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Factors governing rate of invasion: a natural experiment using Argentine ants

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Abstract Predicting the success of biological invasions is a major goal of invasion biology. Determining the causes of invasions, however, can be difficult, owing to the complexity and spatio-temporal heterogeneity of the invasion process. The purpose of this study was to assess factors influencing rate of invasion for the Argentine ant (*Linepithema humile*), a widespread invasive species. The rate of invasion for 20 independent Argentine ant populations was measured over 4 years in riparian woodlands in the lower Sacramento River Valley of northern California. *A priori* predictors of rate of invasion included stream flow (a measure of abiotic suitability), disturbance, and native ant richness. In addition, baits were used to estimate the abundance of Argentine ants and native ants at the 20 sites. A multiple regression model accounted for nearly half of the variation in mean rate of invasion ($R^2 = 0.46$), but stream flow was the only significant factor in this analysis. Argentine ants spread, on average, 16 m year^{-1} at sites with permanent stream flow and retreated, on average, −6 m year^{-1} at sites with intermittent stream flow. Rate of invasion was independent of both disturbance and native ant richness. Argentine ants recruited to more baits in higher numbers in invaded areas than did native ants in uninvaded areas. In addition, rate of invasion was *positively* correlated with the proportion of baits recruited to by native ants in uninvaded areas. Together, these findings suggest that abiotic suitability is of paramount importance in determining rate of invasion for the Argentine ant.

Key words Argentine ants · Biological invasion · Biotic resistance · Disturbance · Rate of invasion

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Introduction

A major aim of invasion biology is to determine the factors governing invasion success (Mooney and Drake 1986; Drake et al. 1989; Kareiva 1996). The establishment and spread of invading species may be influenced by the abiotic environment, attributes of the target community, characteristics of the invader, and interactions between these variables (Orians 1986; Pimm 1991; Lodge 1993). Therefore, predicting invasion success in particular cases requires a detailed understanding of how colonization ability and subsequent population growth are influenced by different features of specific environments. This inherent complexity makes predicting the success of invasions a difficult challenge (Ehrlich 1989; Pimm 1991; Lodge 1993; Kareiva 1996), but one of enormous importance given the increasing ecological havoc wreaked by invading species (Vitousek et al. 1996).

Although many factors contribute to the success of particular invasions, several are considered generally important. The abiotic environment frequently sets clear limits on where species invade. For this reason, there is often a similarity between the abiotic environment of an invader's native range and that in its introduced range (Simberloff 1986; Crawley 1986; Brown 1989). Biotic interactions also influence invasion success. Elton (1958), for example, suggested that invasion success is inversely related to "ecological resistance" (i.e., the summed negative effects of competition, predation, parasitism, and disease). As a corollary, Elton (1958) predicted that areas with high species richness would be harder to invade than areas of low species richness. Although Elton's idea – now usually known as the biotic resistance hypothesis – has recently received renewed interest from ecologists (Diamond and Case 1986; Simberloff 1986; Case 1991; Case and Bolger 1991; Case 1996; Tilman 1997), its generality is hard to assess given the paucity of empirical tests. Lastly, disturbed habitats are often considered vulnerable to invasion. Disturbance may encourage invasions if it increases the availability of a limiting resource (Hobbs 1989) or decreases biotic resistance (Elton 1958).

One way to quantify the factors determining invasion success is to introduce propagules into manipulated environments or into environments that differ in known ways, and to then estimate invasion success through time (Hobbs 1989; D'Antonio 1993; Bergelson et al. 1993). Unfortunately, experimental introductions are often unethical, especially for species with known histories of invasiveness. For such species, studies that examine variation in the success of established populations may be the best method to appraise the factors governing invasion success. Natural experiments (*sensu* Diamond 1986) of this sort have advantages and disadvantages. Compared to manipulative experiments, natural experiments permit little control over the amount of variation within independent variables or among sites but may offer greater realism and generality given the large spatial and temporal scales often involved (Diamond 1986).

