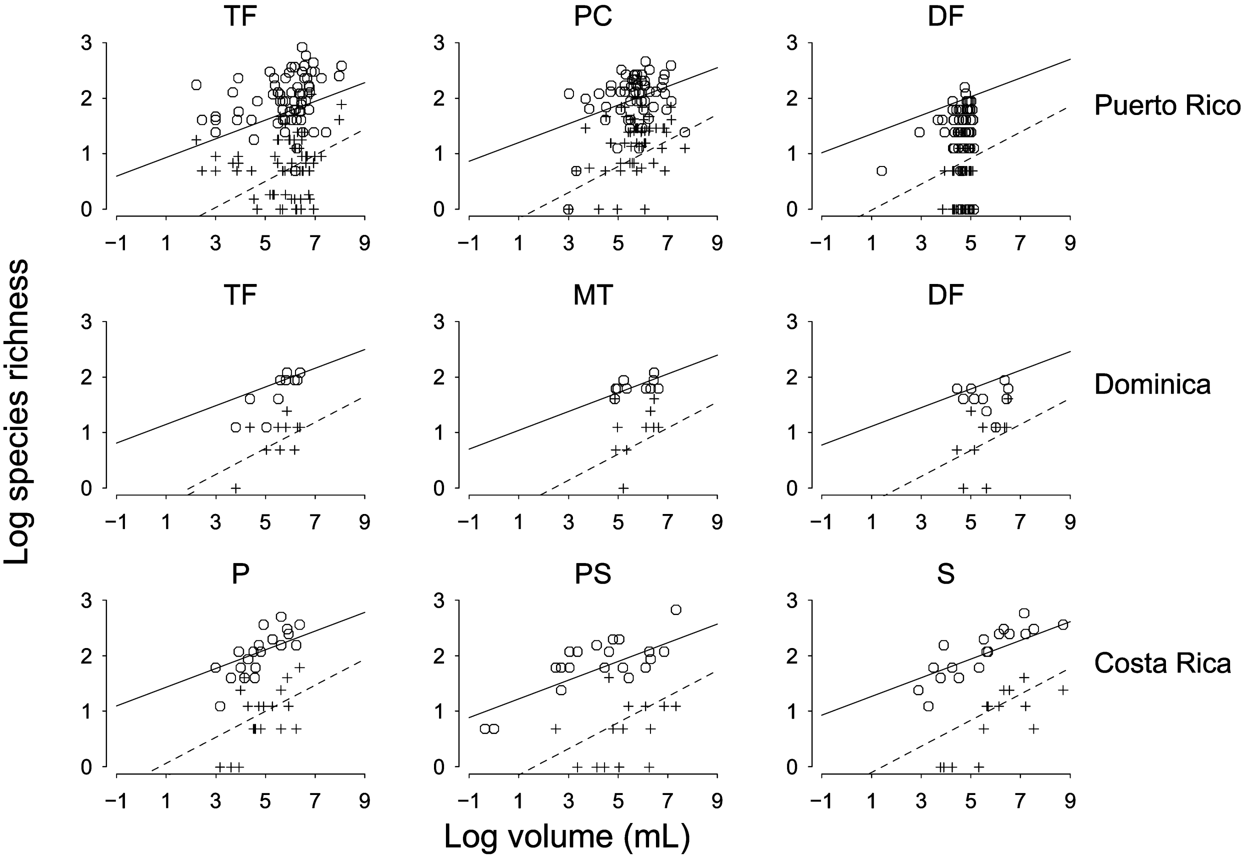

Figure 2: Relationship between bromeliad size (as estimated by volume in mL) and species richness of macroinvertebrate detritivores (*circles*) and predators (*plus signs*). A single mixed-effect model was fitted to all nine data sets (predators, *dashed line*; detritivores, *solid line*); intercepts but not slopes of these regression lines differ between the nine data sets. *TF* = tabonuco forest; *PC* = palo colorado; *DF* = dwarf forest; *MT* = midelevational montane thicket; *P* = primary forest; *PS* = mixed primary and secondary forest; *S* = secondary forest.

of species i to habitat size (i.e., slope of the logistic function). Higher z values are expected when either individual x_i values increase or the exponential distribution of A^* values in the community has lower variance (i.e., higher values of rate parameter λ; Ovaskainen and Hanski 2003).

