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Biotic resistance to an invasive spider conferred by generalist insectivorous birds on Hawaii 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 Hawaii 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: *Achaearanea* 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).

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 Hawaii. *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 [Cyperaeae]) 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 àpapane (*Himatione sanguinea*). Native òmaò (*Myadestes obscurus*), iìwi (*Vestiara coccinea*), àmakihi (*Hemignathus virens*), and èlepaio (*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. unpublished 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 unpublished manuscript), in this paper I focus on an introduced spider, *Achaearanea* cf. *riparia* (Blackwall) (Theridiidae). Like other theridiids, these spiders build small tangle webs between leaves and branches. All three *Achaearanea* species recorded from Hawaii are exotic. The cosmopolitan common house spider (*A. tepidariorum*), present in the islands for at least a century (Kirkaldy 1908), is strictly associated with anthropogenic habitat. *Achaearanea 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 Hawaii Volcanoes National Park and possibly other areas on the island of Hawaii (Gagné 1979; Gruner unpublished data; P. Krushelnycky unpublished 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

3

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.

150 plots (78%). Of the 16 caged plots, *A. riparia* was
151 collected from 15 (94%).
152   Caging significantly increased both density and
153 biomass of *A. riparia* (Figure 1, Table 2). Aver-
154 age density in caged, unfertilized plots (17.09 spi-
155 ders/100 g foliage $\pm$ 6.51 S.E.) was approximately
156 25-fold higher relative to control plots
157 (0.60 ± 0.26) and almost 80 times higher than in
158 fertilized, uncaged plots (0.21 ± 0.12, Figure 1).
159 No individuals longer than 3 mm were collected
160 on uncaged plots, compared to 37 larger (4–
161 5 mm) spiders within cages (Table 1). These data
162 are suggestive only, because small sample sizes in
163 uncaged plots and missing values for size classes
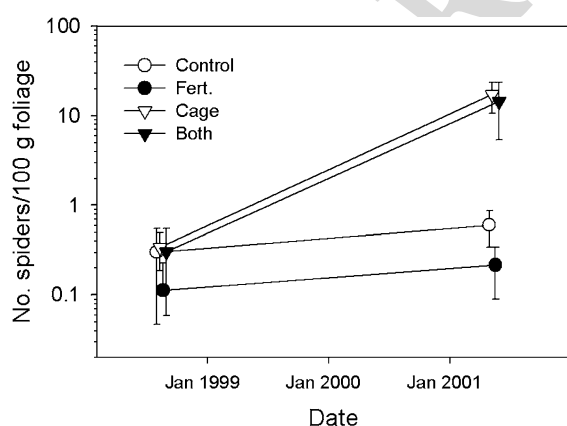164 limit analyses by contingency tables.

Figure 1. Response of *Achaearanea* spider density to fertiliza-tion 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 (± 1 S.E.).

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.

165   Fertilization significantly reduced spider bio-
166 mass, with a greater effect when plots were also
167 caged (significant fertilization × cage interaction,
168 Table 2). The interaction must be viewed with
169 caution because absolute biomass numbers are
170 low in uncaged plots. Nevertheless, a negative
171 fertilization response at fine spatial grain may be
172 due to dilution across increased habitat, as fertil-
173 ization led to a dramatic increase in vegetative
174 biomass overall (Gruner unpublished manu-
175 script). These results did not change when abso-
176 lute biomass (not standardized by foliage mass)
177 was considered (fert.: $F_{1,7} = 8.07$, $P = 0.025$;
178 cage: $F_{1,7} = 23.03$, $P = 0.002$; fert. × cage:
179 $F_{1,7} = 6.28$, $P = 0.041$). The interactive effect dis-
180 appeared when the total biomass of foliage col-
181 lected in samples was included in the model as a
182 covariate, but the significant main effects
183 remained (fert.: $F_{1,7} = 5.52$, $P = 0.051$; cage:
184 $F_{1,7} = 21.95$, $P = 0.002$).
185   It is possible that presence and density of spi-
186 ders were underestimated in the initial collec-
187 tions. As destructive sampling was necessarily
188 more conservative at the experimental outset,
189 foliage samples were smaller than at the conclu-
190 sion of the experiment (overall foliage means
191 $\pm$ S.E., $n = 88$; initial: $81.05 \, \text{g} \pm 5.57$; final:

192 238.28 g $\pm$ 8.18; one-tailed paired $t = -20.39$,
193 df = 138, $P < 0.0001$). Smaller foliage collections
194 may have resulted in a lower probability of sam-
195 pling individuals of rare species if they were pres-
196 ent. Undersampling would result in a higher
197 preponderance of null values (Table 1), possibly
198 depressing the average density found initially
199 (control plot means [no. spiders/100g foliage] $\pm$
200 S.E., $n = 8$; initial: 0.30 ± 0.25; final: 0.68 ± 0.28;
201 one-tailed paired $t = -1.78$, df = 7, $P = 0.059$),
202 but this does not account for the large difference
203 in caged plots. Thus, exclusion of birds had a
204 very strong effect on this single introduced spider
205 species.

