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RANKING THE COMPONENTS OF ECOLOGICAL RESISTANCE TO BIOLOGICAL INVADERS: AN EXPERIMENTAL MANIPULATION IN A SOUTHERN APPALACHIAN RIPARIAN FOREST

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

MaryBeth (Betsy) Von Holle
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DEDICATION

This dissertation is dedicated to my parents, Elizabeth and William Von Holle, who have inspired and supported me in achieving my ambitions.

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ABSTRACT

The theory that communities can withstand introductions of non-natives is called "ecological resistance," which was hypothesized to consist of three interdependent elements: (1) environmental resistance, which may be mediated through natural disturbances; (2) biotic resistance, which is a consequence of plant adaptive strategies; and (3) demographic resistance, which may be expressed as differential dispersal and establishment. I separated the influences of natural disturbance, biotic resistance, and demographic resistance and ranked their contributions to ecological resistance with a field experiment. This research was conducted at Big Stony Creek, a naturally flooded system within the Jefferson National Forest in southwestern Virginia. I manipulated resident diversities and functional group representation along a disturbance gradient and planted differing quantities of invaders into these manipulated plots. Success of an invasion was measured by survivorship and growth of the invader. I found that demographic effects were mostly responsible for invasibility of this riparian system, with environmental and biotic factors contributing much less to the variation in invasibility. The natural disturbance of flooding enhanced resistance to non-indigenous species invasion and was a significant factor in overall invasibility of this habitat. Biotic factors were not significant deterrents to invasion; however I revealed a lack of intra-functional group competition within the biotic component of ecological resistance. I also found a strong influence of canopy and understory functional group composition on invader survivorship and a change in the richness-invasibility relationship across flooding regimes. Additionally, I reviewed the literature in paleoecological, historical, and experimental studies of plant species invasions to illustrate the relevance of biological inertia in plant communities to invasion ecology. I introduce inertia as a fourth component of ecological resistance to biological invasion. This will be an additional component in future studies ranking components of ecological resistance. I predict that in this system the environmental and biotic resistance influences on invader survivorship relative to invader addition pressure are low on a yearly basis and will have great cumulative impact that will grow over long periods of time.

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INTRODUCTION

Ranking the Components of Ecological Resistance to Biological Invaders: An Experimental Manipulation in a Southern Appalachian Riparian Forest

Introduction

The hypothesis that communities withstand introductions of non-natives is called "ecological resistance", which was described by Elton (1958, p.115) as "forces of nature" that keep "numbers down to a level that prevents a species becoming any kind of dominant in the community and damping down or even completely leveling major fluctuations and outbreaks." Chapman (1931) first introduced this idea as "environmental resistance", which included the forces of the biotic community, "biotic resistance", and the environment, "physical resistance", into which the nonindigenous species established. He likened the process of invasion to the physics of current flow:

> "It is possible to calculate the potential number of individuals that a species will produce if we assign a partial biotic potential to the species as the result of an investigation of its sex ratio and the number of young produced in a unit of time under given conditions. It is also possible to measure the number of individuals which are actually present in the environment at any time. The difference between the two numbers thus obtained must represent the reduction of the potential number of individuals by the resistance of the environment, in much the same way that the resistance of an electric circuit reduces the current from its potential to its actual value." (Chapman 1931, p. 195)

Lodge (1993a, b) hypothesized that the outcome of an invasion is affected by three interdependent elements: (1) environmental resistance (temperature, water flow, chemistry, structure, and abiotic resources), (2) biotic resistance (prey availability, competition, predation, disease, parasites), and (3) demographic resistance (numbers introduced, ability to increase when rare). Demographic resistance, as envisioned by Lodge (1993 a, b), is primarily a trait of the invader, and not of the invaded community. Moyle and Light (1996) used these three interdependent elements to extend Elton's (1958) concept of ecological resistance to include demographic resistance. Their model of invasion emphasized environmental resistance as the earliest and strongest factor that would affect an invading species.

Because terminology related to resistance to biological invasion has been duplicated and not thoroughly defined in the past, I establish terms for each factor of resistance to

invaders (noted in bold). The term **biotic resistance** will be used to refer to any direct or indirect interaction between species that are introduced into the area with resident species (Elton 1958). I use the term **environmental resistance** to refer to abiotic influences, such as temperature, flow, structure, chemistry, and abiotic resources (Moyle and Light 1996). I call **ecological resistance** what Chapman (1931) originally referred to as "environmental resistance", which consists of **biotic** and **environmental resistances** (Elton 1958). I use the term **invasibility** to refer to the entire process of invasion that ultimately results in the susceptibility of an area to invasion (Lonsdale 1999). This integration of nonindigenous species into an area can be affected by climate and the level of disturbance (**environmental resistance**), properties of native species and community structure (**biotic resistance**), and properties of invading species and the numbers introduced (**demographic resistance**). These definitions will be used consistently throughout the dissertation. Last, I will introduce (with H. Delcourt and D. Simberloff) the term **biological inertia,** which is the time lag between establishment of an invader and its integration into the recipient community, owing to the microenvironmental influences of the recipient biotic community. **Ecological resistance** will then be used to refer to **biotic inertia** and **environmental** and **biotic resistances** to biological invasion. **Invasibility** will then be used to describe all of the previously-described factors of invasibility, including **biotic inertia**. It is important to note that my definition of ecological resistance is different from that introduced by Lodge (1993a, b) and Moyle and Light (1996), because I do not include demographic resistance as a factor of resistance, rather as a factor in invasibility. All of the factors included within both ecological resistance and invasibility are assumed to be interdependent.

Some communities appear to resist invasions of small numbers of introduced species (Hobbs and Atkins 1988, Baltz and Moyle 1993). The factors that negatively influenced impact of weed biocontrol insects in the Silwood Project on Weed Biocontrol, as ranked in order of importance by percentage of introductions affected by each factor, were climate (44), incompatibility (33), predators (22), competion (12), parasitoids (11), and disease (8) (Crawley, 1986). Thus, abiotic factors (usually bad weather) were the most important in influencing the performance of these introduced herbivores, followed by the biotic factors of predation and competition.

Although there have been studies of the various types of ecological resistance, no quantitative studies have examined the relative importance of these. Historically, ecological resistance studies have focused on biotic resistance (Levine and D' Antonio 1999). Levine and D' Antonio (1999) argued that a long-held dogma that high-diversity systems resist biological invasion has not been supported by experiments and observations. Moyle and Light (1996) suggested that environmental resistance to freshwater fish invasion is stronger than either biotic or demographic resistances. Dantonio (1993) found that the importance of environmental and biotic resistance depended on the plant community. Byers (2001) revealed that physical habitat attributes of a soft-sediment northeastern Pacific coastal area mediated biotic resistance, in the form of predation, on the invasion of a soft-shelled non-indigenous clam. Clearly, future research must test multiple hypotheses to discover the mechanisms of invasion resistance. The study described here is unique in experimentally testing simultaneously both (previously described) components of ecological resistance. The following chapters explore the biotic (community structure and richness) and environmental components of ecological resistance. In the last chapter, I introduce a new component of ecological resistance to biological invaders: biological inertia.

Biotic Resistance

'Biotic resistance' is the theory that the key to the success of an invader is the degree of resistance by the resident biota and that this resistance is somewhat predictable (Simberloff 1986). High species diversities might be expected to decrease nutrient availability and increase competition, predation, disease, and parasites. All of the latter factors may contribute to biotic resistance (Elton 1958, Simberloff 1986, Ricklefs 1987, Pimm 1991). Mathematical models of the diversity-invasibility relationship supported this view (Robinson & Valentine 1979, Post & Pimm 1983, Shigesada et al. 1984, Drake 1988, 1990, Case 1990, 1991; Law and Morton 1996). However, Levine and D'Antonio (1999) point out that many of the underlying assumptions of these models may not exist in real communities. Possible spurious model assumptions included interactions at small spatial scales, invader interactions similar to those of residents, and equilibrium states of the invader and of the invaded communities (Levine and D' Antonio 1999).

Observational studies

Many observational efforts have sought to detect structure in the composition of natural communities by testing for constancy in the proportion of species from each guild. If competition is more severe between species in one guild than between species in different guilds (Pianka 1980, Simberloff and Dayan 1991), the number of species in each guild at a site should be limited. Thus the proportions of species in each guild are expected to be relatively constant among sites if assembly rules are operating (Wilson 1989b). Fox and associates have demonstrated community structure through assembly rules with several data sets of naturally-occurring desert rodents (Fox 1987, Fox 1989, Fox and Kirkland 1992, Fox and Brown 1993, Brown et al. 2000). Stone et al. (1996) randomized the same rodent communities tested in the previous studies and discovered that the evidence for community structure found by the authors rested largely on an unrealistic treatment of the few widespread species. Assembly rules for plants have proven difficult to demonstrate (Wilson 1995). Wilson and colleagues have tested the constancy of proportions of species in different guilds by measuring the relative constancy in the proportion of plant species from each guild (Wilson 1989a, Wilson and Roxburgh 1994, Wilson and Gitay 1995). Wilson (Wilson 1989a) found no proportionality with synusial (height-stratified) guilds in an Australian forest, while Wilson and Gitay (1995) found little evidence of plant guild proportionality in a dune slack at a $40mm^2$ scale. However, at a point scale in lawn communities, (Wilson and Roxburgh 1994)) documented equal proportions of forbs and graminoids. Thus, there has been variable support for assembly rules determining community structure.

The assumption behind comparative studies of invasibility with resident species richness was that a decreasing proportion of non-native species in richer communities would indicate biotic resistance (Cornell 1999). Stohlgren et al. (1999) compared grasslands, mountain meadows, and forests in the intermountain west of the United States. (Lonsdale 1999) compared 162 sites (mostly nature reserves) world-wide. Both studies revealed an increase in the number of non-indigenous species in the areas with the greatest resident diversities.

Experimental studies

Tilman et al. (1996) initially set up experimental plots in tallgrass prairie with varying resident species numbers, keeping density constant across richness treatments. Two years later, there was a significant positive relationship between resident plant cover and species richness. Naeem et al. (2000) used these plots for tests of the diversity-invasibility relationship, which revealed a negative relationship between plot richness and invasibility. Lyons and Schwartz (2001) demonstrated an increase in establishment of the non-indigenous grass, *Lolium temulentum*, with plots in which diversity was experimentally decreased in a field study in the Sierra Nevadas. However, most of the variation in invasion success of the previous studies may be attributed to increased survivorship owing to a decrease in plot biomass that results from experimental reduction of diversity.

Peart and Foin (1985) did not find a relationship between richness and resident species identities with plot invasibility but did establish that resident vegetation biomass influenced invasion. (Palmer and Maurer 1997) revealed a positive relationship between natural weed species recruitment and higher crop plants richness within manipulated plots, after resident biomass was factored out of the relationship. Naeem et al.(2000) controlled for density in their greenhouse study of *Crepis tectorum*, an invasive annual. When they varied species richness of the neighbors of *C. tectorum*, there was a direct negative effect of species diversity on the above-ground biomass. Lavorel et al. (1999b) used a pot experiment to explore the demographic success of a pasture weed, *Echium plantagineum*. They discovered that, when they controlled for density, increasing species richness of co-germinants had no effect on seedling emergence. The single greatest predictor of germination success of *E. plantagineum* was co-germinant density. Dukes (2001) demonstrated that resident species diversities had no effect on grassland microcosm invisibility, when resident density was held constant. Thus, most experiments testing the richness-invasibility relationships that controlled for density showed either no relationship or a positive influence of resident species diversity on invasibility.

I explored the relative importance of these factors of biotic resistance and tested for this relationship across a disturbance gradient (Part II). I kept the original densities constant, which is important in separating out the sole contribution of species diversity on invasibility.

Fox's assembly rule (Fox 1987), that relative dearth of certain functional groups in a community will facilitate invasion of those particular functional groups, serves as the basis for investigation into the functional group effects of biotic resistance (Part I). Here we follow Gitay and Noble (1997) and use **functional group** to mean a non-phylogenetic classification leading to a grouping of organisms that respond in a similar way to a syndrome of environmental factors. Use of functional groups has been demonstrated to be a fruitful way to examine plant communities and ecosystems (Diaz et al. 1994, Campbell et al. 1999, Landsberg et al. 1999, Lavorel et al. 1999a, McIntyre et al. 1999)

Environmental Resistance

Many authors (Moyle and Light 1996, Huston 1979, Burke and Grime 1996, Tilman 1997) have suggested that ecological resistance is mediated by environmental factors (flooding intensity, temperature, wind, light soil type), but few have tested this proposition quantitatively. Some authors have proposed that natural disturbances increase invasibility of systems (di Castri 1990). Environmental resistance is the strongest type of resistance for fish communities and depends on the interactions among environmental variability, predictability, and severity (see Moyle and Light [1996] for literature review).

Ruderal plants may increase in downstream reaches because of anthropogenic disturbances, increases in bank heights, and milder climates, which allow a greater diversity of species possessing varying flooding tolerances (Vannote et al. 1980). Studies by Decamps et al. (1995) and PlantyTabacchi et al. (1996) in France and the northwestern United States support these findings. Pyle (1995) found the frequency and species richness of non-indigenous plants increased with distance from the river (and decreased with inundation duration). Taken together, these studies suggest that many non-native species are unlikely to occupy habitats subjected to high levels of flooding in particular, and perhaps natural disturbance generally. I test this hypothesis by experimentally planting known numbers of invaders into plots along a flooding gradient (Part III).

Demographic Resistance

Demographic resistance studies indicate that the higher the propagule intensity, the greater the probability of successful establishment (Beirne 1975, Veltman et al. 1996, Green 1997). Even when a species is pre-adapted to a new environment, many factors may cause

an introduction to fail. Pimm (1991) suggested that conditions for successful introduction are scarce in time and space. Possible post-establishment limitations in invasion success include Allee effects (lack of sufficient organisms to reproduce in a given area), demographic accidents, and fluctuations in density owing to environmental effects.

Historically, invasibility studies have not separated anthropogenic or natural disturbances from propagule pressure (Simberloff 1986). Pyle (1995) attributed the increase in non-indigenous plant frequency and richness to exogenous disturbance in fragmented and recreationally-used land; this trend could also be due to increased number of propagules, given the higher human traffic in parks. I seeded two different numbers of individuals into experimental plots to test the role of demographic resistance in a riparian forest. The results of the ecological resistance experiment will take more time than this dissertation allows and thus are currently in progress (Von Holle & Simberloff, in progress).

Experimental System and Objectives

The research was conducted at Big Stony Creek (38° 26' N, 81° 50' W), a naturally flooded system within the Jefferson National Forest in southwestern Virginia that experiences little human disturbance. This is a model system for study of the first two proposed components of ecological resistance (environmental, biotic) simultaneously, as all factors operate within contiguous forest cover. I tested a number of hypotheses within each factor, as follows:

Biotic Resistance

I tested the biotic component of ecological resistance by studying the role of plant functional groups in riparian community organization (with Daniel Simberloff, Part **I**). Fox's assembly rule states that, "There is a much higher probability that each species entering a community will be drawn from a different functional group (genus or other taxonomically related group of species with similar diets) until each group is represented, before the cycle repeats" (Fox 1987, p. 201). Our objectives were to test Fox's assembly rule and determine the role and importance of functional groups in plant community structure (Part **I**). The functional groups were: small above-ground biomass, branching and rhizomatous root structure (SB); small-above-ground biomass, taproot (ST); large above-ground biomass,

branching root structure (LB); and large above-ground biomass, taproot (LT). Additionally, I investigated the role and importance of functional groups and biotic diversity in ecological resistance (Parts **I, II**). I also investigated which functional groups can invade preferentially or resist invasions by other propagules (Part **I**). The diversity-invasibility relationship was explored across disturbance regimes (Part **II**). These questions were investigated with a series of field experiments, in which I manipulated resident diversities and functional group representation prior to planting invaders. The resulting interactions are discussed in Parts **I** and **II**.

Environmental Resistance

I determined how invasion was influenced by the abiotic factor of flooding and tested if certain species and functional groups were better invaders of different environmental regimes (Part **III**). This proposition was investigated by planting known numbers of plants into plots that experienced varying flooding disturbances.

Biological Inertia

We reviewed the literature in paleoecology, forest-stand simulation modeling, and historical and experimental studies of plant species invasions to illustrate the relevance of biological inertia in plant communities to invasion ecology (Part **IV**). I did not generate specific tests of this fourth component of ecological resistance in this study system for this dissertation.

Experimental Design and Methods

Biotic Resistance

I tested the biotic component of ecological resistance by studying the role of species and functional group diversity in riparian community organization (Part **II**). 1.5 x 1.5m plots were randomly assigned low (low richness), intermediate (intermediate richness) and high (control and digging control) recipient community richness treatments in two high and two low flooding duration sites. After a two-week period to allow for rerooting of plants, these plots were planted with plants of 10 randomly chosen species from widespread native and introduced species commonly found throughout the floodplains of Big Stony Creek and with similar habitat requirements. I refer to these plants as 'invaders' even though many are

native species (Appendix 1). Success of an invasion was measured by proxy biomass (estimation of total biomass with a regression model of measured characters), growth, and survivorship of the invader. I assigned plant species to functional groups and investigated whether plots with species in particular functional groups resisted invasions by other species in particular functional groups. I tested this relationship with multiple regression models.

Fox's assembly rule

I explored functional group resistance to plant invaders by eliminating or decreasing the number of understory plant species in particular functional groups from plots (Part **I**). My functional groups comprise combinations of above-ground biomass and rooting structure type. I assessed success of an invasion by plant survivorship and growth. Manipulated plots were planted with 10 randomly chosen species from widespread native and introduced plants commonly found throughout the floodplains of Big Stony Creek. I analyzed survivorship of functional groups with loglinear models for the analysis of categorical data in a 4-way table.

Environmental Resistance

I inserted a known number of non-native, "weedy" native, and other native species of differing functional groups into plots that experienced different flooding conditions (Part III). I monitored these plants for 2 years and analyzed the role of plant origin and functional group influence on invader success with t-tests, analysis of variance, and logistic regression.

Summary

The characteristics of non-invaded communities and landscapes have not been thoroughly researched for comparison to invaded areas. Vermeij (1996) suggested that studying attributes of recipient biotas or regions that make them susceptible to invasion is a top priority. Additionally, the primary objective of these experiments "... should be ... not to exclude explanations, but to rank them or to explore their interdependence" (Vermeij 1996, p.8). In fact, there has been a disproportionate emphasis on biotic resistance in ecological resistance studies (Chapin et al. 1997, Levine and D' Antonio 1999). Identifying the relevant components of ecological resistance will guide future resistance research. Understanding mechanisms that govern the addition and deletion of species is important for

understanding ecological community structure. Additionally, this study links complex environmental and biotic factors that can be extended to understand landscape-level interactions such as riverine influence on native biodiversity and invasion. Finally, I introduce (with Hazel R. Delcourt and D. Simberloff) the idea that biological inertia within the resident community is a fourth component of ecological resistance to invasion. This influence of resident on the immigrating species is relevant to studies of ecological resistance because of the lag time inherent in loss of resident species after environmental conditions become suitable for invasion by immigrating species (Part **IV**).

References

Baltz, D. M., and P. B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. Ecological Applications **3**:246-255.

Beirne, B. P. 1975. Biological control attempts by introductions against pest insects in field in Canada. Canadian Entomologist **107**:225-236.

Brown, J. H., B. J. Fox, and D. A. Kelt. 2000. Assembly rules: Desert rodent communities are structured at scales from local to continental. American Naturalist **156**:314-321.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology:776-790.

Byers, J.E. 2001. Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. Oecologia **130:** 146-156.

Campbell, B. D., D. M. Stafford Smith, and A. J. Ash. 1999. A rule-based model for the functional analysis of vegetation change in Australasian grasslands. Journal of Vegetation Science **10**:723-730.

Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. Proceedings Of The National Academy Of Sciences Of The United States Of America **87**:9610-9614.

Case, T. J. 1991. Invasion resistance, species buildup and community collapse in metapopulation models with interspecies competition. Biological Journal of the Linnean Society **42**:239-266.

Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science **277**:500-504.

Chapman, R. N. 1931. Animal ecology: with a special reference to insects. McGraw-Hill Park, New York.

Cornell, H. V. Unsaturation and regional influences on species richness in ecological communities: A review of the evidence. Ecoscience **6(3)**:303-315

Crawley, M.J. 1986. The population biology of invaders. Philosophical Transactions of the Royal Society of London, Series B **314**: 711 - 731.

D' Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. Ecology **74**:83-95.

Decamps, H., A. M. Plantytabacchi, and E. Tabacchi. 1995. Changes in the hydrological regime and invasions by plant species along riparian systems of the Adour River, France. Regulated Rivers-Research & Management **11**:23-33.

Deferrari, C. M., and R. J. Naiman. 1994. A multiscale assessment of the occurrence of Nonindigenous plants on the Olympic Peninsula, Washington. Journal of Vegetation Science **5**:247-258.

Diaz, S., A. Acosta, and M. Cabido. 1994. Community structure in montane grasslands of Central Argentina in relation to land use. Journal of Vegetation Science **5**:483-488.

Di Castri, F. 1990. On invading species and invaded ecosystems: the interplay of historical change and biological necessity, *in*, F. di Castri, A.J. Hansen, and M. Debussche (eds.) Biological invasions in Europe and the Mediterranean Basin. Kluwer, Dordrecht.

Drake, J.A. 1988. Models of community assembly and the structure of ecological landscapes Pages 585-605 in T.G. Hallam, L.J. Gross and S.A. Levin, editors. Mathematical Ecology: Proceedings of the Autumn Course Research Seminars, International Centre for Theorectical Physics.World Press, Singapore.

Drake, J.A. 1990. The mechanics of community assembly and succession. Journal of Theorectical Biology **147**: 213-233.

Dukes, J. S. 2001. Biodiversity and invasibility in grassland microcosms. Oecologia **126**:563-568.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London.

Fox, B. J. 1987. Species assembly and the evolution of community structure. Evolutionary Ecology **1**:201-213.

Fox, B. J. 1989. Small-mammal community pattern in Australian heathland; a taxonomically based rule for species assembly. Pages 91-103 *in* D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig, editors. Patterns in the Structure of Mammalian Communities. Texas Tech University, Lubbock, Texas.

Fox, B. J., and J. H. Brown. 1993. Assembly rules for functional groups in North American desert rodent communities. Oikos **67**:358-370.

Fox, B. J., and G. L. Kirkland. 1992. An assembly rule for functional groups applied to North American soricid communities. Journal of Mammalogy **73**:491-503.

Gitay, H., and I. R. Noble. 1997. What are functional types and how should we seek them? Pages 3-19 *in* T. M. Smith, H. H. Shugart, and F. I. Woodward, editors. Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change. Cambridge University Press, Cambridge, UK.

Glowka, L., F. Burhenne-Guilmin, and H. Synge. 1994. A Guide to the Convention on Biological Diversity. IUCN, Gland.

Green, R. E. 1997. The influence of numbers released on the outcome of attempts to introduce non-indigenous bird species to New Zealand. Journal of Animal Ecology **66**:25-35.

Hobbs, R. J., and L. Atkins. 1988. Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian Wheat-Belt. Australian Journal Of Ecology **13**:171-179.

Hood, W. G., and R. J. Naiman. 2000. Vulnerability of riparian zones to invasion by non-indigenous vascular plants. Plant Ecology **148**:105-114.

Huston, M. 1979. General Hypothesis of Species-Diversity. American Naturalist:81-101.

Landsberg, J., S. Lavorel, and J. Stol. 1999. Grazing response groups among understorey plants in arid rangelands. Journal of Vegetation Science **10**:683-696.

Lavorel, S., S. McIntyre, and K. Grigulis. 1999a. Plant response to disturbance in a Mediterranean grassland: How many functional groups? Journal of Vegetation Science **10**:661-672.

Lavorel, S., A.-H. Prieur-Richard, and K. Grigulis. 1999b. Invasibility and diversity of plant communities: from pattern to processes. Diversity and Distributions **5**:41-49.

Law, R. and R. D. Morton. 1996. Permanence and the assembly of ecological communities. Ecology **77**:762-775

Levine, J. M., and C. M. D' Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos:15-26.

Lodge, D. M. 1993a. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**:133-137.

Lodge, D. M. 1993b. Species invasions and deletions: Community effects and responses to climate and habitat change. Pages 367-387 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic Interactions and Global Change. Sinauer associates, Sunderland, Massachusettes, USA.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology **80**:1522-1536.

Lyons, K. G., and M. W. Schwartz. 2001. Rare species loss alters ecosystem function - invasion resistance. Ecology Letters **4**:358-365.

McIntyre, S., S. Lavorel, J. Landsberg, and T. D. A. Forbes. 1999. Disturbance response in vegetation towards a global perspective on functional traits. Journal of Vegetation Science **10**:621-630.

Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biological Conservation **78**:149-161.

Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos **91**:97-108.

Palmer, M. W., and T. Maurer. 1997. Does diversity beget diversity? A case study of crops and weeds. Journal of Vegetation Science **8**:235-240.

Peart, D. R., and T. C. Foin. 1985. Analysis and prediction of population and community change: a grassland case study. Pages 313-339 *in* J. White, editor. The Population Structure of Vegetation. Junk, Dordecht.

Pianka, E. R. 1980. Guild structure in desert lizards. Oikos **35**:194-201.

Pimm, S. L. 1991. The Balance of Nature? Ecological Issues and the Conservation of Species and Communities. University of Chicago Press, Chicago.

PlantyTabacchi, A. M., E. Tabacchi, R. J. Naiman, C. Deferrari, and H. Decamps. 1996. Invasibility of species rich communities in riparian zones. Conservation Biology **10**:598-607.

Post, W.M, and S.L. Pimm. 1983. Community assembly and food web stability. Mathematical Bioscience **64**: 169-192.

Pyle, L. L. 1995. Effects of disturbance on herbaceous exotic plant species on the floodplain of the Potomac River. American Midland Naturalist **134**:244-253.

Ricklefs, R. E. 1987. Community Diversity : Relative Roles of Local and Regional Processes. Science **235**:167-171.

Robinson, J.V., and W.D. Valentine. 1979. The concepts of elasticity, invulnerability, and invadibility. Journal of Theorectical Biology **81**:91-104.