We calculated incidence functions for all species in two contrasting data sets (secondary forest in Costa Rica and PC in Puerto Rico) to explore how body size and abundance correlate with incidence. Incidence functions were modeled as generalized linear models (GLMs) with binomial errors and a logit link function, using both log bromeliad volume and log detrital mass as measures of habitat size. In the Puerto Rico model, year effects were incorporated as different intercepts and the 1993 intercept was used to estimate A^*. We could not compute incidence functions for species with less than three occurrences or when our maximum likelihood models failed to converge, with the result that incidence functions were calculated for 53 of the 104 species in the two data sets.

Results

Bromeliad volume and detrital mass were both strong predictors of species richness (volume: $F = 118.6$, df = 1,548; detrital mass: $F = 149$, df = 1,548; $P < .0001$ for both). Overall, z values differed between trophic levels (fig. 2) whether bromeliad size was measured as volume (trophic level × volume: $F = 4.01$, df = 1,548, $P = .046$) or detrital mass (trophic level × detrital mass: $F = 8.18$, df = 1,548, $P = .004$). Predicted z values for predators (volume based, 0.234; detrital mass based, 0.293) were substantially higher than those for prey (volume based, 0.168; detrital mass based, 0.197). Individual bromeliads generally had fewer predator species than prey species (trophic level: $F = 740$ and $F = 746$ for volume and detrital-mass models, respectively, df = 1,548, $P <$ .0001; fig. 2).

Can Sampling Effects Explain the Pattern?

Predator species tended to have lower regional abundances than prey species (GLMM, $F = 5.53$, $\text{df} = 1, 129$, $P = .02$; fig. 3). Regional evenness, as estimated by Pielou's J, was similar between trophic levels (bootstrapped 95% CIs overlap). We investigated whether differences in z values between predators and prey were simply due to sampling effects coupled with this difference in regional abundance. Random assembly simulations predicted higher z values for predators than for prey in all nine data sets when volume was used as a measure of habitat size and in eight of the nine data sets when detrital mass was used as a measure of habitat size (table 1). The observed differences in z values between predators and prey were not significantly different from the random assembly simulations in most data sets, with the following exceptions. In the Costa Rica data set, the difference in predator versus prey z values was substantially higher than predicted from the simulations of the secondary forest data set and the mixed forest data set but not the primary forest data set (with habitat size measured as either volume or detrital mass; table 1). The two DF data sets also had greater trophic level differences in z values than was predicted from simulations but only when habitat size was estimated as volume, not detrital mass (table 1).

Does Incidence Correlate with Trophic Rank or Body Size?

We compared incidence parameters between predators and prey in one data set showing a greater effect of trophic level on z values than was predicted by sampling effects (secondary forest in Costa Rica) and in one data set showing differences in z values consistent with sampling effects (PC in Puerto Rico). In the Costa Rica data set, the average x_i value of predators was one to two orders of magnitude higher than that of prey (table 2). Much of this difference was due to the influence of one predatory species, *Mecistogaster modesta*, which was an extreme outlier in the otherwise normal distribution of x_i values (fig. 4). This predatory damselfly switched abruptly from 0% occupancy to near 100% occupancy at a volume of about 138 mL (4.8 g detrital mass). In contrast, x_i values were similar between predators and prey in the Puerto Rico data set (table 2). Only A^* values based on volume in the Costa Rica data set fitted an exponential distribution (Kolmogrov-Smirnov test on prey: $P = .24$; on predators: $P = .36$), and in this data set, the exponential rate parameter λ did not significantly differ between prey ($\lambda = 0.135$, 95%CI $= 0.081$, 0.21) and predators ($\lambda = 0.185$, 95%CI $= 0.046$, 0.480).

The body mass of species did not correlate with either incidence parameter, in either data set, using either volume or detrital mass as an estimate of bromeliad size ($-0.25 < r < 0.14$, $P > .2$). Body size did not differ significantly between trophic levels in either Costa Rica (quasi-likelihood GLM, $P = .45$) or Puerto Rico ($F = 0.13$, $\text{df} = 1, 37$, $P = .72$).

