

Invasion note

Biotic resistance to an invasive spider conferred by generalist insectivorous birds on Hawai’i Island

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Abstract

A central problem for ecology is to understand why some biological invasions succeed while others fail. Species interactions frequently are cited anecdotally for establishment failure, but biotic resistance is not well supported by quantitative experimental studies in animal communities. In a 33-month experiment on Hawai’i Island, exclusion of native and alien forest birds resulted in a 25- to 80-fold increase in the density of a single non-indigenous spider species (Theridiidae: *Achaearana* cf. *riparia*). Caged plots held large aggregations of juveniles and more large-bodied individuals, suggesting potential reproductive individuals are more susceptible to bird predation. Most examples of biotic resistance involve competition for limiting resources among sessile marine animals or terrestrial plants. The present results show that generalist predators can limit the success of introductions, even on oceanic islands, generally assumed less resistant to invasion.

Introduction

A central question in ecology is why some biological invasions succeed while others fail. Numerous mechanisms may alter the fate of non-indigenous species in a foreign range, including the number and quality of introduced propagules (Green 1997), levels of human disturbance (Hobbs and Huenneke 1992), compatibility of physiological tolerances with abiotic site characteristics (Blackburn and Duncan 2001), or biotic resistance of the recipient community (Maron and Vilà 2001).

Following Chapman’s (1931) formulation of the concept of ecological resistance, Elton (1958) proposed that a strongly interacting community of native species may resist invasion, predicting species-rich communities should be more stable

and resistant. Although several examples of resistance exist from marine systems (e.g. Reusch 1998) and sessile organisms in plant communities (e.g. Hector et al. 2001), there have been few experimental evaluations in terrestrial animal communities (Lake and O’Dowd 1991; Schoener and Spiller 1995). Aside from biological control examples in agroecosystems (Luck et al. 1999), most studies have ignored functional diversity and the role of consumers (Maron and Vilà 2001; Duffy 2002). Biotic resistance remains controversial (Simberloff 1995), and quantitative population-level studies are urgently needed to evaluate the generality of the concept (Goeden and Louda 1976; Simberloff and Von Holle 1999).

This paper reports experimental evidence of biotic resistance to invasion by an exotic species

in a forest ecosystem. Exclusion of a guild of generalist insectivorous birds led to an unexpected irruption of an introduced spider. Several experimental examples of invasion resistance in natural terrestrial animal communities now come from oceanic islands, often considered intrinsically less resistant to invasion (e.g. Elton 1958; Pimm 1991).

Materials and methods

For almost 3 years (August 1998 to May 2001), I conducted a factorial experiment to test the community-wide impacts of resources and bird predators in a forest ecosystem. The site was located on the historical basaltic lava flow of 1881 on Mauna Loa, Island of Hawai'i. *Metrosideros polymorpha* Gaudichaud-Beaupré (Myrtaceae) dominates this montane (1280 m a.s.l.), early-successional wet forest (~ 4000 mm a.a.p.), along with ferns (e.g. *Dicranopteris linearis* [Burm.] Underw. [Gleicheniaceae]), sedges (e.g. *Machaerina angustifolia* [Gaud.] T. Koyama [Cyperaceae]) and low shrubs (e.g. *Coprosma ernodeoides* A. Gray [Rubiaceae]).

Birds are the only diurnally active, canopy-foraging vertebrate insectivores in the Hawaiian Islands. The most common birds at this site are Japanese white-eye (*Zosterops japonicus*) and native 'apapane (*Himatione sanguinea*). Native 'oma'o (*Myadestes obscurus*), 'i'iwi (*Vestiaria coccinea*), 'amakihi (*Hemignathus virens*), and 'elepaio (*Chasiempis sandwicensis*), respectively, are present at decreasing frequency. *Zosterops japonicus* and *C. sandwicensis* are predominantly insectivorous, *H. sanguinea* and *V. coccinea* are principally nectarivorous and *M. obscurus* is frugivorous. All take arthropods opportunistically, especially while provisioning nestlings in the spring (Perkins 1903; Baldwin 1953, Ralph et al., unpubl. data).