This study employs a natural experiment to examine the determinants of post-establishment invasion success in the Argentine ant (*Linepithema humile*) in northern California. Native to South America, the Argentine ant has spread via human commerce throughout the world, primarily to areas with Mediterranean and subtropical climates (Hölldobler and Wilson 1990). First recorded in California around 1907 (Newell and Barber 1913), Argentine ants are now widespread, established, and spreading in that state, but are confined to low-elevation areas with permanent soil moisture (Erickson 1971; Tremper 1976; Ward 1987; Knight and Rust 1990; Holway 1995; Suarez et al. in press). Argentine ant invasions offer excellent opportunities to study invasion success. First, Argentine ant invasion fronts advance slowly (typically <100 m year^{-1}; Crowell 1968; Erickson 1971) making it possible to measure spread accurately. Rates of spread are slow because colony reproduction occurs only through budding (queens do not participate in mating flights; Newell and Barber 1913). Second, Argentine ant invasion fronts are often spatially discrete (Erickson 1971; Holway in press a) making it possible to measure spread unambiguously. The well-delineated nature of these invasion fronts stems from the Argentine ant's mode of colony reproduction and from its ability to displace epigeic (i.e., aboveground foraging) native ants.

To clarify how different factors influence the rate of Argentine ant invasions, I followed 20 independent invasion fronts in riparian woodlands in northern California over a 4-year period. At each site and during each year, I measured the rate of invasion and several factors that might influence invasion success: stream flow (a measure of abiotic suitability), disturbance, and native ant richness. I then estimated the relative importance of each factor. Using baiting experiments, I also compared patterns of Argentine ant and native ant abundance across each contact zone to see if Argentine ants recruited more strongly to baits than did native ants and to determine if ant abundance was correlated with rate of invasion. This study offers an unusual opportunity to compare the relative importance of abiotic and biotic determinants of invasion success for a widespread invasive animal.

Methods

Study area

This study was conducted in riparian woodlands in the lower Sacramento River Valley of northern California. This region experiences a Mediterranean climate with a cool wet season (November–April) and a hot dry season (May–October). Argentine ants are common in riparian, urban, and some agricultural habitats (e.g., citrus orchards) in this watershed but are absent from drier areas such as chaparral and oak woodland (Ward 1987). Argentine ants are patchily distributed in riparian woodlands in the Sacramento River Valley (Ward 1987) but are established and spreading where they do occur (Holway 1995). These spatially discrete populations are the product of accidental human introductions and natural downstream dispersal events (Holway 1995). In 1993, I located 16 Argentine ant invasion fronts (and discovered four more in 1994) in riparian corridors bordering streams flowing east out of the Coast Range. Of these sites 17 were along creeks emptying into the Sacramento River; the remaining 3 sites were about 100 km south of the other sites and either drained into the San Joaquin River (two sites) or San Francisco Bay (one site). All 20 sites were in riparian woodland dominated by *Populus fremontii*, *Quercus lobata*, *Juglans hindsii*, *Aesculus californica*, and *Salix* spp. The locations and characteristics of the 20 sites are listed in Table 1.

Methods

I visited each site in July and August for 5 consecutive years (1993–1997) to measure how far Argentine ants had spread. Visits to each site were made on nearly the same date (i.e., within a week) in each year. During each visit, I mapped the distribution of Argentine ants and native ants relative to permanent landmarks (e.g., mature trees, large rocks) and marked the edge of the invasion front. The location of each invasion front was determined using baits (see below) and through visual inspections of potential nest sites (e.g., logs and rocks) and foraging areas (e.g., bare ground and trees). I estimated rate of invasion as the linear distance separating invasion fronts in consecutive years; the location of the invasion front in a given year was defined as the farthest upstream (or downstream) Argentine ant nest. Deterring rate of invasion was greatly simplified by the fact that invasion fronts were discrete and advanced slowly. Moreover, Argentine ants were confined to narrow riparian corridors (10–50 m wide); surrounding habitats were too dry to support this species.

The following three factors were predicted *a priori* as potentially important determinants of rate of invasion.

