REPORTS

ECOLOGICAL RESISTANCE TO BIOLOGICAL INVASION OVERWHELMED BY PROPAGULE PRESSURE

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Abstract. Models and observational studies have sought patterns of predictability for invasion of natural areas by nonindigenous species, but with limited success. In a field experiment using forest understory plants, we jointly manipulated three hypothesized determinants of biological invasion outcome: resident diversity, physical disturbance and abiotic conditions, and propagule pressure. The foremost constraints on net habitat invasibility were the number of propagules that arrived at a site and naturally varying resident plant density. The physical environment (flooding regime) and the number of established resident species had negligible impact on habitat invasibility as compared to propagule pressure, despite manipulations that forced a significant reduction in resident richness, and a gradient in flooding from no flooding to annual flooding. This is the first experimental study to demonstrate the primacy of propagule pressure as a determinant of habitat invasibility in comparison with other candidate controlling factors.

Key words: field experiment; introduction effort; invasibility; plant invaders; richness.

INTRODUCTION

The colonizing success of nonindigenous species is extraordinarily unpredictable and varies by orders of magnitude from one place to another. Establishment of nonindigenous species in an area can be affected by abiotic conditions and disturbance level; properties of native species and community structure; and properties of invading species and the numbers of individuals introduced. Some communities appear to resist invasions of introduced species (Hobbs and Atkins 1988, Baltz and Moyle 1993, Von Holle et al. 2003). Invasibility, defined as the intrinsic susceptibility of an area to invasion (Richardson 2001), has been shown to differ between biomes (Lonsdale 1999). It is unclear whether the abiotic properties of the ecosystem (Burke and Grime 1996, Moyle and Light 1996, Holway 1998), biotic properties of the ecosystem (Levine and D'Antonio 1999), number of individual invaders (Beirne 1975, Veltman et al. 1996, Williamson 1996); or some combination of these factors (Lonsdale 1999, Rejmánek 1999, Williamson and Harrison 2002) determine invasibility. In their conceptual model of aquatic community invasibility, Moyle and Light (1996) identified the importance of habitat invasibility factors (biotic,

abiotic, properties of invaders; Lodge 1993) at each of the three phases of a nonnative invasion (arrival, establishment, and spread; Vermeij [1996]). They emphasized environmental resistance as the earliest and strongest factor that would affect the probability of establishment of an invading nonnative species. However, there has been a disproportionate emphasis on "biotic resistance" (ways in which the resident species repel invaders) in invasion resistance studies (Levine and D'Antonio 1999). Additionally, the relationship between propagule pressure and biotic and abiotic conditions in determining invasibility of natural habitats remains unclear (D'Antonio et al. 2001, Lockwood et al. 2005). Although there has been research on the various possible determinants of invasibility, no experimental studies have examined their relative importance. To elucidate the mechanisms governing habitat invasibility, we experimentally manipulated community richness in plots that experienced yearly or no flooding and inserted two treatments of invader addition into a riparian forest that experiences little human disturbance. The research described here is unique in simultaneously testing three components of invasibility: biotic and abiotic properties of the recipient ecosystem, or ecological resistance (Lodge 1993), and propagule pressure, the number of invaders introduced into the system.

Our nested experimental design crossed propagule pressure of invaders with abiotic and biotic resistance

PLATE 1. The floral structure of *Parnassia asarifolia*, a streambank herb, found in the streamside site of the study area. Photo credit: B. Von Holle.

factors. Our objective was to assess the relative importance of these three interdependent factors on the invasibility of a naturally flooding riparian forest. We define propagule pressure as the composite measure of the number of individuals released into a region to which they are not native, which incorporates both the absolute number of individuals involved in any one introduction event (propagule size), and the number of discrete release events (propagule number) (Lockwood et al. 2005). Our four-year study focuses on the establishment of seedling and adult plants transplanted in two discrete release events. For many plant species, the conditions for establishment are more stringent than the germination stage (Turnbull et al. 2000). We used plants and seedlings as invaders rather than seeds, because ecological resistance may be more important to plant establishment than to the germination of nonnative invaders. We used plants growing in the watershed as invaders to avoid the potential introduction of novel genetic variation. We call these plants "invaders" even though some are native species (Appendix A). We planted both native and nonnative invaders to understand differences in ecological resistance factors to establishment by native and nonnative plants.

