

Predator-Dependent Species-Area Relationships

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ABSTRACT: In addition to having a positive effect on species richness (species-area relationships [SARs]), habitat area can influence the presence of predators, which can indirectly influence prey richness. While these direct and indirect effects of area on richness occur simultaneously, no research has examined how predation might contribute to SAR variation. We extend MacArthur and Wilson's equilibrium theory of island biogeography by including predation-induced shifts in prey extinction and predict that predators will reduce slopes of prey SARs. We provide support for this with data from two insular ecosystems: orthopteran richness in Ozark glades (rocky herbaceous communities within a forested matrix) with and without insectivorous lizards and zooplankton richness in freshwater ponds with and without zooplanktivorous fishes. Our results emphasize that anthropogenic activities yield simultaneous changes in processes altering diversity and that it is critical that we understand how these components of anthropogenic change interact to impact diversity.

Keywords: biodiversity, habitat loss, island biogeography, neutral theory, predation.

The relationship between species richness and habitat area is one of the most fundamental and well-studied patterns in ecology (Schoener 1976; Rosenzweig 1995; Lomolino 2000). Species-area relationships (SARs) are central to a general framework for understanding the distribution and abundance of species in nature because (1) the majority of species assemblages exhibit positive SARs (Connor and McCoy 1979; Drakare et al. 2006), (2) such relationships are summarized by simple mathematical associations between the increase in species richness with increasing habitat area (Arrhenius 1921; Rosenzweig 1995; He and Le-

gendre 1996; Tjørve 2003), and (3) key ecological and evolutionary processes are responsible for generating variation in these relationships (Rosenzweig 1995; Lomolino 2000; Drakare et al. 2006). Furthermore, against the backdrop of biodiversity loss as a result of global change and regional habitat destruction, understanding how habitat area is related to species richness is becoming an increasingly important applied problem (Bierregaard et al. 2001; Rosenzweig 2003; Ibanez et al. 2006).

Many functions have been applied to species-area data (reviewed in Tjørve 2003); however, the power law, $S = CA^z$, is the most common model formulation, where S and A are species richness and area, respectively, and C and z are curve-fitting parameters (Arrhenius 1921; He and Legendre 1996). Often, this equation is log-transformed to make it linear, giving $\log S = \log C + z \log A$. Several factors have been proposed to create variation in the slope (z) of log-transformed SARs. These include nonbiological factors such as the spatial scale of sampling methodology (Scheiner et al. 2000; Scheiner 2003, 2004), but important variation still exists even when methodology is controlled (e.g., Drakare et al. 2006). Biological factors that have been invoked to explain variation in z include habitat or ecosystem type, body mass, latitude, and trophic position (reviewed in Connor and McCoy 1979; Rosenzweig 1995; Holt et al. 1999; Lomolino 2000; Drakare et al. 2006).

Here, we focus on how top predators may alter SARs. Top predators play a significant role in the richness of their prey communities (reviewed in Chase et al. 2002), vary predictably with habitat area (Holt 1996), and are often disproportionately influenced by anthropogenic habitat loss (Terborgh et al. 2001; Laurance et al. 2002). Furthermore, predators often increase the probability of extinction of their prey species (Sih et al. 1985; Schoener et al. 2001). As a result, variation in the presence of top predators might be an important factor influencing variation in SARs across systems (Toft and Schoener 1983), and exploring the interaction between predation and SARs may provide deeper insight into understanding how communities will respond to losses of habitat and changes in the abundance of top predators.

Two primary mechanisms underlying the positive relationship between species richness and area are (1) environ-

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mental heterogeneity, whereby positive SARs are generated as a result of increases in the number of habitat types, and thus available “niches,” with area, and (2) demographic colonization-extinction dynamics, whereby larger habitats maintain larger populations leading to higher colonization rates and/or lower extinction rates (MacArthur and Wilson 1967; Connor and McCoy 1979; Drakare et al. 2006). We explore theoretically how predators will alter the latter mechanism by incorporating predation-induced shifts in prey species extinction rates into the equilibrium theory of island biogeography (ETIB; Preston 1962a, 1962b; MacArthur and Wilson 1963, 1967). Results from our simple theoretical exploration reveal an important general prediction: the slope (z) of SARs should be lower in habitats with predators. We conclude by comparing this model prediction with data from SARs with and without predators in a terrestrial and an aquatic ecosystem.