Shigesada, N., K. Kawasaki, and E. Teramoto. 1984. The effects of interference competition on stability, structure, and invasion of a multispecies system. Journal of Mathematical Biology **21**: 97-113.

Simberloff, D. 1986. Introduced Insects: A biogeographic and systematic perspective. Pages 3-24 *in* H. A. Mooney and J. A. Drake, editors. Ecology of Biological Invasions in North America and Hawaii. Springer-Verlag, New York.

Simberloff, D., and T. Dayan. 1991. The Guild Concept and the Structure of Ecological Communities. Annual Review Of Ecology And Systematics **22**:115-143.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs:25-46.

Stone, L., T. Dayan, and D. Simberloff. 1996. Community-wide assembly patterns unmasked: The importance of species' differing geographical ranges. American Naturalist **148**:997-1015.

Tabacchi, E. 1995. Structural variability and invasions of pioneer plant communities in riparian habitats of the middle Adour River (SW France). Canadian Journal of Botany-Revue Canadienne De Botanique **73**:33-44.

Tilman, D. 1997. Community invasibility ; recruitment limitation ; and grassland biodiversity. Ecology:81-92.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature **379**:718-720.

United States Congress. 1993. Harmful Non-Indigenous Species in the United States. Office of Technology Assessment, Washington, D.C.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. River continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130-137.

Veltman, C. J., S. Nee, and M. J. Crawley. 1996. Correlates of introduction success in exotic New Zealand birds. American Naturalist **147**:542-557.

Vermeij, G. J. 1996. An agenda for invasion biology. Biological Conservation **78**:3-9.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience **48**:607-615

Wilson, J. B. 1995. Testing for community structure : A Bayesian approach. - Folia Geobotanica & Phytotaxonomica 461-469.

Wilson, J. B. 1989a. A null model of guild proportionality, applied to stratification of a New Zealand temperate rain forest. Oecologia **80**:263-267.

Wilson, J. B. 1989b. Relations between native and exotic plant guilds in the Upper Clutha. New Zealand. Journal of Ecology **77**:223-235.

Wilson, J. B., and H. Gitay. 1995. Community structure and assembly rules in a dune slack : variance in richness ; guild proportionality ; biomass constancy and dominance/diversity Relations. Vegetatio **116**:93-106.

Wilson, J. B., and S. H. Roxburgh. 1994. A demonstration of guild-based assembly rules for a plant community ; and determination of intrinsic guilds. Oikos **69**:267-276.

PART I

Testing Fox's assembly rule: Does plant invasion depend on recipient community structure?

This part is a lightly revised version of a manuscript with the same name by B. Von Holle & D. Simberloff:

Von Holle, B. and D. Simberloff. 2002, in review. Testing Fox's assembly rule: Does plant invasion depend on recipient community structure? Oikos

My use of "we" in this part refers to my coauthor and me. My primary contributions to this paper include (1) Selection of the topic (2) selection of the field site (3) most of the experimental manipulations and censuses (4) all of the statistical analyses and interpretation of the results and (5) most of the writing

Abstract

Fox's assembly rule, that relative dearth of certain functional groups in a community will facilitate invasion of that particular functional group, serves as the basis for investigation into the functional group effects of invasion resistance. We explored functional group resistance to plant invaders by eliminating or decreasing the number of understory plant species in particular functional groups from plots at a riparian site in southwestern Virginia, USA. Our functional groups comprise combinations of above-ground biomass and rooting structure type. We assessed success of an invasion by plant survivorship and growth. Manipulated plots were planted with 10 randomly chosen species from widespread native and introduced plants commonly found throughout the floodplains of Big Stony Creek. We analyzed survivorship of functional groups with loglinear models for the analysis of categorical data in a 4-way table. There was a significant interaction between functional groups removed in the plot and survivorship in the functional groups added to those plots. However, survivorship of species in functional groups introduced into plots with their respective functional group removed did not differ from survivorship when any other functional group was removed. Additionally, growth of each of the most abundant species did not differ significantly among plots with different functional groups manipulated. Specifically, species did not fare better in those plots that had representatives of their own functional group removed. Fox's assembly rule does not hold for this plant community;

however, composition of the recipient community is a significant factor in community assembly.

Introduction

Fox's assembly rule (1987), that relative dearth of certain functional groups in a community will facilitate invasion by species of that particular functional group, serves as the basis for investigation into the functional group effects on resistance. Historical debate among theoretical ecologists has focused on two different views of community structure. The 'Individualistic' concept of Gleason (1926) assumes little direct interaction among species. The only constraints on a species' establishment are ability to disperse and survive under the current environmental conditions. This concept can be viewed as a null model, where species coexistence is unrelated to guild membership (Connor and Simberloff 1979). The opposite view holds that competitive exclusion between species results in assembly rules. The general idea is that competitive filters sort communities into a predictable cohort of species (Diamond 1975). This notion was further generalized by Fox (1987) to predict community assembly by functional groups. These same assembly rules based on competition hold in Fox's view; however, exclusion occurs at the level of the functional group, not the species. The only input required to predict community composition is prior knowledge of how the pool of species fit into functional or taxonomic groups (Fox 1987). Fox's assembly rule states that, "There is a much higher probability that each species entering a community will be drawn from a different functional group (genus or other taxonomically related group of species with similar diets) until each group is represented, before the cycle repeats" Fox, 1987, p. 201). This statement was proposed as a general rule, and Fox and Brown (1993) encouraged tests of this rule with different taxa. This supposition was based on animals rather than plants; however it has been tested several times for plant communities with both positive and negative results (Weiher and Keddy 1995). Our objectives were to test Fox's assembly rule and determine the role and importance of functional groups in plant community structure. This is the first experimental test of a hypothesis that has molded discussions of community assembly and structure.

Many observational efforts have sought to detect structure in the composition of natural communities by testing for constancy in the proportion of species from each guild. If competition is more severe between species in one guild than between species in different guilds (Pianka 1980, Simberloff and Dayan 1991), the number of species in each guild at a site should be limited. Thus the proportions of species in each guild are expected to be relatively constant within sites if assembly rules are operating (Wilson 1989a). Fox and associates have demonstrated community structure through assembly rules with several data sets of naturally-occurring desert rodents (Fox 1987, 1989, Fox and Kirkland 1992, Fox and Brown 1993, Brown et al. 2000). Stone et al. (1996) randomized the rodent communities tested in the previous studies and suggested that the evidence for community structure found by the previous authors rested largely on an unrealistic treatment of the few widespread species. Assembly rules for plants have proven harder to demonstrate (Wilson 1995). Wilson and colleagues have tested the constancy of proportions of species in different guilds by measuring the relative constancy in the proportion of plant species from each guild (Wilson 1989b, Wilson and Roxburgh 1994, Wilson and Gitay 1995). Wilson (1989b) found no proportionality with synusial (height-stratified) guilds in an Australian forest, while Wilson and Gitay (1995) found little evidence of plant guild proportionality in a dune slack at a $40mm^2$ scale. However, at a point scale in lawn communities, Wilson and Roxburgh (1994) documented equal proportions of forbs and graminoids. They concluded that the lack of evidence for assembly rules noted in the past may have been due to inability to detect them and that finer scale methods are more appropriate to detect plant community structure.

Plant morphology varies with environmental conditions (Shugart 1997). Subjective assignment of growth form categories has been a successful way of assigning functional group membership because these classifications reflect broad ecosystem functions (Aguiar et al. 1996) and correlate with other sets of physiological and morphological traits (Grime et al. 1988, Leishman and Westoby 1992). We followed Gitay and Noble (1997) and used functional group to mean a non-phylogenetic classification leading to a grouping of organisms that respond similarly to environmental factors. 'Environmental factors' can include biotic and abiotic processes that change as a result of a perturbation to the

system. In this paper, we consider morphological traits of functional groups as they relate to their biotic mechanisms of competition for space. We use the term "functional group" in this paper; related terms include guild (Simberloff and Dayan 1991), life-form (Raunkiaer 1934), form (Box 1981), strategy (Grime 1974, 1977, Tilman 1988), and temperament (Oldeman and van Dijk 1991).

We designed experiments to gain insight into how community composition affects invasion into a community. The central question is: do invaders whose functional group has been reduced or removed perform better than those that have their functional group represented? We pose three specific hypotheses to address this central issue (Table 1):

1. When a functional group has been removed a community will becomes more susceptible (in general) to invasion of new species of any functional group.

2. The probability of successful invasion of a plot with a functional group of low or zero diversity (manipulated) will be higher for species of that functional group than when this functional group is not manipulated.

3. Different morphologically based functional groups will have different invasion success depending on inherent biological traits.

Methods

Functional groups

The research was conducted at Big Stony Creek (38° 26' N, 81° 50' W), a naturally flooded system within the Jefferson National Forest in southwestern Virginia that experiences little human disturbance. We studied the role of plant functional groups in riparian invasion by manipulating community composition. Our functional groups were established *a priori* using the deductive method (*sensu* Gitay and Noble [1997]) based on our knowledge of stresses that a new plant might face in these communities: competition from the existing community and flooding by the adjacent stream. Our functional groups are defined by their physical occupancy of space and comprise combinations of above ground biomass and rooting structure type. These morphological characteristics differentiate a plant's use of space: branching shoots and roots use shallow, horizontal spaces, and tall (long) roots and shoots use deeper, vertical areas in the soil matrix and canopy (Figure 1).

Soil water dynamics differ at different soil depths and reflect differences in rooting depth (Wieland and Bazzaz 1975, Knoop and Walker 1985, Cody 1986, Davis and Mooney 1986, Sala et al. 1989, 1992). Additionally, the horizontal structure of plants is a determinant of their ability to use resources that are heterogeneously distributed in space (Pitelka and Ashmun 1986). Thus, plant morphology has been found to influence resource acquisition directly. All plants are characterized by their potential adult classification, though that may not be the state of the individual at the time of collection (e.g., a large, taprooted individual <1/2m tall will not be in its adult state). Although they may not presently be in the adult state that confers the functional group status, these groupings have different correlates for total dry weight (Table 2) at the <1/2m state. The functional groups are small above-ground biomass, branching and rhizomatous root structure (SB); small above-ground biomass, taproot (ST); large above-ground biomass, branching root structure (LB); and large above-ground biomass, taproot (LT) (Appendix 1 and Fig. 1).

Experimental Design

Community Manipulation

A randomized block design was employed across four plots to test hypotheses 1 and 2 (Figure 2). Two plots are adjacent to the creek, and the other two are in the second level of the floodplain, which was never flooded during our experiment. Each plot encompasses a 70 x 10m area. Each of these areas had four rows with 1m between rows. All subplots in each of the four rows had the same functional group manipulated. One plot in each of the streamside and upper terrace (further away from the stream) areas, each containing 40 subplots, was censused and manipulated in 1999. The second pair of plots, each with 28 subplots, were censused and manipulated in 2000 (Figure 2). Each subplot was 1.5 x 1.5m. Plot treatment was assigned randomly

Representation of functional groups within plots was manipulated by either 1) eliminating a functional group, or 2) leaving only one species to represent that functional group. The "one representative species" treatment was created by eliminating all but one randomly-picked representative species from each manipulated functional group. There were four 'one representative species' treatments; in each, a different functional group was manipulated (Fig. 2). This treatment was conceived to ascertain whether one functional

group member could represent an entire functional group, or if species within functional groups are redundant in ability to resist invasive plants. A paired treatment eliminated all species from the given manipulated functional group (lack of functional group). There were four "lack of functional group" treatments. In each, all species of one randomly-picked functional group were removed. If the functional group that was chosen randomly for manipulation in that plot was missing, another plot was chosen randomly. Plots to control for the effect of uprooting and replanting species were manipulated by uprooting and replanting all the plants of one randomly chosen functional group per plot (digging control). Other control plots were maintained where there was no plant manipulation. Any significant difference in success of invasion between the digging control and the control plots will indicate the effect of digging.

While we reduced or removed the representation of a functional group within a plot, we maintained the original density of the plot through replacement. Biomass of the "one representative species" treatment plots did not change, as equivalent biomasses of plants were replanted in each hole created by removal of a plant, using the one species of that functional group randomly selected to remain in that plot. Additionally, the biomass of the "lack of functional group" plots did not change, as randomly chosen species of the remaining functional groups were propagated to fill the vacant spots to provide the equivalent biomass. The control plots were left with the original complement of species. All manipulated plants were shorter than 0.5 meter.

Invader input

After a two-week period to allow for rerooting of plants, these 1.5 x 1.5 m plots were planted with seedling or adult plants (<1/2 m) of 10 randomly chosen species from widespread native and introduced species commonly found throughout the floodplains of Big Stony Creek. These species all had similar habitat requirements (as in Burke and Grime (1996), Appendix 1). We refer to these plants as 'invaders' even though many are native (Appendix 1). These 136 plots were within streamside and upper terrace areas. Eighty of the plots had two additions of 10 invaders. The 10 invaders were added in 1999 and 2000. This treatment with two sets of invader additions is referred to as the 2X treatment, with each plot having a total of 20 planted invaders. The other 56 plots had only one addition of

10 invaders, in 2000; this addition is referred to as the 1X treatment (Figure 2). The "one representative species" and "lack of functional group" treatments within the 1X treatment had only two functional groups manipulated, LB and LT (Appendix 1). Success of an invasion was measured by survivorship, estimation of total biomass, and growth of the invader. Our three year study focuses on the integration phase of invasion (Vermeij 1996). The previous phase, establishment, is when the resistance of the community is hypothesized to be the strongest (Vermeij 1996). The establishment phase of invasion might have very different community dynamics and results

The first invader additions of the 2X treatment invaders in 1999 were composed of 58.4% native, 29.7% non-indigenous, and 11.9% unknown provenance (n=800). The 800 invaders of the second invader addition of the 2X treatment in 2000 were composed of 62.25% native, 33.5% non-indigenous, and 4.25% unknown provenance. The 560 invaders of the 1X treatment were composed of 53.6% native, 45.5% non-indigenous, and .009% unknown provenance.

Trait measurement

Our proxy measure for each functional group's above- and below-ground dry weight is a unique set of traits. The set of characteristics for each functional group that allows the best estimation of total biomass was determined by randomly collecting 60 plants along 2 transects away from the creek, measuring six morphological traits, taking the dry weight, and correlating these traits with total dry weight (Table 2). The traits were measured in the field, *in situ*, as follows:

1) Stem diameter: Measured at ground level, using calipers.
2) Canopy length: The longest length of the canopy area of the leaves, measured with a ruler, parallel to the ground
3) Canopy width: Measured with a ruler, perpendicular to the length and parallel to the ground.
4) Stem height: Measured with a ruler from the ground to the top of highest chlorophyll-containing structure.
5) Number of leaves: The count of all leaves across all ramets. Compound leaves

were counted as one. Immature and dying leaves were counted if greater than half the leaf area contained green tissue.

6) Internode length: The length between the first internode (closest to the ground) and the second, measured with a ruler.

Support for our *a priori* functional group classification is provided by the unique combination of characteristics that determines the biomass of each functional group and their differential survival (Table 2 and Fig. 1). All the traits that significantly correlate to total dry weight for the functional group of each invading species are measured two weeks after the invasion, and every summer following, to estimate biomass change. Survivorship was measured by death at a census period. A plant was counted as dead if it had no chlorophyll left in any structures or was missing from the spot where it was planted. If the marker tag was absent the plant was counted as missing. Some plants counted as 'dead' resprouted the following summer, as evidenced by the greater number of interactions in the year 2 census than the year 1 census (Table 3).

Statistical Analyses

We tested to see if successful invasion was more likely in plots with a functional group removed or the diversity of a functional group lowered to one species. Additionally, we tested for the effect of digging on the survivorship of the invading plants by comparing survivorship in the digging control plots and control plots. Logistic regression analyses (PROC LOGISTIC of SAS) were performed with survivorship (dead or alive) as the dependent variable and treatment as the independent variable. Logistic regression describes the relationship between a categorical response variable (i.e. survivorhip) and a set of explanatory variables (i.e. plot treatment, functional group manipulated, functional group invading). This method of analysis employs a comparative approach, where one variable is always used as a reference variable and the response and explanatory variables fit the logistic regression model via maximum likelihood estimation (Stokes et al. 2000). Thus, to get all combinations of functional group removed by functional group invaded, we had to perform two logistic regressions, using different reference groups each time. The probability of an event (plant mortality) is modelled for each variable, and the model is then tested with goodness of fit tests for statistical significance. To correct for multiple testing, we took the

p-values from the analyses, ranked them, and used the sequential Bonferroni technique of dividing a critical value of 0.05 by the rank of the p-values (Rice 1989). Because reference groups are employed in logistic regression, data may sometimes appear duplicate (as in Table 4b), when few groups are available to serve as reference groups. Logistic regressions were performed on each census period of all three invader sets. Each invader addition was tested separately, unless specified below. Site location had no significant effect on the functional-group-remvoved-by-functional-group-invaded interaction, so we combined streamside and non-streamside plots in analyses of treatment effects (logistic regression).

We tested for differential invasion success of invaders when their functional group is represented and when it is not (Hypothesis 2, Table 1). These analyses (PROC LOGISTIC of SAS) were performed with logistic regression with survivorship (dead or alive) as the dependent variable.

Additionally, growth of the most abundant invading species in 1999 and 2000 was analyzed using Kruskall-Wallis tests to determine if Fox's assembly rule would be manifested at the species level. There was no difference in survivorship between plants invading plots with their respective functional group removed completely or reduced to one species in 1999, so we lumped both of these functional group manipulations. Thus, the most abundant species introduced into plots were tested for differences in stem diameter growth between when their functional group was removed or reduced and when any other functional groups were removed or reduced. The differences were used only for plots where there was a functional group manipulation (e.g., no controls were used). The plants that we used for this purpose were the first and second sets of invader additions of the 2X treatment. We subtracted the stem diameter of these plants the year they were planted from the stem diameter the following year for the growth measurement. We then used PROC NONPAR1WAY WILCOXON for these analyses.

Lastly, to determine if plant traits influence the success of functional groups, we grouped plants into size classes: small (SB & ST) and large (LB & LT) and root classes: branched (SB & LB) and taprooted (ST & LT). We tested if species with a particular size or root class had greater survivorship when plants with that size or root class was removed.

The degree of persistence of functional groups three years after planting were analyzed with a Kaplan-Meier survivorship analysis (Lee 1992). The first invader addition of the 2X treatment was the only invader set with all four functional groups represented in the invader pool and thus appropriate for this analysis. The survivorship data for these analyses were gleaned from the censuses that occurred two weeks, one year, and two years after planting, respectively. We considered deaths only up to the third year, after which the invaders were censored and not represented in the analysis. We used PROC LIFETEST of SAS for this analysis.

We have identified 49, 52, 38 and 31 species in the SB, ST, LB and LT groupings, respectively, using the nomenclature and species descriptions of Gleason & Cronquist (Gleason and Cronquist 1991) supplemented by field observations and experiments (Appendix 1, experiment described under *Methods, "Trait measurement"*). There are 15, 19, 1, and 1 non-indigenous species in these groupings, respectively. Specimens were pressed and catalogued in the University of Virginia Mountain Lake Biological Station Herbarium. All annuals were removed from tests that considered data for more than two weeks after planting. All analyses were performed with SAS version 7.1.

Results

Survivorship of added invaders of the species randomly chosen from widespread native and introduced species was 83% in 1999 (n=800) and 92% in 2000 (n=1600) 2 weeks after planting. Survivorship was significantly lower for the LT functional group in 1999 across all treatments ($p=0.0006$, Chi-square=17.26, n=510). Thus, in 2000, we removed the LT functional group from the randomly-picked invader pool (Second invader addition of the 2X- and the first invader addition of 1X- planting).

There were no significant differences in survivorship of the invaders across treatments in each of the three experiments (logistic regression, Fig. 4). The removal of a functional group does not make that community more susceptible to invasion (Hypothesis 1, Table 1). Additionally, there were no differences in overall invader survivorship between the one representative species and lack of functional group treatments. Last, there were no differences in invader survivorships between the digging control and control treatments.

There were significant interactions between functional groups removed from plots and survivorship of the members in functional groups added to those plots in three of the six experimental runs. The logistic regressions for censuses 1 and 2 of the 2X, first invader addition treatment, and the second census of the 2X, second invader addition treatment, had significant interactions between functional group removed and functional group invaded (Tables 3-5). This means that, when a functional group was removed, at least one functional group had significantly greater or lesser survivorship in these plots than in other plots with different functional groups removed. Thus, when the ST functional group was removed in year 1 of the 2X, first invader addition treatment (Table 3a), species in the SB functional group had significantly lower survivorship in these plots than in plots with other functional groups removed ($p=0.0004$, $n=8$). Taprooted species with large biomass (LT) had significantly higher survivorship the second year of the treatment when SB was removed than when any other functional group was removed ($p=0.0002$, $n=19$, Table 3b). The second census of the 2X, second invader addition treatment, had a significant overall functional-group-removed-by-functional-group-invaded interaction. However, none of the tests of specific functional group invading and specific functional group removed were significant, after adjustment for multiple tests (Table 4).

Following the second hypothesis (Table 1), we expected to find that invaders in the functional group that was eliminated from a plot were more likely to succeed because that particular soil horizon and above-ground space was unused in those plots. We analyzed survivorship of functional groups with loglinear models for the analysis of categorical data in a 4-way table. Survivorship was not greater for any functional group in plots from which species from that functional group were removed than for plots with any other manipulated functional group (Tables 3-5). The removal of a particular functional group does not affect survivorship of species in that same functional group planted in that plot two weeks later. There were 18 tests (each experiment had two censuses) of Fox's assembly rule (specific functional group removed with potentially greater invasion success by members of the same functional group), and none of these interactions were statistically significant. Additionally, abundant invading species showed no response to removal of species in their respective functional group in the recipient plot. There were no differences in the stem diameter

growth of the 17 most abundant invaders in the two invader additions of the 2X treatment (1999 & 2000) between plants in plots with species in their respective functional group removed and plants in plots that retained species in their functional group (Table 6).

We tested each data set for both census periods (two week census, one year later) for an influence of removal of a particular root or a size class on success of species of that root or size class into a plot. Of the six censuses for the three experiments, we found one significant root effect: individuals of species in functional groups that invaded plots with their respective root type removed (branching or tap-rooted) of the second invader addition of the 2X treatment, one year later, had decreased survivorship ($p=0.048$, Chi-Square= 3.91). There were no significant size-removed-by-size-invaded effects for any of the six censuses. In other words, neither large nor small plants showed a difference in survivorship when either large or small plants were removed from those plots.

The survival analysis indicated that there is a significant difference in the survivorship of the first invader addition of the 2X treatment, across three years. Median survivorship, after being planted, of species in the different functional groups was in the order: SB =27.5 months >LB=18.87 months >ST=12.68 months >LT=11.33 months after being planted, respectively (Fig. 3). Because more than one half of the SB plants were alive at the last census period, the estimate of 27.5 months is a projected median time, assuming the same survival curve as displayed for the last two time periods. The rest of the functional group median survival times were estimated by linear interpolation.

Discussion

Many studies support assembly rules for both plants and animals, and many studies fail to detect them (see Weiher and Keddy [1995], Gotelli and Graves [1996] for lists of references). It has been suggested that the presence of assembly rules is so well established that future research needs to turn to establishing what the assembly rules are and how they vary along gradients and taxa (Weiher and Keddy 1995). Wilson (1995) suggested that field experiments to test plant community structure have been burdened with several drawbacks. The addition of a digging control would elucidate results of field experiments that are confounded by this disturbance. The lack of digging effects on invader survivorship

validates our treatments and results. We propose that experimental studies such as this one will further resolve the question of the existence of such rules and, if they exist, the mechanisms by which they operate.

Invader survivorship in the one representative species treatments did not differ from that in the lack of functional group treatments. Thus, the diversity of species within one functional group in this recipient community had no effect on invasion into plots; there was no difference in invader survivorship in treatments with no species, one species, or all original species of a functional group represented in the recipient plot. Because there was no difference in invader survivorship between the functional group removal treatments and those that kept the functional groups intact, we cannot say whether or not one species can represent a functional group. Different levels of representation of a functional group had no effect on the survivorship of invading species of that functional group. Other researchers have observed a lack of community structure for plants (Wilson 1989b, Wilson and Gitay 1995). They found non-uniform variances in the number of plant species belonging to functional groupings in communities and inferred from this a lack of assembly rules for plant communities. Intra-functional group competition may not be a major influence on community structure, or, alternatively, assembly rules cannot be revealed with this null model technique (Weiher and Keddy 1999). The lack of evidence for assembly rules using both null models and our experimental approach constitutes strong support for the lack of intra-functional group competition as a major force in community structure.

Survivorship of species in a particular functional group depends significantly on which functional group has been removed: three of six experimental runs, or 50%, showed significant interactions. These were functional-group-removed-by-functional-group-invaded interactions. However, only two of sixty-eight specific functional-group-removed-by-functional-group-invaded interactions, or 3%, were statistically significant, after comparing the p-values to Bonferroni-adjusted alpha values. It is possible that relay floristics (Egler 1954) are occurring here, where the environmental conditions of a site are made more or less amenable by the co-occurence of species or functional groups. Connell and Slayter (1977) described several observational and experimental studies that demonstrate relay floristics,

where ruderal species colonize bare substrate and ameliorate adverse environmental

conditions. An example of this phenomenon is the preferential establishment of *Mitchella repens* under primary *Tsuga canadensis* and pine canopies in Massachusetts (Whitney and Foster 1988).

Indirect interactions are important to community ecology and often overlooked (Levine 1999). Indirect interactions may be more important for community structure of this riparian community than direct competitive effects. If plants in different functional groups are competitive mutualists (Pianka 1980), our results may have been, in part, the outcome of multiple, positive, indirect interactions with a net larger effect than the direct competition between functional group members. Future experiments could include manipulations of various functional group combinations, to reveal if there are mutualisms and/or inter-dependencies of particular species and functional groups.