Many factors can covary with the species richness of an area, such as disturbance, nutrients, climate, and propagule pressure. These extrinsic factors influence invaders and residents alike and appear to affect relationships between species richness and invasibility (Levine and D'Antonio 1999, Naeem et al. 2000). By directly manipulating the plot richness in situ we reduced the influence of these covariates on invader survival. We separated the effects of propagule pressure from those caused by stream flooding by planting the same number of invading individuals per plot along a flooding gradient. This naturally flooding riparian area is a model system to study properties of ecological resistance (biotic plus abiotic factors; Lodge [1993]) simultaneously, as all factors operate within contiguous forest cover.

MATERIALS AND METHODS

We conducted the research at Big Stony Creek (38°26′ N, 81°50′ W), a second-order creek (Leopold et al. 1964) within the Jefferson National Forest in southwestern Virginia that experiences little human disturbance and floods naturally (see Plate 1). All plots were located under canopies of evergreen or deciduous temperate forests. The vegetation types were *Tsuga canadensis* forest with *Rhododendron maximum* understory in the streamside regions and *Liriodendron tulipifera–Quercus alba–Q. rubra–Acer saccharum* forest with *Kalmia latifolia*, *Ilex opaca*, and *Rhododendron maximum* understory in the upper terrace sites (Suiter and Evans 1999).

To determine how spatial distribution of nonnative species varies with distance from the creek, we surveyed 64, 2 m diameter, circular plots within transects that were perpendicular to the river for nonnative species richness and abundance under riparian forest can-

opy. These 64 plots were surveyed under forest canopy and at 1, 5, 20, and 40 m from the creek within 16 randomly chosen transects along the length of Big Stony Creek.

Ecological resistance

We tested the role of the biotic component of ecological resistance by manipulating resident species richness prior to the propagule pressure treatment. Randomly chosen plots located in two streamside and upper terrace sites that experience yearly and no flooding, respectively, were assigned low (low richness), intermediate (intermediate richness), and high (control and digging control) species richness subplot treatments of the resident communities. All experimental plots were located under forest canopy and each covered a 70 × 10 m area of level ground. Each plot had four rows of 1.5 × 1.5 m subplots: two plots were established in each of the streamside and upper terrace areas. The first pair comprised the 2× treatment, with 10 subplots per row, and was manipulated, and first censused, in 1999. The second pair comprised the 1× treatment, with 14 subplots per row, and was manipulated in 2000 (Appendix B). Species richness and stem densities were censused in each subplot prior to manipulation. Subplot species richnesses were lowered for low- and intermediate-richness treatments or left unchanged for high-richness treatments. We manipulated subplot species richness of the low-richness treatment by reducing the number of species in the plot to two randomly picked species per functional group, for a total of eight species per plot. We classified plants into four functional groups based on aboveground biomass (small vs. large) and root structure (taprooted vs. branching or adventitious) for a separate study concerning invasion by functional groups (Von Holle and Simberloff 2004). These functional groups were; SN (small aboveground biomass, non-taprooted structure), LN (large aboveground biomass, non-taprooted structure), LT (large aboveground biomass, taproot), and ST (small aboveground biomass, taproot) (Von Holle and Simberloff 2004). Another set of subplots had one randomly picked functional group either removed or lowered to one species (intermediate richness). The ''high-richness'' treatment was left with the original complement of plants (control plots). In plots to control for the effect of digging, all the plants of the randomly chosen functional group per plot were uprooted and replanted (digging control). Although we manipulated subplot richness, we left manipulated subplots with their original densities. We did this by filling the empty holes left by removed resident plants with individuals of the randomly picked species that were selected to remain in the subplots. These replacement plants were collected from a nearby, forested, transplant area. Thus, we manipulated the plot richness while allowing plot density to vary naturally. All manipulated plants were less than 0.5 m tall.