The Model

The ETIB predicts that the equilibrium number of species (\hat{S}) in an insular habitat will be a function of maximum immigration rate (I), maximum extinction rate (E), and the number of species in the mainland pool (P), resulting in

$$\hat{S} = \frac{IP}{I + E}. \quad (1)$$

For clarity, immigration and extinction rates can also be thought of as per-species probabilities of immigration/extinction (i.e., I/P and E/P are constant per capita rates). To derive SARs under the ETIB, two assumptions must be made (MacArthur and Wilson 1963, 1967): population sizes for each species must be proportional to island area, and species extinction rates must decrease with increasing population size. Under these assumptions, large islands will have larger population sizes and lower extinction rates than small islands ($E_s > E_L$) and will therefore harbor more species. In log-transformed SARs, this increase in species number from small (\hat{S}_s) to large (\hat{S}_L) islands divided by the change in island size (A) gives z , the slope of log-transformed SARs:

$$z = \frac{\log \hat{S}_L - \log \hat{S}_s}{\log A_L - \log A_s}. \quad (2)$$

To explore how SARs vary with predation, we extend the ETIB by adding the assumption that predators increase extinction rates of prey species by reducing prey population sizes independent of island size (fig. 1). We also assume that predation is neutral with respect to prey spe-

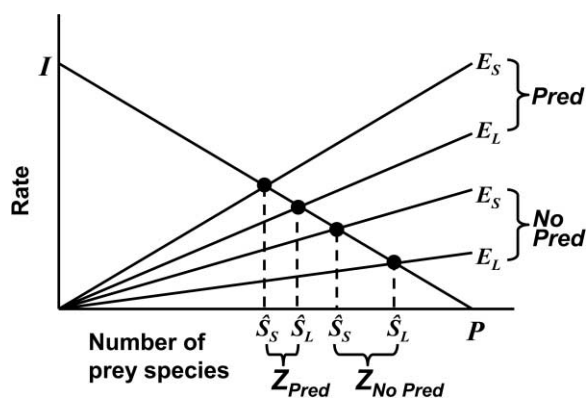


Figure 1: Effect of predators incorporated into the equilibrium theory of island biogeography (model parameters are defined in text). Straightened immigration and size-specific extinction curves (E_s and E_L) demonstrate increases in the equilibrium number of species with island area ($\hat{S}_L > \hat{S}_s$), the species-area relationship (SAR). Islands with predators (*Pred*) have higher prey species extinction probabilities than islands of similar size without predators and therefore harbor fewer prey species at equilibrium (\hat{S}_L predator $<$ \hat{S}_L no predator; the same for \hat{S}_s). This results in a smaller increase in species number from small (\hat{S}_s) to large (\hat{S}_L) islands in the presence of predators (i.e., a smaller z value for SARs with predators).

cies; all prey species are equally susceptible to predators. The total extinction rate of prey species then becomes the summation of extinction contributions from island size (E_{size}) and predators (E_{pred}) because both now affect prey population sizes. This assumption is the key to generating predictions about how z varies with predation, and this modifies equation (1) as follows:

$$\hat{S} = \frac{IP}{I + E_{size} + E_{pred}}. \quad (3)$$

Here, islands with predators will have smaller prey population sizes and higher extinction probabilities than islands of similar size without predators and will therefore harbor fewer prey species (fig. 1; \hat{S}_L predator $<$ \hat{S}_L no predator; the same for \hat{S}_s). Substituting equation (3) for \hat{S}_s and \hat{S}_L in equation (2), rearranging logarithmic notation, and simplifying gives

$$z = \frac{\log\left(\frac{I + E_s + E_p}{I + E_L + E_p}\right)}{\log\left(\frac{A_L}{A_s}\right)}, \quad (4)$$

where E_L and E_s are extinction rates for large and small islands, respectively, and E_p is the extinction rate when

predators are present. Because extinction rates are higher on small islands than on large islands ($E_s > E_L$; ETIB), the numerator of the species term of equation (4) must be >1 . When predators are present ($E_p > 0$), both numerator and denominator of this species term are increased by E_p , which results in a decrease of the numerator and therefore the value of z (fig. 1).

Methods

We explored the generality of this model prediction by studying prey species richness in two disparate ecosystems with insular properties that vary considerably in size and in the presence or absence of important top predators: terrestrial glades and freshwater ponds. Prey species richness in both systems is known to be influenced by both habitat area (glades: Ö. Östman et al. 2007; ponds: Dodson 1992; Oertli et al. 2002) and top predators (lizards in glades: Van Zandt et al. 2005; fish in ponds: Hall et al. 1970; Knapp et al. 2001). Thus, these ecosystems are ideal for testing whether top predators yield shifts in the slope of the species-area relationship of their prey.