If there was substantial intra-functional group competition, invaders from those functional groups that were represented in the plots would be less successful than invaders from functional groups that were absent or reduced. Conversely, the total or partial lack of a functional group in a plot would allow invaders from that functional group to flourish in the absence of competition. However, species did not respond to removal of their particular functional group. The total absence of a particular functional group had no apparent influence, within the limits of this study, on the success of invading species from that functional group. Our results are consistent with the work of others who found no evidence of intra-guild structure in various plant communities (Wilson 1989b, Wilson and Gitay 1995). Although our experiments indicate that there is inter-functional group interaction, we find no evidence that intra-functional group interactions structure the community. Thus the community will not become saturated with plants of functional groups as envisioned by Fox (1987).

When we tested the '*a posteriori*' characterization (*sensu* Lavorel et al. [1997]), which identifies sets of attributes represented in species that belong in the same response group, we found evidence that the root type of plants is the trait that confers success in the functional-group-removed-by-functional-group-invaded interactions. Invaders with branching roots (SB, then LB) were better general invaders of all plots than taprooted invaders. Half of the plots are in the first terminal of a flood plain (streamside), where some of them were

regularly flooded during this experiment. Plants in environmentally-disturbed systems may have traits that converge on resistance to the disturbance that affects them (Weiher and Keddy 1995). Species adapted to stressful environments (where primary production is restricted by resource limitations imposed by the physical environment) tend to exhibit the same adaptations and might converge on the same functional characteristics because of the particular abiotic conditions (del Moral et al. 1985). Stress-tolerant plants tend to have low stem dry weights (Hills et al. 1994), are low to the ground (Grime 1974), have short roots, and are not laterally extensive (Grime et al. 1988). Abiotic conditions may override biotic stressors in morphological selection on riverine plants.

Above-ground plant size did not confer invasion success. Wilson (1988), in a literature review of root/shoot competition experiments, found that root competition is more intense than shoot competition. This finding suggests that competition for soil space is a possible explanation for community organization. Root competition might be more strongly influenced by the type, rather than the overall size, of the root. Future research on determinants of plant community structure should focus on root competition as a possible mechanism.

It is possible that there are other, more important traits that we did not consider in our morphological classification of functional groups. Morphology may not be the determining factor of this understory community, as it was for other communities (Fox 1987, 1989, Wilson and Roxburgh 1994, Brown et al. 2000). Our view of resource gathering may be quite different from that of an autotrophic organism (Simberloff and Dayan 1991).

This is the only experimental test of Fox's assembly rule to date. Using an experimental design of adding a random suite of species from various functional groups into plots with varying degrees of representation of these same functional groups, we were able to test directly intra-functional group competition as a mechanism for community structure. We propose that there is community structure, as indicated by our significant functional-group-removed-by-functional-group-invaded interactions. However, mechanisms for this structure operate at a level beyond the testing capabilities of this experiment. Positive, indirect interactions may be more important in structuring this community than negative, direct interactions between functional group members.

Conclusion

Invasion depends upon community composition. It may follow some sort of initial floristic model, where the presence or absence of a certain functional group may or may not facilitate the establishment of another functional group.

While there may be significant associations between various species and functional groups, there is no clear evidence that intra-functional group competition and assembly rules structure this plant community. Fox's assembly rule does not hold for this plant community: Plants are not more likely to survive in plots from which their functional group was removed or reduced than in any other plot.

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References

Aguiar, M. R., Paruelo, J. M., Sala, O. E. and Lauenroth, W. K. 1996. Ecosystem responses to changes in plant functional type composition: An example from the Patagonian steppe. - Journal of Vegetation Science 3: 381-390.

Box, E. O. 1981. Macroclimate and plant forms: An introduction in predictive modeling in phytogeography. - Dr. W. Junk.

Brown, J. H., Fox, B. J. and Kelt, D. A. 2000. Assembly rules: Desert rodent communities are structured at scales from local to continental. - American Naturalist 3: 314-321.

Burke, M. J. W. and Grime, J. P. 1996. An experimental study of plant community invasibility. - Ecology 776-790.

Cody, M. L. 1986. Structural niches in plant communities. - In: Diamond, J. M. and Case, T. J. (ed.),Community ecology. Harper and Row, pp. 381-405.

Connell, J. H. and Slayter, R. O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. - The American Naturalist 1119-1144.

Connor, E. F. and Simberloff, D. 1979. The assembly of species communities - chance or competition. - Ecology 6: 1132-1140.

Davis, S. D. and Mooney, H. A. 1986. Water-use patterns of 4 coccurring chaparral shrubs. - Oecologia 2: 172-177.

del Moral, R., Clampitt, C. A. and Wood, D. M. 1985. Does interference cause niche differentiation - evidence from sub-alpine plant-communities. - American Journal of Botany 12: 1891-1901.

Diamond, J. M. 1975. Assembly of species communities. - In: Cody, M. L. and Diamond, J. M. (ed.),Ecology and evolution of communities. Harvard University Press, pp. 342-444.

Egler, F. E. 1954. Vegetation science concepts. I. Initial floristic composition - a factor in old-field vegetation development. - Vegetatio 412-417.

Fox, B. J. 1987. Species assembly and the evolution of community structure. - Evolutionary Ecology 201-213.

Fox, B. J. 1989. Small-mammal community pattern in australian heathland; a taxonomically based rule for species assembly. - In: Morris, D. W., Abramsky, Z., Fox, B. J. and Willig, M. R. (ed.),Patterns in the structure of mammalian communities. Texas Tech University, pp. 91-103.

Fox, B. J. and Brown, J. H. 1993. Assembly rules for functional-groups in North American desert rodent communities. - Oikos 2: 358-370.

Fox, B. J. and Kirkland, G. L. 1992. An assembly rule for functional-groups applied to north- american soricid communities. - Journal of Mammalogy 3: 491-503.

Gitay, H. and Noble, I. R. 1997. What are functional types and how should we seek them? - In: Smith, T. M., Shugart, H. H. and Woodward, F. I. (ed.),Plant functional types: Their relevance to ecosystem properties and global change. Cambridge University Press, pp. 3-19.

Gleason, H. A. and Cronquist, A. 1991. Manual of vascular plants of Northeastern United States and adjacent Canada. - New York Botanical Garden.

Gotelli, N. J. and Graves, G. R. 1996. Null models in ecology. - Smithsonian Institution Press.

Grime, J. P. 1974. Vegetation classification by reference to strategy. - Nature 26-31.

Grime, J. P. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. - American Naturalist 982: 1169-1194.

Grime, J. P., Hodgson, J. G. and Hunt, R. 1988. Comparative plant ecology : A functional approach to common British species. - Allen & Unwin.

Hills, J. M., Murphy, K. J., Pulford, I. D. and Flowers, T. H. 1994. A method for classifying European riverine wetland ecosystems using functional vegetation groups. - Functional Ecology 2: 242-252.

Knoop, W. T. and Walker, B. H. 1985. Interactions of woody and herbaceous vegetation in a Southern African savanna. - Journal of Ecology 1: 235-253.

Lavorel, S., McIntyre, S., Landsberg, J. and Forbes, T. D. A. 1997. Plant functional classifications: From general groups to specific groups based on response to disturbance. - Trends in Ecology & Evolution 12: 474-478.

Lee, E.T. 1992. Statistical methods for survival data analysis. Wiley, New York.

Leishman, M. R. and Westoby, M. 1992. Classifying plants into groups on the basis of associations of individual traits evidence from Australian semiarid woodlands. - Journal of Ecology 3: 417-424.

Levine, J. M. 1999. Indirect facilitation: Evidence and predictions from a riparian community. - Ecology 5: 1762-1769.

Oldeman, R. A. and van Dijk, J. 1991. Diagnosis of the temperament of tropical rain forest trees. - In: Gómez-Pompa, A., Whitmore, T. C. and Hadley, M. (ed.),Rain forest regeneration and management. UNESCO, pp. 21-66.

Pianka, E. R. 1980. Guild structure in desert lizards. - Oikos 2: 194-201.

Pitelka, L. F. and Ashmun, J. W. 1986. Physiology and integration of ramets in clonal plants. - In: Jackson, J. B. C., Buss, L. W. and Cook, R. E. (ed.),Population biology and evolution of clonal organisms. Yale University Press, pp. 399-435.

Raunkiaer, C. 1934. The life forms of plants and statistical plant geography. - Oxford University Press.

Rice, W. R. 1989. Analyzing tables of statistical tests. - Evolution 1: 223-225.

Sala, O. E., Golluscio, R. A., Lauenroth, W. K. and Soriano, A. 1989. Resource partitioning between shrubs and grasses in the patagonian steppe. - Oecologia 4: 501-505.

Sala, O. E., Lauenroth, W. K. and Parton, W. J. 1992. Long-term soil-water dynamics in the shortgrass steppe. - Ecology 4: 1175-1181.

Shugart, H. H. 1997. Plant and ecosystem functional types. - In: Smith, T. M., Shugart, H. H. and Woodward, F. I. (ed.),Plant functional types: Their relevance to ecosystem properties and global change. Cambridge University Press, pp. 20-46.

Simberloff, D. and Dayan, T. 1991. The guild concept and the structure of ecological communities. - Annual Review Of Ecology And Systematics 115-143.

Stokes, M. E., Davis, C. S. and Koch, G. G. 2000. Categorical data analysis using the SAS system. - SAS Institute.

Stone, L., Dayan, T. and Simberloff, D. 1996. Community-wide assembly patterns unmasked: The importance of species' differing geographical ranges. - American Naturalist 6: 997-1015.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. - Princeton University Press.

Vermeij, G. J. 1996. An agenda for invasion biology. - Biological Conservation 1-2: 3-9.

Weiher, E. and Keddy, P. 1999. Assembly rules as general constraints on community composition. - In: Weiher, E. and Keddy, P. (ed.), Ecological assembly rules: Perspectives, advances, retreats. University Press, pp. 251-271.

Weiher, E. and Keddy, P. A. 1995. Assembly rules, null models, and trait dispersion - new questions from old patterns. - Oikos 1: 159-164.

Whitney, G. G. and Foster, D. R. 1988. Overstory composition and age as determinants of the understorey flora of woods of central New England. - Journal of Ecology 3: 867-876.

Wieland, N. K. and Bazzaz, F. A. 1975. Physiological ecology of three codominant successional annuals. - Ecology 3: 681-688.

Wilson, J. B. 1988. Shoot competition and root competition. - Journal of Applied Ecology 1: 279-296.

Wilson, J. B. 1989a. Relations between native and non-indigenous plant guilds in the Upper Clutha ; New Zealand. - Journal of Ecology 223-235.

Wilson, J. B. 1989b. A null model of guild proportionality, applied to stratification of a New-Zealand temperate rain-forest. - Oecologia 2: 263-267.

Wilson, J. B. 1995. Testing for community structure : A Bayesian-approach. - Folia Geobotanica & Phytotaxonomica 461-469.

Wilson, J. B. and Gitay, H. 1995. Community structure and assembly rules in a dune slack : Variance in richness ; guild proportionality ; biomass constancy and dominance/diversity relations. - Vegetatio 93-106.

Wilson, J. B. and Roxburgh, S. H. 1994. A demonstration of guild-based assembly rules for a plant community ; and determination of intrinsic guilds. - Oikos 267-276.

Appendix

Figure 1. Representative species in each guild: a) Small above-ground biomass, branching and rhizomatous root structure (SB) - *Lycopodium digitatum*; b) Large above-ground biomass, branching root structure (LB) - *Amelanchier arborea*; c) Small-above-ground biomass, taproot (ST) - *Rubus sp.*; and d) Large above-ground biomass, taproot (LT) - *Quercus rubra.* These plants are commonly found in our study site. Note the use of vertical space by the tap-rooted plants, whereas the branching-rooted species use shallow, wide spaces with their root structure.

Figure 1.

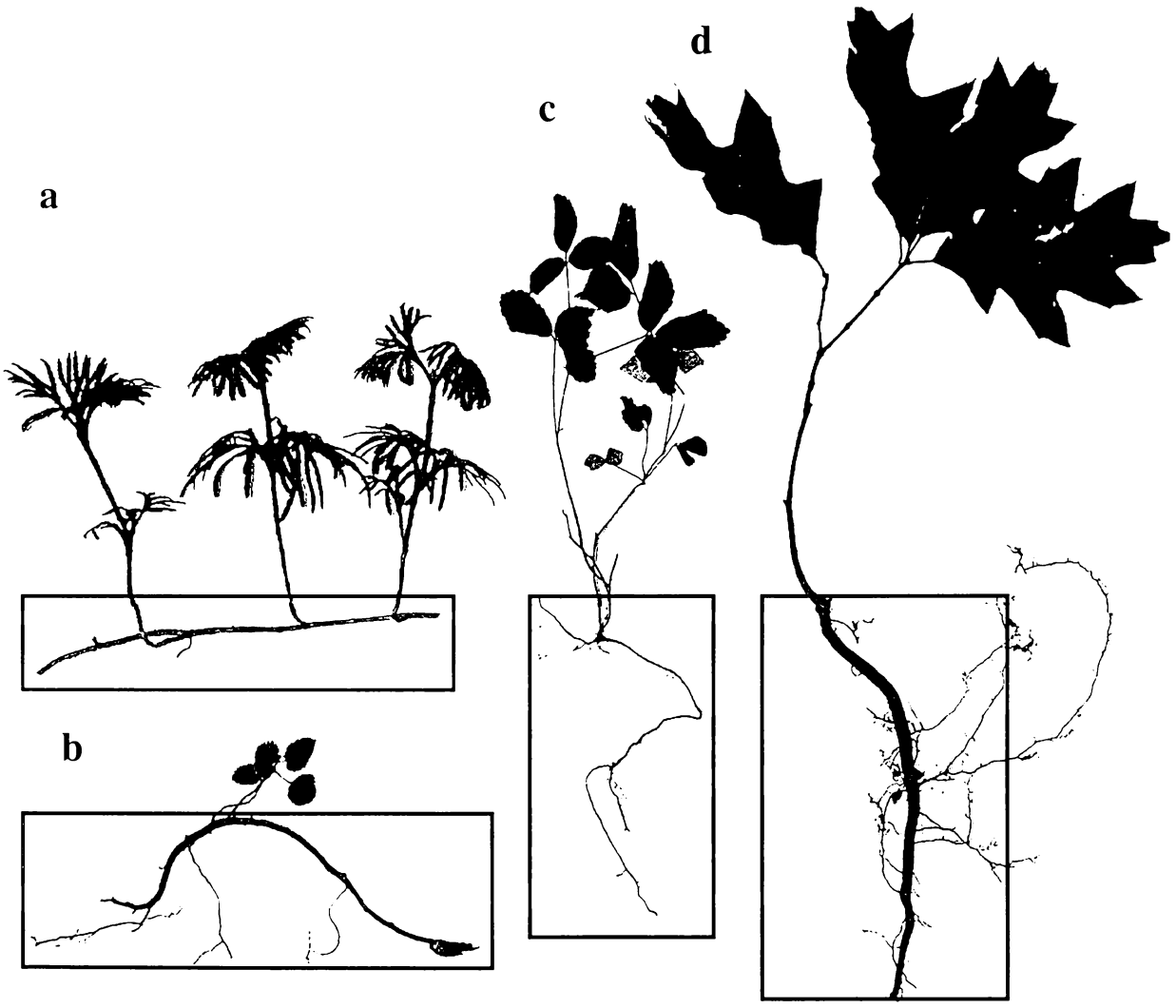

Figure 2. Experimental design for the invaders placed in the138 subplots sampled in this study. Numbers in parentheses indicate number of replicates, or subplots. The boxes with the functional groups indicated (SB, ST, LB, LT) are the number of subplots that have those functional groups manipulated for each treatment above. For the 'one representative species' treatment, SB (small above-ground biomass, branching root structure), LB (large above-ground biomass, branching root structure), LT(large above-ground biomass, taproot), ST (small above-ground biomass, taproot) indicate functional groups with only one species in each of these functional groups left in the plot. For the 'lack of functional group' treatment, SB, LB, LT, and ST indicate eliminated functional groups in those plots. The 138 subplots were divided among 4 larger plots, having 1X and 2X treatments, and further split by site location (streamside and non-streamside). The gray box indicates the invaders planted into the manipulated plots. The first invader addition of the 2X treatment was planted in 1999. A second invader addition was planted into these same 80 plots, one year later. The separate 1X plots were planted in 2000 and are identical, except that they have only LB and LT removed (indicated in bold) and a total of 56 plots.

Figure 2.

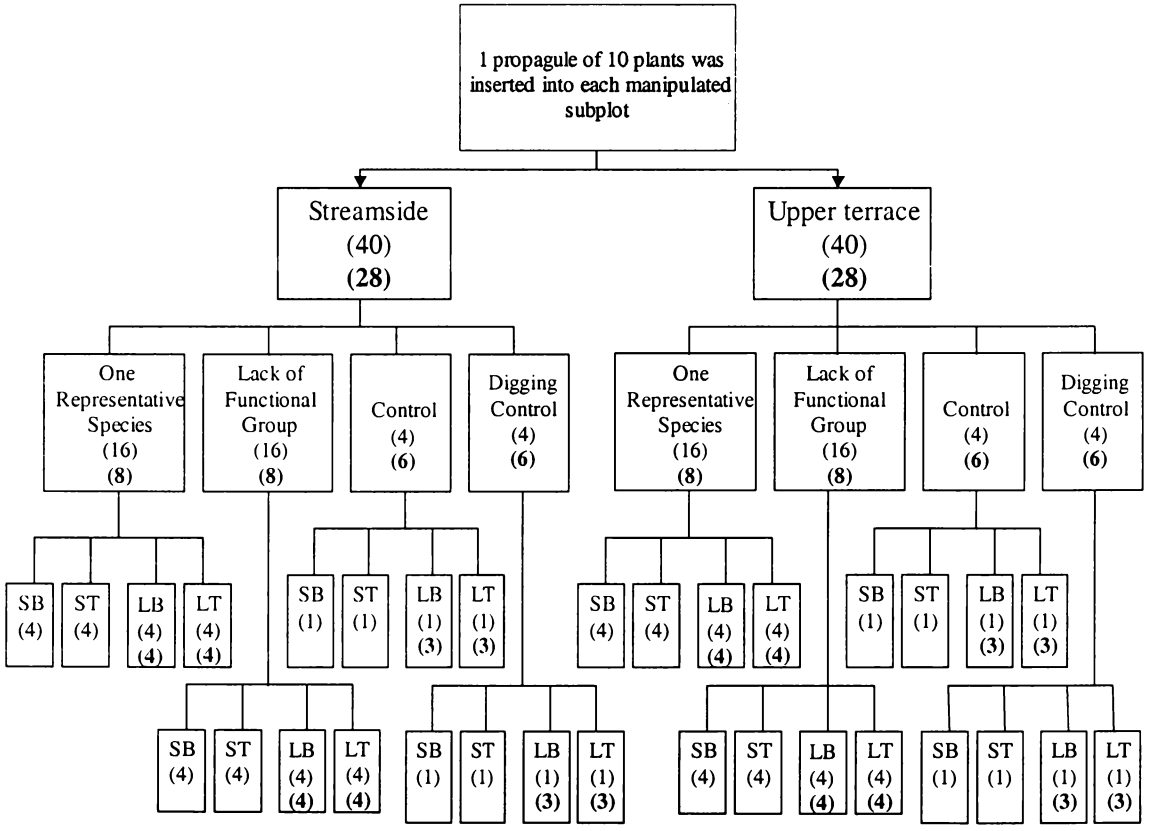
1 propagule of 10 plants was inserted into each manipulated subplot
Streamside (40) (28)
Upper terrace (40) (28)
One Representative Species (16) (8)
Lack of Functional Group (16) (8)
Control (4) (6)
Digging Control (4) (6)
SB (4)
ST (4)
LB (4) (4)
LT (4) (4)
SB (1)
ST (1)
LB (1) (3)
LT (1) (3)

Figure 3. Kaplan-Meier survivor analysis of the different functional groups across three years. The plants analyzed were from the first invader addition of the 2X treatment, across the three census years: 1999, 2000 and 2001. The functional group survivorships are: SB>LB>ST>LT. Note that the x axis is in natural log scale and the y-axis is in the natural log of the negative of the natural log scale.

Figure 3.

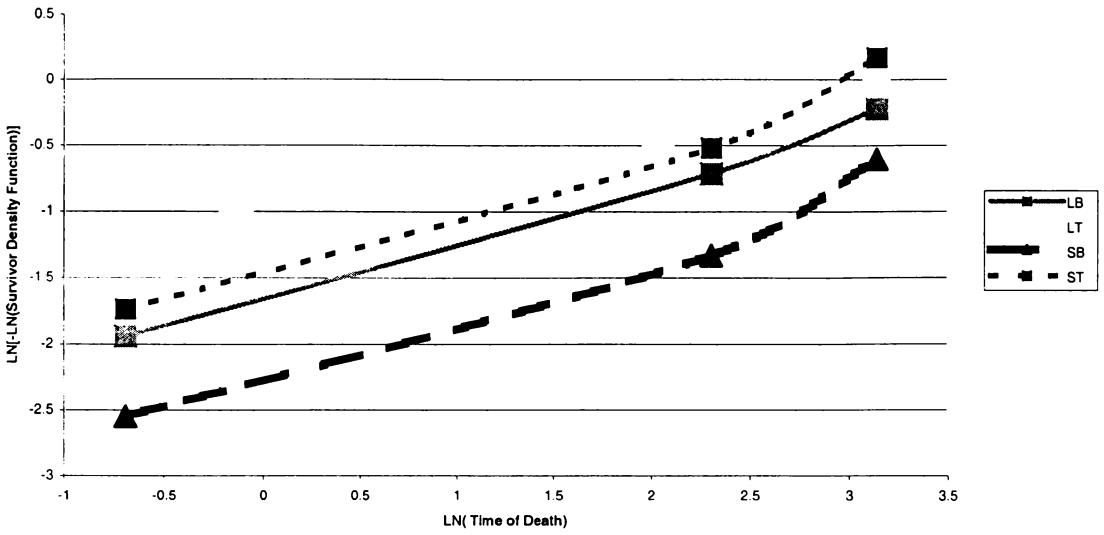
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-1
-0.5
0
0.5
1
1.5
2
2.5
3
3.5
LN[-LN(Survivor Density Function)]
LN(Time of Death)
LB
LT
SB
ST

Figure 4. Percent survivorship of all invaders in each treatment, for all three experiments. The four treatments in each of the 3 logistic regressions did not differ significantly. The logistic regression was carried out on each of the three data sets in 1999 and 2000. These data were summed in this figure for ease of representation.

Figure 4.

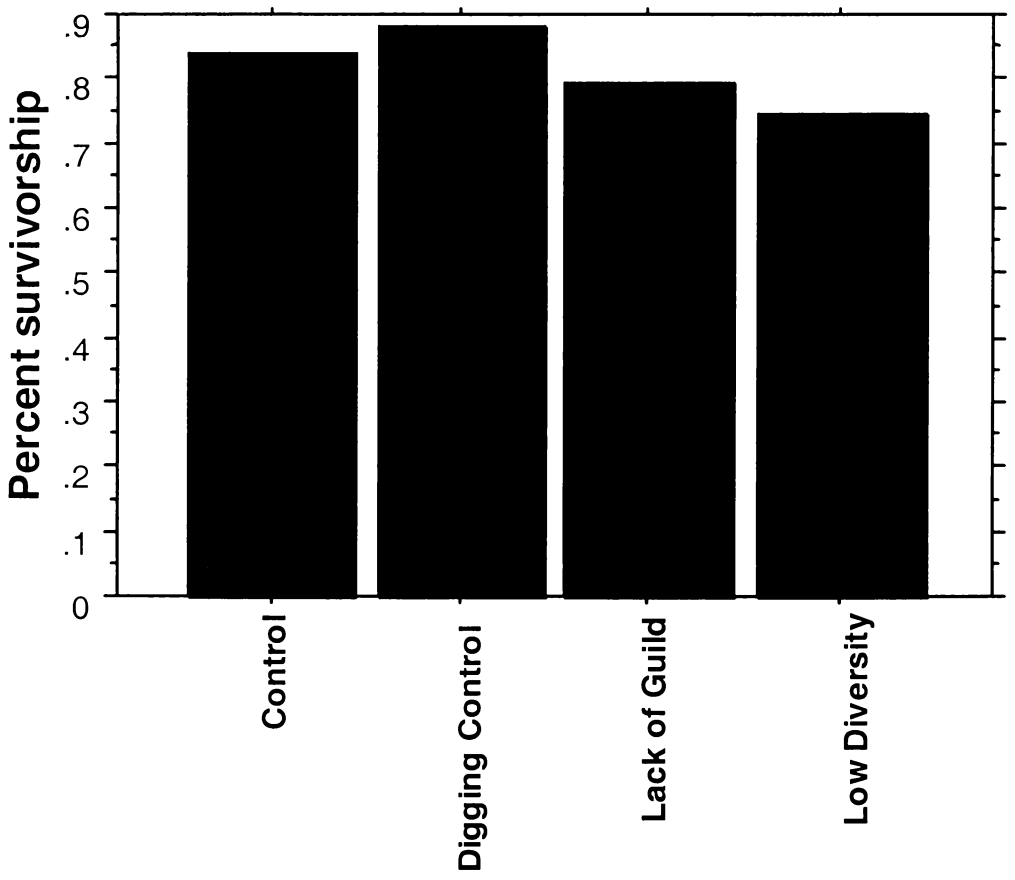
Percent survivorship
0
.1
.2
.3
.4
.5
.6
.7
.8
.9
Control
Digging Control
Lack of Guild
Low Diversity

Table 1.

Hypotheses tested in this experiment.

Hypothesis	
1	When a functional group has been completely removed from a community, that community will become more susceptible (in general) to invasion of new species of any functional group.
2	The probability of successful invasion of plots manipulated to create low or zero diversity within functional groups will be higher for species of that particular functional group.
3	Different morphologically based functional groups will have different invasion success depending inherent biological traits.

Table 2.