Abiotic influences on native and nonnative invader survival were explored by placing these manipulated subplots along a flooding gradient and monitoring invader survival (see the *Invasibility* section below for description of invaders). Site treatments were assigned to incorporate yearly flooding. Although there were frequent floods, they were not large enough to cover the entire streamside treatment area during the drought winter years that occurred in the southern Appalachians from 1999 through 2001. Thus, only 24 out of 96 streamside subplots were regularly flooded. The two ''streamside'' plots (adjacent to the creek) were frequently and partially flooded every year from approximately December through April (Von Holle 2002) and the two ''upper terrace'' plots (in the second level of the floodplain) were not flooded during the experimental time frame. We use the term ''flooding condition'' to indicate whether that subplot flooded (flooded or unflooded) during the previous year. Subplot flooding status was confirmed by the presence of debris covering the subplots after the yearly spring floods.

Invasibility

We explored the role of propagule pressure concurrently with ecological resistance by planting a total of 10 native and nonnative invader individuals per transplant event, and with two discrete release events, in the manipulated subplots along the flooding gradient. After a two-week period to allow for rerooting of the manipulated resident plants, the experimental subplots were planted with 10 adults and/or seedlings (<0.5 m) of individual invader species randomly chosen from widespread native and introduced species commonly found throughout the floodplains of Big Stony Creek and with similar, forested, habitat requirements. We planted experimental plots with two treatments of propagule pressure and monitored individual invader survival and establishment. Some of these plots—the one-time propagule pressure treatment, 1× treatment (1120 individual native and nonnative invaders in 112 subplots)—received the planting treatment only in the second year, 2000. The two-time propagule treatment, or 2× treatment, comprised 80 subplots that each received 10 transplanted individual invaders in both 1999 and 2000 (800 native and nonnative invaders into 80 subplots, Appendix B). These invaders were taken from 50-m transects laid perpendicularly to Big Stony Creek in forested areas. One nonnative or native species (in order of priority) was systematically sought and dug up every 5 m. These 10 native and nonnative invaders were inserted into the subplot as equidistantly as possible, placed on three parallel, diagonal lines, with the middle line the hypotenuse of two equilateral triangles comprising the inner 1 × 1 m of the subplot. Subplots received different species mixes. Owing to the random selection of 10 individuals, it is possible that there could be more than one individual of one species within a subplot. Each plant was marked with metal tags and

watered daily for one week and then once every other day the following week. Survival data for these analyses were gleaned from the censuses that occurred two weeks after planting and every year thereafter for three ($1\times$ and $2\times$, second invader addition) and four years ($2\times$, first invader addition), respectively. The first invader addition of the $2\times$ treatment was the only invader set with four years of data. We considered deaths only up to the third or fourth year, depending on propagule pressure addition, after which time the transplants were censored and not represented in the analysis.

Statistical analyses

Ecological resistance.—We compared the influence of abiotic, biotic, and propagule pressure variables on the invasion success of transplanted invaders by plant origin (native, nonnative). We performed multiple regressions of percentage survival of invaders by origin (native, nonnative) within each plot in the final census year as dependent upon the presence of other transplants (i.e., $2\times$ treatment or not), duration of flooding that occurred in 2002 (measured by taking the distance from the ground to the top of the flood debris that accumulated above plots; this is a proxy for yearly flooding inundation/duration), manipulated plot richness as of 2001, plot density as of 2001, soil volumetric water content, soil carbon, light penetration, and size of nearest overstory shrub and tree. We removed any factors that we did not a priori consider to be important to invader survival or that exhibited multicollinearity.

