Invasive Plants Have Scale-Dependent Effects on Diversity by Altering Species-Area Relationships

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Kristin I. Powell,[1]* Jonathan M. Chase,[2] Tiffany M. Knight[1]

Although invasive plant species often reduce diversity, they rarely cause plant extinctions. We surveyed paired invaded and uninvaded plant communities from three biomes. We reconcile the discrepancy in diversity loss from invaders by showing that invaded communities have lower local richness but steeper species accumulation with area than that of uninvaded communities, leading to proportionately fewer species loss at broader spatial scales. We show that invaders drive scale-dependent biodiversity loss through strong neutral sampling effects on the number of individuals in a community. We also show that nonneutral species extirpations are due to a proportionately larger effect of invaders on common species, suggesting that rare species are buffered against extinction. Our study provides a synthetic perspective on the threat of invasions to biodiversity loss across spatial scales.

Many empirical studies show dramatic reductions of native biodiversity in the presence of invasive species (1–3). However, evidence that invasive species cause native species extinctions is rare, although it might be expected given the overwhelming evidence of their negative effects (4–7). Although invasive predators and parasites are known to have caused extinctions of many species (8), competition with invasive plants is rarely implicated in extinction (5, 9). In fact, in some cases the presence of invasive plants can actually increase species richness, leading to questions about whether most invasive species are really a leading threat to the conservation of native biodiversity (9, 10).

A difference in the spatial scales of investigation might explain the controversy between studies that find reductions in biodiversity and those that find no effects or positive effects on biodiversity. Studies that find invasive-plant–mediated reductions in biodiversity typically investigate small spatial scales (<25 m^2), whereas studies that find little evidence for negative effects of plant invaders on extinctions take place at much broader spatial scales (2). We hypothesized that this discrepancy can be resolved by understanding whether and how invasive species alter the scaling of species richness with area [the species-area relationship (SAR), $S = cA^z$, where S is species number, A is area, and c and z are constants). Specifically, the effect of invasive species will become increasingly tempered with sampling scale if the invader decreases the intercept (c) and/or increases the slope (z) of the log-log SAR [$\log(S) = z\log(A) + \log(c)$].

We examined the scale-dependent influence of invasive plant species, which we define as the subset of nonnative plant species that have high rates of population growth and become dominant members of the community to which they are in-

troduced (11–13). The influence of non-native plant species that do not achieve such dominance is not as controversial and has little negative influence on species richness at any scale. We haphazardly chose three disparate, forested biomes from across the United States that are experiencing established but ongoing invasions. We chose species with disparate growth forms and physiology across biomes in order to explore possible generality of their effects on diversity. Our study systems were as follows: hardwood hammock forests in central Florida that are being invaded by *Dianella ensifolia* (cerulean flax lily), a dense mat-forming understory herb introduced from Asia and Africa (14); oak-hickory forests in eastern Missouri that are being invaded by *Lonicera maackii* (Amur honeysuckle), a mid-story shrub introduced from East Asia that creates low light levels and soil allelopathy (15, 16); and tropical mesic forests on the Big Island of Hawai'i that are being invaded by *Morella faya* (fire tree),

a nitrogen-fixing canopy tree introduced from Macaronesia (17).

We identified multiple pairs of sites on opposite sides of each ongoing invasion front. Invaded communities were dominated (>90% cover) by the focal invader, which was present for at least 30 years (based on population structure and conversations with local managers). To minimize variation among site conditions other than the presence of the invader, paired 500-m^2 communities were identified according to the following three criteria: they were spatially proximate and occurred on similar soil and topographic conditions; they had very low densities of the invasive species but had a population structure indicative of future growth (for example, many individuals of each stage class); they had the same dominant and subdominant native overstory species, suggesting similarity in the underlying environmental conditions (fig. S1) (18).

We found a universally lower intercept (c) and steeper slope (z) of the SAR in invaded communities relative to uninvaded communities across biomes (Fig. 1 and fig. S2). Each plant invader caused large species richness reductions at small scales but a much smaller proportional reduction in species richness at broad scales (Fig. 1 and fig. S3). These patterns support our hypothesis that the discrepancy between studies that find larger or smaller influences of invasive species on native biodiversity can be reconciled by considering spatial scale.