Functional group characteristics that correlate with total biomass. The dependent variable was total dry biomass and the independent variables were all of the plant characters listed in the first column. Using step-wise backwards regression we selected the best model for each functional group. The characters that comprised the best model were then measured yearly in the field and are marked by an '*'. The most significant models for a given functional group are,

SB total biomass = -2.16 SD + 0.322 CL + 0.28 CW – 1.56 IL + $(-2.16\ SD)^2$

ST total biomass = 0.345 SD + 0.013 CL

	Functional Group			
Plant character	**SB**	**ST**	**LB**	**LT**
Stem diameter	*	*		*
Canopy Length	*	*	*	
Canopy width	*		*	*
Internode length	*			
Plant height				*
No. of leaves				*
Model R^2 and p-value	1.00, p<0.0001	0.791, p<0.0001	0.9981, p<0.004	0.9982, p<0.063

LB total biomass = -1.68 CL + 4.46 CW

LT total biomass = 0.37 SD + 0.025 PH – 0.081 CW + 0.371 NOL.

Table 3.

Loglinear regressions of the first (A) and second censuses (B) of the first invader addition of the 2X treatment. Eight hundred plants were planted in 1999 for this experiment. The first census occurred two weeks after transplantation and the second occurred one year later, in 2000. The first sequential Bonferroni-adjusted α-value was .0016. Significant p-values that are below the sequentially-ranked α- values are marked in bold. P-values are listed for the test of whether members of the functional group invading had significantly different success when invading plots that had that functional group removed. The numbers of these tests are in parentheses, following the p-values.

A)
2 Weeks

Functional	**Invading functional group**			
group removed	**LB**	**LT**	**SB**	**ST**
LB	0.04 (6)	0.47 (20)	0.01 (39)	0.02 (69)
LT	0.03 (15)	0.18 (10)	0.04 (56)	0.02 (57)
SB	0.91 (14)	0.11 (18)	0.35 (24)	0.15 (84)
ST	0.004 (3)	0.47 (11)	**0.0004 (8)**	0.85 (86)

Overall functional-group-removed-by-functional-group-invaded p-value=0.01, n=599

B)
1 Year

Functional	**Invading functional group**			
group removed	**LB**	**LT**	**SB**	**ST**
LB	0.65 (8)	0.15 (11)	0.09 (45)	0.68 (72)
LT	0.26 (20)	0.34 (10)	0.19 (58)	0.008 (61)
SB	0.17 (16)	**0.0002 (19)**	0.39 (28)	0.009 (85)
ST	0.08 (7)	0.18 (12)	0.25 (10)	0.22 (97)

Overall functional-group-removed-by-functional-group-invaded p-value=0.007, n=646

Table 4. Loglinear regression of the first (A) and second (B) censuses of the second invader addition of the 2X treatment. The 800 plants for this experiment were planted in 2000. The first census occurred 2 weeks after transplantation and the second occurred one year later, 2001. The table-wide sequential Bonferroni-adjusted α-value was .0016. No p-values fell below this value; thus it is safe to assume that all tests are not significant at the level of the table-wide α level. P-values are listed for the test of whether members of the functional group invading had significantly different success when invading into plots with that functional group removed. The numbers of these tests are in parentheses, following the p-values.

A)
2 Weeks

Functional	**Invading functional group**			
group removed	**LB**	**LT**	**SB**	**ST**
LB	(...) (9)	(...)	.65 (57)	.65 (95)
LT	.92 (24)	.51 (1)	.93 (62)	.94 (74)
SB	.79 (13)	(...)	.81 (58)	.81 (93)
ST	(...) (15)	.69 (1)	.83 (54)	.82 (90)

Overall functional-group-removed-by-functional-group-invaded p-value =0.39, n=646

B)
1 Year

Functional	**Invading functional group**			
group removed	**LB**	**LT**	**SB**	**ST**
LB	.4243(9)	(...)	.0129(50)	.0856 (94)
LT	.6269(24)	(...)	.1273(61)	.0250(73)
SB	.8121(12)	(...)	.0992(54)	.6171(84)
ST	.4358(14)	(...)	.0137(53)	.8256(90)

Overall functional-group-removed-by-functional-group-invaded p-value= .0185, n=626

Table 5. Loglinear regression analyses of the first (A) and second (B) censuses of the 1x treatment. The 336 plants for this experiment were planted in 2000. The first census occurred 2 weeks after transplantation and the second occurred one year later, 2001. The sequential Bonferroni-adjusted α-value was 0.003. No p-values fell below this value; thus it is safe to assume that all tests are not significant at the level of the table-wide α level. P-values are listed for the test of whether member of the functional group invading had significantly different success when invading into plots that had the indicated functional group removed. The numbers of these tests are in parentheses, following the p-values.

A)
2 Week

Functional	**Invading functional group**			
group removed	**LB**	**LT**	**SB**	**ST**
LB	0.24 (103)	(...) (3)	0.10 (11)	0.09 (39)
LT	0.43 (89)	(...) (11)	0.38 (17)	0.87 (42)

Overall functional-group-removed-by-functional-group-invaded p-value of p=0.18, n=336

B)
1 Year

Functional	**Invading functional group**			
group removed	**LB**	**LT**	**SB**	**ST**
LB	0.84 (2)	0.26 (4)	0.21 (14)	0.58 (52)
LT	0.84 (8)	0.26 (10)	0.21(15)	0.58 (34)

Overall functional-group-removed-by-functional-group-invaded p-value of 0.5397, n=139

Table 6.

Abundant invaders of the 2X treatment planted in 1999 and 2000 that had no stem diameter growth response to their particular functional group being removed or reduced. '*' indicate nonindigenous species. P-values and (n) are listed in the cells. The stem diameter growths after one year were tested with Kruskal-Wallis tests. The first sequential Bonferroni-corrected α =.0046. No p-values fell below this value, so it is safe to assume that all tests are not significant at the level of the table-wide α level.

Species	**Functional group**	**Planted in 1999**	**Planted in 2000**
Acer rubrum	LT	.3120(19)	(...)
Aster divaricatus	ST	.7418(13)	.3515(12)
Cerastium vulgatum	SB	(...)	.2636
Desmodium sp.	ST	.2243(12)	(...)
**Duchesnia indica*	ST	.6879(11)	(...)
Aster sp. A	ST	.1312(22)	(...)
Hamamalis virginiana	LB	.1783(12)	(...)
Maianthemum canadense	SB	.5617(11)	.7552(25)
Mitchella repens	SB	.7304(29)	(...)
Oxalis stricta	ST	(...)	.1675(7)
Parthenocissus quinquefolia	ST	.4758(18)	(...)
Potentilla canadensis	ST	(...)	.0159(16)
Potentilla simplex	ST	(...)	.2929(20)
**Prunella vulgaris*	ST	.0994 (39)	.0976(12)
Rosa multiflora	LB	(...)	.4795(3)
Veronica officinalis	SB	(...)	.1031(15)
Viola septentrionalis	ST	.1220(28)	.1895(24)

PART II

Testing Elton's notion of biotic resistance: Does plant invasion success depend upon species richness of the recipient community?

Abstract

I investigated the role and importance of biotic diversity and natural flooding disturbance in resistance to plant invaders in a floodplain forest in southwestern Virginia. I tested the biotic component of ecological resistance by studying the role of plant and functional group understory richness in riparian community organization. Additionally, I assessed the role of the canopy composition on invasion. Randomly chosen 1.5 x 1.5m plots of two streamside and two upper terrace sites with different flooding occurrences were randomly assigned low (low richness), intermediate (intermediate richness) and high (control and digging control) species richness treatments of the recipient communities. After a two-week period to allow for rerooting of plants, these plots were planted with seedlings or adult plants (<1/2m) of 10 randomly chosen species from widespread native and introduced species commonly found throughout the floodplains of Big Stony Creek and with similar habitat requirements. Success of an invasion was measured by proxy biomass, growth, and survivorship of the invader. I assigned plant species to functional groups and investigated which functional groups resisted invasions by other species. The most significant biotic influences on invader survivorship in this system of streamside and upper terrace plots were the overstory of *Rhododendron maximum* and the understory functional composition. Invader survivorship increased with distance from *R. maximum* and with species richness of the understory small above ground, branching-rooted functional group. Survivorship was positively correlated with recipient community species richness and negatively correlated with recipient plots density. However, the richness-invasibility relationship is different in areas that have been flooded with a negative relationship between plot species richness and invader survivorship. Density is an important factor that should be analyzed simultaneously with species richness of recipient plots, in order to disentangle their separate contributions to invasion resistance. Full understanding of Elton's notion of biotic resistance requires a further exploration of the role of natural disturbance regimes.

Introduction

Elton (1958) invoked the notion of biotic resistance to non-native invaders as the justification for the extreme degree of invasion of species-poor systems such as islands and anthropogenically-disturbed areas. 'Biotic resistance' is the hypothesis that the key to the success of an invader is the degree of resistance offered by the resident biota and that this resistance is somewhat predictable (Simberloff 1986). Higher species richnesses might be expected to decrease nutrient availability and increase competition, predation, disease, and parasites. These factors may, in turn, contribute to biotic resistance. The relationship between the biotic resistance and invasibility of a system is typically called the "diversity-invasibility" relationship and most hypotheses testing this relationship are referring to species richness as the index of diversity. To clarify the hypothesis, I use the term richness-invasibility relationship. The effect of resident biota richness on plant invasibility has been most often researched in open systems such as grasslands, with both observational and experimental studies (Part **IV**). These studies have provided evidence of positive (Robinson et al. 1995, Planty-Tabacchi et al. 1996, Wiser et al. 1998, Stohlgren et al. 1999), negative (Tilman 1997, Levine 2000, Naeem et al. 2000) and no effects (Lavorel et al. 1999, Dukes 2001) of species richness on community invasibility. In a review of the diversity-invasibility hypothesis, Levine and D'Antonio (1999) discovered that observational studies of natural systems tended to indicate a positive relationship between diversity and invasibility. Invader addition studies that did not manipulate the resident communities and experimental studies that directly manipulated the recipient plant communities both produced mixed results for this relationship (Robinson et al. 1995, Tilman et al. 1996, Palmer and Maurer 1997, Tilman et al. 1997). Clearly, Elton's hypothesis regarding invasibility has not been resolved. However, empirical and theoretical studies of this hypothesis have provided a clear mandate for future empirical work. A number of factors have been proposed as to why empirical work has shown such variable support for this hypothesis.

Covarying factors

Many factors can covary with species richness, such as disturbance, nutrients, climate and propagule pressure (number of seeds introduced). 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, Wardle 2001). Additionally, resident cover and biomass covary with species richness. In order to elucidate the unique influence of species richness on invasion, experiments are necessary that separate these covarying factors from resident species richness by manipulating species richness *in situ*.

Flooding

It has been suggested that environmental stress or disturbance will change the richness-invasibility relationship. Hood and Naiman (2000) predicted that in more communities (not affected by flooding), the diversity-invasibility paradigm will hold, but in disturbed communities there will not be a negative relationship between resident species richness and invasibility. The proposed mechanism for this difference is the overriding influence of abiotic rather than biotic factors in plant survivorship (Gasith and Resh 1999, Hood and Naiman 2000). This relationship is influenced by whether the observational or experimental plots are under a natural disturbance regime.

Functional groups

Use of functional groups is a fruitful way to examine plant invasibility. Wiser (1998) revealed that a non-indigenous perennial herb, *Hieracium lepidulum*, invaded a subset of plots in a New Zealand mountain beech forest that had more species in the same morphological guild. Dukes (2000) found that the presence of more functional groups inhibited invasion into grassland microcosms in California. However, Lavorel et al (1999) discovered no relationship between functional group richness **or** species richness and invasibility of experimentally manipulated plant communities in France, Portugal and Australia.

Objectives

My objectives were to explore the role and importance of biotic factors in species invasion and ecological resistance in a closed-canopy system. I expected that the overstory influence of a closed-canopy system would have a major impact on community invasibility. I tested the hypothesis that biotic resistance to the establishment of invaders exists. In other words, I determined if decreasing resident species richness increases invasibility. I reduced natural plot species richnesses to create a low richness treatment; ambient richness (control) and digging control (digging control) plots served as high richness treatments, while

maintaining original plot density, through individual plant replacement. I inserted "invaders" into high, intermediate, and low richness plots. Manipulating plot species richness removed covarying extrinsic factors, and retaining original plot densities allowed me to isolate the effect of species richness on invasibility. I tested intrinsic effects of resident species richness on invasibility and checked whether this relationship changes with a natural disturbance of flooding by placing these manipulated plots along a gradient of flooding. To my knowledge, this is the first field experiment conducted on Elton's hypothesis in a closed-canopy system.

I predicted that the probability of successful invasion would increase with decreasing species richness of the recipient community, if density is unchanging. I also predicted that the richness-invasibility relationship would not hold in communities subjected to substantial flooding. I tested the prediction that certain functional groups would be better at resisting invaders than others. Lastly, I explored overstory effects on invasibility of the plots in different flooding regimes.

Experimental Design and Methods

Experimental system

To capture the highest biological species richness in this riparian system, and thus the highest possible level of biotic resistance, all of my plots were located in the most heterogeneous habitat (Vannote et al. 1980), in the midreaches of Big Stony Creek (38° 26' N, 81° 50' W), in southwestern Virginia. The vegetation types in my study sites 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). These are the closed forest types of Trianosky (1994) and are evergreen and deciduous temperate forests. Regeneration patterns differ under *Rhododendron maximum* canopy than other forest types (Clinton and Boring 1994), possibly owing to differences in light, soil nutrients, and water under this canopy (Nilsen et al. 2001). The surface soil layer was deeper in the upper terrace areas, as there were fewer *Rhododendron maximum* roots occupying this space. Because flooding frequency varies with elevation (Menges and Waller 1983), elevation differences are a necessary component of a study of different flooding

regimes. However, differences in elevation are also correlated with differences in edaphic factors (Ware et al. 1992, Bridge and Johnson 2000) and these differences may influence species composition (Clinton and Boring 1994, Kwit et al. 1998, Brosofske et al. 2001) and probability of establishment of certain exotic species (McNab and Loftis 2002). The elevational differences among my sites were slight (personal observation) but are associated with statistically significant differences in edaphic conditions (Table 1).

All manipulated plants were less than half a meter tall. My functional groups were defined by the way they physically occupy space and so comprise variations of all possible combinations of aboveground biomass and rooting structure type. These combinations reflect, in part, traits that may allow a plant to withstand flooding disturbance. All plants were characterized by their potential adult classification, though that may not have been the state of the individual at the time of experimental manipulation. The functional groups were small aboveground biomass, with branching and rhizomatous root structure (SB); small-above-ground biomass, with taproot (ST); large aboveground biomass, with branching root structure (LB); and large aboveground biomass, with taproot (LT) (Appendix 1 & Part **I**).

Plot design

The topography of the field site was a typical stream bank and terrace system. All plots were located on level terraces to control for changes in plant interactions on sloped versus level ground. Two streamside plots were adjacent to the creek and were flooded yearly. The other two were in the second level of the floodplain and were not flooded during the experimental time frame. I will use the term "site position" to indicate the position of the treatment plot (first level, or stream-side plots were positioned near the stream and second level, or upper terrace plots were located one terrace up from the first level) that the invader was planted into. I will use the term "flooding condition" for the flooded and unflooded subplots to indicate whether flooding occurred over that subplot during the prior year. All experimental plots were located under forest canopy. Each plot encompassed a 70 x 10m area. One plot in each of the streamside and upper terrace areas, each containing 40 subplots, was censused and manipulated in 1999. The second pair of plots, with 56 subplots, was censused and manipulated in 2000 (Figure 1). These two different experiments are referred to as "1999 invaders" and "2000 invaders", respectively. Optimal plot size was determined from a

species-area curve generated from 10 nested samples in the floodplain area of Big Stony Creek (Figure 2). Because sites differ in observed proportion of total taxon richness with sample size (Cao et al. 2002), I attempted to obtain the highest number of species within my site by appropriately-sized sample subplots. Williamson et al. (2001) suggested that the species-area relationship does not have an asymptote.

Thus, I chose the subplot size at the first leveling-off of the species-accumulation curve (Cain 1938, Bunge and Fitzpatrick 1993, Soberon and Llorente 1993). These 1.5 x 1.5m subplots had high species richness, and consequently the greatest hypothesized species interactions, at the first asymptote of the species-accumulation curve (Cain 1938).

Subplot species richnesses (total number of species) and stem densities were censused in each subplot, prior to manipulation. The term 'density', used throughout this paper, indicates the number of plant individuals per subplot. Subplot species richnesses were lowered or left the same for low and high richness treatments, respectively. Manipulated subplots were left with their original densities, as the randomly picked species that were to remain in the plots were propagated and inserted into the empty holes left by removed plants. I dug up these replacements either from other subplots that required removal of those individuals or in a nearby forested area used for transplants. Subplot species richnesses were manipulated by lowering the number to two randomly-picked species per functional group (**low richness**), for a total of eight species per plot. Biomass of the 'low richness' treatment subplots was maintained, as equivalent biomass of plants was replanted in each hole created by removal of that plant, using either of the two species of the four functional groups randomly selected to remain in that plot. Another set of subplots had one randomly-picked functional group either removed or lowered to one species (**intermediate richness**). Biomass of the 'intermediate richness' treatment plots did not change, as equivalent biomasses of plants were replanted in each hole created by removal of a plant, using either the one species of that functional group randomly selected to remain in that plot (half of the intermediate subplots) or randomly chosen species of the remaining functional groups (other half of the intermediate subplots) when one functional group was totally removed to study the effects of functional group removal (Part **I**). 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**). The digging controls for the intermediate and the low richness subplots had one and all functional groups dug up and replanted, respectively. Any significant difference in success of invasion between the digging control and the control plots indicates the effect of digging. Randomly chosen subplots in each of the 4 plots located in two streamside and upper terrace sites which experience yearly and no flooding, respectively, were randomly assigned low (low richness), intermediate (intermediate richness) and high (control and digging control) species richness treatments of the recipient communities (Figure 1). In order to reduce stress related to transplanting, immediately following planting, all subplots were watered every day for a week and then every other day for another week.

Invader input

After this two-week period to allow for rerooting of plants, these 1.5 x 1.5 m subplots were planted with adult and seedling plants (<1/2 m) of 10 randomly chosen species from widespread native and introduced species commonly found throughout the floodplains of Big Stony Creek and with similar habitat requirements (as in Burke and Grime (1996). I identified 37, 44, 38 and 29 species in the SB, ST, LB and LT groups, respectively, using the nomenclature of Gleason & Cronquist (1991). These groups contain 11, 23, 1, and 2 non-indigenous species, respectively (Appendix 1). I refer to these plants as 'invaders' even though many are native species (Appendix 1). These 10 invaders were inserted into the plot as equidistantly from each other as possible, following three parallel, diagonal lines, with the middle line the hypotenuse of 2 equilateral triangles comprising the inner 1m of the plot. Each plant was marked with metal tags and watered daily for one week and then once every other day for the following week. I transplanted 800 invaders into the 80 subplots in 1999. I planted 1120 invaders in 112 subplots in two separate plots in 2000.

Monitoring invaders

Success of an invasion was measured by survivorship and growth of the invader. All invaders were monitored two weeks after transplantation, and every year following. Survivorship was measured by death at a census period. A plant was counted as dead if it had no chlorophyll left in any structures or was missing from the spot where it was planted.

If the marker tag was absent the plant was counted as missing. The following traits were measured to estimate growth, in the field, *in situ*, as follows:

1) Stem diameter: Measured at ground level, using calipers.
2) Canopy length: The longest length of the canopy area of the leaves, measured with a ruler, parallel to the ground
3) Canopy width: Measured with a ruler, perpendicular to the length and parallel to the ground.

Overstory community characteristics

To investigate the relationship of the impact of overstory on invader survivorship, I censused the distance, size and canopy cover of the adult overstory trees and shrubs near the subplot. I measured the diameter at breast height (DBH) of the largest tree and shrub within three meters of the edge of each subplot. I also recorded the distance of this tree and shrub from the subplot. If the largest tree or shrub was within the 1.5 meter subplot, then the distance was recorded as negative, from the closest edge of the plot. To estimate tree and shrub canopy cover, I measured the diffuse penetration coefficent, or measurement of sky visible beneath the plant canopy (Norman and Campbell 1989), of each subplot with a digital hemispheric canopy lens (CID-110, CID, Inc.) at 1.5m above ground level. All censuses took place in August of 2001.

Statistics

Percentage of plot invader survivorship was transformed with Anscombe's transformation (Zar 1999). The percentage data were the percent of invaders that survived out of the original ten individuals planted in the plot. All species richness treatments (high, intermediate, low) were used in the analyses, unless otherwise noted. To test the relationship between resident species or functional group species richness relationship and plot invasibility, I conducted multiple regressions with transformed percent invader survivorship as the dependent variable, while the independent variables were species richness, density, flooding condition, and the interaction of site location or flooding condition with species richness and density of the recipient subplots. These analyses were conducted for the censuses of the invaders two weeks after they were planted and each year following, for both sets of invaders. I tested survivorship of the invaders across the site location they were

inserted into as a measurement of transplant stress in each treatment plot (streamside and upper terrace). I tested invader survivorship across the flooding condition (whether the plot was flooded) as a measurement of flooding disturbance to the plant. To evaluate the effect of overstory on understory invasibility, I performed multiple regressions with percent invader survivorship as the dependent variable and LB and LT diameter at breast height (DBH) and distance from plot as the independent variables. I used the R^2 –C(p) selection method for all multiple regressions, where the model with the least variables and the highest R^2 was selected, given that the C(p) was no greater than the number of variables in the model (Mallows 1973, Daniel and Wood 1980).

To correct for multiple testing, I took the p-values from the analyses, ranked them, and used the sequential Bonferroni technique of dividing a critical alpha of 0.05 by the rank of the p-values (Rice 1989).

To explore the potential overstory effects on invasibility, I investigated canopy cover relationship with invader survivorship. I performed a simple regression of the diffuse penetration coefficients, which are a measure of sky visible beneath the plant canopy, with percent invader survivorship.

The stem diameter, canopy length, and canopy width were measured in the field for each invader for every census in 2000 and 2001. I determined growth of each invader by subtracting the stem diameter, canopy length, and canopy width measurements of year 2001 from the year 2000 measurements of invaders planted in 2000 (n=1120). Kruskal Wallis tests were performed for the change in each of these three measured characteristics and the proxy biomass for each plant within flooding conditions, from year 2000 to 2001. The plants in the low and the high richness treatment subplots were analyzed, to obtain the greatest difference in resident plot species richness on plant growth.

I estimated the proxy biomass for each invader using equations that predict functional group biomass using plant characters that were generated by Von Holle and Simberloff (Part I). I tested for differences in biomass of invaders between the low and high richness plots for each functional group, using Kruskal-Wallis tests.

To investigate treatment effects on invader survivorship, I conducted a Kaplan-Meier survivorship (Lee 1992) test on invader survivorship across time and treatment plots.

To test for changes in resident plant diversity after plot manipulation, I conducted Student t-tests across low and high richness treatments

Evidence of herbivory and fungal infection was recorded for each invader in all plots in 2001. Percentage of invaders in plots that evidenced herbivory was arc-sine square root transformed and regressed against plot species richness and density to determine if richer or denser plots attract more herbivores. These analyses were not possible for pathogens, as only two cases of fungal infection were recorded for the 956 survivors in 2001.

Results

Survivorship of transplanted invaders was significantly lower in the flooded than the unflooded streamside subplots in year 2001. However, there was a trend for higher survivorship in the flooded subplots in the 1999 invaders (Table 2). Overall survivorship of the transplanted invaders was also significantly lower in the unflooded streamside plots than in the unflooded upper terrace plots. Clearly there are both site and flooding disturbance effects on survivorship of transplanted invaders.

There is no difference in invader survivorship between the digging control and control plots as indicated by a Kaplan-Meier test on survivorship across time and treatment plots (Figure 3). The plot species richnesses were significantly different across high (control and digging control subplots) and low species richness (low richness subplots) treatments by a Student t-test ($t=3.00$, $p=0.004$, Means: low species richness = 7.6, high species richness=11.02). However, the plot species richnesses of the low richness plots were not significantly lower than those of the control plots, one year after manipulation ($t=0.369$, $p=.71$, Means: low species richness=9.79, high species richness = 10.17). This was due to germination of individual plants from the seed bank or resprouting from residual roots accidentally left after plot species richness manipulations. These individuals added to the plot species richness but were generally not abundant.

Understory Community Characteristics

Plot species richness effects on survivorship

Because I expected to find that invaders are more likely to survive in low richness plots, I used the pairs of plots with the highest degree of difference of species richness for

the analysis of invasibility with plot species richness, i.e. high and low richness treatment subplots. High species richness plots were represented by the control and digging control plots and the low species richness plots were represented by the low richness treatment. There was no difference in growth of stem diameter, canopy length, or width between the different species richness treatments in the different flooding conditions by Kruskal-Wallis tests.

I found no significant differences in biomass between the low and high richness plots for each functional group, using Kruskall-Wallis tests.

Site and invasibility

To explore the site-invasibility relationship and whether it changes with flooding, I analyzed the effect of site location on this relationship. The site variables that had the biggest influence on invader survivorship changed with time after transplantation. Common relationships arose from both cohorts, even though they were planted in different years. Density showed a marginally significant negative effect on invader survivorship within the first two weeks of the 1999 transplants but became insignificant after comparison with the Bonferonni-adjusted alpha. The site position of the year 2000 transplants was significantly negatively correlated with invader survivorship two weeks following the initial insert. The greatest two-week mortality occurred under the *Tsuga Canadensis/ Rhododendron maximum* canopy in the streamside plots. The different edaphic characters under this canopy may be the cause for this transplant stress (Table 3A). These streamside plots had lower soil water and percent carbon and nitrogen content.

Flooding and invasibility

To explore the richness-invasibility relationship and whether it changes with flooding, I analyzed the effect of flooding on this relationship. Overall, species richness was strongly positively correlated with one-year invader survivorship for the year 2000 transplants (Table 3B). One year later, density was the most significant (and negative) influence on invasion success in the 1999 transplant cohort. There was no relationship of the independent variables with invader survivorship two years after the first set was transplanted (Table 3B). The B4 interaction of the 2000 cohort was a negative relationship compared to the positive richness-invasibility relationship for all of the plots. The different sign of B4

than the overall diversity-invasibility relationship suggests that flooded plots have a negative richness-invasibility relationship. After flooding, the flooded plots have a negative richness-invasibility relationship while the unflooded plots have a positive richness-invasibility relationship (Figure 4). Last, the relationship between species richness and invasibility was positive when density was held constant in the regression model. Biotic characteristics of the understory became more important later in the establishment period (Figure 5).