Invasibility.—To explore the relative importance of these three factors to habitat invasibility, we used a log-linear Poisson regression model. Habitat invasibility was assessed by the total number of native and nonnative invaders that survived to the end of the experimental time period, or net invasion success, within each subplot. The variables used in the analysis to predict number of surviving invaders per plot were invader pressure treatment ($1\times$, $2\times$), flooding treatment (flooded or not), richness (we used the richness as surveyed in 2001 because manipulated plot richness changed over time), and naturally varying plot density, censused in 2001. We used number of surviving native and non-indigenous invaders from each plot in the years 2000 to 2002, or the years that the $2\times$ treatment was complete. Poisson regressions were used instead of a nested ANOVA analysis because of the unbalanced experimental design. The $2\times$ treatment had no low-richness treatments and there were no flooded, intermediate-richness treatment subplots in the $1\times$ treatment (Appendix B). Poisson regression tests the number of survivors of each treatment through time (Stokes et al. 2000). We could test invasibility of the plot to net invasion by combined native and nonnative invaders, as subplots within each propagule pressure treatment received equal numbers of all invaders (native and nonnative invaders, combined). However each plot had different proportions of plant origins, making an invasi-

bility analysis by plant geographic origin (native, nonnative) impossible. All analyses were performed with SAS version 8.2 (SAS Institute 2001).

RESULTS

Nonnative species abundance and richness was unrelated to distance from the river, according to regression analysis, indicating that there are no inherent gradients of nonnative species with distance from the river. There were no significant differences in invader survival between the digging control and the control plots, as indicated by logistic regression analysis. This result validates our experimental method of reducing subplot richness by transplanting resident community members. Additionally, there was no difference between survival of plants in the outer 0.5-m perimeter of the plot with those of the inner 1×1 m of the plot, as indicated by contingency table analysis, which suggests that there are no edge effects on the survival of transplanted invaders. Thus, our experimental treatments designed to test ecological resistance factors important to native and nonnative survival and net habitat invasibility are not confounded by these habitat and methodological issues.

Ecological resistance

Ecological resistance to invasion depended upon the geographic origin of the invading plant. Survival of native transplants in the invader pool was significantly, positively influenced by the presence of co-occurring invaders (native and nonnative transplants combined) and negatively affected by flooding and overstory tree size. By contrast, factors important for ecological resistance to nonnative species invasion were quantitatively different (Table 1). Flooding significantly facilitated invasion by nonnative species, while greater resident richness significantly decreased the percentage of surviving individuals of nonnative species.

Invasibility

Propagule pressure was the only experimental treatment that significantly predicted the number of surviving invaders per plot over time, as indicated by yearly number of surviving native and nonnative plants in plots from 2000 to 2002 (Table 2). The interaction between propagule pressure and plot density was statistically significant, indicating that the net number of surviving invaders in the $1\times$ treatment increased with increasing resident density (Fig. 1), a factor allowed to vary naturally in the study design. Resident plant density is important in modifying the role of propagule pressure. Propagule pressure treatment was the only statistically significant variable (parameter estimate = -0.5151, $P < 0.0001$, with reference group as propagule pressure treatment $2\times$, nonflooded plots) in a model using only main effects. However, the model with the interaction (pressure $\times$ density) had a significantly better fit (Table 2). Plots with the two-time in-

TABLE 1. Ecosystem factors that determine resistance to invasion, as determined by multiple regression.

	Regression parameters		
Response variable	All invaders	Native	Nonindigenous
Co-occurring invaders	0.2071**	0.2373**	0.1562
Flooding	−0.0055	−0.0106*	0.0189**
Plot richness	−0.0046	0.0010	−0.0251*
Plot density	−0.0004	−0.0003	0.0010
Soil water	0.7631	0.6317	−0.0746
Soil carbon	−1.576	−2.272	3.007
Light penetration	0.1740	0.2079	0.8307
Overstory shrub size	0.0045	0.0092	−0.0149
Overstory tree size	−0.0043	−0.0060*	−0.0019
Overall r^2	0.2207	0.2212	0.1940
Overall F (P)	2.01 (0.0519)	1.99 (0.0555)	1.63 (0.1264)