The influence of invasive species on the slope of the SAR (z) results from the tension between four non–mutually exclusive mechanisms: a neutral sampling effect, nonneutral shifts in the relative abundance of species, local species extirpations, and/or shifts in the aggregation among individuals (19–21). First, by reducing the absolute number of individuals in invaded habitats (3, 22, 23), invasive species can decrease c and increase z through a neutral sampling effect, so long as the
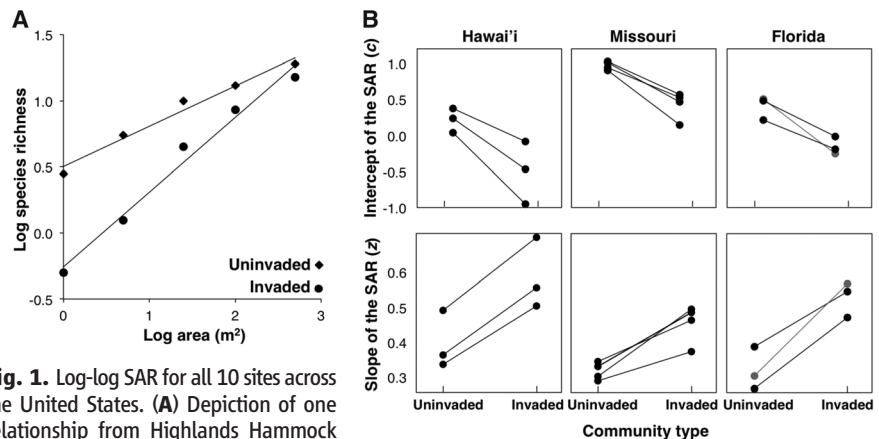

Fig. 1. Log-log SAR for all 10 sites across the United States. (**A**) Depiction of one relationship from Highlands Hammock State Park, Florida [(B), shown in gray], highlighting how increases in the SAR slopes (z) in invaded communities lead to smaller species richness declines with increasing spatial scale. (**B**) Decreases in the intercepts (c) and increases in the slopes (z) of the invaded SAR for Hawai'i (invasive plant *M. faya*: c, $t = 4.702$, $P = 0.042$; z, $t = 15.541$, $P = 0.004$), Missouri (invasive plant *L. maackii*; c, $t = 7.219$, $P = 0.005$; z, $t = 6.151$, $P = 0.009$), and Florida (invasive plant *D. ensifolia*; c, $t = 5.194$, $P = 0.035$; z, $t = 6.783$, $P = 0.021$).

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SAR has a maximum species richness (2, 19, 24). Second, invasive species can alter the shape of the relative species abundance distribution (SAD) through nonneutral effects on species' abundances (2, 21, 25). If native communities become more even in the presence of invaders, z will increase, whereas if native communities become less even, z will decrease. Third, both sampling effects and shifts in the shape of the SAD due to an invader can increase deterministic and stochastic local extirpations, which will decrease z. Fourth, the degree of intra- and interspecific aggregation of individuals within a community will influence z; less aggregated communities have a steeper z than that of more aggregated communities (18, 21, 25).

To dissect the relative influence of the four main mechanisms on z, we used null model analyses on spatially explicit abundance data collected in 50 1-m^2 plots evenly distributed within each 500-m^2 SAR plot (18). Because dissecting the effects of aggregation versus local extirpations requires a different type of null model, it was not possible to dissect all of the possible mechanisms in a single analysis. Thus, we first determined whether there were differences in aggregation between invaded and uninvaded communities by measuring the bias—or difference in area under curves—between the species rarefaction (nonspatially explicit null expectation) and accumulation (spatially explicit) curves [modified from (26)]. We found no significant difference in bias between invaded compared with uninvaded communities within or across sites (paired t tests for each plant invader, $-1.015 < t < 1.924$, $0.194 < P < 0.994$) (fig. S4) (18), indicating that differences in aggregation are unlikely to be a cause of observed shifts in z.

We next devised a null model approach to dissect the effects of invasive species due to neutral sampling effects, local species extirpations, and shifts in the shape of the SAD (table S1) (18). In all cases, there was a large reduction in the number of individuals in the invaded community (ranging from 65 to 91% loss of individuals), which led to large increases in z due to the sampling effect (Fig. 2 and Table 1). However, predicted changes in z solely due to the sampling effect were universally higher than the observed changes in z (Fig. 2) (18). We found that species extirpations moderated the influence of neutral sampling effects on z. In all invaded communities, there were fewer species in our largest sample area than expected from neutral sampling, suggesting that these species were subject to a deterministic or stochastic negative influence of small populations on extirpation. Although one site did show a more even SAD in the invaded community, species extirpations outweighed the influence of invaders on the shape of the SAD (Fig. 2).