1. *Stream flow*. To assess the importance of this factor, I divided the 20 sites into two categories based on late summer stream flow: sites with intermittent stream flow and sites with perennial stream flow (Ward 1987).
2. *Disturbance*. I estimated disturbance using a composite index modified from Ward (1987). This index was the sum of six factors, each estimated on a scale of 0 to 2: encroachment by non-native trees (e.g., *Ailanthus*, *Tamarix*), absence or scarcity of large native trees, replacement of native understory plants by exotic species, presence of garbage, soil disturbance, and degree of human modification of habitats surrounding riparian corridor.
3. *Ant species richness*. For each site, ant species richness was estimated as the number of epigeic native ants recorded in an area

Table 1 Locations and characteristics of the 20 invasion fronts in this study (*rate* average rate of spread, m year^{-1}, *richness* native ant richness)

Creek	Location	Start	Rate	Flow	Disturbance	Richness
1. Putah	1.2 km E Monticello Dam	1993	49	1	6	9
2. Putah	2.3 km W Putah Cr. & Pleasants Val. Rd.	1993	21	1	2	10
3. Putah	0.6 km W Putah Cr. & Pleasants Val. Rd.	1993	23	1	5	5
4. Putah	1.4 km E Putah Cr. & Pleasants Val. Rd.	1993	−1	1	7	10
5. Putah	0.5 km NW Putah Cr. Rd. & McNeill Ln.	1993	−16	0	9	6
6. Putah	0.5 km N of S Fk. of Putah Creek confluence	1993	3	0	5	4
7. Putah	adjacent to the UCD Equestrian Center	1993	5	0	8	9
8. Putah	adjacent to the UCD Arboretum	1993	0	0	6	8
9. Putah	5 km E Mace Rd.	1993	17	1	5	4
10. Ulatis	0.3 km SE Ulatis Cr. & Pleasants Val. Rd.	1993	−21	0	7	4
11. Ulatis	0.3 km W Ulatis Cr. & Bucktown Lane	1993	0	0	5	5
12. Cache	2.75 km W Cache Cr. & Rd. 94B	1994	16	1	4	6
13. Cache	1.00 km W Cache Cr. & Rd. 94B	1993	19	1	8	7
14. Cache	0.75 km E Cache Cr. & Rd. 94B	1993	23	1	8	8
15. Willow Slough	1.2 km S Winters Canal & Rd. 23	1994	0	0	3	4
16. Willow Slough	0.1 km E Willow Slough & Rd. 102	1994	4	1	9	6
17. Gordon Slough	1 km W of Rd. 94B along Rd. 20	1994	6	1	3	8
18. Corral Hollow	3.3 km SW I-580	1993	19	1	2	6
19. Corral Hollow	2.7 km SW I-580	1993	12	1	4	4
20. Arroyo Del Valle	0.6 km S US Veterans Administration Hospital	1993	4	1	3	4

defined by the invasion front in the first year of the study and a point 100 m beyond. I kept a cumulative list of all epigeic ants recorded at each site; at most sites, few new species were added after the first year.

I used baits to confirm the location each invasion front and to estimate ant abundance. Baits are commonly used to survey ant faunas (Hölldobler and Wilson 1990) and are especially useful for detecting dominant, epigeic species (Ward 1987; Porter and Savignano 1990). During my annual visits to each site in 1993–1996, I established a 120-m bait transect oriented perpendicular to the invasion front (and parallel to the riparian corridor). Placing baits every 4 m in an approximately straight line, I put 10 baits behind the invasion front in the area occupied by Argentine ants and 20 baits ahead of the invasion front in the area still held by native ants. Thus, each bait transect extended 40 m into the invaded area and 80 m into the uninvaded area. The precise location of invasion fronts was not always known at the time baits were first placed on the ground. In such cases, I added several baits to both ends of the transect. For each transect, I identified and estimated the number of ant workers present at each bait after 120 minutes. I conducted all baiting in the morning (0800–1000 hours) over temperature intervals in which most common species were active. Baits were placed on numbered index cards and consisted of about 2.5 g of canned tuna in oil and 2.5 g apple jelly representing sources of lipids, proteins, and carbohydrates (Lynch et al. 1981; Fellers 1987).

Statistical analysis

I used multiple regression to estimate how stream flow, disturbance, and native ant species richness affect mean rate of invasion (m year^{-1}) over 4 years (or over 3 years for the four 1994 sites). Stream flow was entered as a dummy variable in the regression model: sites with intermittent stream flow (0) and sites with permanent stream flow (1). Standard regression diagnostics indicated that these data met the assumptions of multiple linear regression (SYSTAT 1992). In addition, multicollinearity did not appear to be a problem: independent variables were uncorrelated with each other, and tolerance values were high (SYSTAT 1992). Using paired *t*-tests, I also compared the proportion of baits to which Argentine ants recruited in the invaded portion of the transect with the proportion of baits to which native ants recruited in the uninvaded portion of the transect. The data points in each of these comparisons were the mean proportion of baits (at each site over 4 years, or over 3 years for the four 1994 sites) at which ants were present and to which >50, >100, and >200 workers recruited after 120 min. Because the raw data in these comparisons were proportions, they were arcsin transformed prior to analysis. All statistical analyses were performed using SYSTAT version 5 (SYSTAT 1992).