Notes: All independent variables were entered and retained for each model. Three models were run (df = 9): all invaders combined, native species, and nonindigenous species percentage survivorship as dependent on response variables, by plot in 2002.
* $P \leq 0.05$; ** $P \leq 0.01$ for tests of significant difference of parameter values from 0.

vasion addition, on average, contained more than twice the number of surviving native and nonnative invaders than those with the one-time addition treatment (mean ± SE number of surviving invaders in 2002 by treatment; 1×, 2.72 ± 0.20; 2×, 6.54 ± 0.30; unpaired t test, df = 145, t = 10.5, P < 0.0001).

Invader survival by origin

Native and nonnative plants did not differ in establishment success across the two flooding treatments, according to two-way analyses of variance of one- and two-year survivorship. Nevertheless, survival curves of nonindigenous and native species differed significantly, according to a Kaplan-Meier (Lee 1992) survivorship analysis (log-rank chi-square = 158.9, df = 1, P < 0.0001). Nonindigenous species had slightly higher survival two weeks after transplanting, but their survival declined precipitously relative to native survival during the following one-, two- and three-year censuses.

TABLE 2. Experimentally manipulated and naturally occurring ecosystem factors that determine number of surviving invaders from 2000 to 2002, as determined by a Poisson regression model.

Response variable	df	Parameter estimate	P
Propagule pressure	1	−0.65	<0.0001
Flooding	1	0.06	0.1967
Plot richness	1	0.005	0.3133
Plot density	1	−0.001	0.0213
Density × pressure	1	0.002	0.0005

Notes: The reference group in this analysis was propagule-pressure treatment 2×, nonflooded plots. Parameter estimates and P values provided indicate tests between each parameter and the chi-square values, which were conducted after the Poisson analysis of goodness of fit for the model. Model fit is valid, as indicated by the nonsignificant chi-square value of the log-likelihood difference test between the full interaction model and the current model (χ^2_{10} = 3.00, df = 550, P = 0.981).

DISCUSSION

Invasibility

The positive density-dependent interaction of native and nonnative invaders with resident plant density might have resulted from the severe drought in the southern Appalachians during the experimental years. In the low invader-propagule treatment, facilitation between invaders and resident plants might have occurred during this stressful environmental period, as facilitation between plants generally increases along stress gradients (Bertness and Callaway 1994, Callaway et al. 2002). A threshold for the positive effects of resident plant density might have been crossed with the two-time invader addition treatment, with the number of surviving invaders in the 2× treatment stable across varying resident densities.
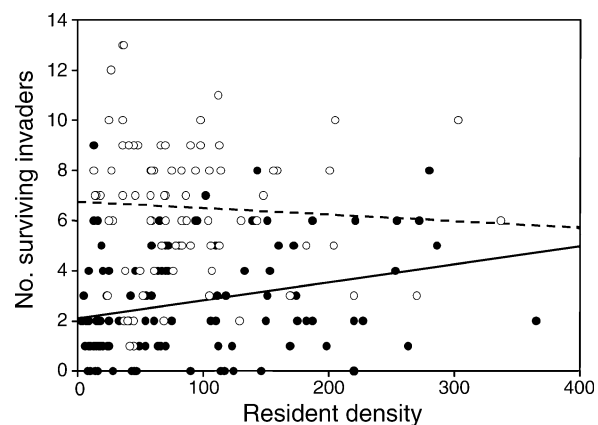

FIG. 1. Dependence of number of surviving invaders (per plot) on naturally varying resident densities of plots. Solid circles indicate 1× treatment subplots, and open circles are 2× treatment subplots (one-time propagule treatment, or 1×, n = 114; two-time propagule treatment, or 2×, n = 80). Simple regression lines are provided for each propagule-pressure treatment: dashed line for the 2× treatment and solid line for the 1× treatment.

