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Habitat Area Affects Arthropod Communities Directly and Indirectly Through Top Predators

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Both habitat area and predators are known to affect the diversity and composition of species that live in a locality. In addition, habitat area can influence the presence of predators, indirectly affecting the diversity of prey. Thus, habitat area may influence species diversity directly and indirectly through the presence of top predators. Here we examine the effects of habitat area and predators on the species richness and composition of a foliage living arthropod community in a fragmented complex of glades (small grassland patches within a forested matrix) in the Ozark Plateau, Missouri. We find that a top predator, the eastern collared lizard *Crotaphytus collaris collaris*, occurs primarily on larger glades. Glade area was positively correlated with arthropod diversity, but only after removing the effect of collared lizard presence. Moreover, collared lizards reduced overall arthropod richness, and shifted the dominance from predatory arthropods (*e.g.* spiders) and Orthopteran grasshoppers to Homopterans (planthoppers). This study shows the importance of accounting for variation in the presence of a top predator when studying the effect of landscape-level processes on species richness and composition.

Habitat area has long been known to directly affect patterns of species richness in natural communities (reviewed in Lomolino 2000, Drakare *et al.* 2006). Smaller habitats generally contain fewer species, in part because of increased risk of extinction due to demographic stochasticity (Brown and Kodric-Brown 1977, Hanski 1999, Fahrig 2003). However, in communities where interspecific interactions, such as competition and predation, are strong, the relationship between habitat area and species richness can be more ambiguous (Toft and Schoener 1983, Holyoak 2000, Gotelli and Ellison 2006, Schoener and Spiller 2006).

The number of trophic levels that occur in a habitat generally increases with habitat area; predators are more likely to be present and abundant in larger habitat patches (Schoener 1989, Holt 1996, Holt *et al.* 1999, Post 2002, Holt and Hoopes 2005). Increases in the presence and/or abundance of predators owing to habitat area could in turn alter patterns of species richness and composition of the prey community (reviewed in Chase *et al.* 2002). For example, Schoener and Spiller (2006) found that web-building spider richness increased with island area, but that the intercept was lower with predatory Anolis lizards (Toft and Schoener 1983). Similarly, Gotelli and Ellison (2006) showed that the presence of a top predatory insect larvae had much larger effect on food web structure than variation in habitat size in water-filled leaves of pitcherplants. Likewise, within a trophic level, habitat area might alter the probability of the presence/abundance of competitively dominant species (reviewed in Amarasekare 2003). While the direct effects of habitat area on patterns of species diversity are expected to be rather straightforward, the indirect effects, through interspecific interactions, can lead to rather complex habitat area-species richness relationships. Moreover, the direct and indirect effects of habitat area are not only likely to change species richness but also species com-

position (Chase *et al.* 2002, Amarasekare 2003).

Here we present results of how species richness and density of a foliage living arthropod community vary with habitat area and the presence of a top predator, the eastern collared lizard *Crotaphytus collaris collaris*,in a fragmented glade complex in the Ozark Plateau, Missouri (USA). We suggest that habitat area affects arthropod richness and composition of the studied groups both directly and indirectly by altering the distribution of the predatory collared lizard.

Methods

Study site: Ozark glades

Our study site is a collection of glades at Taum Sauk Mountain State Park and the adjoining Missouri Department of Conservation land in southeastern Missouri (Iron County). Glades are small openings (0.1-2 ha in this study) of rocky (Rhyolite on Taum Sauk Mountain) outcrops scattered throughout oak-hickory and pine forests in the Ozark Plateau. The soil layer is thin, and the flora contains many endemic species that are similar to grassland and prairie species (Ware 2002). The fauna is also similar to other grasslands in the Midwest United States, but has in addition some relict species that are adapted to a warm and dry climate (*e.g.* scorpions, tarantulas, collared lizards). The distribution of Ozark glades used to be much more widespread, but because of fire-suppression and other forms of habitat destruction, glade habitat in Missouri is now much reduced and greatly fragmented (Templeton *et al.* 2001, Brisson *et al.* 2003). Furthermore, the remaining glades differ in area. Because of the high proportion of endemics they maintain, and the scarcity of glades in the Ozark region, a variety of efforts are being made to restore these habitats and their resident flora and fauna, mostly notably, prescribed fires (Templeton *et al.* 2001, Brisson *et al.* 2003). The glade complex in our study at Taum Sauk Mountain State Park is regularly burned every 2-3 yr (2003 was the last burn prior to this study).