Functional group species richness/density and invasibility

In another multiple regression analysis, where the dependent variable was invader survivorship and the independent variables were species richnesses within the functional groups present in the plot, there was only one significant relationship observed in the two different experiments (Table 4A). Plot species richness of the SB functional group had a significant positive association with invader survivorship (R^2 =.23, p=0.0008) in 2001, one year after these plants were transplanted. LT species richness had a marginally significant association with invader survivorship. However, the two other tests of the censuses showed no significant relationships between within-functional group species richnesses and invader survivorship (Table 4A).

Additionally, I investigated the relationship of the densities of the functional groups in the recipient plots with the survivorship of invaders in those plots and found one significant relationship in two census years of one experiment and no significant relationships in the other experiment (Table 4). The model that included SB and LB densities was significantly related to increased invader survivorship in the year 2001, one year after the 2000 plants were transplanted (R^2= 0.1968, p=0.002).

Herbivores

I recorded herbivory on the invaders in the 2001 census (41 plants experienced herbivory out of 956 plants censused). To test for increased predation by herbivores occurring in higher species richness plots, I analyzed the percentage of invaders with herbivory in 2001. These data were arcsine square root transformed and regressed against plot species richness and density for each experiment. There was an insignificant trend towards increased herbivory in subplots with higher species richnesses and decreased herbivory in subplots with higher densities in multiple regressions of percent herbivory with

plot species richness and density for both experiments (1999, F=1.53, p=0.22; 2000, F=2.08, p=0.13).

Overstory community characteristics

I investigated the relationship of the impact of overstory trees and shrubs on invader survivorship. Invader survivorship was regressed against the overstory characteristics for each experiment at each census period. Plots set up and planted in 1999 showed no relationship of invader survivorship in any of the census periods with the overstory trees and shrubs composition (Table 5A). However, the plots that were set up in year 2000 showed a significant relationship between invader survivorship and the overstory composition (Table 5B). Because the interaction between the overstory functional groups and site location on invader survivorship was significant, each site location was analyzed separately for the overstory composition effect on invader survivorship in 2001. Streamside plots had increased invader survivorship the further they were from a large biomass, branching rooted plant, and had decreased invader survivorship under the larger overstory large biomass, tap-rooted plants (Table 5B). The most abundant LB plants in the streamside plots were *Rhododendron maximum, Hamamelis virginiana* and *Ilex opaca* and the most abundant LT plants in the streamside plots were *Tsuga Canadensis* (eastern hemlock), *Acer rubrum* and *Nyssa sylvatica.* Plants in the upper terrace plots had increased survivorship the further they were from a large biomass, branching rooted plant (Table 5B, R^2=0.2409, p=0.02). The most abundant plants in the upper terrace plots and in the LB functional groups were *Ilex opaca*, *Kalmia latifolia* and *Rhododendron maximum.*

The mechanism for overstory effect on invasibility was explored by examining amount of sky available under the plant canopy (diffuse penetration coefficient). There was no relationship between the diffuse penetration coefficient, and invader survivorship in the 1999-planted plots, by simple regression. Plots with invaders transplanted in 2000 did show a positive relationship between invader survivorship and light penetration (Figure 6, R^2=0.03, p=0.04 ; R^2=0.035 , p=0.05; for years 2000 and 2001 respectively). However, the level of variance in invader survivorship that the overstory composition accounted for was much greater than that accounted for by light penetration alone.

Discussion

Overstory community characteristics

The strongest predictor of invader survivorship was the functional group composition of the overstory. The further away from the overstory LB of the plot (*Rhododendron maximum* in flooded plots and *Ilex opaca* in unflooded plots), the more likely an invader would survive in both flooding regimes. Additionally, invaders near larger members of the LT functional group (*Tsuga canadensis*) were less likely to survive one year of flooding. Light availability did not account for much of the variance of invader survivorship. Thus, other factors besides light accounted for the overstory canopy effect on invader survivorship. Communities made up of overstory dominants that cast deep shade and have dense root systems such as eastern hemlock and *Rhododendron* exert powerful micro-environmental effects on the recruiting understory (Clinton and Boring 1994, Nilsen et al. 2001). *Rhododendron maximum* has been shown to reduce canopy recruitment through both above- and below-ground competition with red oak seedlings (Clinton and Boring 1994, Nilsen et al. 2001). This effect has implications for understanding the mechanims of biotic resistance under a closed-canopy system. The canopy was more important than the resident understory species and functional group diversities in invader survivorship. Thus, the biggest component of biotic resistance in closed-canopy systems might be the influence of adult tree and shrub composition, rather than understory species richness.

Functional group species richness/density and invasibility

Von Holle and Simberloff (Part I) revealed that, while there was no evidence in this community for intra-guild competition and the associated assembly rules, significant associations existed between different functional groups. This fact bears on the discovery in this study that a significant predictor of increased invader survivorship was the understory functional group species richness of SB and density of SB and LB. SB might be provide optimal establishment environments for incoming invaders, as they provide low lying cover and are shallowly-rooted. The low stature of these species may allow greater light to the establishing invader. This SB cover might inhibit also soil water transpiration. Further studies of the interactions between invaders and the SB functional group would be necessary to understand the mechanisms of this facilitation.

Site and invasibility

The site where the invader was planted was the best predictor of the initial survivorship of the 2000 invaders. The environmental conditions of the streamside plots were most likely stressful and caused the increased mortality during the transplant period. The streamside areas were dominated by *Rhododendron maximum* and *Tsuga canadensis* and had lower light availability and soil nutrients and water content than the unflooded areas. The soil layer was not as deep as in the upper terrace area and the invaders that failed within the first 2 weeks were in the streamside area. This failure was not due to flooding at this time as it did not flood during this two-week interval. This finding suggests that abiotic conditions were the most important determinant of initial invader success. The high stress in the flooded areas under the *R. maximum/ T. canadensis* canopy was the greatest factor in invader survivorship. Whether those plants were adapted to the site characteristics of the flooded plots determined their immediate survivorship.

Plot species richness effects on survivorship

My result of increasing invasibility with higher understory community richness is consistent with the finding by Pugnaire and Luque (2001) that facultative interactions between a leguminous shrub, *Retama spaherocarpa*, and its associate understory species showed a net decrease in facilitation with decreased stress along an environmental gradient in southeastern Spain. Facultative interactions were more important than competitive interactions in the semi-arid plant communities where they based their studies. In my experiment, after the invaders spent a full year in the plots, resident density and species richness became the most significant predictors of invader survivorship. Denser plots might inhibit light interception or nutrient availability and cause a decrease in survivorship. However, this interaction was not as strong as the richness-invasibility interaction, as demonstrated by the results. Mutualisms between native species and invaders can be a stronger influence on community invasibility than the long-held competition-based paradigm of increasing species richness decreasing invasibility (Richardson et al. 2000).

Flooding and invasibility

These facilitative relationships might become reduced under flooding regimes. The richness-invasibility relationship became negative in the flooded areas one year after they were transplanted. This fact suggests that the diversity-invasibility relationship may change in the different flooding regimes. Disturbances are thought to increase resource availability while simultaneously decreasing competition from resident species (Prieur-Richard and Lavorel 2000). Hood and Naiman (2000) suggested that survivorship of plants in areas with flooding would be more influenced by abiotic than biotic factors and would consequently have no relationship with resident diversity. In contrast, my data accord with the mutualism-based model of invasibility (Richardson et al. 2000) and further suggest that the diversity-invasibility relationship changes from positive to negative with flooding. If mutualism really is important in this system, then the change in sign is because these facilitative interactions become decreased in strength in flood-disturbed conditions.

Open questions

Future experiments that evaluate biotic influences on invasibility should further explore herbivory and pathogens as a factors. Fungal pathogens would be better detected in spring and fall censuses, which were not undertaken during these studies. Herbivore diversities increase in higher plant diversity plots (Mortimer et al. 1998, Koricheva et al. 2000, Siemann et al. 1998). Prieur-Richard et al. (2002) found that this increased herbivore diversity owing to higher resident plant diversities also led to increased herbivory on two experimentally-introduced species, *Conyza bonariensis* and *C. canadensis* in Mediterranean annual communities. This might be a significant, indirect, negative influence of richer systems on invasion.

Resident vegetation biomass

Density covarying with resident species richness

The objective of this experiment was to test Elton's original hypothesis regarding invasion as influenced by the number of species present in a site. An explanation for the variable subsequent support (Levine and D'Antonio 1999) for Elton's (1958) biotic resistance hypothesis might be that researchers often did not control density when experimentally manipulating richness. Future experiments could test the relative strengths of

resident plant density and diversity to understand which of these covarying factors most influences invasibility. Because density can covary with species richness, 'low richness' experimental plots may also indicate a lower density if density has not been controlled. Tilman and colleagues (1996) initially set up experimental plots in grasslands to have different species numbers, keeping density constant across species richness treatment. However, these plots were weeded for species that did not belong to that treatment, without replacement. Two years later, there was a significant positive relationship between resident plant cover and species richness. Naeem and colleagues (2000) used these plots for tests of the diversity-invasibility relationship. Plot species richness covaried with density for this experiment; thus their conclusions that invasibility is related to species diversity *per se* may be misleading. Control for resident species biomass or cover is necessary before the true influence of diversity or species richness on invasibility can be revealed. Lyons and Schwartz (2001) demonstrated an increase in establishment of the non-indigenous grass *Lolium temulentum* with experimentally-decreased diversity plots in a field study in the Sierra Nevadas. However, most of the variation in this invader's success may be attributed to increased survivorship owing to a decrease in plot biomass that results from experimental reduction of diversity. Their results might simply be due to the fact that high species richness control plots supported the original plant biomass, whereas the experimentally-reduced diversity plots had lower biomasses. (Levine 2000) suggested that the increased invasion in his experimentally manipulated high richness treatment plots might have been due to plant cover positively covarying with richness treatments. (Huston 1997) suggested that resident biomass needs to be separated from richness, in order to disentangle the intrinsic effects of species richness on invasion.

Many researchers have intimated that resident biomass is the most important determinant of community invasibility (Peart and Foin 1985, Burke and Grime 1996, Crawley et al. 1999, Lavorel et al. 1999). Rejmánek (1989) suggested that the only really significant determinant of degree of plant invasion is the amount of resident biomass or cover. This conclusion was supported by findings of Burke and Grime (1996) that the single greatest predictor of plot invasibility was bare ground within plots. If these results are

universal, density or biomass must be controlled in species richness treatments or misleading interpretations may occur.

Density controlled

Peart and Foin (1985) did not find a relationship between the species richness and resident species identities with plot invasibility but did establish that resident vegetation biomass influenced invasion. Palmer and Maurer (1997) revealed a positive relationship between weed species recruitment and higher crop plant species richness within manipulated plots, after resident biomass was factored out of the relationship. Naeem et al. (2000) controlled for density in their greenhouse study of *Crepis tectorum*, an invasive annual. When they varied species species richness of the neighbors of *C. tectorum*, there was a direct negative effect of species diversity on the above-ground biomass. However, this result could be due to a sampling effect, as in their Figure 6 they lumped all one- and two- species treatments together in their analysis of *C. tectorum* biomass, instead of plotting each treatment separately. Lavorel et al. (1999) used a pot experiment to explore the demographic success of a pasture weed, *Echium plantagineum*. They discovered that, when they controlled for density, increasing species richness of co-germinants had no effect on seedling emergence. The single greatest predictor of germination success of *E. plantagineum* was co-germinant density. Dukes (2001) demonstrated that resident species diversities had no effect on grassland microcosm invasibility, when resident density was held constant. Thus, most experiments testing the richness-invasibility relationships that controlled for density showed either no relationship or a positive influence of resident species diversity on invasibility.

Conclusion

Mortality occurring because of the micro-environmental conditions produced by the *Tsuga Canadensis/ Rhododendron maximum* canopy occurred immediately. Plot understory species richness, density, and functional group characteristics, and overstory functional group characteristics become significant only after one year. This is possibly because inter-guild and inter-specific interactions take longer than two weeks to affect survivorship and growth. The biotic interactions that influence invasibility change during different stages of the invader establishment. Additionally, this positive richness-diversity relationship changed

in different flooding regimes. The biotic factors that influence invasion success differ from those found in open-canopied systems in that the characteristics of the large adult species play a greater factor in invader survivorship. Keeping density constant across species richness treatments allowed me to isolate the effect of resident species richness on invasion. Additionally, I am confident that the survivorship effects of the invaders were due to biological effects of the manipulated treatments, as covarying environmental factors were removed. My model of community invasibility suggests that biotic factors become more important later in the establishment period. The effects of the abiotic factor of flooding that influences invasibility (Part **III**) may be mediated by biotic factors in this system.

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References

Bridge, S. R. J., and E. A. Johnson. 2000. Geomorphic principles of terrain organization and vegetation gradients. Journal of Vegetation Science **11**:57-70.

Brosofske, K. D., J. Chen, and T. R. Crow. 2001. Understory vegetation and site factors: implications for a managed Wisconsin landscape. Forest Ecology and Management **146**:75-87.

Bunge, J. and M. Fitzpatrick. Estimating the number of species: A review. Journal of the American Statistical Association. 88: 364-373.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology:776-790.

Cain, S. A. 1938. The species-area curve. American Midland Naturalist **19**:573-581.

Cao, Y., D.D. Williams, and D.P. Larson. 2002. Comparison of ecological communities: the problem of sample representativeness. Ecological Monographs 72: 41-56.

Clinton, B. D., and L. R. Boring. 1994. Regeneration patterns in canopy gaps of mixed-oak forests of the southern Appalachians - Influences of topographic position and evergreen understory. American Midland Naturalist **132**:308-319.

Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters **2**:140-148.

Daniel, C., and F. Wood. 1980. Fitting Equations to Data, Revised edition. John Wiley & Sons, Inc., New York.

Dukes, J. S. 2001. Biodiversity and invasibility in grassland microcosms. Oecologia **126**:563-568.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London.

Gasith, A., and V. H. Resh. 1999. Streams in Mediterranean climate regions: Abiotic influences and biotic responses to predictable seasonal events. Annual Review Of Ecology And Systematics **30**:51-81.

Hood, W. G., and R. J. Naiman. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecology **148**:105-114.

Huston, M. A. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. Oecologia:449-460.

Kwit, C., M. W. Schwartz, W. J. Platt, and J. P. Geaghan. 1998. The distribution of tree species in steepheads of the Apalachicola River Bluffs, Florida. Journal of the Torrey Botanical Society **125**:309-318.

Lavorel, S., A.-H. Prieur-Richard, and K. Grigulis. 1999. Invasibility and diversity of plant communities: from pattern to processes. Diversity and Distributions **5**:41-49.

Lee, E. T. 1992. Statistical Methods for Survival Data Analysis, 2nd edition. Wiley, New York.

Levine, J. M. 2000. Species diversity and biological invasions: Relating local process to community pattern. Science **288**:852-854.

Levine, J. M., and C. M. D' Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos:15-26.

Lyons, K. G., and M. W. Schwartz. 2001. Rare species loss alters ecosystem function - invasion resistance. Ecology Letters **4**:358-365.

Mallows, C. L. 1973. Some comments on Cp. Technometrics **15**:661-675.

McNab, W. H., and D. L. Loftis. 2002. Probability of occurrence and habitat features for oriental bittersweet in an oak forest in the southern Appalachian mountains, USA. Forest Ecology and Management **155**:45-54.

Menges, E. S., and D. M. Waller. 1983. Plant strategies in relation to elevation and light in floodplain herbs. American Naturalist **122**:454-473.

Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. Oikos **91**:97-108.

Nilsen, E. T., B. D. Clinton, T. T. Lei, O. K. Miller, S. W. Semones, and J. F. Walker. 2001. Does *Rhododendron maximum* L. (Ericaceae) reduce the availability of resources above and belowground for canopy tree seedlings? American Midland Naturalist **145**:325-343.

Norman, J. M., and G. S. Campbell. 1989. Canopy structure. Pages 301-325 *in* R. W. Pearcy, J. Ehleringer, H. A. Mooney, and P. W. Rundel, editors. Plant Physiological Ecology: Field Methods and Instrumentation. Chapman and Hall, London.

Palmer, M. W., and T. Maurer. 1997. Does diversity beget diversity? A case study of crops and weeds. Journal of Vegetation Science **8**:235-240.

Peart, D. R., and T. C. Foin. 1985. Analysis and prediction of population and community change: a grassland case study. Pages 313-339 *in* J. White, editor. The Population Structure of Vegetation. Junk, Dordecht.

PlantyTabacchi, A. M., E. Tabacchi, R. J. Naiman, C. Deferrari, and H. Decamps. 1996. Invasibility of species rich communities in riparian zones. Conservation Biology **10**:598-607.

Prieur-Richard, A.-H., and S. Lavorel. 2000. Invasions: the perspective of diverse plant communities. Austral Ecology **25**:1-7.

Pugnaire, F. I., and M. T. Luque. 2001. Changes in plant interactions along a gradient of environmental stress. Oikos **93**:42-49.

Rejmánek, M. 1989. Invasibility of plant communities. Pages 369-388 *in* J. A. Drake, H. A. Mooney, F. d. Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. Biological Invasions: a Global Perspective. John Wiley and Sons, Chichester, UK.

Rice, W. R. 1989. Analyzing Tables of Statistical Tests. Evolution **43**:223-225.

Richardson, D. M., N. Allsop, C. D. Antonio, S. J. Milton, and M. Rejmanek. 2000. Plant invasions---the role of mutualisms. Biological Review **75**:65-93.

Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. Ecology:786-794.

Simberloff, D. 1986. Introduced Insects: A biogeographic and systematic perspective. Pages 3-24 *in* H. A. Mooney and J. A. Drake, editors. Ecology of Biological Invasions in North America and Hawaii. Springer-Verlag, New York.

Soberon, J.M., and J. Llorente. 1993. The use of species accumulation functions for the prediciton of species richness. Conservation Biology. 7: 480-488.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs:25-46.

Suiter, D. W., and D. K. Evans. 1999. Vascular flora and rare species of New River Gorge National River, West Virginia. Castanea **64**:23-49.

Tilman, D. 1997. Community invasibility ; recruitment limitation ; and grassland biodiversity. Ecology:81-92.

Tilman, D., C. L. Lehman, and K. T. Thomson. 1997. Plant diversity and ecosystem productivity: Theoretical considerations. Proceedings of The National Academy of Sciences of The United States Of America:1857-1861.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature **379**:718-720.

Trianosky, P. A. 1994. A classification of the terrestrial plant communities of West Virginia-Draft. West Virginia Natural Heritage Program Technical Report 94-2, Elkins.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. River continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130-137.

Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility - evidence of a biological mechanism or a consequence of sampling effect? Oikos **95**:161-170.

Ware, S., P. L. Redfearn, G. L. Pyrah, and W. R. Weber. 1992. Soil-pH, Topography and forest vegetation in the central Ozarks. American Midland Naturalist **128**:40-52.

Williamson, M., K.J. Gaston, W.M. Lonsdale. 2001. The species-area relationship does not have an asymptote! Journal of Biogeography 28: 827-830.

Wiser, S. K., R. B. Allen, P. W. Clinton, and K. H. Platt. 1998. Community structure and forest invasion by an exotic herb over 23 years. Ecology **79**:2071-2081.

Zar, J. H. 1999. Biostatistical Analysis, 4th edition. Prentice-Hall, Englewood Cliffs, N.J., USA.

Appendix

Figure 1. Experimental design for the invaders placed in the192 subplots sampled in this study. The numbers on top and in parentheses indicate the number of subplots of the 2000 invaders. The numbers in bold and on the bottom are the 1999 invader subplot numbers. Numbers in parentheses indicate number of replicates, or subplots. The boxes with the functional groups indicated (SB, ST, LB, LT) are the number of subplots that have those functional groups manipulated for the intermediate species richness treatment. SB (small above-ground biomass, branching root structure), LB (large above-ground biomass, branching root structure), LT(large above-ground biomass, taproot), ST (small above-ground biomass, taproot) indicate functional groups that have been eliminated or had one representative species of that functional group in those plots. The 192 subplots were divided among 4 larger plots in two different flooding regimes (flooding and non-flooding).

Figure 1.

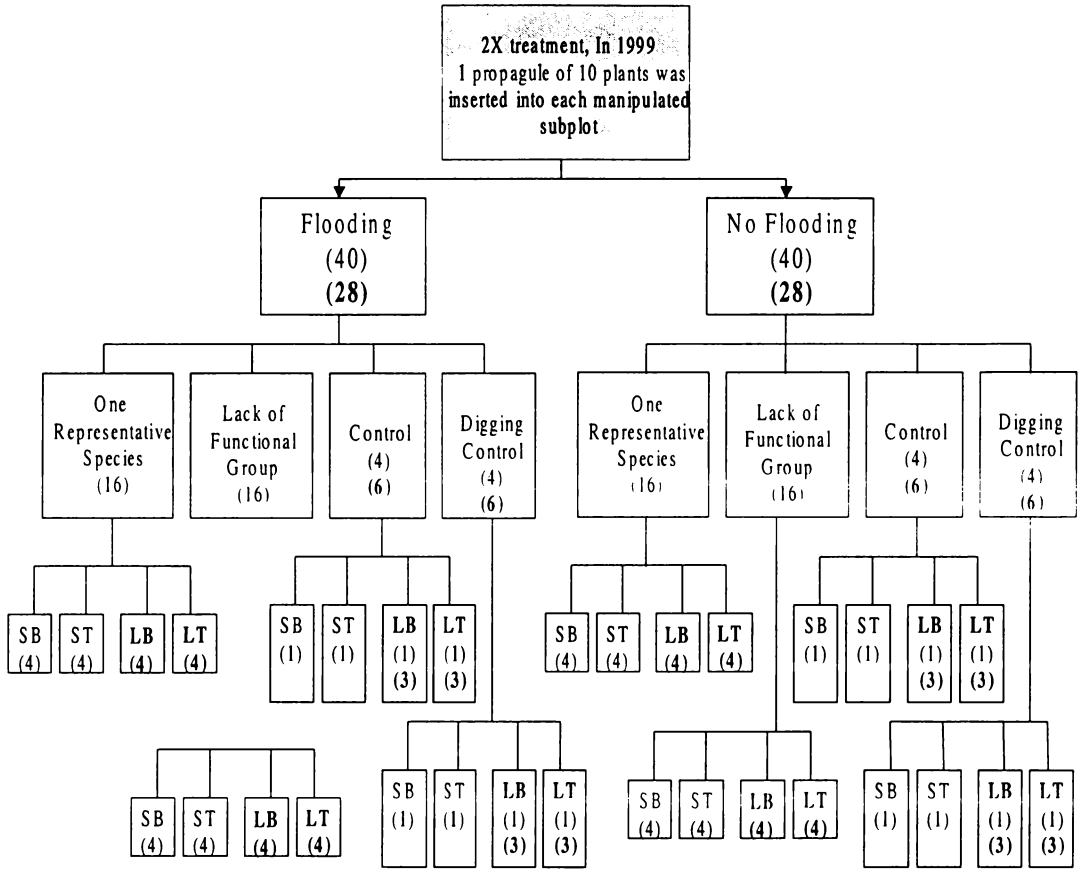

2X treatment, In 1999
1 propagule of 10 plants was inserted into each manipulated subplot
Flooding
(40)
(28)
No Flooding
(40)
(28)
One Representative Species
(16)
Lack of Functional Group
(16)
Control
(4)
(6)
Digging Control
(4)
(6)
SB
(4)
ST
(4)
LB
(4)
LT
(4)
SB
(1)
ST
(1)
LB
(1)
(3)
LT
(1)
(3)

Figure 2. Species-area curve for species along a 50-m transect in the Big Stony Creek watershed

Figure 2.

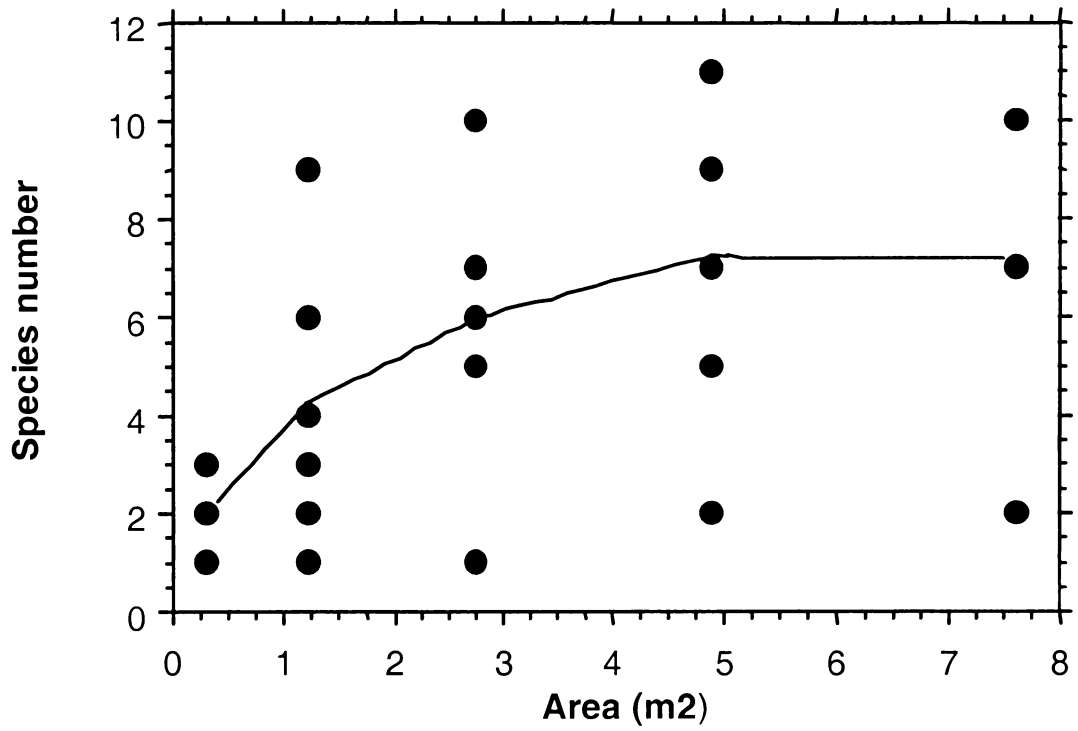


Figure 3. No significant difference in survivorship of all invaders in the 1999 (n=800) cohort between plot treatments, by Kaplan-Meier survivorship analysis across the three census years: 1999, 2000 and 2001. Note that the x axis is in natural log scale and the y-axis is in the natural log of the negative of the natural log scale.