Propagule pressure has been assigned a special importance in invasibility (Simberloff 1989, Williamson 1996). Levine (2000) established that the resident species richness of experimentally manipulated riparian plots in Southern California did not have as great an effect on invader survival as did the number of individual invaders added. Additionally, the intensity of propagule pressure, rather than any environmental factor, best explained the invasion of South Africa's Agulhas Plain by three woody invasive species (Rouget and Richardson 2003). It has been suggested that propagule pressure may be the most important factor in establishment success of nonnative species of various taxa in a variety of ecosystems worldwide (Lonsdale 1999, Fine 2004). This is the first experimental study to demonstrate the dominance of propagule pressure as the primary determinant of habitat invasibility in comparison with other candidate controlling factors. The physical environment (flood regime) and the number of established resident species had negligible impact on net native and nonnative invasion success as compared to propagule pressure, in spite of manipulations that forced a significant reduction in resident richness, and a flooding regime that varied drastically among plots. Policy implications are clear: any reduction in the rate at which propagules of nonindigenous species arrive at sites is likely to reduce greatly the probability that invasions will succeed.

Ecological resistance

The factors in this study that we found to be important for ecological resistance to nonnative invaders accord with classic invasion biology theory (Elton 1958), which predicts that invasion is facilitated by disturbance and inhibited by richer communities. However, this result conflicts with large-scale observational studies reporting a positive relationship between resident species richness and invasibility (Stohlgren et al. 1999, Brown and Peet 2003). The reason for this discord may be that habitat diversity accounts for this relationship at a large scale but not at a small one (Lonsdale 1999). Additionally, the interaction of native biodiversity with nonnative invaders may depend on abiotic conditions (Von Holle 2005). Interactions between particular invader species and community types may be too idiosyncratic to extrapolate to ecosystem resistance at the landscape scale (Higgins et al. 1996). Our study assessed neighborhood-scale resistance to invasion. In our system, the ecosystem factors that account for resistance to nonnative species differ categorically from those that inhibit native species establishment.

Flooding and the number of resident species did not substantially influence overall habitat invasibility, whereas the number of plants added to the plots and the density of residents did. The positive density-dependent response in the low propagule pressure treatment to resident density indicates that positive inter-

actions between invaders and native communities may be more common than assumed previously (Richardson et al. 2000). In this system, propagule pressure overwhelmed ecological resistance to invasion. However, these findings are tempered by the fact that we extracted all invaders from habitats similar to our plots. Given their presence in this forested riparian system, the nonnative invader species chosen may have already overcome environmental resistance to their establishment. Additionally, our experiment measured ecosystem effects on establishing seedlings and adult plants. Ecological resistance might have different impacts on natural seed dispersal. Nevertheless, our finding of the importance of propagule pressure and its interaction with the resident biota for invader establishment success, if confirmed more widely, has profound implications for invasibility studies. Propagule-pressure studies of animals indicate that the higher the propagule intensity, the greater the probability of successful establishment (Beirne 1975, Veltman et al. 1996, Green 1997). This result, like ours, suggests that the most useful types of study for determining the mechanisms of invasion into natural areas would concern propagule pressure factors (e.g., life history characteristics of the invader, Allee affects, or association with human sources) and the community simultaneously (D'Antonio et al. 2001), rather than simple tests of community influence on invasion. Finally, knowledge that the ecosystem factors that inhibit invasion by nonnative species differ qualitatively from those that inhibit establishment by natives can serve as guidelines to conserve habitats likely to repel invasion by nonnatives and promote native establishment.

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APPENDIX A

A table listing, by origin and growth form, the plant species in the study site is available in ESA's Electronic Data Archive: *Ecological Archives* E086-174-A1.

APPENDIX B

A figure showing the experimental design for the invaders placed in the 192 subplots sampled in this study is available in ESA's Electronic Data Archive: *Ecological Archives* E086-174-A2.