Twelve glades were chosen for the study (Table 1). These were chosen because they were part of a long-term collared lizard population study (Brisson *et al.* 2003) and were similar in vegetative/rock substrate. Additionally, six of the glades had persisting collared lizard populations and six did not. The area of each glade was measured from the interactive GIS-map on the Missouri Department of Conservation's home-page (<http://mdcgis.mdc.mo.gov/website/statewidedoqqtruecolor/viewer.asp>). Glade area was measured using a continuous forest edge as the boundary; therefore, small patches of trees within a glade were included in the measurement. The whole glade complex was ca 100 ha (including forests between glades).

Table 1. Descriptive data (size and collared lizard presence) and arthropod community structure (species richness and abundance of each group) at each studied glade. Pred – predatory arthropods, Orth – Orthoptera, Hom – Homoptera.

Glade	Area (ha)	Collared lizards	Isolated – connected	Arthropod species richness					Arthropod abundance				
				Total	Pred	Orth	Hom	Other	Total	Pred	Orth	Hom	Other
TS-3	0.82	Yes	Iso	12	2	2	5	3	48	5	4	26	13
TS-4	0.11	No	Iso	15	5	2	6	2	46	8	6	24	8
TS-5	0.21	No	Iso	16	6	3	3	4	41	7	5	19	10
TS-7	0.66	No	Iso	24	6	9	3	6	67	8	21	11	27
27	1.15	Yes	Con	19	5	4	7	3	55	8	6	30	11
28	1.75	Yes	Con	22	4	4	9	5	67	6	13	31	17
29-A	0.9	Yes	Con	17	5	3	5	4	48	6	4	25	13
29-B	1.64	Yes	Con	21	5	5	7	4	45	7	6	24	8
30	0.96	Yes	Con	18	6	4	5	3	40	7	8	16	9
TS-2L	0.05	No	Con	20	7	6	4	3	72	8	28	14	22
TS-2M	0.66	No	Iso	23	8	4	5	6	63	12	11	14	26
TS-2U	0.05	No	Con	19	8	3	5	3	64	12	9	24	19

Collared lizards

Eastern collared lizards *Crotaphytus collaris collaris* (Iguanidae: Crotaphytinae), have naturally occurred on glades in the Ozarks for at least 8000 yr, and the population at Taum Sauk Mountain has probably been present for the majority of that time period (Templeton *et al.* 2001). Because of their strict preference for open habitats, lizard populations are fragmented on isolated glades, and individuals do not live in the surrounding forests. Individuals are, however, capable of occasionally dispersing through forests with a sparse understory (Brisson *et al.* 2003). Collared lizards are the largest vertebrate predator confined to the glades (snout to vent length 9-11 cm), and are territorial sit-and-wait predators adapted to foraging for arthropods (5-30 mm in length) and other prey items in xeric environments (Fitch 1956, McAllister 1985, Husak and McCoy 2000). In glades where collared lizards only occur sporadically, the smaller eastern fence lizards (Sceloporus undulatus, snout to vent length 6-7 cm) are a top predator (Van Zandt *et al.* 2005). Sceloporus also feed on arthropods, but consume smaller prey than collared lizards, ranging from 1 to 20 mm (average 5 mm, Rose 1976). Birds are rarely seen foraging in these glades, most likely because forest birds are not adept at foraging in these grasslands, and the isolated patches are too small to maintain viable populations of open grassland bird species.