Results

About half of the variation in mean rate of invasion was accounted for by the multiple regression model (Table 2; $R^2 = 0.46$). However, the only significant factor in this model was stream flow; rate of invasion was independent of both disturbance and native ant richness (Table 2). On average, Argentine ants advanced 16.3 ± 3.5 m year^{-1} (mean ± 1 SEM) at sites with permanent stream flow ($n = 13$) and retreated −5.9 ± 3.8 m year^{-1} at sites with intermittent stream flow ($n = 7$). At sites where Argentine ants advanced consistently, invasion fronts were well-defined and native ant colonies failed to persist behind the advancing front (Fig. 1A). On occasion, Argentine ant nests became established a few meters ahead of the main invasion front in one year only to be enveloped by it in the next. At sites where they did not advance, Argentine ants were patchy and, perhaps as a consequence, native ants occurred more often along the inside edges of these fronts (Fig. 1B).

The mean proportion of baits at which Argentine ants were present in the invaded portion of the transect was not different from the mean proportion of baits at which native ants were present in the uninvaded portion of the transect (Fig. 2). However, Argentine ants recruited to a higher proportion of baits in the invaded portion of the transect than did native ants in the uninvaded portion of the transect; this difference held irrespective of what threshold number of workers was

Table 2 Multiple regression of the effects of stream flow, disturbance, and native ant richness on rate of invasion of Argentine ants at 20 invasion fronts. **A** ANOVA for full multiple regression model; **B** parameter estimates for the intercept and the three independent variables from the full regression model. The dependent variable in the regression was average rate of invasion (m year^{-1}) over 4 years (or over 3 years for 4 of the 20 sites)

Source	SS	*df*	*F*	*P*	R^2
A Analysis of variance					
Model	2037.7	3	4.53	0.018	0.46
Error	2398.9	16			
Total	4436.6	19			

Variable	Parameter estimate	Standard error	*t*	*P*
B Parameter estimates				
Intercept	−6.06	10.96	−0.55	0.59
Stream flow	18.34	6.13	3.00	0.01
Disturbance	−0.86	1.32	−0.65	0.52
Native ant richness	1.26	1.43	0.88	0.39

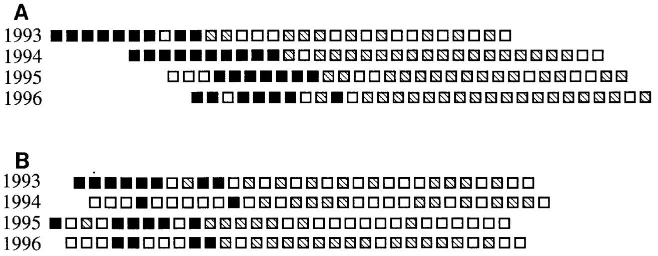

Fig. 1 Depictions of two Argentine ant invasion fronts through time for **A** a site (no. 19) where Argentine ants advanced every year, and **B** a site (no. 5) where Argentine ants failed to advance (each row shows the results of a bait transect: *filled squares* baits recruited to by Argentine ants, *shaded squares* baits recruited to by native ants, *open squares* baits to which no ants recruited). In the field, baits were placed 4 m apart in an approximately linear transect. In this figure, the bait transects within each site are oriented to demonstrate year-to-year movements of the invasion front