Figure 3.

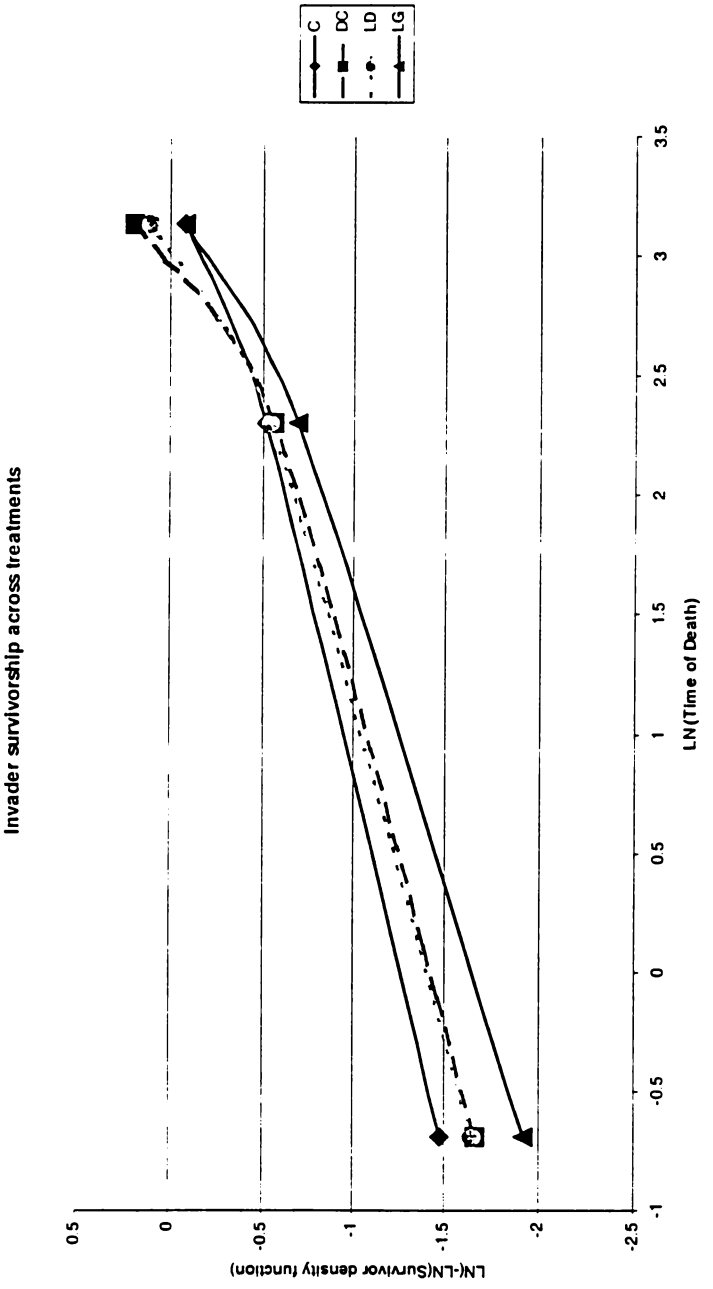
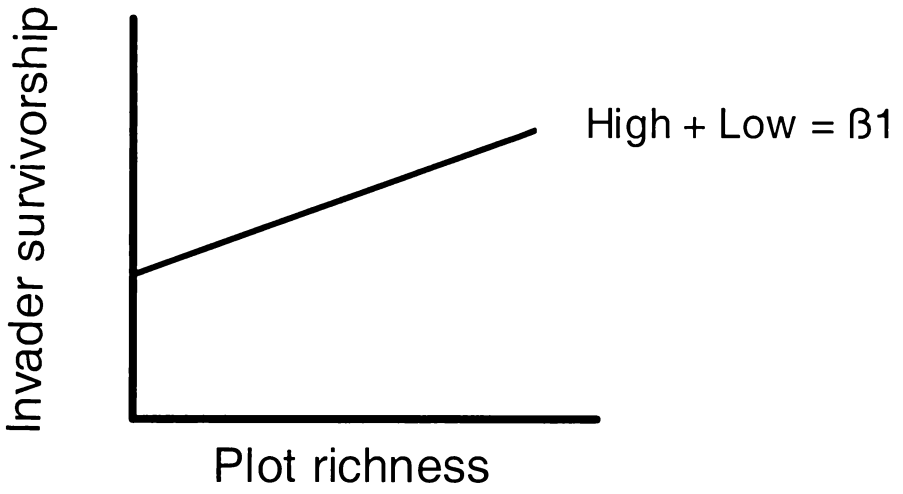

Invader survivorship across treatments
C
DC
LD
LG
LN(-LN(Survivor density function))
LN(Time of Death)
0.5
0
-0.5
-1
-1.5
-2
-2.5
-1
-0.5
0
0.5
1
1.5
2
2.5
3
3.5

Figure 4. A schematic of the richness-invasibility relationship, as revealed by individual regression coefficients. Note that ß4 is the contribution of flooded plots to the overall diversity-invasibility relationship, ß1. If the sign of ß4 differs from that of ß1, then the flooded plots exhibit a different relationship with plot species richness to invasibility. A. Observed relationship of invader survivorship with plot species richness, ß1. ß1 is the overall richness-invasibility relationship across both flooded and unflooded plots. B. The richness-invasibility relationship in each flooding regime. With a dummy variable for flooding condition, for relationship of survivorship with plot diversity in each of the flooding treatments, flooded plots show a different relationship than that of the overall positive relationship of invader survivorship with plot species richness. The regression models for each flooding treatment are as follows: Flooded=(α +ß3) + (ß1 + ß4)Diversity+ ß2Density. Unflooded= α +ß1Diversity + ß2Density. The individual multiple regression parameters of the observed relationships can be found in Table 2.

Figure 4.

A.


Invader survivorship
High + Low = ß1
Plot richness

B.

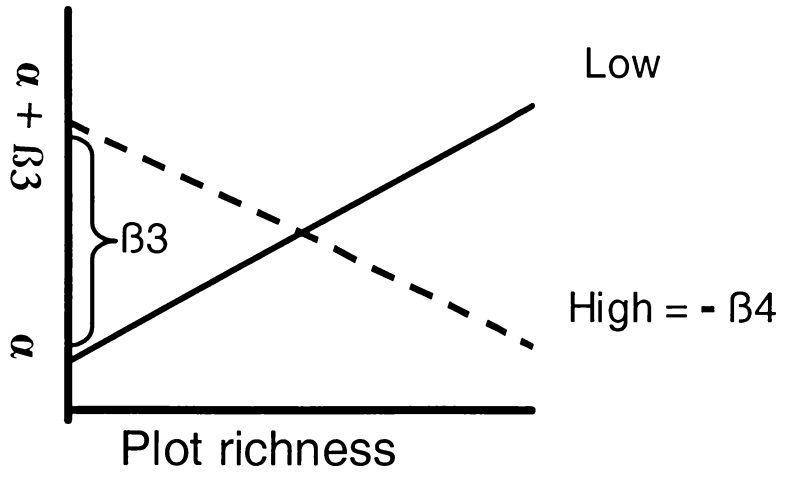

Low
ß3
High = - ß4
Plot richness

Figure 5. Overall site variable effects on invader survivorship, at different establishment times. This diagram shows the invader at the top of the figure, and undergoing the site variable pressures, as indicated with arrows. Arrows pointing down indicate an inferred negative impact by that variable on invader survivorship; arrows pointing up indicate a positive effect by that variable on invader survivorship. These relationships were inferred from the multiple regressions of plot density, species richness and site position on invader survivorship (Table 2). The positive invader survivorship relationship to site characters in the unflooded plots at two weeks is only in relation to that of the relationship to flood condition.

Figure 5.

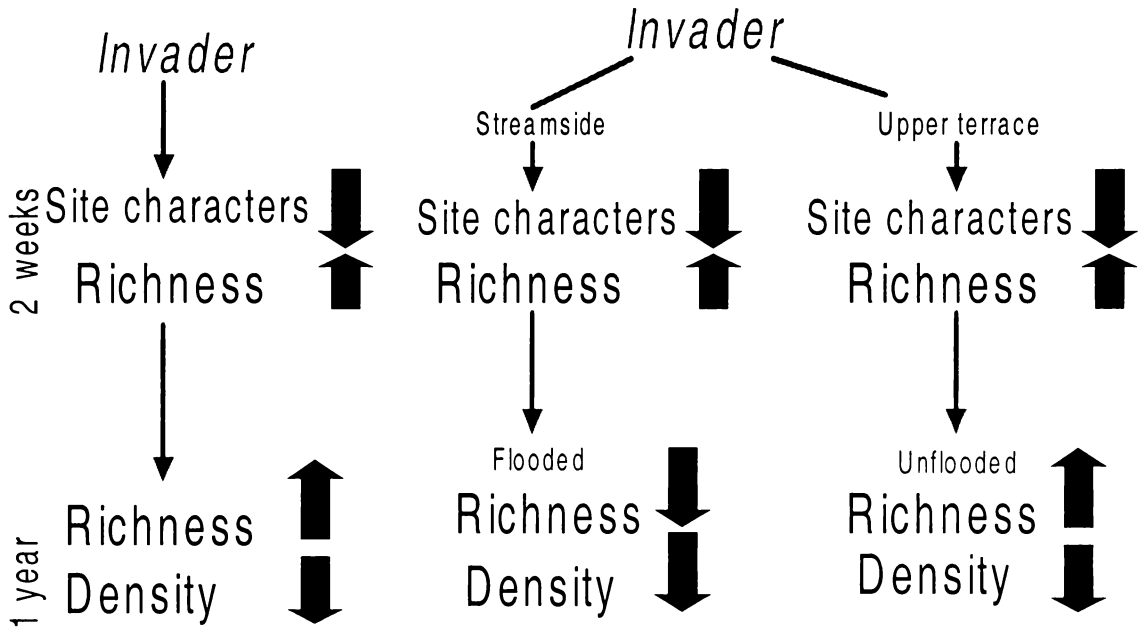
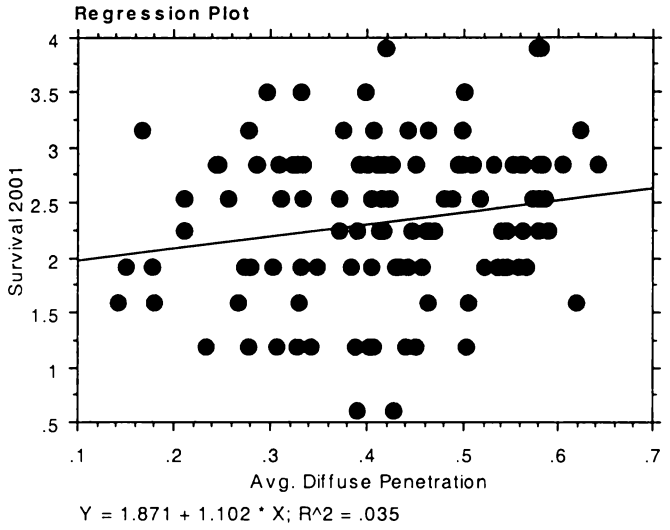

Invader
2 weeks
Site characters
Richness
1 year
Richness
Density
Invader
Streamside
Site characters
Richness
Flooded
Richness
Density
Upper terrace
Site characters
Richness
Unflooded
Richness
Density

Figure 6. Significant relationships between incident light and survivorship of the 1X invaders, at yearly census periods; A. 2001, B. 2000.

Figure 6.

A. Year 2001



B. Year 2000

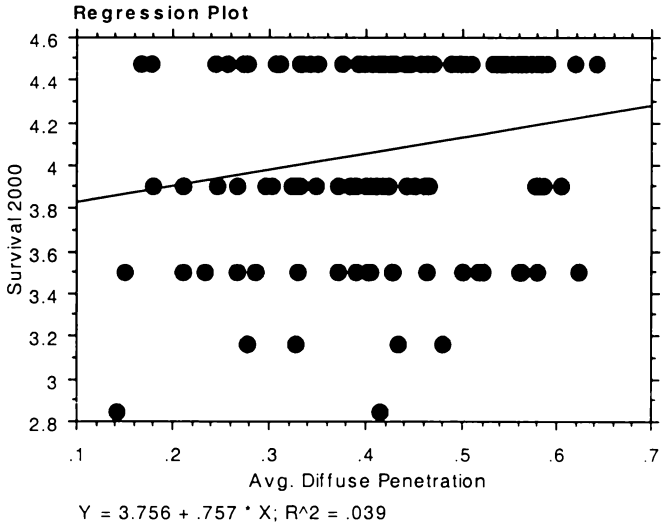


Table 1. Differences in edaphic factors between the different site locations. Cell values are means plus and minus one standard deviation.

	Flooding treatment (MEAN± SD)			
Site variable	**Streamside**	**Upper terrace**	**t-value**	**p-value**
VWC	11.05 ± 3.15	19.2 ± 6.61	-7.441	<0.0001
CARBON(%)	2.02 ± 0.63	3.18 ± 1.31	-5.433	<0.0001
SULFUR(%)	0.05 ± 0.02	0.04 ± 0.02	2.096	0.0390
NITROGEN (%)	0.087 ± 0.02	0.133 ± 0.002	-6.206	<0.0001
Ph	3.928 ± 0.22	3.820 ± 0.167	2.602	0.0109
SAND	10.78 ± 0.85	10.34 ± 1.76	1.493	0.1392
SILT	2.011 ± 0.897	3.532 ± 1.61	-5.487	<0.0001
CLAY	2.211 ± 0.85	1.129 ± 1.084	5.180	<0.0001

Table 2. A. Tests of 2001 survivorship between subplots that were within the same streamside site that were flooded and unflooded. B. Tests of 2001 invader survivorship between unflooded subplots in different site locations (streamside and upper terrace).

A.

	Site location and Flooding condition (MEAN ± SD)			
Census time	**Streamside Flooded**	**Streamside Unflooded**	**t-value**	**p-value**
Invaders 1999, 2 years later (2001)	2.31 ± 0.61	1.96 ± 0.56	1.88	0.0673
Invaders 2000, 1 year later (2001)	1.69 ± 0.63	2.23 ± 0.75	-2.22	0.0305

B.

	Site location and Flooding condition (MEAN ± SD)			
Census time	**Streamside Unflooded**	**Upper Terrace Unflooded**	**t-value**	**p-value**
Invaders 1999, 2 years later (2001)	1.96 ± 0.56	2.14 ± 0.58	-1.18	0.2425
Invaders 2000, 1 year later (2001)	2.23 ± 0.75	2.59 ± 0.64	-2.61	0.0105

Table 3. Influence of site condition and plot variables on invader survivorship, two weeks after transplanting (A). Influence of flooding condition and plot variables on invader survivorship, one year and two years after transplanting. Only the subplots that were flooded were used in these analyses after the first and second years in the plots (B). All analyses are multiple regressions, conducted with percent invader survivorship transformed using Anscombe's transformation (Zar 1999). Cell numbers of the first six columns are parameter estimates of five multiple regressions carried out on the invader survivorship versus the independent variables denoted as the column headings. All individual parameter p-values were compared to a Bonferonni-adjusted alpha of 0.0125, to adjust for multiple tests within one model. Statistically significant individual parameter estimates are in bold. Only independent variables that comprise the overall best model are indicated. The right-most column indicates the model R^2 and p-value. All significant models have R^2 and p-values in bold.

A.

Census time	**Intercept = α**	**Richness = β1**	**Density = β2**	**Site = β3**	**Rich*Site = β4**	**Dens*Site = β5**	**R^2/ (p-value)**
Invaders 1999							
2wk census	**3.67801**	--	-0.00182	-0.14668	--	--	0.0679 (0.0667)
Invaders 2000	**4.17820**	**--**	--	**-0.48082**	**0.05576**	-0.00209	
2wk census							**0.1121 (0.0051)**

B.

Census time	**Intercept = α**	**Richness = β1**	**Density = β2**	**Flooding = β3**	**Rich*Flood = β4**	**Dens*Flood = β5**	**R^2/ (p-value)**
Invaders 1999							
1 year later	**2.7475**	0.0222	**-0.0035**	--	--	--	**0.0923 (0.0240)**
2 years later	**2.2362**	-0.0135	--	0.4724	--	-0.0016	0.0616 (0.1821)
Invaders 2000							
1 year later	**1.7959**	**0.0585**	--	--	-0.0491	--	**0.1539 (<0.0001)**

Table 4. Multiple regression for functional group species richness of recipient plot with invader survivorship. All analyses are multiple regressions, conducted with percent invader survivorship (in each plot) transformed using Anscombe's transformation (Zar 1999). Cell numbers are parameter estimates of five multiple regressions carried out on the invader survivorship versus the independent variables denoted as the column headings. All individual parameter p-values sequentially compared to a Bonferonni-adjusted alpha of 0.0125 to adjust for multiple tests. Statistically significant individual parameter estimates are in bold. Proportion of invader survivorship censused in 2001 from the 80 plots where invaders were planted in 1999. Proportion of invader survivorship censused in 2000 and 2001 for the invaders that were planted in year 2000. Only independent variables that comprise the overall best model are indicated. All overall models are statistically significant, except when indicated by 'ns'.

A. Plot species richness of functional groups

Census time	Intercept = α	LB	LT	SB	ST	Model R^2
Invaders 1999, n=80						
2 years later, ns	**2.1332**	-0.0970	0.1057	--	--	0.0973
Invaders 2000, n=112						
2wk census, ns	**3.8673**	0.0605	--	-0.0232	--	0.0220
1 year later	**1.5291**	--	0.1336	**0.1343**	--	**0.2301**

B. Plot density of functional groups

Census time	Intercept = α	LB	LT	SB	ST	Model R^2
Invaders 1999, n=80						
2 years later, ns	**2.1881**	--	0.0181	-0.0030	--	0.0547
Invaders 2000, n=112						
2wk census, ns	**3.9115**	-0.0072	--	0.0010	0.0057	0.0293
1 year later	**2.0183**	0.0159	--	0.0030	--	**0.1968**

Table 5. Multiple regression for the size and distance of the largest tree and shrub to the recipient plot with invader survivorship. All analyses are multiple regressions, conducted with percent invader survivorship transformed using Anscombe's transformation (Zar 1999). Cell numbers are parameter estimates of five multiple regressions carried out on invader survivorship versus the independent variables denoted as the column headings. All individual parameter p-values sequentially compared to a Bonferonni-adjusted alpha of 0.0125 to adjust for multiple tests. Statistically significant individual parameter estimates are indicated by bold. Only the independent variables that comprise the overall best model are indicated. All overall models are statistically significant, except when indicated by 'ns'.

A. Tree and shrub dbh and distance from plot, for invaders that were planted in 1999

Census time	LB DBH	LB Distance	LT DBH	LT Distance	Model R^2
Invaders 1999, n=80					
2 wk census, ns	--	-0.0009	--	--	0.0173
1 year later, ns	--	--	--	-0.0014	0.0254
2 years later, ns	-0.0315	--	--	--	0.0395

B. Tree and shrub dbh and distance from plot, for invaders that were planted in 2000

Census time	LB DBH	LB Distance	LT DBH	LT Distance	Model R^2
Invaders 2000, n=112					
2 wk census, ns	0.0133	--	--	--	0.0178
1 year later Streamside	--	0.0023	-0.0161	--	**0.1464**
1 year later Upper terrace	-0.0379	**0.0032**	--	--	**0.2409**

PART III

Does flooding disturbance facilitate invasion by non-indigenous species?

Abstract

Ecological resistance to biological invaders might be mediated by environmental factors, but there have been few quantitative tests of this hypothesis. Many natural disturbances, such as flooding, may be accompanied by increased invader additions of non-indigenous species, so it is necessary to separate this covarying factor from the physical effect of disturbance to isolate the effect of natural disturbance on invader establishment. I determined how invasion is influenced by the natural disturbance of flooding and tested if the origin of species (non-indigenous or native) or their morphologically-defined functional group determined invasion success. I conducted these experimental field studies in the floodplain forest Big Stony Creek, a naturally flooded system within the Jefferson National Forest in southwestern Virginia, USA. Non-indigenous species had significantly greater canopy length and width growth than natives in the unflooded plots than native species. Native species had higher survivorship than non-indigenous species in both flooded and unflooded conditions. Plants with large above-ground biomass and branching roots (LB) had higher survivorship than other functional groups after one year, across flooding treatments. According to Elton's (1958) original biotic resistance theory, non-indigenous invaders should have been better invaders of these low diversity, highly disturbed stream habitats than natives. The fact that this prediction does not hold true suggests that flooding inhibits invasion by non-indigenous species in this system.

Introduction

The theory that communities withstand introductions of non-natives is called "ecological resistance", which was described by Elton (1958, p.115) as "forces of nature" that keep "numbers down to a level that prevents a species becoming any kind of dominant in the community and damping down or even completely leveling major fluctuations and outbreaks". The most frequently studied component of ecological resistance has been biological resistance. These studies have revealed both positive and negative impacts of diversity on invaders (Levine and D' Antonio 1999). Many authors (Huston 1979, Rejmánek 1989, Tilman 1997) have suggested that ecological resistance is caused by environmental

factors (flooding intensity, etc.), but few have tested this proposition quantitatively (Burke and Grime 1996, Smith and Knapp 1999). Moyle and Light (1996) argue that environmental resistance is the strongest type of resistance for California fish communities. Many case studies have shown that anthropogenic and natural disturbances increase invasibility of a system.

Both anthropogenic and natural disturbances are assumed usually to increase invasion into a system. The proposed cause for this increase is that the decreased number of the resident species in the highly disturbed systems would present less resistance to invaders (Elton 1958). Simberloff (1986) suggested that the best test for this hypothesis would be in natural disturbed habitats. Anthropogenically disturbed habitat may be more suitable for non-indigenous species and invaders may accompany the humans who created the disturbances. These habitats are often novel to the area and consequently non-indigenous species are better adapted than natives are in this habitat (Crosby 1986). Seeds of non-indigenous species may be carried by natural disturbance agents; such as rivers, or anthropogenic disturbance agents, such humans. Thus, it is unknown whether the physical disturbance itself increases invasibility of a system or if it is the increased invader addition pressures that accompany anthropogenic and natural disturbances or the novel nature of the habitat. For example, increased invasion could be due to the physical scouring of the banks during flooding, or it could be due to the increased number of seeds that are deposited on the scoured banks, or a change in disturbance regime that alters the substrate. In order to separate these covarying factors, I planted non-indigenous and native plants of varying functional groups along a flooding gradient. By planting the same number of invaders per plot, I was able to separate the covarying factor of invader addition pressure from the physical disturbance of stream flooding. These invaders were inserted at different times into experimental plots and with two types of invader addition treatments. My objectives were to determine how invasibility is influenced by this abiotic factor and to test if certain species and functional groups are better invaders in different environmental regimes.

I expected that invaders are less likely to survive in sites with high flooding intensities. Thus, I anticipated that the overall probability of successful invasion would be lower in these flooded plots than in equivalent unflooded forest plots. I hypothesized that

non-indigenous invaders were less likely than native invaders to survive in sites with high flooding rates because natives should be better adapted to local, historical, natural disturbance regimes. I predicted that morphological adaptations exist that increase plant survivorship after flooding. Last, I analyzed invasion success in relation to several other environmental variables: soil texture, moisture, pH, and chemical composition.

To my knowledge, this is the first experimental field test of the hypothesis that the natural disturbance of flooding decreases habitat invasibility. This study is unique in introducing known numbers of invaders along a natural disturbance gradient and tracking their outcome. Using this experimental design, I was able to assess the success or failure of specific invader groups under varying flooding regimes.

Experimental system and objectives

Experimental site

The experimental site was located at Big Stony Creek (38° 26' N, 81° 50' W), a naturally flooded system within the Jefferson National Forest in southwestern Virginia that experiences little human disturbance. The community closest to the stream is largely dominated by hemlock (*Tsuga canadensis*) and *Rhododendron maximum*, and the community further away from the stream is a mixed deciduous hardwood forest. A seasonally highly flooded site is the streamside treatment. An unflooded site is the upper terrace treatment (Table 1). These two sites have significantly different physical conditions, most likely because of differences in elevation and distances from the stream (Part II). All experimental plots were located under forest canopy. The topography of the field site was a typical stream bank and terrace system. All plots were located on level terraces to control for changes in plant interactions on sloped versus level ground. Plots were censused and manipulated in 1999 in 2000 for a separate study on the biotic components of ecological resistance to invaders (Parts **I, II**).

Soil properties

In addition to the experimental manipulations, I collected other environmental variables (soil texture, moisture, pH and chemical composition) in 2001 to test if invasion success significantly correlated with any of these factors. I characterized the soil properties

by systematically taking three soil samples from each 1.5 x 1.5m plot. These soil cores were taken from the first 10 centimeters of mineral soil, and composited to form a single sample. Composites were air dried, sieved (<2mm), and analyzed for texture using a Lamont soil texture unit (Forestry Suppliers). Millimeters of sand and silt were measured and clay was estimated from a 15 mm soil sample for the soil texture characterization. The composites were further sieved (<250 um), and analyzed for pH in water with an Orion meter (SA720). The sieved composites were tested with an elemental analyzer (LECO CNS-2000) for percentage soil carbon and nitrogen. Soil water content was measured in July of 2001 in the field with a volumetric water content analyzer (Hydrosense, Decagon Services, Inc.).