Glades are fire-maintained rocky outcrops often clustered on southern or southwestern exposures of mountains that create complexes of insular desertlike or dry prairie microhabitats embedded within a forested matrix (Nelson 1985). Glades in the Ozark ecosystem (spanning Arkansas, Missouri, and Oklahoma) contain relatively simple food webs. At the top of the glade food web, eastern collared lizards *Crotaphytus collaris collaris*, which are restricted to glade habitats, are the most important predators of insect herbivores (Blair and Blair 1941; McAllister 1985; Bergmann and Chaplin 1992). However, because fire maintains glade habitats as well as dispersal corridors for collared lizards, these predators were extirpated from many glades due to fire suppression by European settlers (Templeton et al. 2001; Brisson et al. 2003). Natural fire regimes were restored more than 20 years ago (Templeton 1996; Templeton et al. 2001), and collared lizards have been reintroduced in several glade communities but have not yet established in others, creating opportunities to explore how predators alter prey SARs in Ozark glades. Orthopterans (e.g., grasshoppers) represent the majority of the herbivore biomass of these communities ($>80\%$; Van Zandt et al. 2005; W. A. Ryberg, unpublished data), and, because of their high richness, relative ease of sampling and identification, and high susceptibility to predation by collared lizards, we focused on this group of species. Using standard sweep net protocols (Evans et al. 1983; Evans and Bailey 1993), we sampled orthopteran richness in 31 glades of varying sizes (750–29,500 m²) in the St. Francois Mountains section of the Ozark Highlands of southeastern Missouri (Shannon and Carter Cos.). Seventeen of these glades

occurred on a mountain where collared lizards were reintroduced in 1984, and 14 glades were on an adjacent mountain that collared lizards have not yet recolonized (Templeton et al. 2001). Because glades with and without predatory lizards were segregated spatially, we recognize that differences in orthopteran SARs may result from factors other than predation (e.g., productivity, habitat heterogeneity, isolation). We only sampled glades lacking significant variation in these factors in order to minimize this problem (ANCOVA; productivity: $F = 2.31$, $df = 1, 28$, $P = .14$; habitat heterogeneity: $F = 1.11$, $df = 1, 28$, $P = .30$; t -test, isolation: $F = 0.066$, $df = 1, 29$, $P = .80$).

In east-central Missouri, except in river flood plains and sinkhole ponds, few natural ponds exist because of the karst geology (Unklesbay and Vineyard 1992). However, a large number of ponds have been constructed for agriculture, wildlife, recreation, and conservation purposes (Shelton 2005). Although there are many predators of herbivorous taxa in ponds, fish often have the most dramatic impact on prey species diversity (Hall et al. 1970; Shurin 2001). Importantly, fish are often highly dispersal limited and, as such, their presence is often independent of pond size and other environmental characteristics. In the ponds used in this study, fish colonized ponds as a result both of human intervention (deliberate and accidental) and natural colonization (e.g., flooding rivers). We considered a pond to be fishless if no fish were found after seining 10%–20% of a pond's surface area with a 4.5-m, 10-mm-mesh seine. Fish ponds had one or more species of Centrarchidae sunfishes (primarily *Lepomis cyanellus* green sunfish, *Lepomis macrochirus* bluegill, and *Micropterus salmoides* largemouth bass), which are among the most common and voracious predators in small ponds. Ponds that had only smaller fish, including Cyprinidae minnows or *Gambusia affinis* mosquito fish, were not included because these fish are known to be less effective predators. For this study, we focused on the effects of pond area and fish predators on the richness of Crustacean (cladoceran and copepod) zooplankton, which were diverse and readily identifiable to species under a dissecting microscope. These crustaceans represent a major component of herbivore biomass in this system (Vadeboncoeur et al. 2002), and their diversity typically co-varies positively with other aquatic taxa (Dodson et al. 2000). As such, if we expanded our surveys to other taxa, we expect qualitatively similar results. Zooplankton were sampled in July–August by pulling a 10-cm-diameter 80- μ m zooplankton net using standard protocols (e.g., Harris et al. 2000). We sampled 30 ponds that varied in surface area (range 92–5,834 m²), were constructed more than 10 years before sampling, and were known to retain permanent standing water in most years. Other factors, including pond canopy coverage, pH,

and conductivity, were measured, but for this comparison, ponds were specifically chosen to be similar in these factors, and these factors showed no significant covariation (ANCOVA, canopy coverage: $F = 1.49$, $df = 1, 27$, $P = .23$, pH: $F = 0.96$, $df = 1, 27$, $P = .34$, conductivity: $F = 0.007$, $df = 1, 27$, $P = .93$). Sampled ponds all occurred in natural areas less than approximately 250 km from St. Louis, Missouri, within a matrix of mixed prairie and oak-hickory woodlands with minimal direct connection to populated areas or agriculture.