The collared lizard populations on glades at Taum Sauk Mountain State Park have been monitored since 1998 (Brisson *et al.* 2003). Glades were grouped into those with persisting collared lizard populations and those without lizards based on this monitoring (Table 1). Although lizards have been found on almost all glades in this study, they were almost never found on those glades that we consider to lack lizard populations. Instead, on occasions in these smaller glades, a single lizard or two were observed (usually juvenile males dispersing to new territories) for a few days before moving on (Brisson *et al.* 2003, Strasburg and Brisson unpubl.). Although collared lizards have some natural enemies (birds of prey, predatory mammals, and snakes), the effect of these predators on the demography and distribution of collared lizards on and near this study site seems to be minimal (Sexton *et al.* 1992). We therefore ignored that aspect of the food web here.

Sampling arthropods

Foliage arthropod communities were sampled in 12 glades, which had complete information on collared lizard presence since the inception of the monitoring study. In each glade, arthropods were sampled by two sets of 20 sweeps by a single observer (Ö. Ö.) with a 0.5 m diameter sweep-net in vegetation dominated by grasses and narrow-leafed herbs of 10-30 cm height. We choose to standardize the number of samples taken per glade, rather than sample proportional to glade area, so that we could examine differences in species richness while holding the sample area (and presumably abundance of individuals sampled) constant (a sampling "rarefaction"). Sampling took place in August, 2004, when a majority of insects were present on glades, and advanced in life-stage enough to readily identify.

Sweep-net sampling is the standard methodology for sampling grassland arthropods because of its simplicity and its ability to collect relatively sparsely distributed species (Southwood and Henderson 2000). However, like any other method, sweep-netting differentially samples some groups of arthropods relative to others. For example, ground dwelling arthropods, such as many beetles and hunting spiders, are rarely captured in sweep nets, and pitfall traps are better for sampling these organisms; because of the rocky substrate, pitfalls were not possible in this ecosystem type. Furthermore, because our analysis is primarily focused on comparing arthropod communities among glades, the systematic focus on one group of arthropods (foliage dwelling species readily encountered in sweep netting) should not alter our qualitative conclusions. Because temperature and wind can affect sweep-net capture efficiency (Southwood and Henderson 2000), glades were randomly sampled with respect to area and collared lizard presence, and only during a limited time window when temperature was similar, and when there was minimal wind.

Samples were stored in a cooler with ice and brought to the laboratory where they were frozen. All collected arthropods, which included Orthoptera (grasshoppers, katydids and crickets), Coleoptera (beetles), Homoptera (aphids, leaf- and planthoppers), Heteroptera (true bugs), and Araneae (spiders) were identified to species (or in cases where species could not readily be discerned, morphospecies) using standard identification guides (Jaques 1951, Helfer 1963, Slater and Baranowski 1978, White 1983, White and Borror 1998, Milne and Milne 2000); information about trophic level was also collected from these guides.

Statistical analysis

The influence of glade area and collared lizard presence on arthropod species richness and density was estimated with ANCOVA, where glade area was a continuous, independent variable and the presence or absence of a viable collared lizard population was a categorical variable. We also included the interaction term between area and predators, since predators can alter the slope of the species area relationship (Schoe-

ner and Spiller 2006). Patch isolation can also affect species richness (reviewed in Cadotte 2006). To control for differences in patch isolation, glades were categorized as either isolated (five glades with 170-250 m of forest to nearest larger or similar sized glade) or connected (seven glades with 20-60 m of forest to nearest larger or similar sized glade). Both the interaction between area and predators, as well as isolation, were removed from the model (in a backward manner) if $p > 0.1$ to increase statistical power.

We further examined the influence of glade area and collared lizard presence on the densities of different taxonomic and functional groupings using ANCOVA. Densities of other arthropod groups were removed if $p > 0.1$. This allowed us to explore any possible covariation among arthropod groups that might indicate interactions between species groups and the influence of glade area and/or collared lizard presence. While a path-analysis (or other structural equation modeling approach) would have been a direct way to explore these indirect interactions, we did not have the sample size necessary for such analyses.

Glade area, species richness and densities were $\log_{10}$-transformed, and proportions were arcsin-square root transformed prior to statistical analyses. The z-values of the species area relationship were caculated from the slope of the regression coefficient between $\log_{10}$ (species richness) versus $\log_{10}$ (area) (corrected for isolation). All statistical analyses were performed with SAS version 9.1.3 (Anon. 2003).