Flooding

Large floods every spring (after snowmelt) scour the banks of Big Stony Creek (USGS historical stream flow data, http://water.usgs.gov/). These floods are short but exert great force and mechanical stress on the surrounding vegetation (personal observation). Thus, though flooding is infrequent, it might select for plants able to withstand this infrequent, intense stress. The inundation frequency of the site was used as the measure of environmental disturbance (Figure 1). The inundation frequency was estimated by temperature differentials between ground and canopy temperature monitors. Elevation, slope, and distance from the stream channel indirectly measure inundation frequency (Menges and Waller 1983). Elevation and distance from stream channel are as equal as possible within flood treatment type. All plots are on level slopes. I deployed 4 Tidbit temperature loggers (Forestry Suppliers, Alabama) to record the ambient temperature every 15 minutes from September to May of each year of the experiment. Three of these monitors were located on the ground at varying distances from the stream, and one monitor was in the canopy. A temperature differential occurs between an underwater logger and one in the canopy immediately above it, thus recording the flooding gradient throughout the wet season (H. Wilbur, personal communication). A positive value of the difference between the underwater and ambient air temperatures would indicate flooding in the colder months while negative differences between the underwater and ambient air temperature would indicate flooding in the warmer months. Flooding was assumed to occur when there was a temperature difference between the underwater and canopy monitors that exceeded that of

the temperature range of the unflooded ground and the canopy monitors (Figure 1). These temperature loggers are distributed in the 2X planting regime (see next section). The flooding data were confirmed by the presence of debris covering the plot after the yearly spring floods. Although there were frequent floods (Figure 1), they were not large enough to cover the entire high flooding treatment area during the drought winter years of 1999 through 2001. Thus, only 18 plots were flooded in the 2X treatment and six plots in the 1X treatment.

Plant origin

Plants were classified into one of three groups: Native, "weedy" native and non-indigenous species. Native species are plants that have historically been in the state of Virginia and are not spreading outside of their natural range. "Weedy" natives are those species thought to be native to Virginia, but that are spreading elsewhere in the world according to Gleason and Cronquist (1991) and/or Uva et al. (1997). These weedy native species are expected to have the ruderal nature of many non-indigenous species. It is possible that some of the species categorized in this study as native would spread outside their range, given adequate introduction pressure by humans. These plants would then be considered "weedy"; however, these possibilities are unknown, as they were not introduced or there were inadequate data. Non-indigenous species are those species not native to Virginia.

Functional groups

My functional groups were established *a priori* using the deductive method (*sensu* Gitay and Noble (1997)) based on my knowledge of stresses that a new plant might face in these communities: competition from the existing community and flooding by the adjacent stream. The functional groups are defined by their physical occupancy of space and comprise combinations of above ground biomass and rooting structure type. These morphological characteristics differentiate a plant's use of space: branching shoots and roots use shallow, horizontal spaces, and tall (long) roots and shoots use deeper, vertical areas in the soil matrix (Part I). The functional groups are: small above-ground biomass, branching and rhizomatous root structure (SB); small-above-ground biomass, taproot (ST); large above-ground biomass, branching root structure (LB); and large above-ground biomass,

taproot (LT). All manipulated plants are less than half a meter tall. I expected the functional groups to respond differently to different flooding treatments. For example, an individual with large above-ground biomass and a single taprooted structure was predicted to be less able to withstand a flood. Though a large shrub and a large tree may both offer the same resistance to the force of moving water, the large tree with one taproot has only one point of attachment to the soil matrix, and a shrub with branching roots has many. All plants are characterized by their potential adult classification, though that may not be the state of the individual at the time of collection (i.e. a large, taprooted individual <1/2m tall will not be in its adult state). However, there are statistically significant differences in survivorship between functional groupings at this size (Part I).

Invader input

After a two-week period to allow for rerooting of plants, 1.5 x 1.5 m plots were planted with seedling and adult plants (<1/2m) of 10 randomly chosen species from widespread native and non-indigenous species commonly found throughout the floodplains of Big Stony Creek. These species all had similar habitat requirements (as in Burke and Grime (1996), Appendix 1). I refer to these plants as 'invaders' even though many are native (Appendix 1). These 192 plots were within stream- flooded and unflooded areas. Eighty of the plots had two additions of 10 invaders. The input of 10 invaders occurred in 1999 and 2000. This treatment with two sets of invader additions is referred to as the 2X treatment, with each plot having a total of 20 planted invaders. The other 112 plots had only one addition of 10 invaders, in 2000; these are referred to as the 1X treatment (Table 1). Survivorship was significantly lower for the LT functional group in 1999 across all treatments (Part I). Thus, in 2000, I removed the LT functional group from the randomly-picked invader pool (second invader addition of the 2X- and the first invader addition of 1X- planting). All invaders were watered once daily for one week after transplanting and every other day for one subsequent week. The recipient communities of these plots were manipulated prior to the insertion of the invaders for a study of the interactions of the resident with the invading species (Part **I,** Part **II**). I lowered the species diversity of experimental plots by removing randomly-picked functional groups or randomly picking eight species to remain in those plots. The densities of these plots were kept at their original

levels, through replacement. Control plots that maintained their original diversities and densities were maintained. Thus, invaders were planted into plots with varying diversities. However, flooded plots had significantly lower overall average diversities (H = 10.14 ± 6.89, L = 12.86 ± 3.85, t=-3.41, p=0.0008) and densities (H = 69.97 ± 70.64, L = 140.26 ± 96.44, t=-5.78, p<0.0001) than unflooded plots, both before and after manipulations. The flooded plots conform to Elton's (1958) assumption that the lower-diversity plots occur in the highly-flooded areas.

The first invader additions of the 2X treatment invaders in 1999 were composed of 56% native, 11% weedy native, 24% non-indigenous, and 9% unknown provenance (n=800). The 800 invaders of the second invader addition of the 2X treatment in 2000 were composed of 51% native, 13% weedy native, 33% non-indigenous, and 4% unknown provenance. The 1,120 invaders of the 1X treatment were composed of: 39% native, 18% weedy native, 44% non-indigenous, and 2% unknown provenance.

Monitoring invaders

Success of an invasion was measured by survivorship and growth of the invader. All invaders were monitored two weeks after transplanting, and every subsequent year. Mortality was measured by death at a census period. A plant was counted as dead if it had no chlorophyll in any structures or if it could not be located. If the marker tag was absent and that species of plant was not present in the plot, the plant was counted as missing and was assumed to be dead for statistical analyses. The following traits were measured to estimate growth, in the field, *in situ*, as follows:

1) Stem diameter: Measured at ground level, using calipers.
2) Canopy length: The longest length of the canopy area of the leaves, measured with a ruler, parallel to the ground
3) Canopy width: Measured with a ruler, perpendicular to the length and parallel to the ground.

Statistical Analyses

Each year, the success of an invader was indicated by four measurements: 1) the length of time it survived and change in morphological characteristics of 2) stem diameter, 3) canopy length, and 4) canopy width. Two-week survivorship of plants was analyzed

according to plot position within the flooding treatment (streamside or upper terrace). One-year survivorship of the plants was analyzed according to the flooding condition of the subplot. Thus, some subplots near the stream that I had expected to be flooded were not, and these subsequently were counted as unflooding subplots.

Environmental resistance

Stress and flooding

To analyze the separate stresses of transplanting and flooding on the invading plant, plot survivorship was analyzed within a plot after both transplanting and flooding. To analyze whether invader survivorship was lower in the streamside treatment plots because of transplant stress, survivorship was calculated by dividing the number of living invaders by the original 10 invaders, two weeks after transplanting. To analyze whether invader survivorship was lower in plots that experienced flooding, I compared invader survivorship in the flooded subplots to that in the unflooded subplots. The survivorship after stream flooding, which occurs one year after transplanting, was the number of living invaders at that census period divided by the number of living invaders at the previous census period. Student's t-tests were performed between flooded and unflooded subplots for all invaders. Nonparametric tests were used (Wilcoxon 2-sample test) if the populations were not normally distributed.

Plant origin

To determine if weedy natives and native plants outperformed non-indigenous species after transplanting to flooded treatment areas, I performed logistic regressions on invader survivorship by plant origin and site location (streamside and upper terrace). To analyze whether invader survivorship was lower in plots that experienced flooding, I compared invader survivorship in the flooded subplots to that in the unflooded subplots. Two-week deaths were removed from all flooding condition analyses, to separate those deaths caused solely by transplanting from those caused by flooding. To understand the sole contribution of plant origin on invader success, all analyses of plant origin were controlled for plant functional group. This was done because many of the non-indigenous species were of the ST functional group (Appendix 1), and this disproportion could confound the origin results.

Functional groups

I performed logistic regressions on invader survivorship to determine which functional groups had differential success across flooding treatments and conditions. The survivorship data were analyzed according to plant functional group and plot flooding treatment for transplant stress analyses. To analyze the impact of stream flooding on functional group survivorship, I analyzed the survivorship data of plant functional groups within plots with different flooding conditions (flooded and unflooded). To understand the exclusive contribution of functional group to invader success, I controlled all analyses of functional groups for plant origin.

Growth

To investigate differences in plant origin and functional group survivorship further, I performed analysis of variance on plant growth each year after transplanting. The changes in the measured plant characteristics (stem diameter, canopy length and width) were used as indicators of plant growth. These analyses were performed for each plant origin and functional group across each flooding condition. Tukey-Kramer post-hoc tests were used to investigate any statistically significant differences between functional groups in different flooding conditions.

Soil properties

If any soil property is correlated with invasion success, this might account for unexplained variance of the components of the ecological resistance model described in this experiment. I performed a multiple regression with plot invader survivorship as the dependent variable and soil characteristics as the independent variables, for all censuses of all treatments. Even though soil characteristics were measured only in the summer of 2001, it is assumed that these soil properties remained constant throughout the experiment. These characteristics were soil water content, percent carbon, percent nitrogen, pH, sand, silt, and clay. Percent plot survivorship was transformed using Anscombe's transformation, since I had proportional data (Zar 1999). The percent carbon and nitrogen data were arc-sine square-root transformed for normality. I checked all variables for interactions with site location by checking significant location-by-independent variable interactions. If these interactions were not statistically significant, I lumped streamside and upper terrace

treatment plots together. I used the R^2 –C(p) selection method, where the model with the least variables and the highest R^2 was selected, given that the C(p) was no greater than the number of variables in the model.

Results

Environmental resistance

Stress

In general, invading plants had lower post-transplant survivorship in streamside plots. Invading plants in the 56 streamside treatment plots of the 1X treatment displayed statistically significantly lower average plot survivorship (3.98± 0.46 8 s.d.) than in the second level treatment plots (4.18± 0.42 s.d.) by a Wilcoxon 2-sample test, with a normal approximation (Z=-2.34, p= 0.0191). There were no statistically significant differences in plot survivorship in any of the 2X treatment invader additions (Wilcoxon 2-sample tests).

Flooding

I expected the highest probability of invader survivorship in the less flooded areas. Invading plants showed no response to flooding. After one year, there were no statistically significant differences between survivorship of plants in subplots that had been flooded and those that had not (unpaired t-tests and Wilcoxon 2-sample tests). The trends in plant survivorship after flooding were increased survivorship (2X treatment, 1st invader addition, years one and two) and decreased survivorship in flooded plots (1X treatment, year one). These variable, insignificant results may have been due to low sample size of flooded plots or simply a lack of a general response. Although there were frequent floods (Figure 1), they were not large enough to cover the entire high flooding treatment area during the drought winter years of 1999 through 2001. Thus, only 18 plots were flooded in the 2X treatment and six plots in the 1X treatment.

Plant origin

Stress

Non-indigenous species survive transplanting more frequently than native species. Logistic regressions of two-week invader survivorship revealed greater survivorship of weedy natives and non-indigenous species than native species in the streamside plots for the

2X, second invader addition treatment (Table 2). In the second-level plots, non-indigenous species had higher survivorship than both natives and weedy natives in the 2X treatment, first invader addition (Table 2). All other logistic regressions were not significant. These results indicate the greater success of plants with ruderal habits after transplant stress.

Flooding

One year later, the situation was quite different for the plants that had survived transplanting. Native species had significantly higher survivorship than non-indigenous species in unflooded subplots. This was true for the 2000 and 2001 censuses of the unflooding plots of the first and second invader additions of the 2X treatment and the 1X treatment plants (Table 3). Natives also had significantly higher survivorship than weedy natives in the second invader addition of the 2X treatment and in the 1X treatment. Weedy natives had statistically higher survivorship than non-indigenous species in all three of these censuses. This trend of natives exhibiting greater invasion success than non-indigenous species was similar in the flooded subplots; however, owing to low sample sizes of flooded plots (as indicated earlier), the overall trend was not significant (Table 3). Additionally, this trend holds true in the flooded subplots, however, the results are not statistically significant. An interesting result that was superficially incongruous with the survivorship trend was the significantly greater canopy length and width growth of non-indigenous species than growth of both classes of natives in the unflooded plots (Figure 2). This result suggests that, while most natives species have overall higher survivorship than most non-indigenous species in both flooding conditions, the few surviving non-indigenous species have higher fitness than the diverse surviving natives. This suggestion is evidenced by field observations of certain non-indigenous species, such as *Rumex acetosella*, that would exhibit rapid growth after transplanting.

Numbers of non-indigenous species continue to diminish with time. Two years later, natives had even greater invasion success than non-indigenous species in the unflooded plots. The difference between natives and weedy natives was not significant (Table 4).

Functional groups

Stress

Species in the smaller functional groups had generally higher survivorship after transplanting, across flooding treatments. The 1X treatment plants exhibited the only statistically significant transplant survivorship trend, with ST having greater survivorship than SB plants (Table 5).

Flooding

One year later, large above ground biomass, branching-rooted (LB) plants had higher survivorship than did plants in other functional groups. This was true in three of the five censuses. LB plants had significantly higher survivorship than both SB and ST plants in the 2001 census of the 1X treatment (Table 6). LB plants also had significantly greater stem diameter growth than the other functional groups in the unflooded plots (Figure 3).

The only planting that had all four functional groups included in the invader input (2X, 1st invader addition) revealed a significantly greater survivorship of SB plants than of LT plants, which in turn survived at a significantly greater rate than ST plants, in the unflooded plots two years after transplantation (Table 7).

Soil characteristics

Soil characteristics of a plot did not influence plant transplant success but did affect long-term plant survivorship. Invader survivorship in plots was positively correlated with soil water content, one year after transplanting. This correlation occurred in two multiple regression analyses of plot survivorship with soil characteristics (Table 8, 2X, 2nd invader addition, streamsided site and 1X). The survivorship of plants in flooded plots was also negatively correlated with percent carbon, pH, and silt in the soil. The survivorship of the 1X plants was also negatively correlated with sand content. The only significant models predicting invader survivorship resulted one year after transplanting.

Discussion

Stress

Invader transplant success is lower in the streamside than in the second level treatment plots. This result is most likely due to the low light and dense root mass provided

by the *Rhododendron maximum/ Tsuga canadensis* canopy cover (Part **II**). The plants that were the most stressed by transplanting were natives, as ruderal plants (weedy native and non-indigenous species) exhibited greater survivorship after transplanting than natives. Additionally, larger plants were not as successful in surviving transplanting than smaller ones. The act of digging up plants and reinserting them into the ground is a form of anthropogenic disturbance. All these results support the idea that ruderals are more highly adapted to human disturbance than non-ruderal native species (Crosby 1986).

Flooding

I expected most plants to have higher survivorship in the unflooded areas. However, the variable results for this test did not show any clear survivorship trends. This could be because there were not enough flooded subplots, or because plants of differing functional groups and origins had contrasting survivorship trends, which may have produced no overall trend for plant survivorship.

The performance of invaders of differing origins in the flooded plots conformed to my original predictions. Native plants (including weedy natives) generally had higher survivorship than non-indigenous species in the flooded plots. This is probably due to adaptations of native species to the natural disturbance of flooding. However, there were few subplots that actually flooded. I project that this trend could have been statistically significant, if there were greater sample sizes for this test. According to Elton's (1958) original biotic resistance theory, non-native species should have been better invaders of these low-diversity, highly disturbed stream habitats than were natives. The fact that this prediction is not borne out suggests that flooding inhibits invasion by non-indigenous species in this system. Additionally, the fact that non-native species did not outperform natives in the flooded areas implies that previous studies that found high invasibility of flooded areas may actually have been due to the increased numbers of invader propagules that accompanied the anthropogenic or natural disturbance regimes.

Native species also outperformed non-indigenous species at the same time in the unflooded plots. Native species are clearly better invaders of closed-canopy forest than non-indigenous invaders. The role of *Rhododendron maximum* cover in non-indigenous species performance is currently being investigated with additional experiments (Part **II**). The

higher survivorship of LB plants in the flooded subplots contradicted my expectation that the smaller biomass branching-rooted plants would have higher survivorship than other groups. The deep root system of the LB plants may allow these species to withstand flooding, either by physically remaining on the bank or through physiological adaptations to anoxia. This result is also interesting in light of the fact that the SB plants were better overall survivors in all plots (Part **II**). These results imply that morphological adaptations to flooding do exist. Other researchers have found evidence of functional group characteristics that adapt species to anthropogenic (Diaz et al. 1994, Campbell et al. 1999, Landsberg et al. 1999, Lavorel et al. 1999, McIntyre et al. 1999) and natural disturbances (Hills et al. 1994, Weiher et al. 1999).

My three-year study focuses on the integration phase of invasion. The establishment phase of invasion might have very different invasion dynamics and results.

Conservation implications

Vannote et al. (1980) hypothesized that the increase in anthropogenic disturbances in downstream reaches caused a pattern of increased ruderal species richness downstream. Additional explanations for the increase of downstream ruderals were increases in bank heights and a milder climate, which allow a greater diversity of species possessing varying flooding tolerances. Studies by Decamps et al. (1995) and Planty-Tabacchi et al. (1996) in France and the northwestern U.S. support these findings. Pyle (1995) found the frequency and species richness of non-indigenous plants increased with distance from the river (and decreased with inundation duration). Taken together, these studies suggest that non-native species are unlikely to occupy habitats subjected to high levels of flooding, and perhaps of other natural disturbances. With greater sample size, I predict that native species would be significantly better invaders of flooded areas than non-indigenous species.

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References

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology:776-790.

Campbell, B. D., D. M. Stafford Smith, and A. J. Ash. 1999. A rule-based model for the functional analysis of vegetation change in Australasian grasslands. Journal of Vegetation Science **10**:723-730.

Chapin, F. S., B. H. Walker, R. J. Hobbs, D. U. Hooper, J. H. Lawton, O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. Science **277**:500-504.

Crosby, A. W. 1986. Ecological Imperialism: The Biological Expansion of Europe, 900-1900. Cambridge University Press, Cambridge.

Decamps, H., A. M. Plantytabacchi, and E. Tabacchi. 1995. Changes in the hydrological regime and invasions by plant species along riparian systems of the Adour River, France. Regulated Rivers-Research & Management **11**:23-33.

Diaz, S., A. Acosta, and M. Cabido. 1994. Community structure in montane grasslands of central Argentina in relation to land use. Journal of Vegetation Science **5**:483-488.

Elton, C. S. 1958. The Ecology of Invasions by animals and plants. Methuen, London.

Fox, M. D., and B. J. Fox. 1986. The susceptibility of natural communities to invasion. Pages 57-66 *in* R. H. Groves and J. J. Burdon editors. The Ecology of Biological Invasions. Cambridge University Press, Cambridge, U.K.

Gitay, H., and I. R. Noble. 1997. What are functional types and how should we seek them? Pages 3-19 *in* T. M. Smith, H. H. Shugart, and F. I. Woodward, editors. Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change. University Press, Cambridge, UK.

Gleason, H. A., and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada, 2nd edition. New York Botanical Garden, Bronx, N.Y., USA.

Hills, J. M., K. J. Murphy, I. D. Pulford, and T. H. Flowers. 1994. A method for classifying European riverine wetland ecosystems using functional vegetation groups. Functional Ecology **8**:242-252.

Huston, M. 1979. General hypothesis of species-diversity. American Naturalist:81-101.

Landsberg, J., S. Lavorel, and J. Stol. 1999. Grazing response groups among understorey plants in arid rangelands. Journal of Vegetation Science **10**:683-696.

Lavorel, S., S. McIntyre, and K. Grigulis. 1999. Plant response to disturbance in a Mediterranean grassland: How many functional groups? Journal of Vegetation Science **10**:661-672.

Levine, J. M. 2000. Species diversity and biological invasions: Relating local process to community pattern. Science **288**:852-854.

Levine, J. M., and C. M. D' Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos:15-26.

McIntyre, S., P. Y. Ladiges, and G. Adams. 1988. Plant species-richness and invasion by exotics in relation to disturbance of wetland communities on the riverine plain ; NSW. Australian Journal of Ecology **13**:361-373.

McIntyre, S., S. Lavorel, J. Landsberg, and T. D. A. Forbes. 1999. Disturbance response in vegetation towards a global perspective on functional traits. Journal of Vegetation Science **10**:621-630.

Menges, E. S., and D. M. Waller. 1983. Plant strategies in relation to elevation and light in floodplain herbs. American Naturalist **122**:454-473.

Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biological Conservation **78**:149-161.

Planty-Tabacchi, A. M., E. Tabacchi, R. J. Naiman, C. Deferrari, and H. Decamps. 1996. Invasibility of species rich communities in riparian zones. Conservation Biology **10**:598-607.

Pyle, L. L. 1995. Effects of disturbance on herbaceous exotic plant species on the floodplain of the Potomac River. American Midland Naturalist **134**:244-253.

Rejmánek, M. 1989. Invasibility of plant communities. Pages 369-388 *in* J. A. Drake, H. A. Mooney, F. d. Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. Biological invasions: A Global Perspective. John Wiley and Sons, Chichester, UK.

Simberloff, D. 1986. Introduced Insects: A biogeographic and systematic perspective. Pages 3-24 *in* H. A. Mooney and J. A. Drake, editors. Ecology of Biological Invasions in North America and Hawaii. Springer-Verlag, New York.

Smith, M. D., and A. K. Knapp. 1999. Exotic plant species in a C-4-dominated grassland: invasibility ; disturbance ; and community structure. Oecologia **120**:605-612.

Tilman, D. 1997. Community invasibility ; recruitment limitation ; and grassland biodiversity. Ecology:81-92.

Uva, R. H., J. C. Neal, and J. M. DiTomaso. 1997. Weeds of the Northeast. Comstock Publishing Associates, Ithaca.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. River continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130-137.

Von Holle, B. in progress. (Part II) Testing Elton's notion of biotic resistance: Does plant invasion success depend upon species richness of the recipient community? For submission to Ecology.

Von Holle, B., and D. Simberloff. (Part I) in review. Testing Fox's assembly rule: Does plant invasion depend on recipient community structure? Oikos.

Weiher, E., A. van der Werf, K. Thompson, M. Roderick, E. Garnier, and O. Eriksson. 1999. Challenging Theophrastus: A common core list of plant traits for functional ecology. Journal of Vegetation Science **10**:609-620.

Zar, J. H. 1999. Biostatistical Analysis, 4th edition. Prentice-Hall, Englewood Cliffs, N.J., USA.

Appendix

Figure 1. Temperature difference between ground and canopy monitors from September 1999 to May 2000, in degrees Celsius. The maximum temperature difference of the ground monitor that was never flooded from the canopy monitor is –16°C to 3°C. This temperature range is bracketed by the dashed lines in the figure. Any difference values above this bracket indicate flooding in cold months and those below the bracket indicate flooding in warmer months, when the water temperature is lower than the air temperature.

Figure 1.

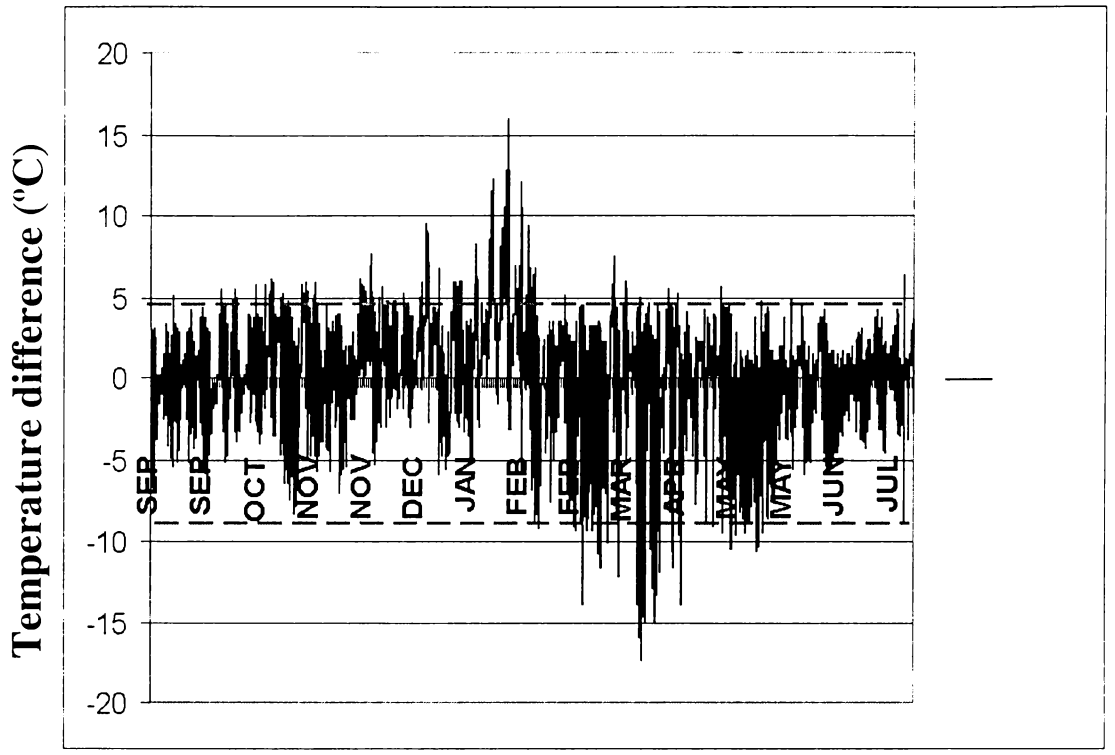
Temperature difference (°C)
20
15
10
5
0
-5
-10
-15
-20
SEP
SEP
OCT
NOV
NOV
DEC
JAN
FEB
MAR
MAY
JUN
JUL

Figure 2. Non-indigenous species had greater growth than native species in unflooded subplots for the second invader addition of the 2X treatment. Invader canopy length and width growth was measured (in cm) in 2001 and 2000. Analyses of plant origin and flooding condition were conducted with ANOVAs, with Tukey-Kramer post-hoc tests.