Although the observed shifts in the slope of the SAR (z) were largely due to neutral sampling effects moderated by local extirpations, we asked whether the local extirpations might have resulted because rarer species were inherently more susceptible to invaders or, instead, simply victims of low population numbers. We examined abundance changes in each species' response to invaders and determined the deviation of their abundance in the invaded community relative to that expected from neutral sampling effects (18, 27). Species that were common in uninvaded communities tended to deviate negatively from abundances expected from sampling effects (they were more strongly influenced by the invader), whereas species that were rarer in uninvaded communities tended to deviate positively from expected abundances (they were less strongly influenced) (Table 1 and fig. S5). This result could have emerged from at least two nonexclusive mechanisms, including common species having greater niche overlap with invaders (28) and/or rare species possessing life history traits—such as shade tolerance or growth under low-resource conditions (29)—that allow them to proportionally maintain their abundance in the presence of invaders (30).
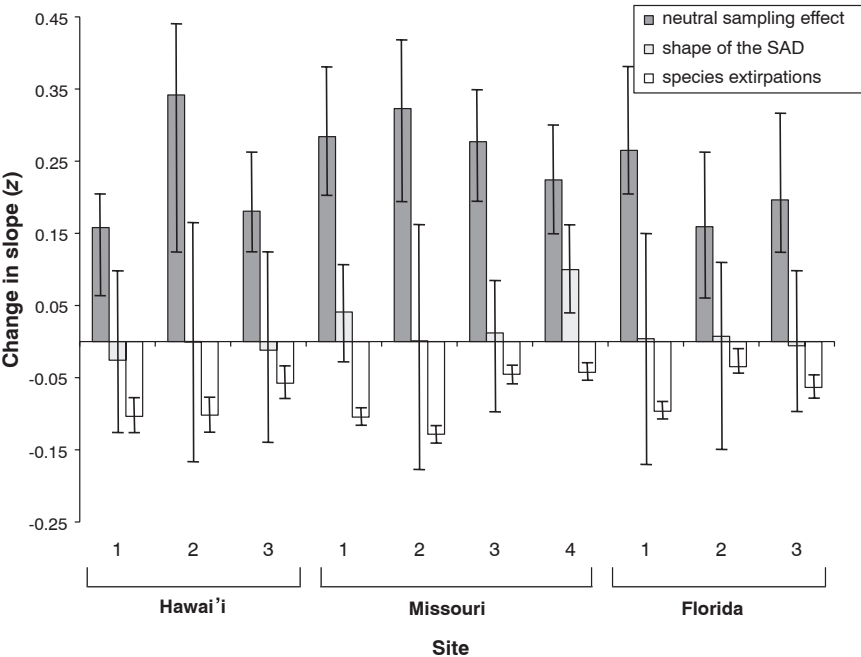

Fig. 2. Contribution of neutral sampling effects (dark gray bars), nonneutral changes in the relative species abundance distribution (light gray bars), and species extirpations beyond those expected from sampling (white bars) to the observed difference in the slope (z) of the SAR between invaded and uninvaded communities. The sum of the bars for each site is equivalent to the observed change in slope between invaded and uninvaded communities across 50 1-m^2 plots. Positive bars contribute to a higher slope observed in the invaded relative to the uninvaded community, whereas negative bars moderate the observed difference in slopes. Error bars are 95 percentile confidence intervals (table S1) (18).

Table 1. The loss of individuals (excluding the focal invader) and Kendall's rank correlation explaining shifts in species' abundances for all sites. Kendall's rank correlations show the relationship between a species' abundance in the uninvaded community and its deviation from its expected abundance in the invaded community. Significant P values reflect larger negative effects of plant invaders on common as compared with rare species.

Site	Sampled site	Individuals in uninvaded community	Individuals in invaded community	Kendall's rank correlation coefficient (τ)	Kendall's rank correlation P value
Hawai'i	1	223	77	−0.231	0.109
	2	163	17	−0.405	0.014
	3	241	59	−0.369	0.010
Missouri	1	4378	374	−0.381	<0.001
	2	1460	228	−0.378	<0.001
	3	840	98	−0.442	<0.001
	4	4348	486	−0.407	<0.001
Florida	1*	569*	120*	−0.482*	<0.001*
	2	362	127	−0.230	0.072
	3	369	129	−0.308	0.040

*Corresponds to the Highlands Hammock State Park example shown in Fig. 1A.