Thirty-two 20 × 20 m plots grouped in eight blocks were established in a randomized block design. Sixteen plots were fertilized at 6-mo intervals ('NPT' of Raich et al. 1996). A randomly selected clump of 1–6 individual *M. polymorpha* trees within the central 8 × 8 m were either left open or caged using sheer agricultural polypropylene mesh (2 × 2 cm, Ross Daniels Incorporated),

supported by a frame of aluminum conduit piping 4 m tall (cages ~ 20 m circumference).

I sampled tree clumps at experimental outset and conclusion by clipping 5–10 branches, shaking and beating branches onto a lab table, and collecting all arthropods with an aspirator. I scored and identified them to species, measured body length to the nearest millimeter, and estimated dry biomass using length-mass regressions (Gruner 2003). I dried clippings at 70 °C to constant mass and weighed both foliar and woody components. Arthropod numbers were summed per plot and calculated as loads per 100 g foliar dry mass.

Although I quantified the entire arthropod fauna of focal trees (Gruner 2004), this paper focuses on an introduced spider, *Achaearenea* cf. *riparia* (Blackwall) (Theridiidae). Like other theridiids, these spiders build small tangle webs between leaves and branches. All three *Achaearenea* species recorded from Hawai'i are exotic. The cosmopolitan common house spider (*A. tepidariorum*), present in the islands for at least a century (Kirkaldy 1908), is primarily associated with anthropogenic habitat. *Achaearenea riparia* and *A. acorensis* were reported recently as new state introductions (Beatty et al. 2000). Although their current distributions are poorly understood (Nishida 2002), contemporary sampling with comparison to historical record suggest *A. riparia* is expanding within Hawai'i Volcanoes National Park and possibly other areas on the island of Hawai'i (Gagné 1979; D.S. Gruner unpubl. data; P. Krushelnycky, unpubl. data).

Final *A. riparia* density and biomass were log transformed ($\ln[x + 1]$) and analyzed using a mixed general linear model with type III sums of squares in SAS 8.02 (SAS Institute, Cary, NC). Bird exclusion and fertilization were treated as fixed factors, with blocks and their 2-way interactions as random effects.

Results

At the start of the experiment, only 15 *A. riparia* spiders were collected from 9 of 32 plots (28%; Table 1). In contrast, at the end of the study, 1399 individuals were collected from 25 of 32

Table 1. Total abundance^a and frequency^b (in parentheses) of *Achaearanea* cf. *riparia*, by treatment and size class, from initial and final collections.

Size class (mm)	Initial (32)	Treatment (8)			
		Control	Fert.	Cage	Both
0.5–1.5	10 (5)	18 (5)	7 (4)	700 (8)	389 (5)
1.5–2.5	3 (2)	2 (1)	1 (1)	132 (8)	34 (5)
2.5–3.5	2 (2)	2 (2)	0 (0)	73 (7)	4 (2)
3.5–4.5	0 (0)	0 (0)	0 (0)	33 (5)	3 (3)
4.5–5.5	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
All sizes	15 (9)	22 (5)	8 (5)	939 (8)	430 (7)

^a Number of individuals of given size class across all plots of a given treatment.

^b Number of plots in which individuals of given size class were collected; total pools of plots considered for this frequency are given in headings (in parentheses).

plots (78%). Of the 16 caged plots, *A. riparia* was collected from 15 (94%).

Caging significantly increased both density and biomass of *A. riparia* (Figure 1; Table 2). Average density in caged, unfertilized plots (17.09 spiders/100 g foliage \pm 6.51 SE) was approximately 25-fold higher relative to control plots (0.60 \pm 0.26) and almost 80 times higher than in fertilized, uncaged plots (0.21 \pm 0.12; Figure 1). No individuals longer than 3 mm were collected on uncaged plots, compared to 37 larger (4–5 mm) spiders within cages (Table 1). These data are suggestive only, because small sample sizes in uncaged plots and missing values for size classes limit analyses by contingency tables.