Results

Collared lizard presence

The distribution of collared lizard populations was concentrated in larger glades ($t_{1,10} = 15$, $p = 0.003$, $n = 12$). The average area of glades was 1.2 ha for those with collared lizards, and 0.3 ha for those without collared lizards.

Arthropod species richness

Total foliage arthropod species richness was positively correlated with glade area and was lower in glades with collared lizards (Figure 1, Table 2). Although the z-value (slope) was higher among glades with collared lizards ($z = 0.35$) than without ($z = 0.27$), this difference was non-significant ($p = 0.5$), possibly as a result of the somewhat small sample sizes reported in this study. The observed correlations were not an effect of different abundances in the samples, because the results did not qualitatively change when we rarified the richness data to account for slight differences in the number of individuals sampled among the glades (Table 2).

Arthropod communities mainly consisted of three groups, Orthoptera (mainly grasshoppers and katydids, *i.e.* relatively large, chewing herbivores), Homoptera (mainly leaf-and planthoppers, *i.e.* relatively small, sucking herbivores), and predatory arthropods

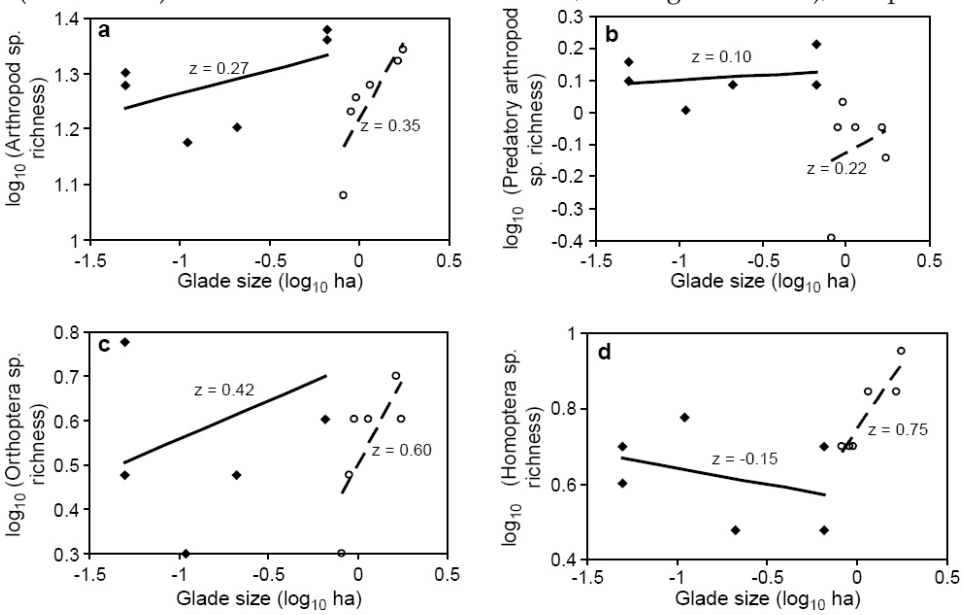

Fig. 1. Species richness in absence of collared lizards (filled diamonds, solid line) or in presence of collared lizards (open circles, dashed line). (a) Total arthropod species richness, (b) predatory arthropod species richness (corrected for isolation, Table 2), and (c) Orthoptera species richness were all positively correlated with glade area and was lower when collared lizards were present. There was no significant main effect of glade area on Homoptera species richness (d) but an interaction between glade area and collared lizard presence. z-values are regression coefficients between glade area and species richness (when corrected for isolation, see Methods).

Table 2. Results from ANCOVAs of effects of glade area, collared lizard presence, and isolation (categorical variable, see Methods) on the dependent variables. For density analyses, the densities of the other arthropod groups were included as covariates. The interaction between area and collared lizard presence, isolation and densities of other arthropod groups were removed from the model if $p > 0.1$, whereas area and collared lizard presence were not removed because they were our focal variables. DF is the degree of freedom for the error term in each model, all independent variables had DF = 1. n = 12 for all models.