Discussion

Overall, predator diversity was more affected by bromeliad size than prey diversity was. This increase in z values with trophic rank is consistent with the TRH. However, it is likely that bromeliad insects do not conform to the stacked specialist food webs (see the introduction to this article), which is required in the original formulation of the TRH (Holt et al. 1999). In this article, we ask whether TRH

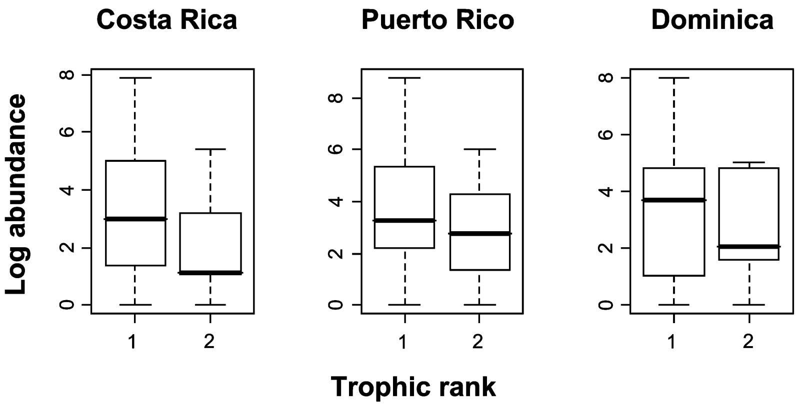

Figure 3: Box plots of the regional abundance (log transformed) of prey (trophic rank = 1) and predators (trophic rank = 2) in bromeliads in three countries. Box plots illustrate the median (*line*), the interquartile range of the data (*box*), and the tails of the distribution (bars = 1.5 × interquartile range).

Table 1: Observed and simulated differences in z values between predators and prey and the probability that observed differences are greater than simulated mean differences by chance

	Volume			Detrital mass		
Country, habitat	Observed	Simulated	P	Observed	Simulated	P
Costa Rica:						
P	.138	.332	.95	.214	.223	.54
PS	.133	.053	.047	.157	.064	.030
S	.192	.063	.011	.234	.071	.006
Puerto Rico:						
TF	−.052	.099	.99	−.074	.117	.99
PC	.072	.068	.48	.098	.080	.39
DF	.438	.014	.003	.046	.0001	.28
Dominica:						
TF	−.089	.046	.82	−.739	.0262	.99
MT	.087	.131	.61	−.086	.113	.97
DF	.258	.006	.019	−.022	−.0054	.54

Note: Simulations for nine data sets are based on random assembly of individuals in bromeliads from the regional pool, irrespective of trophic requirements. P = primary rainforest; PS = mixed primary and secondary rainforest; S = secondary rainforest; PC = palo colorado; DF = dwarf forest; TF = tabonuco forest; MT = midelevational montane thicket.

processes are needed to explain trophic-level differences in z values or whether simpler explanations based on sampling effects or body size would suffice.

Sampling Effects

When mean abundance per species or species evenness differs between any two groups of species (e.g., predators and prey), our simulation results (fig. 1) show that simple sampling effects can result in a difference in z values. In the case of bromeliad insects, sampling effects are predicted to result in higher z values for predators than for prey in almost all data sets, likely as a result of the lower regional abundance of predator species than prey species. Evenness was broadly similar among trophic levels, so it may have been less important in causing sampling-based differences in z values. Colonization of bromeliads by insects may be usefully approximated by a random assembly process from the region, because all propagules arrive from outside the bromeliad (i.e., oviposition by terrestrial adults) rather than from within. Annelids, ostracods, and mites have within-bromeliad population dynamics but account for a very small percentage of individuals.

Most of the observed differences between predator and prey z values were comparable to those predicted simply by sampling effects. This suggests that the most parsimonious explanation for observed z value differences need not include information on predator-prey interactions or species differences in colonization. However, four data sets had large differences between predator and prey z values, beyond those predicted by sampling effects: two data sets that included bromeliads from Costa Rica secondary forest and two data sets of bromeliads from high-elevation DF.