206 Discussion

207 Crawley (1987) defines a successful invasion as
208 when an invader is able to increase from rarity.
209 By this definition, *A. riparia* was present but not
210 invasive until birds were excluded. Not only was
211 this spider rare in my initial samples (Figure 1),
212 but it also was absent from *Metrosideros* at a site
213 less than 15 km away (F.S. Fretz, personal com-
214 munication) and from extensive quantitative
215 arthropod collections at 5 sites on 3 islands (Gru-
216 ner and Polhemus 2003, Gruner unpublished
217 data). Although *A. riparia* appears to be expand-
218 ing its range, this study explains its continued
219 rarity at the present site, and provides the first
220 experimental demonstration of community resis-
221 tance mediated by generalist birds. While anec-
222 dotes describing biotic resistance are abundant,
223 particularly in highly modified biological control
224 situations (Goeden and Louda 1976; Luck et al.
225 1999), experimental demonstrations of this phe-
226 nomenon in natural terrestrial animal communi-
227 ties are rare (Schoener and Spiller 1995). In an
228 interesting example, red crabs (*Gecarcoidea natal-
229 is*) prey on introduced African snails (*Achatina
230 fulica*) in undisturbed native forests on Christmas
231 Island in the Indian Ocean (Lake and O'Dowd
232 1991). Another invasive species, the long-legged,
233 or yellow crazy ant (Formicidae: *Anoplolepis gra-
234 cilipes*), preys on red crabs, negating the resis-
235 tance and indirectly facilitating the invasion of
236 snails (O'Dowd et al. 2003).
237 In the present case, an introduced species may
238 enhance biotic resistance to other invasive spe-

239 cies. *Zosterops japonicus,* the most abundant bird
240 at the site and throughout the Hawaiian Islands
241 overall, thrives both in highly modified habitats
242 and in native forests from sea level to 2000+ m
243 in elevation (Scott et al. 1986). Comparative evi-
244 dence suggests *Z. japonicus* competes for
245 resources with native birds (Mountainspring and
246 Scott 1985), which implies food resources are
247 limiting for birds at some times or places. Spiders
248 are among the most important prey for five of
249 the six commonest passerines at this site, includ-
250 ing *Z. japonicus* (Perkins 1903; Baldwin 1953;
251 CJ Ralph et al. unpublished data). Neverthe-
252 less, these birds forage predominantly within
253 tree canopies, leaving many microhabitats where
254 these spiders and other introduced species may
255 gain a foothold and persist in novel environ-
256 ments.
257 The observed effect of local invasion resistance
258 thus results from predation by generalist, oppor-
259 tunistic predators. Biotic resistance is predicted
260 to be strong where omnivores or generalists are
261 abundant (Crawley 1986). Theoretical models
262 predict that mobile generalist predators can also
263 confer ecosystem stability (McCann et al. 1998),
264 which has been linked, although controversially,
265 to ecological resistance and diversity (Elton 1958;
266 Pimm 1991). In case studies in terrestrial (Lake
267 and O'Dowd 1991; Schoener and Spiller 1995)
268 and aquatic systems (e.g. Reusch 1998; Miller
269 et al. 2002), resistance also was attributable to
270 generalist predators. In terrestrial plant commu-
271 nities, where there are more positive examples of
272 biotic resistance (e.g. Hector et al. 2001), the
273 potential effects of consumers remain unclear
274 (Louda and Rand 2003).
275 Climatic constraints may have primacy over
276 biotic resistance in many regions. For instance,
277 Blackburn and Duncan (2001) linked the estab-
278 lishment success of introduced birds primarily to
279 abiotic conditions at introduction sites world-
280 wide. If sufficient propagules colonize the most
281 conducive microhabitats, invading organisms
282 would be less constrained by abiotic factors, and
283 failure to invade may be more related to species
284 interactions. More than 80% of the world's cli-
285 matic regimes are found in the Hawaiian Islands
286 (Juvik et al. 1978). Patterns of bird introduction,
287 distribution and local extinction were consistent
288 with competitive exclusion as an explanation for

the failure of introduced species to establish in Hawaii (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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