To elucidate the impacts of predators on SARs, we regressed prey richness (the number of species observed in each insular habitat) with and without predators against habitat area on log-transformed axes. We tested predator and predator-free regressions for equality of slopes (ANCOVA; Sokal and Rohlf 1995; Systat Software) to determine whether predators altered the slope, z , of the SAR.

Results and Discussion

We found 27 species of orthopterans (18 Acrididae, six Tettigoniidae, two Gryllidae, one Tetrigidae; Capinera et al. 2004) in the glades and 22 species of Crustacean zooplankton (16 cladocerans and six copepods; Balcer et al. 1984; Thorp and Covich 1991) in the ponds. We found strong differences between SARs with and without predators for both terrestrial glades (fig. 2A) and freshwater ponds (fig. 2B). While prey species richness increased with area in both predator and predator-free habitats, the slope (z) of the SAR was much steeper without predators than with predators in both community types (ANCOVA on log-transformed data: test for equality of slopes [TES], glades: $F = 11.39$, $df = 1, 27$, $P < .05$; ponds: $F = 5.02$,

$df = 1, 26$, $P < .05$; fig. 2). Thus, for two very different types of insular habitats, the results support our general model prediction that top predators reduce the slope of the SAR and weaken the effects of area on prey species richness.

Our model derives this general prediction that SAR slopes should be shallower with predators from the assumption that habitats with predators have higher prey species extinction probabilities than habitats of similar size without predators and therefore harbor fewer prey species at equilibrium ($\hat{S}_L \text{ predator} < \hat{S}_L \text{ no predator}$; the same for \hat{S}_s). Such reductions of prey species richness with predators are often observed in natural systems (reviewed in Chase et al. 2002), and our results support this in all but the smallest glades and ponds (fig. 2A, 2B). However, the higher richness of prey species in the smallest habitats suggests a possible role for other mechanisms (e.g., keystone predation: Paine 1966; Leibold 1996) leading to increased species richness with predators in those habitats. This highlights the potential importance of scale for future empirical and theoretical explorations of SAR slope variation.

In our model, predators alter prey species richness by increasing prey extinction rates neutrally, despite the fact that predators are often not neutral with respect to their effects on different prey species (reviewed in Chase et al. 2002). Our goal with this approach was to develop the simplest possible model to explore how predators might alter prey SARs and to compare those predictions with data from different ecosystem types. This general approach might also offer an opportunity to incorporate trophic interactions into other models grounded in island biogeography theory, such as Hubbell's (2001) "unified neu-

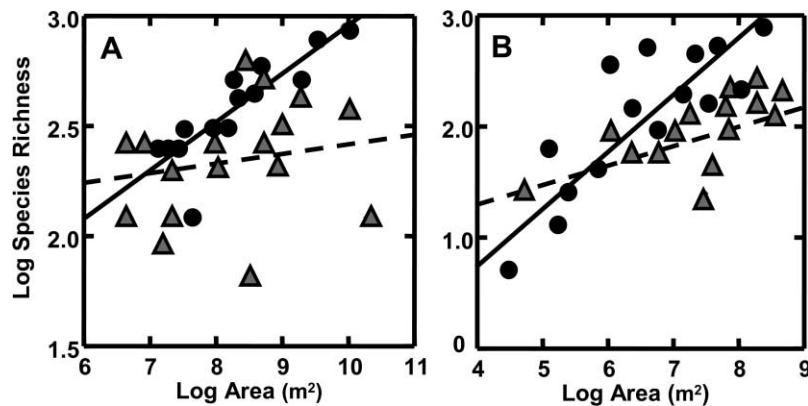


Figure 2: Log-transformed SARs with (*triangles*) and without (*circles*) predators for terrestrial glade (A) and freshwater pond (B) ecosystems. Slopes (z) of predator-free regressions (*solid lines*) are significantly higher than regression slopes for habitats with predators (*dashed lines*) in glade (predators, $y = 0.22x + 0.77$, $r^2 = 0.72$, $P < .05$; no predators, $y = 0.07x + 1.77$, $r^2 = 0.08$, $P = .27$) and pond (predators, $y = 0.46x - 0.90$, $r^2 = 0.67$, $P < .05$; no predators, $y = 0.20x + 0.49$, $r^2 = 0.45$, $P < .05$) ecosystems.