We begin by examining the results from the Costa Rica secondary forest. Predator species in this forest tended to have different incidence functions than prey species, notably having higher x_i values (i.e., they were more sensitive to bromeliad size), but had similar clustering of A^* values. All else being equal, high x_i values correspond to high z values (Ovaskainen and Hanski 2003). This difference in x_i value was due to a single predator species, *Mecistogaster modesta*, whose occupancy switched abruptly from near 0% in bromeliads with volumes of <138 mL to near 100% in larger bromeliads. It is not surprising that the effect of *M. modesta* is limited to Costa Rica secondary forest: in Costa Rica, secondary-forest bromeliads have much higher abundances of damselfly larvae than do primary-forest bromeliads (Srivastava et al. 2005). Damselflies do not occur in either the Puerto Rico or the Dominica bromeliads.

Even in the case of *M. modesta*, we doubt that its high x_i value conforms to the stacked specialist food webs required in the original formulation of the TRH (Holt et al. 1999). *Mecistogaster modesta* consumes virtually all possible prey species that are smaller in body size (D. S. Srivastava, unpublished feeding trials and fecal dissections). The sharp threshold in the incidence of *M. modesta* is related instead to adult damselfly behavior. Male damselflies obtain matings by defending bromeliads (typically only those >100 mL volume). Females oviposit primarily in bromeliads >100 mL in volume (D. S. Srivastava and J. T. Ngai, unpublished data). These adult preferences for

Table 2: Comparison of the incidence function parameter x_i between predator and prey species for two data sets

	Costa Rica secondary rainforest				Puerto Rico palo colorado			
Mean x_i	Predators	Prey	F^a	P	Predators	Prey	F^b	P
Volume based	19.1 ± .6	.94 ± .02	7.73	.012	5.89 ± .81	.38 ± .03	.37	.55
Detrital mass based	94.2 ± 3.1	.83 ± .01	7.73	.012	.95 ± .02	.84 ± .04	.02	.88

Note: See "Methods" for the definition of x_i. Differences in mean values were tested with quasi-likelihood generalized linear mixed models.

[a] df = 1, 18.

[b] df = 1, 31.

large bromeliads likely reflect the drought risk associated with small bromeliads. *Mecistogaster modesta* larvae must remain in bromeliads for several months before pupation, which can extend the larval stage into the dry season (D. S. Srivastava, personal observation). This contrasts with larval durations of 2–6 weeks for common detritivores such as chironomid, tipulid, and mosquito larvae (D. S. Srivastava and B. A. Richardson, personal observation).

The sensitivity of *M. modesta* to bromeliad size may represent a more general pattern of predator sensitivity to disturbance associated with small habitat size. For example, in the Bahamas, hurricane risk for animals is greatest on small islands (Schoener et al. 2001). The top predators on these islands—lizards, spiders, and parasitoids—are much more affected by hurricanes than are their herbivore prey (Spiller and Schoener 2007). In West African reserves, extirpation rates of large mammals through hunting are higher on small reserves, and this reserve size effect is stronger for carnivores compared with herbivores (Brashares et al. 2001).