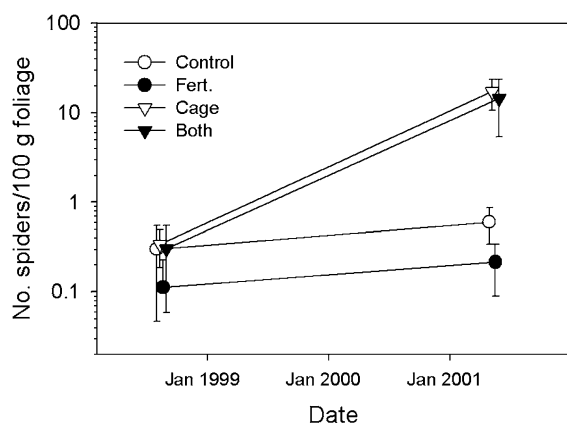


Figure 1. Response of *Achaearanea* spider density to fertilization and bird exclusion cages over a 33-mo manipulation. Shaded symbols (●, ▼) represent fertilized treatments, and upside down triangles (▽, ▼) are bird exclusion treatments. Plots are offset slightly to emphasize error bars (\pm 1 SE).

Table 2. Results of general linear model analysis of final *Achaearanea* density and biomass.

Source ^a	df	MS	F	P ^b
Density^c				
Fertilization (F)	1	3.023	4.343	0.076
Cage (C)	1	21.402	20.738	0.003
F \times C	1	0.999	1.346	0.284
Block (B)	7	1.966	2.649	0.111
F \times B	7	0.696	0.937	0.533
C \times B	7	1.032	1.391	0.337
Error	7	0.742		
Biomass^c				
Fertilization (F)	1	1.208	5.780	0.047
Cage (C)	1	4.914	15.120	0.006
F \times C	1	0.775	5.366	0.054
Block (B)	7	0.387	2.679	0.108
F \times B	7	0.209	1.448	0.319
C \times B	7	0.325	2.247	0.154
Error	7	0.144		

^a Italicized effects were treated as random; others were fixed.

^b Bold-face P-values are significant at $\alpha = 0.05$.

^c Spider density and biomass (numbers/100 g dry foliage) were transformed [$\ln(x + 1)$] prior to analysis.

Fertilization significantly reduced spider biomass, with a greater effect when plots were also caged (significant fertilization \times cage interaction; Table 2). The interaction must be viewed with caution because absolute biomass numbers are low in uncaged plots. Nevertheless, a negative fertilization response at fine spatial grain may be due to dilution across increased habitat, as fertilization led to a dramatic increase in vegetative biomass overall (Gruner 2004). These results did not change when absolute biomass (not standardized by foliage mass) was considered (fert.: $F_{1,7} = 8.07$, $P = 0.025$; cage: $F_{1,7} = 23.03$, $P = 0.002$; fert. \times cage: $F_{1,7} = 6.28$, $P = 0.041$). The interactive effect disappeared when the total biomass of foliage collected in samples was included in the model as a covariate, but the significant main effects remained (fert.: $F_{1,7} = 5.52$, $P = 0.051$; cage: $F_{1,7} = 21.95$, $P = 0.002$).

It is possible that presence and density of spiders were underestimated in the initial collections. As destructive sampling was necessarily more conservative at the experimental outset, foliage samples were smaller than at the conclusion of the experiment (overall foliage means \pm SE, $n = 88$; initial: 81.05 g \pm 5.57; final: 238.28 g \pm 8.18; one-tailed paired $t = -20.39$,

df = 138, $P < 0.0001$). Smaller foliage collections may have resulted in a lower probability of sampling individuals of rare species if they were present. Undersampling would result in a higher preponderance of null values (Table 1), possibly depressing the average density found initially (control plot means [no. spiders/100 g foliage] \pm S.E., $n = 8$; initial: 0.30 ± 0.25 ; final: 0.68 ± 0.28 ; one-tailed paired $t = -1.78$, $df = 7$, $P = 0.059$), but this does not account for the large difference in caged plots. Thus, exclusion of birds had a very strong effect on this single introduced spider species.