tral theory" (UNT). For example, the two major theorems of the UNT, that ecological community dynamics are a zero-sum game and that relative species abundances are lognormal-like under zero-sum drift processes, stem from an assumption of organism saturation in landscapes implying that the density of individuals is a constant, ρ (Hubbell 2001, pp. 54–55). Indeed, the universal biodiversity number, θ , is a function of ρ . Our model assumes that predators decrease individual density in a way that is proportional to prey species abundance (i.e., neutral), which causes variation in species richness through demographic processes. A similar assumption could be made for the UNT, where predators (or any other factor altering ρ [e.g., productivity, disturbance]) decrease ρ , and therefore θ , which alters other predicted patterns (e.g., rank-abundance relationships, β -diversity).

There are several explicit assumptions in our modeling framework: first, species are noninteractive, having no influence on each other's colonization and extinction rates (MacArthur and Wilson 1963, 1967); second, species population densities are constant, and extinction probabilities are inversely proportional to population size (MacArthur and Wilson 1963, 1967); and finally, predators increase prey extinction rates by reducing their population sizes. In addition to these explicit assumptions, our model implicitly assumes that prey species immigration rates do not change with predators or island isolation. Changing either of these assumptions could alter our predicted effect of predators on SARs. For example, habitat selection by prey species that preferentially avoid predators (e.g., Resetarits 2005) might result in lower immigration rates that decrease the magnitude of predator effects on SARs in those groups. Alternatively, increasing island isolation (i.e., comparing "near" vs. "far" islands) might decrease island immigration probability, which increases the magnitude of predator effects on SARs. Furthermore, it is important to note that different model formulations with different underlying assumptions often can predict similar patterns (e.g., Chave et al. 2002; Wilson et al. 2003). Thus, as for MacArthur and Wilson's (1963, 1967) ETIB and Hubbell's (2001) UNT, in order to discern among models, it will be necessary to generate and compare predictions other than SARs, such as patterns of species turnover in time and/or space (Simberloff and Wilson 1969; Chase 2005).

With the goal of simplicity, the first generation of our model has limitations that leave several opportunities for future development. First, rooted in the ETIB, our model explores how predators might alter prey SARs generated from independent sampling regimes (i.e., samples from nonoverlapping areas of different size). However, SARs are also generated from nested sampling designs (i.e., larger areas contain all smaller areas sampled). While predators may also depress slopes of nested SARs, the mechanism

for this pattern cannot be modeled as a shift in island colonization-extinction rates. Second, with limited empirical data, we only examine interactions between two trophic levels (i.e., predators and their prey). For systems with three or more trophic levels, we would predict alternating impacts of predation on the slopes of SARs such that top predators would decrease the SAR slopes of their prey, but the prey of the prey could in turn increase their population sizes, decrease their extinction rates, and increase their SAR slopes. Investigating how robust the qualitative predictions of our model are to changes in the aforementioned assumptions (and others) and exploring other predicted patterns in addition to SARs will be the subject of future theoretical work (W. A. Ryberg and J. M. Chase, unpublished manuscript).

By focusing on changes in SARs for communities with and without predators, our study provides the means to more accurately predict how habitat loss translates into species loss under different community structures, which are also probably shifting in the face of global change and habitat destruction (Terborgh et al. 2001; Laurance et al. 2002; Ibanez et al. 2006). More generally, it is becoming increasingly evident that processes altering diversity often interact in complex ways (Mackey and Currie 2001; Mittelbach et al. 2001). For example, Proulx and Mazumder (1998) showed that the effects of predators on patterns of diversity depended critically on the productivity of a system. Likewise, Kneitel and Miller (2003) and Östman et al. (2006) found that the effects of predators and disturbance on patterns of diversity, respectively, were strongly influenced by the degree of isolation of those communities. Consequently, as anthropogenic activities yield simultaneous changes in habitat area, isolation, productivity, disturbance regime, and the presence of top predators, it is of critical importance that we understand how these components of anthropogenic change interact to alter diversity.

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