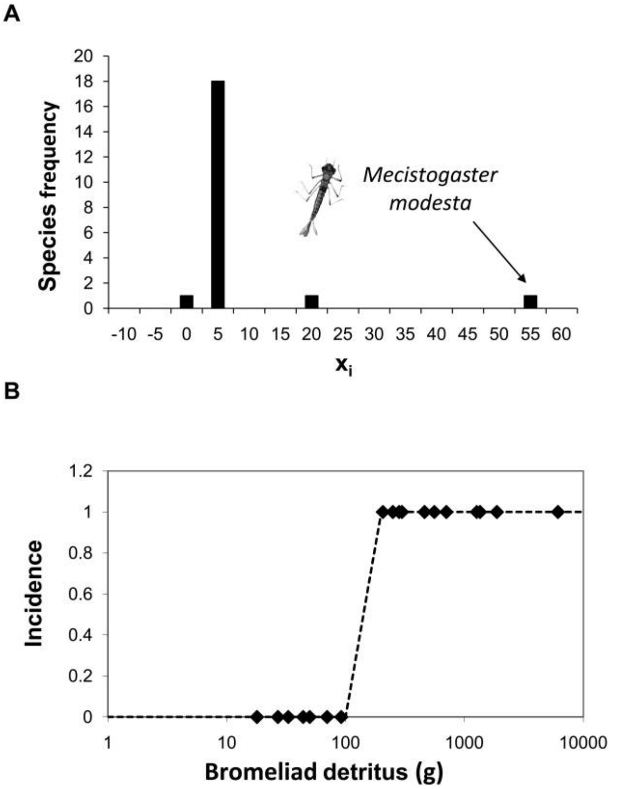

Figure 4: *A*, Distribution of x_i values, based on bromeliad volume, for all macroinvertebrates with >2 occurrences in bromeliads in Costa Rican secondary forest, in 2002. The outlier is identified as the damselfly *Mecistogaster modesta*. *B*, Incidence function for *M. modesta* from the same data set (*symbols*, observed incidence; *dotted line*, fitted incidence function).

In most data sets, observed and simulated z values based on bromeliad volume were generally similar to those based on bromeliad detrital mass. The exceptions were the two DF data sets, where trophic differences in z values based on volume—but not on detrital mass—were significantly greater than those predicted from sampling effects. In DFs, detrital mass is uncorrelated with bromeliad volume (Puerto Rico, $r = 0.14$, $P = .14$; Dominica, $r = 0.08$, $P = .83$), unlike the other seven data sets ($0.57 > r > 0.94$, $P < .026$). This pattern may reflect stochasticity in litter entrapment by DF bromeliads due to high wind disturbance and uneven canopy cover coupled with low rates of litterfall (Richardson 1999). In both DFs, detritivore z values were higher for detrital mass than for bromeliad volume, whereas the reverse was true for predator z values. This suggests that, at least in DFs, detritivore richness tends to track detrital resources, whereas predator richness tends to track bromeliad water capacity. Many predators characteristic of low-elevation bromeliads are missing in impoverished DF bromeliads (Richardson 1999). Instead, the dominant predators are corethrellids (Richardson 1999), which largely prey on mosquitoes in the water column and thus may be particularly sensitive to bromeliad volume.

Body Size Effects

We also considered whether covariance between body size and trophic level could cause the observed trophic-level differences in z values. Predators tend to be larger than their prey, especially when predation is via engulfment and is therefore gape limited. Recent synthetic studies have shown that *z* values are higher for large-bodied species than for small-bodied species (Matter et al. 2002; Drakare et al. 2006) and for multicellular organisms than for unicellular organisms (Hillebrand and Blenckner 2002). These patterns have been explained in terms of correlations between small body size and either high dispersal ability (Finlay et al. 1998; Drakare et al. 2006) or sensitivity to environmental stochasticity (Matter et al. 2002). For birds, body size is positively correlated both with *z* values and the incidence parameter x_i; the latter correlation is proposed to be the proximate cause of the former (Cook and Hanski 1995; Matter et al. 2002; Ovaskainen and Hanski 2003). In bromeliad invertebrates, in contrast, we found no correlation between body size and either incidence parameter. We also found no overall difference in body size between predator and prey taxa, perhaps because many predators in bromeliads can consume prey larger than themselves through piercing mouthparts (e.g., tabanid larvae, tanypodine chironomids, planaria). Together, these observations suggest that differences in *z* values between trophic levels in bromeliads are not simply the result of body size effects on incidence.

In summary, we have shown that an increase in *z* values with trophic rank is a necessary condition but is not sufficient to prove the TRH. The same pattern is also predicted by simple sampling effects, as well as by covariance of trophic level with species traits such as body size. In our empirical example of the bromeliad-inhabiting insect, we found that differences in *z* values between predators and prey were not consistent with body size effects but could reflect sampling effects coupled with differences in population densities between trophic levels. The interesting question, then, is not why species-area curves differ between trophic levels but why predators are rare. In addition to these sampling effects, the long larval stage of predatory damselfly larvae increases the sensitivity to drought of this species (inversely correlated with habitat size), leading to unusually high x_i values and hence high predator *z* values. In DFs, stochastic decoupling of bromeliad volume and detrital mass may also lead to divergent *z* values between trophic levels. These results emerged from sampling a common system in multiple habitats and countries, demonstrating the power of this approach. Most important, our study illustrates how careful partitioning of species-area relationships can lead to deeper insights about the ecological processes responsible for spatial patterns in diversity.

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