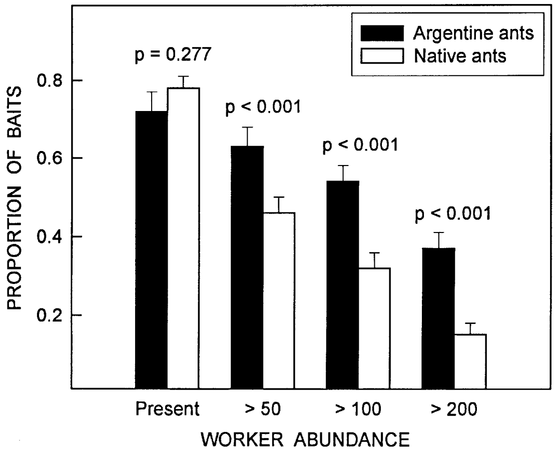

Fig. 2 Results of baiting experiments. Each *bar* depicts the mean (+1 SEM) of the mean proportions of baits at which ants were present and to which ants recruited (for three categories of abundance). *Filled bars* are for baits in the invaded part of the transect (i.e., baits with Argentine ants), and *open bars* are for baits in the uninvaded portion of the transect (i.e., baits with native ants). The proportion for each site and category (i.e., native ants or Argentine ants) is the mean from four bait transects conducted on successive years (or from three bait transects for the four 1994 sites). Sample size for each bar is 20 sites. The *P*-value above each pair of bars is from a paired *t*-test

used in the analysis (Fig. 2). Using the mean proportion of baits to which more than 50 workers recruited as an estimate of ant abundance, mean rate of invasion was positively correlated with both Argentine ant abundance ($r = 0.649$, $n = 20$, $P < 0.002$) and native ant abundance ($r = 0.438$, $n = 20$, $P < 0.05$). In addition, Argentine ant abundance and native ant abundance were positively correlated with one another ($r = 0.670$, $n = 20$, $P < 0.001$). The abundances of both Argentine ants and native ants were uncorrelated ($P > 0.05$) with measures of disturbance and native ant species richness.

Discussion

This study monitored the fates of 20 independent invasion fronts over a 4-year period. At each site, tens of thousands of Argentine ants and native ants interacted in a structurally complex and spatially heterogeneous environment. Because of the spatial and temporal scales involved, experimental manipulations of either Argentine ants (e.g., introductions) or native ants (e.g., selective removals) would have been nearly impossible to conduct with precision. Although natural experiments may lack the perceived rigor of manipulative experiments, they are the best way to quantify certain ecological phenomena (Diamond 1986).

Factors governing rate of invasion

Stream flow was the only highly significant predictor of rate of invasion in this study (Table 1). This finding reflects the physiological limitations of the Argentine ant and corresponds well to its regional distribution in California. Tremper (1976) found that, compared to ants native to California, Argentine ants desiccated more easily and were less tolerant of high temperatures. Moreover, unlike many native ants, Argentine ants nest superficially in the soil (Newell and Barber 1913), increasing their vulnerability to desiccation and heat stress. These characteristics confine Argentine ants to habitats that are relatively cool and moist, greatly restricting their range in California to areas along the coast, which receive moisture through summer fog, and mesic areas in the interior (Tremper 1976; Ward 1987; Knight and Rust 1990; Holway 1995; Suarez et al. in press). In riparian woodlands in the lower Sacramento River Valley, Argentine ants are found more often along permanent streams than intermittent streams (Ward 1987). Together these findings suggest that abiotic factors limit both the establishment and the subsequent spread of Argentine ant populations in California.

The results of this study also suggest that competitive resistance from the native ant community does little to curb the rate of invasion. Rate of invasion was independent of native ant species richness (Table 1) but *positively* correlated with native ant abundance. These findings run counter to the biotic resistance hypothesis (Elton 1958) and are surprising given the importance of interspecific competition in structuring ant communities (Hölldobler and Wilson 1990). A probable explanation for this result is that the competitive asymmetry between Argentine ants and native ants is so strong (Human and Gordon 1996; Holway, in press b) that rate of invasion is largely determined by abiotic suitability. Abiotic factors predominate as determinants of invasion success in other invasions as well (Simberloff 1986; Moyle and Light 1996). Although Argentine ants and native ants compete intensely for food resources (Human and Gordon 1996; Holway, in press b), these interactions appear relatively unimportant in affecting population-level processes, such as rate of spread. A similar result was reported by Bennett (1990) who found that house finches and house sparrows compete aggressively for nest sites, but that population-level changes at larger scales appeared independent of interspecific competition between the two species. Factors controlling ecological processes at one scale are often different from those controlling ecological processes at larger scales (Wiens 1986; Levin 1992).