Thus, rarer species may be more buffered from extinction than expected from neutral sampling effects. However, time-lagged extinctions due to extinction debt may lead to additional species loss (*31*).

Although an examination of how hundreds of common and rare species were disproportionately influenced by invaders is beyond the scope of this study, we can glean insights by examining the traits of common and rare species at the study sites. For example, in Hawai'i the native sedge *Carex wahuensis* was rare in the absence of the invader but became proportionately more common in the presence of the invader, likely because it could tolerate lower light and/or take advantage of higher nitrogen imposed by the invasive *M. faya* (*32*). Likewise, in Missouri several native species known to be shade tolerant (such as *Desmodium glutinosum* and *Trillium recurvatum*) (*33*) were proportionately less influenced by the invasive *L. maacki* than were shade-intolerant species.

Overall, by explicitly focusing on scale-dependent processes, the results from our study reconcile the differences observed among local- and broad-scale effects of invasive plant species on biodiversity. Decreased intercepts (*c*) and increased slopes (*z*) of the SAR were primarily caused by neutral sampling effects. In addition, disproportionately smaller effects on rare species' abundances moderated species loss at the broadest spatial scale. Understanding the mechanisms by which invasive species shift species abundance distributions could improve our ability to forecast future invasion-induced extinctions. Although

particularly harmful to native biodiversity at small spatial scales, invasive species' effects may be reversed through targeted control to increase native species abundances, at least until future extinction debt is paid.

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Supplementary Materials

www.sciencemag.org/cgi/content/full/339/6117/316/DC1
Materials and Methods
Figs. S1 to S5
Table S1
Reference (*34*)

Structure of Histone mRNA Stem-Loop, Human Stem-Loop Binding Protein, and 3'hExo Ternary Complex

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Metazoan replication-dependent histone messenger RNAs (mRNAs) have a conserved stem-loop (SL) at their 3'-end. The stem-loop binding protein (SLBP) specifically recognizes the SL to regulate histone mRNA metabolism, and the 3'-5' exonuclease 3'hExo trims its 3'-end after processing. We report the crystal structure of a ternary complex of human SLBP RNA binding domain, human 3'hExo, and a 26-nucleotide SL RNA. Only one base of the SL is recognized specifically by SLBP, and the two proteins primarily recognize the shape of the RNA. SLBP and 3'hExo have no direct contact with each other, and induced structural changes in the loop of the SL mediate their cooperative binding. The 3' flanking sequence is positioned in the 3'hExo active site, but the ternary complex limits the extent of trimming.

Metazoan replication-dependent histone mRNAs have a conserved stem-loop (SL) structure at their 3'-end (*1*, *2*), distinct from the polyadenylate tail found on all other known eukaryotic mRNAs (*3*, *4*). The stem-loop binding protein (SLBP) (*5*), also known as hairpin binding protein (*6*), is a central regulator of histone mRNA metabolism. SLBP and the U7 small nuclear ribonucleoprotein (snRNP) (*7*) are required

for the 3'-end processing of histone pre-mRNAs (fig. S1). SLBP is also required for the export, stability, and translation of mature mRNAs. The 3'-5' exonuclease 3'hExo (also known as Eri-1) forms a tight ternary complex with SL and SLBP. 3'hExo can trim three nucleotides in vitro from the processed histone mRNA 3'-end, and SLBP protects against further trimming (*8*–*11*). 3'hExo is required for replication-dependent histone mRNA

degradation (*12*). It is also involved in microRNA homeostasis (*13*) and 5.8*S* rRNA 3'-end maturation (*14*, *15*). The stem-loop RNA consists of a six–base pair stem and a four-base loop, as well as flanking sequences at both ends (fig. S1). SLBP (31 kD) has high affinity for the SL (dissociation constant $K_d = 1$ to 10 nM) (*16*–*20*). It contains a ~70-residue RNA binding domain (RBD) (Fig. 1A and fig. S2). 3'hExo (40 kD) consists of an N-terminal SAP domain (~60 residues) followed by a nuclease domain (~220 residues) that belongs to the DEDDh superfamily (Fig. 1A and fig. S3) (*9*–*11*, *21*).

We report here the crystal structure at 2.6 Å resolution of the ternary complex of human SLBP RBD, human 3'hExo (SAP and nuclease domains), and a 26-nucleotide SL with consensus sequence (Fig. 1, A and B, and table S1) (*22*). Clear electron density was observed for all 26 nucleotides of the SL (Fig. 1C). The stem (nucleotides 6 to 11 and 16 to 21) has a slightly flattened

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