Discussion

Crawley (1987) defines a successful invasion as when an invader is able to increase from rarity. By this definition, *A. riparia* was present but not invasive until birds were excluded. Not only was this spider rare in my initial samples (Figure 1), but it also was absent from *Metrosideros* at a site less than 15 km away (F.S. Fretz, pers. comm.) and from extensive quantitative arthropod collections at 5 sites on 3 islands (Gruner and Polhemus 2003; D.S. Gruner, unpubl. data). Although *A. riparia* appears to be expanding its range, this study explains its continued rarity at the present site, and provides the first experimental demonstration of community resistance mediated by generalist birds. While anecdotes describing biotic resistance are abundant, particularly in highly modified biological control situations (Goeden and Louda 1976; Luck et al. 1999), experimental demonstrations of this phenomenon in natural terrestrial animal communities are rare (Schoener and Spiller 1995). In an interesting example, red crabs (*Gecarcoidea natalis*) prey on introduced African snails (*Achatina fulica*) in undisturbed native forests on Christmas Island in the Indian Ocean (Lake and O'Dowd 1991). Another invasive species, the long-legged, or yellow crazy ant (Formicidae: *Anoplolepis gracilipes*), preys on red crabs, negating the resistance and indirectly facilitating the invasion of snails (O'Dowd et al. 2003).

In the present case, an introduced species may enhance biotic resistance to other invasive species. *Zosterops japonicus*, the most abundant bird

at the site and throughout the Hawaiian Islands overall, thrives both in highly modified habitats and in native forests from sea level to 2000+ m in elevation (Scott et al. 1986). Comparative evidence suggests *Z. japonicus* competes for resources with native birds (Mountainspring and Scott 1985), which implies food resources are limiting for birds at some times or places. Spiders are among the most important prey for five of the six commonest passerines at this site, including *Z. japonicus* (Perkins 1903; Baldwin 1953; C.J. Ralph et al., unpubl. data). Nevertheless, these birds forage predominantly within tree canopies, leaving many microhabitats where these spiders and other introduced species may gain a foothold and persist in novel environments.

The observed effect of local invasion resistance thus results from predation by generalist, opportunistic predators. Biotic resistance is predicted to be strong where omnivores or generalists are abundant (Crawley 1986). Theoretical models predict that mobile generalist predators can also confer ecosystem stability (McCann et al. 1998), which has been linked, although controversially, to ecological resistance and diversity (Elton 1958; Pimm 1991). In case studies in terrestrial (Lake and O'Dowd 1991; Schoener and Spiller 1995) and aquatic systems (e.g. Reusch 1998; Miller et al. 2002), resistance also was attributable to generalist predators. In terrestrial plant communities, where there are more positive examples of biotic resistance (e.g. Hector et al. 2001), the potential effects of consumers remain unclear (Louda and Rand 2003).

Climatic constraints may have primacy over biotic resistance in many regions. For instance, Blackburn and Duncan (2001) linked the establishment success of introduced birds primarily to abiotic conditions at introduction sites worldwide. If sufficient propagules colonize the most conducive microhabitats, invading organisms would be less constrained by abiotic factors, and failure to invade may be more related to species interactions. More than 80% of the world's climatic regimes are found in the Hawaiian Islands (Juvik et al. 1978). Patterns of bird introduction, distribution and local extinction were consistent with competitive exclusion as an explanation for the failure of

introduced species to establish in Hawai'i (Moulton and Pimm 1983), although without direct evidence of biotic interactions (Simberloff and Boecklen 1991).

Since prehistoric times, extinction rates of birds on oceanic islands have vastly exceeded rates on continents (Steadman 1995). This study suggests that further loss of insectivorous birds or changes in species composition, as with forest fragmentation (Sekercioglu et al. 2002) and global climate change (Benning et al. 2002), may have ripple effects altering invasibility of island communities. The complete evolutionary absence or disproportionate loss of functional groups, such as top predators (Duffy 2002), may predispose habitats to decreased biotic resistance or increased ecological impact of introduced species. However, although islands may be more susceptible to the negative impacts of biological invasions (Levine and D'Antonio 1999), it clearly is premature to dismiss islands as inherently less resistant (D'Antonio and Dudley 1995; Simberloff 1995). Further additions of introduced species to island faunas may accelerate 'invasional meltdown' (Simberloff and Von Holle 1999; O'Dowd et al. 2003), or may slow the invasion of additional species by augmenting functional diversity and ecological resistance.

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