Another unexpected result of this study was that rate of invasion was independent of disturbance (Table 2). Like other "tramp ants," Argentine ants are often viewed as thriving in disturbed habitats (Hölldobler and Wilson 1990). In southern France, for example, Argentine ants occur only around human habitation (Passera 1994). Likewise, in riparian woodlands in the lower Sacramento River Valley of California, Argentine ants occurred more often in disturbed areas than in less disturbed areas (Ward 1987). The findings of this study, however, suggest that disturbance (as defined here) does not influence rate of invasion. At least for the habitats in this study, the association between disturbance and the presence of Argentine ants may be correlational rather than causal (Simberloff 1989). Because Argentine ants are commonly introduced by people and because sites often visited by people tend to be disturbed, disturbed riparian areas may receive a disproportionate share of accidental introductions. Furthermore, because Argentine ants spread so slowly on their own, it may take years for Argentine ants to spread from disturbed points of introduction into less disturbed areas.

A caveat to the above interpretation is that relevant components of disturbance were not measured in this study. The exact manner in which disturbance abets invading species is often difficult to ascertain with clarity given the many kinds of disturbance, the different scales upon which they act, and the diversity of ways organisms may respond (Orians 1986). Nonetheless, some generalizations can be made. Hobbs (1989) predicted that disturbance will promote invasion if it increases availability of a limiting resource. In this system, food and nest sites may often be limiting, but it is hard to envision how disturbance (at least as defined here) might directly affect the availability of these resources. Elton (1958) and others have suggested that disturbed habitats have lower biotic resistance, but biotic resistance, at least in the form of interspecific competition from ants, appears of minor importance with respect to rate of invasion in this system. Tschinkel (1988), however, speculated that the occurrence of thief ants (specialized predators of other ants) in undisturbed habitats in Florida limited imported fire ants to disturbed areas where thief ants were absent. If correct, both disturbance and biotic resistance (in the form of predation) interact to control the success of fire ant invasions. The role that thief ants play in Argentine ant invasions remains an unexplored but interesting problem.

Comparisons with other invasions

Because Argentine ant colonies reproduce through budding, this species spreads slowly compared to other organisms. The observed mean rate of spread (16 m year^{-1}) was three orders of magnitude lower than the mean rate for ten terrestrial organisms (74.2 ± 40.7 km year^{-1}) listed by Grosholz (1996) (one-sample *t*-test: $t_9 = -13.36$, $P < 0.001$). Argentine ants also spread much less quickly than other invasive Hymenoptera, such as the africanized honey bee (Winston 1991) and the monogyne form of the imported fire ant (Wilson and Brown 1958). However, the rate of invasion reported here was strikingly similar to the rate (10–40 m year^{-1}) reported by Porter et al. (1988) for the polygyne form of the imported fire ant which, like the Argentine ant, reproduces chiefly through colony budding.

Although budding reproduction prevents Argentine ants from spreading quickly on their own, colonies are commonly introduced into new areas by jump-dispersal events such as human transport and floods (Newell and Barber 1913; Lieberburg et al. 1975). Because jump-dispersal events quickly carry Argentine ant colonies long distances, they are an important component of the large-scale dynamics of this invasion. For example, Argentine ants may be unable to colonize isolated mesic areas in interior California unless introduced there by humans. A qualitatively similar pattern of invasion was described by Johnson and Carlton (1996) for the zebra mussel (*Dreissena polymorpha*) which colonizes lakes, reservoirs, and areas upstream from established populations only though adventitious human introduction.

Conclusions

The results of this study suggest that abiotic factors (e.g., soil moisture) are the principal determinants of rate of invasion for Argentine ants. Although generally considered important, both disturbance and biotic resistance failed to influence rate of invasion in this system. An unexplored issue, however, is the role of biotic resistance and disturbance in the establishment of new Argentine ant populations. Because populations of competitively dominant species may often be impacted more by the abiotic environment than by interspecific competition, perhaps it is not surprising that abiotic factors govern rate of invasion for Argentine ants. However, if invasive species are often strong competitors, then abiotic factors should commonly be more important than biotic resistance (at least from interspecific competition) in controlling the success of such invasions. This hypothesis calls into question the generality of the biotic resistance hypothesis and should be tested with other species of invading organisms.

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