Dep. variable	Total richness DF = 8	Rarefied richness DF = 8	Total density DF = 8	Predator richness DF = 8	Predator density DF = 8	Orthoptera richness DF = 8	Orthoptera density DF = 8	Homoptera richness DF = 8	Homoptera density DF = 7	Richness of other herbivores DF = 9	Density of other herbivores DF = 8
Area	F = 127***	F = 32***	F = 0.1	F = 7.7*	F = 1.6	F = 9.7*	F = 2.2	F = 3.6	F = 2.3	F = 16**	F = 0.6
Lizard	F = 151***	F = 26**	F = 0.8	F = 29***	F = 8.8*	F = 11**	F = 6.6*	F = 4.5	F = 4.4*	F = 10*	F = 0.9
Isolation	F = 120***	F = 23**		F = 24**	F = 4.1	F = 8.6	F = 4.5				
Area × lizard								F = 5.9*	F = 6.9*		
Orthoptera density									F = 8.8*		F = 5.5*

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

(mainly spiders and predatory Heteroptera), which together comprised 73% of all sampled individuals. The remaining 27% of individuals were herbivorous and omnivorous Heteroptera and Coleoptera species. The species richness of the three main groups differed in their relationships with glade area and collared lizard presence. Predatory arthropod and Orthoptera species richness was positively correlated with glade area, and was lower (on average by 35 respectively 11%) in the presence of collared lizards (Table 2, Figure 1). The z-values (slopes) did not differ between glades with (z = 0.22 for predatory arthropods and z = 0.60 for Orthopthera) and without collared lizards (z = 0.10 respectively z = 0.42). Species richness of Homoptera showed no response to any of the main effects, but there was an interaction in that richness increased with area (z = 0.75) when collared lizards were present but not when collared lizards were absent (z = -0.15, Table 2, Figure 1). For the remaining arthropods lumped (herbivorous Heteroptera and Coleoptera), species richness increased with glade area and was lower in presence of collared lizards (Table 2).

Arthropod density

Total arthropod density did not differ with glade area or between glades with and without collared lizards (Table 2). Neither was the density of any single group of arthropods correlated with glade area (Table 2). Predatory arthropods and Orthoptera densities decreased, and Homoptera density increased in the presence of collared lizards, whereas the density of the remaining herbivores was not affected (Table 2). The density of predatory arthropods and Orthoptera were on average 28 and 43% lower in the presence of collared lizards, respectively. The average increase in Homoptera density in the presence of persisting collared lizard populations was 51%. Moreover, there was an interaction between glade area and collared lizard presence on Homoptera density (Table 2) because there was an increase in density with glade area among glades with collared lizards and a decrease among glades with collared lizards absent. The density of Homoptera was negatively correlated to the density of Orthoptera (Table 2), but otherwise there was no significant correlation between densities of the different arthropod groups.

Discussion

Our study highlights that the role of food web interactions represents an important complexity in the study of species-area relationships. Specifically, we found that the presence of top predatory collared lizards is related to glade habitat area, and that both hab-

itat area and collared lizard presence is related to foliage inhabiting arthropod species richness. Thus, the species-area relationship in these insular glade habitats is more complicated than the classically observed monotonic rise of species richness with area.

Although the vast majority of studies on species-area relationships find positive relationships (reviewed in Drakare *et al.* 2006), there is considerable variation in the strength of those relationships. That is, the slope (z) of the species-area relationship is highly variable. Some of this variation can be explained by methodological differences, and other variation can be explained by differences in geographical, evolutionary, and ecological variation among systems (Drakare *et al.* 2006). Few studies have explicitly examined how predators might alter the shape of the species-area relationship (Toft and Schoener 1983, Schoener and Spiller 2006, Ryberg and Chase unpubl.). Nevertheless, it is well known that predator presence is often influenced by the area of a given habitat, being more likely to be presence on larger habitat patches (reviewed in Holt and Hoopes 2005). As such, we suggest that some of the variation observed both within and among studies on species-area relationships might be at least partially explained by variation in the presence of predatory species, which in turn influence the richness of their prey.

In our study, if we did not account for the presence of predatory collared lizards, and their influence on arthropod species richness, we might have erroneously concluded that area had no influence of species richness (overall results in Figure 1a). Indeed, when we controlled for the negative effect of collared lizards on arthropod species richness, we found that there was a strong effect of area on species richness both in glades with and without collared lizards (Figure 1a). Although not presented in the same context, a careful examination of the data in Toft and Schoener (1983; Figure 3, p. 420) show a similar pattern of spider species richness and predatory Anolis lizard presence on small Bahamian islands.

In addition, to overall species richness and species abundance co-varying with both area and collared lizard presence (Figure 1a), we found that this relationship differed considerably among the different arthropod groups (Figure 1b-d). Collared lizard presence was correlated with a decrease in the overall richness of arthropod species, as well as in the richness and density of Orthoptera and predatory arthropods. This result is partly consistent with other studies on the effects of predatory lizards on arthropod communities (Spiller and Schoener 1994, Schoener and Spiller 1996, Chase 1998, Van Zandt *et al.* 2005). Our results, however, differed from these other studies in that collared lizards had little effect on the total density of the entire arthropod community. This stems from the fact that the decrease in density of Orthoptera and predatory arthropods was offset by an increase in density of smaller Homoptera (Figure 1). We suggest that this compensation of density and species richness by the smaller species when the larger species are removed could be an indirect effect mediated by the collared lizards. Collared lizards are important predators of Orthoptera and larger predatory arthropods; gut content analysis of Ozark collared lizards showed that Orthoptera constitutes about 75% (mass) of prey (McAllister 1985). However, these relatively large lizards are not likely to be important predators of smaller Homopterans (< 1% of all prey items [McAllister 1985]). Thus, a possible scenario for our differential results among the species groups could be that because collared lizards reduced the abundance and richness of their preferred orthopteran prey, homopterans, which are not preferred prey, but likely competitors of orthopterans (Denno *et al.* 1995), were able to increase in abundance. Alternatively, because predatory arthropods were also reduced by the presence of collared lizards, homopterans could have increased because of reduced predation pressure by these predators (Rosenheim 1998).

Since our data are correlative, we can not with certainty state that habitat area is the primary factor that causes collared lizards to only persist on larger glades, and that both area and lizard presence interact to influence arthropod richness. There are many unmeasured variables that are not accounted for in our sampling design that might covary with habitat area and/or lizard presence. Of course, these limitations are the same for any correlative study, and we have attempted to minimize this variation with our choice of study sites. Nevertheless, the most direct way to test the direct and indirect effects of habitat area and collared lizard presence on patterns of species richness and composition would be to perform experimental manipulations. Unfortunately, in the context of the present study, these collared lizard populations are greatly reduced by habitat loss, and considered threatened in the state of Missouri. Thus, any experimental manipulation of their presence at this site is not possible. However, it is well known that experimental reductions of other lizard species have had strong influences on arthropod species richness (Schoener and Spiller 1996, Chase 1998). Furthermore, preliminary information from other nearby Ozark glade sites where recently extinct collared lizards have been experimentally restored to some glade complexes, but have not yet recolonized others (Templeton *et al.* 2001) suggests a causal relationship between collared lizard presence and arthropod species richness (Ryberg and Chase unpubl.).

It is well known that top predators are often disproportionately influence by habitat area relative to their

prey (Holt 1996, Post 2002, Holt and Hoopes 2005). It is further well known that predators can often have strong effects on the abundance and biodiversity of their prey species (reviewed in Chase *et al.* 2002). As such, we expect that our results, that habitat area and predators interact to determine patterns of community structure are rather general (Toft and Schoener 1983, Gotelli and Ellison 2006, Schoener and Spiller 2006). Thus, even though the species-area relationship remains one of the most well documented patterns in all of ecology (Drakare *et al.* 2006), we suggest that in cases where habitat area also influences the presence of important top predators, ecologists will be well served to consider the interactive roles of area and species interactions when examining the effects of habitat area variation. The effects of habitat area on predator presence and indirect effects on communities is particularly important when trying to understand the consequences of habitat loss on community structure (Terborgh *et al.* 2001).

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