Figure 2.

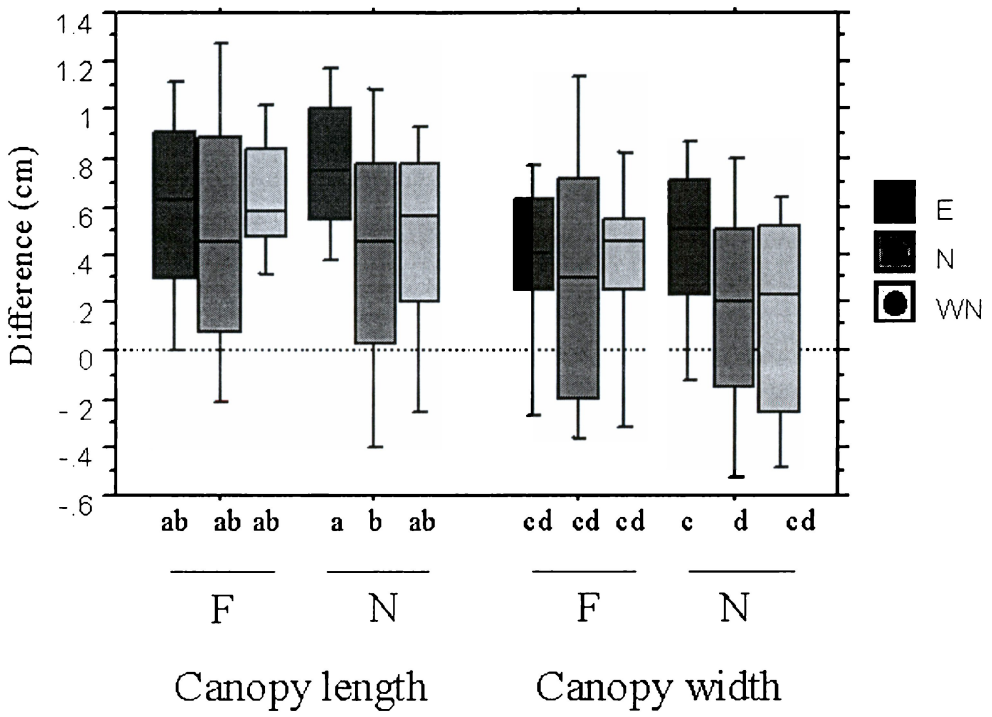
Difference (cm)
1.4
1.2
1
.8
.6
.4
.2
0
-.2
-.4
-.6
ab ab ab a b ab cd cd cd c d cd
F N F N
Canopy length
Canopy width
E
N
WN

Figure 3. Large-biomass, branching-rooted (LB) plants had significantly greater growth in unflooded subplots than plants of other functional groups for the second invader addition of the 2X treatment. Stem diameters were measured (in mm) in 2001 and 2000. Analyses of plant functional group and flooding condition were conducted with ANOVAs, with Tukey-Kramer post-hoc tests.

Figure 3.

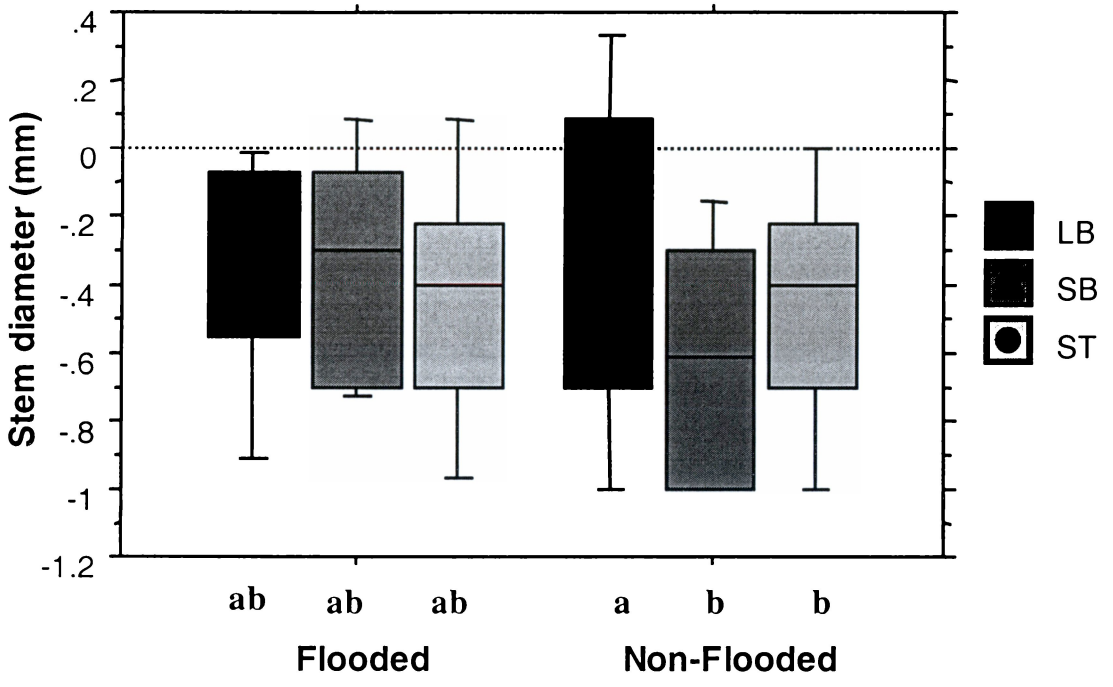
Stem diameter (mm)
.4
.2
0
-.2
-.4
-.6
-.8
-1
-1.2
ab
ab
ab
a
b
b
Flooded
Non-Flooded
LB
SB
ST

Table 1.

Experimental design for the 192 plots sampled in this study. Numbers in parentheses indicate number of replicates, or subplots. Note that the second invader addition of the 2X treatment was planted into the plots that were established and planted with the first invader addition plants in 1999.

		2X Treatment, 1st invader addition, 1999 (80)	**2X Treatment, 2nd invader addition, 2000 (80)**	**1X Treatment, 2000 (112)**
Stie location:	**Floodplain position**			
	Streamside (flooded) (96)	(40)	Planted into plots established in 1999 (previous column).	(56)
	Upper terrace (unflooded) (96)	(40)	Planted into plots established in 1999 (previous column).	(56)

Table 2.

Logistic regressions of survivorship on the origin of invading species and the site into which they were planted, streamside and upper terrace treatments. Functional group is held constant in these analyses. This is an analysis of 2-week invader transplant stress. There were 40 streamside and upper terrace subplots for each of the 2X treatments and there were 56 subplots for each of the streamside and upper terrace treatments of the 1X treatment. Cell numbers are percent survivorship of the groups by their site location and invader addition treatment. P-values listed in the right-most column. Significant values in bold.

2-week survivorship

Site treatment	**Origin of Invading Species**			
	Non-indigenous	**Weedy Native**	**Native**	Wald Chi-Square (p-value)
STREAMSIDE				
2X-P1, 1999	94.90	75.00	76.21	(0.1070)
2X-P2, 2000	94.17_a	94.92_a	85.07_b	**(0.0128)**
1X, 2000	90.87	86.90	91.39	(0.4213)
UPPER TERRACE				
2X-P1, 1999	94.90_a	75.00_b	76.21_c	**(0.0007)**
2X-P2, 2000	85.92	88.64	83.25	(0.5278)
1X, 2000	95.29	98.18	92.61	(0.2718)

Table 3.

Logistic regressions of survivorship on the origin of invading species and the flooding condition of the subplots they were planted into, flooded and unflooded. Functional group is held constant in these analyses. This is an analysis of one-year invader survivorship after flooding disturbance. There were 18 flooded and 62 unflooded subplots for the 2X treatment and 6 flooded and 106 unflooded subplots for the 1X treatment. Cell numbers are percent survivorship of the groups by their flooding condition and invader addition treatment. P-values listed in the right-most column. Significant values in bold.

1 year survivorship

Flooding condition	**Origin of Invading Species**			
	Non-indigenous	**Weedy Native**	**Native**	Wald Chi-Square (p-value)
FLOODED				
2X-P1, 2000	62.86	...	77.00	(0.1870)
2X-P2, 2001	46.27	50.00	61.54	(0.2024)
1X, 2001	30.00	58.33	30.00	(0.1448)
UNFLOODED				
2X-P1, 2000	47.59_{a}	80_{b}	79.02_{ab}	**(<0.0001)**
2X-P2, 2001	39.20_{a}	41.18_{b}	67.64_{c}	**(<0.0001)**
1X, 2001	35.12_{a}	59.06_{b}	59.84_{c}	**(<0.0001)**

Table 4.

Logistic regressions of survivorship on the origin of invading species and the flooding condition of the subplots they were planted into, flooded and unflooded. Functional group is held constant in these analyses. This is an analysis of two-year invader survivorship after flooding. There were 18 flooded and 62 unflooded subplots for the 2X treatment and 6 flooded and 106 unflooded subplots for the 1X treatment. Cell numbers are percent survivorship of the groups by their flooding condition and invader addition treatment. P-values listed in the right-most column. Significant values in bold.

2 year survivorship

Flooding condition	**Origin of Invading Species**			
	Non-indigenous	**Weedy Native**	**Native**	Wald Chi-Square (p-value)
FLOODED				
2X-P1, 2001	57.14	...	61.00	(0.7740)
UNFLOODED				
2X-P1, 2001	17.93_{a}	44.00_{ab}	57.69_{b}	**(<0.0001)**

Table 5.

Logistic regressions of survivorship of the functional group of invading species and the site location into which they were planted, streamside and upper terrace site treatments. Plant origin is held constant in these analyses. This is an analysis of 2-week invader transplant stress. There were 40 streamside and upper terrace subplots for each of the 2X treatments and there were 56 subplots for each of the streamside and upper terrace treatments of the 1X treatment. Cell numbers are percent survivorship of the groups by their flooding and invader addition treatment. P-values listed in the right-most column. Significant values in bold.

2-week survivorship

Site treatment	**Invading functional group**				
	SB	**LB**	**ST**	**LT**	Wald Chi-Square (p-value)
STREAMSIDE					
2X-P1, 1999	86.67	81.82	82.91	67.39	(0.1070)
2X-P2, 2000	86.67	92.50	92.08		(0.3634)
1X, 2000	87.12	79.49	92.69	...	**(0.0078)**
UPPER TERRACE					
2X-P1, 1999	90.57	76.92	84.83	65.00	(0.0163)
2X-P2, 2000	84.11	75.00	87.80		(0.0579)
1X, 2000	92.21_{a}	88.89_{ab}	96.01_{b}	...	(0.2226)

Table 6.

Logistic regressions of survivorship on the functional group of invading species and the flooding condition of the subplots they were planted into, flooded and unflooded. Plant origin is held constant in these analyses. This is an analysis of one-year invader survivorship after flooding disturbance. There were 18 flooded and 62 unflooded subplots for the 2X treatment and 6 flooded and 106 unflooded subplots for the 1X treatment. Cell numbers are percent survivorship of the groups by their flooding condition and invader addition treatment. P-values listed in the right-most column. Significant values in bold.

1 year survivorship

Site treatment	**Invading functional group**				
	SB	**LB**	**ST**	**LT**	Wald Chi-Square (p-value)
FLOODED					
2X-P1, 2000	64.10	66.67	80.60	68.75	(0.2734)
2X-P2, 2001	50.85	57.14	55.21		(0.8411)
1X, 2001	...	...	35.56	...	(...)
UNFLOODED					
2X-P1, 2000	83.06	71.43	62.98	67.44	(0.1976)
2X-P2, 2001	55.06	58.73	53.21		(0.9385)
1X, 2001	48.46_a	71.05_b	45.51_c	...	**(0.0003)**

Table 7.

Logistic regressions of survivorship on the functional group of invading species and the flooding condition of the subplots they were planted into, flooded and unflooded. Plant origin is held constant in these analyses. This is an analysis of two-year invader survivorship after flooding disturbance. There were 18 flooded and 62 unflooded subplots for the 2X treatment and 6 flooded and 106 unflooded subplots for the 1X treatment. Cell numbers are percent survivorship of the groups by their flooding condition and invader addition treatment. P-values listed in the right-most column. Significant values in bold.

2 year survivorship

Flooding condition	**Invading functional group**				
	SB	**LB**	**ST**	**LT**	Wald Chi-Square (p-value)
FLOODED					
2X-P1, 2001	46.15	60.00	67.16	68.75	(0.2229)
UNFLOODED					
2X-P1, 2001	65.32_{a}	47.62_{abc}	33.97_{b}	41.86_{c}	**(0.0001)**

Table 8.

Multiple regression of percent plot survivorship with soil properties. All survivorship data are transformed with Anscombe's transformation and the percent carbon and nitrogen are square-root, arcsine transformed.

Invader Census time	Intercept = α	HYD	C (%)	N (%)	pH	Sand	Silt	Clay	Model R^2
2X-P1, n=80									
2 weeks	**2.8017**	-0.0369	8.5068						0.1421 (0.0587)
1 year later	0.4562				0.5449		0.1230		0.0755 (0.2342)
2 years later	-0.1302	-0.0191			0.7113				0.0859 (0.2174)
2X-P2, n=80									0.0913
2 weeks	**5.0168**	0.0295		-46.6346					(0.1339)
1 year later: Flooded	**16.4185**	0.0666	-15.2415		-2.9514		-0.2809		**0.4879 (0.0098)**
Unflooded	-0.1667	...	...	...	1.3429	-0.2096	...	...	0.2747 (0.0652)
1X, n=112									
2 weeks	**1.5967**	0.0145	4.6923	-211.8573	0.5227				0.1453 (0.2271)
1yr later	**4.1486**	0.0553				-0.2541			**0.3058 (0.0012)**

PART IV

The importance of biological inertia in plant community resistance to invasion

This part is a lightly revised version of a manuscript with the same name by B. Von Holle, H. Delcourt, and D. Simberloff:

Von Holle, B., H. Delcourt, and D. Simberloff. 2002, in review. The importance of biological inertia in plant community resistance to invasion

My use of "we" in this part refers to my coauthors and me. My primary contributions to this paper include (1) Half of the research and literature review of the topic (2) the proposed model of ecological resistance with biological inertia included and (3) half of the writing.

Abstract

Insights into the ecology of historic invasions can be gained by studying long-term invasion patterns as well as through experimental studies. In this paper, we review the literature in paleoecology, forest-stand simulation modeling, and historical and experimental studies of plant species invasions to illustrate the relevance of biological inertia in plant communities to invasion ecology. Ecological resistance to invasion occurs in part because of environmental, demographic, and biotic factors influencing the arrival and establishment of invading species. We propose that biological inertia within the resident community is a fourth component of ecological resistance to invasion, because of the lag time inherent in eliminating resident species after environmental conditions become suitable for invasion by immigrating species. Microclimatic conditions created by the existing vegetation that are favorable for the existence of the present community or population promote the continuity of the present community. This is a form of biological inertia to invasion that is an outcome of the life-history characteristics of the resident species. Biological inertia varies with (1) the magnitude, duration, direction, rate, and variability of climate or other environmental changes; (2) proximity of the community to critical ecotones; (3) heterogeneity of the landscape near ecotone boundaries; and (4) changes in the natural or anthropogenic disturbance regime.

Introduction

Invasion ecologists generally agree that there is a need for a unified framework for understanding the ecology of invasive species (Ewel et al. 1999, Parker et al. 1999, Richardson et al. 2000). Most recent work in invasion ecology has stressed three basic elements of the process of biological invasion, all of which emphasize the adaptive strategy of the colonizing species: (1) arrival; (2) establishment; and (3) spread or integration within natural communities (Moyle and Light 1996). Ecological resistance has historically been considered the sum of environmental, demographic, and biotic factors influencing the invading species (Lodge 1993 a, b). Environmental conditions during the invasion process act as a major filter that can induce a significant lag time between arrival and spread of an alien invader (Lodge 1993 a, b; Kowarik 1995). Persistence of the resident community beyond the time that environmental conditions change in favor of exotic species invasions is a form of biological inertia to invasion that is an outcome of the life-history characteristics of the resident species. Microclimatic conditions created by the existing vegetation that are favorable for the existence of the present community or population may also promote the continuity of the existing community. These are two mechanisms of biological inertia to biological invasion. The strength of inertia can change with the magnitude of the microenvironmental conditions created by resident stands and the longevity of the individuals. In this paper, we propose that biological inertia constitutes a fourth component of ecological resistance to biological invaders. Biological inertia, the resistance of late-successional vegetation to change, can contribute to lag times for invasion of plant communities by exotic species.

We use the term 'time lag' for the length of time it takes for an invader to arrive, establish and integrate in an ecosystem (Kowarik 1995, Crooks and Soulé 1999). We suggest that biotic inertia significantly contributes to this time lag. Thus, the time lag that we refer to can be thought of as the additional time it takes for an invader to establish in a new environment, and the community composition that it establishes into can lengthen this time to integrate. This usage differs from the use of the term 'time lags' or 'delayed density-dependence' that pertains to models of species dynamics, which can cause complex or chaotic dynamics (Gurney et al. 1980, Turchin 1990, Turchin and Taylor 1992, Kot 2001).

Time lags, or delayed density-dependence, of mathematical models denote time delay mechanisms that past generations have on future generations of organisms, such as density-mediated changes in habitat quality, parental effects of population density on offspring quality, and population regulation through predator-prey or host-pathogen interactions (see references in Crone 1997).

In this paper, we review the literature to evaluate the importance of biological inertia to community ecology. We discuss the relevance of biological inertia to invasion and to conservation strategies. We use Williamson's (1996) definition of invasion as: "Biological invasion happens when an organism, any sort of organism, arrives somewhere beyond its previous range" (p. 1). We suggest that insights into the ecology of historic plant invasions can be gained by studying both long-term invasion patterns as well as through experimental studies. The field of invasion ecology has largely disassociated itself from the field of succession ecology (Davis et al. 2001), and it has not included insights from the paleoecological literature into the process of invasion (Davis et al. 1998). Additionally, the invasion of native communities by exotic species is emphasized over native range extensions, even though it has been shown that there are no differences in invasive characteristics of some native and some exotic invasive plants (Thompson et al. 1995). Thus, we will treat historical range extensions of native species as equivalent to the introduction of exotic species beyond their natural ranges. Studying the history of species invasions on time scales ranging from tens to thousands of years can offer insight into current and future species range expansions (Davis et al. 1998, Lodge 1993b, Vermeij 1996). Communication between the largely separate disciplines of invasion ecology, succession ecology, and paleoecology is essential for understanding processes of contemporary invasions and ecological resistance. This review will link the common ground and areas of prospective research among the fields of succession ecology, paleoecology, and invasion biology fields.

Origins of the concept

Watt (1947) was the first ecologist to allude to biological inertia: "The effect on the structure of a community of drought or other efficient cause may persist long after the cause has ceased to operate. In fact, at any given time, there may be no correspondence between

structure and the current meteorological factors. The point is best illustrated by reference to communities with long-lived dominants" (Watt 1947, p. 12). Gorham (1957) coined the term "biological inertia" to describe the perpetuation of bog plant species long after the environmental conditions suitable for their persistance had disappeared. He used the example of sedges persisting in the sere, even after the habitat conditions were more suitable for *Sphagnum* colonization. They survived in the moss cushions by keeping their roots in the richer peat or in the flowing groundwater beneath the peat (Du Rietz 1949). In a second example, he observed that the reed *Phragmites* persists in a "dwarfed and sterile state" at the edge of pine bogs in Fennoscandia under nutrient and acidic conditions far too severe for its establishment. Gorham thought that this population might be a relic of the time when the bogs were shallow ponds and lakes with richer and less acidic edges (Gorham 1957).

Pearsall (1959) extended the original definition of biological inertia by incorporating the time it would take for colonizing species to take advantage of a change in climate or other environmental conditions. He observed that invaders enter a closed climax forest only where there are windfalls creating openings into which they may establish. According to Pearsall (1959), dense vegetation cover presents great inertia to invasion. He estimated that 500 to 1,000 years would be required for an 'appreciable' change in composition of a climax forest in the absence of human disturbance.

Smith (1965) suggested that community inertia is related to the environmental tolerance thresholds, or critical physiological limits, of species. According to Smith (1965), a change in habitat that would not kill existing individual plants but would prevent their regeneration is a likely scenario. If, for example, a climate change occurs that is just above the critical physiological threshold for existence of an invading species (the non-native can barely tolerate this climate), and if it affects only marginal microhabitats, then regeneration of the existing vegetation with its high production of propagules would be favored, slowing the rate at which an invading species can spread. In this case, biological inertia would extend well beyond the lifetimes of individual plants dominating existing communities. If, on the other hand, the environmental change was great enough to be unfavorable for persistence of pre-established species, then the effects of biological inertia would be limited to the life span of existing individual plants. Smith (1965) concluded that, in the long sweep of postglacial

history, the immigration and expansion of species thus depends not only on their competitive abilities and the efficiency of their dispersal mechanisms, but upon the nature and extent of climate change as it relates to the passage of critical tolerance thresholds.

There is a distinction between *inertia* (resistance of the undisturbed vegetation to change, increasing during succession) and *resilience* (ability to recover rapidly from a disturbance, which decreases during succession) (Grime 1979, Shrader-Frechette and McCoy 1993) In the course of secondary succession, initially rapid turnover takes place from one successional stage to the next as annual herbs are replaced by perennials. Inertia thus increases over the course of succession as lags occur in the replacement of short-lived species by increasingly longer-lived species. Resilience of late-successional vegetation is diminished both by slow rates of replacement of dominant species and by limiting factors such as nutrient availability in the soil (Grime 1979).

Thus, inertia was first used to describe the persistence of individuals after the environmental conditions for their establishment had disappeared. The notion evolved towards the usage of inertia as a property of a community. We propose that this term should be used as a component of ecological resistance to biological invasion because of its distinctly different nature from both environmental and biological resistances to invasion. We consider it entirely separate from these two forms of resistance to invasion because inertia is an abiotic influence that is created by a biotic factor. Thus, any environmental influence that is not created by an organism is abiotic and falls under the environmental resistance category. Direct interactions between two or more organisms, i.e. competition, predation, parasitism, disease, and allelopathy are forms of biological resistance to invasion. Biological inertia is the indirect effect of living organisms on others, mediated through environmental means, such as microenvironmental conditions created by forests on recruiting plants. Additionally, these conditions can last longer than the lifetimes of the residents, such as chemicals remaining in soils after the resident allelopathic organism has died. The impact of forest tree longevity on invasion can be both due to biotic resistance and biological inertia; tree presence and subsequent space competition (biotic resistance) and their microenvironmental influence (biological inertia). We consider these four components of ecological resistance to invasion be interdependent.

Evidence for 'biological inertia'

Holocene invasions

Paleoecological studies yield long-term data sets appropriate for determining rates of spread and lag times for range extensions of species into pre-existing communities of long-lived organisms such as trees (Watts 1973, Davis 1981, Huntley and Birks 1983, Cole 1985, Cwynar and MacDonald 1987, Davis 1987, Delcourt and Delcourt 1987, Birks 1989, Clark 1998, Davis et al. 1998). Watts (1973) described fossil pollen and seed diagrams as a composite record of the dynamics of plant populations. Given an accurate time scale with a series of radiocarbon dates (the age of a paleontological specimen determined from the content of carbon 14, which does not directly correspond to a calendar year) or annually laminated sediments, pollen records can be used to study the process of plant invasions in response to climate change on time scales of hundreds to tens of thousands of years. Watts (1973) described the process of postglacial range extension of eastern white pine (*Pinus strobus*) into a forest dominated by spruce (*Picea*) and jack pine/red pine (*Pinus banksiana/resinosa*) in northern Minnesota based on pollen analysis of annually laminated sediments from Lake of the Clouds. The initial time of invasion was influenced by the long distance from which the species had migrated from its Pleistocene refuge in the southeastern United States (Davis 1981, 1987, Delcourt and Delcourt 1987). Eastern white pine was represented in the pollen record by consistent but low pollen percentages from around 9400 to 7350 years ago. During that time interval, it was spreading northward and westward across the Great Lakes region into Minnesota. The pollen grains entering Lake of the Clouds were either derived from a source area beyond the local watershed or from a very small population of trees growing near the lake. Between 7350 and 6400 years ago, eastern white pine pollen increased to 20% of the pollen assemblage. Watts (1973) interpreted the changes in pollen percentages of eastern white pine in the Lake of the Clouds as invasion and local population expansion occurring over a time interval of 700 to 1000 years. A significant time lag thus occurred between the arrival and successful establishment of eastern white pine and its incorporation into the forest community. Watts (1973) suggested that disturbances, including fire and windthrows, were the primary mechanisms that facilitated establishment of seedlings of eastern white pine and that eventually allowed it to overcome

the biological inertia inherent in the pre-existing forest community. Canopy gaps created by resident adults killed by these disturbances would have been colonized by eastern white pine. Thus, range extensions appear to be strongly influenced by the biological inertia of the recipient communities.

Cole (1985) explicitly invoked vegetational inertia to describe a significant time lag observed for species turnover rates in the Grand Canyon after the climate changed from Pleistocene to Holocene conditions. He evaluated the plant macrofossil record spanning the past 24,000 years from packrat middens collected along the cliff faces of the eastern Grand Canyon. Cole (1985) found that vascular plant species that dominated in the Pleistocene were eliminated first from marginal habitats, yet they persisted in the most favorable habitats and were outcompeted slowly during the 1000 to 3000 years following the initial climate change. He suggested that "the time required for vegetational change would then depend upon the reproductive ability of the invading species and upon the proximity of resident species to their critical climatic thresholds" (Cole 1985, p. 299). The creation by the resident community of an unfavorable microclimate for species to extend their ranges, in addition to the lag time for changes in soil conditions, may have contributed to vegetational inertia in the Grand Canyon.

MacDonald and Cwynar (1991) used fossil pollen analysis of seven lake sites to study population growth rates of lodgepole pine (*Pinus contorta* ssp. *latifolia*) during its postglacial range extenstion across western Canada. Lodgepole pine spread into the western interior of Canada from a refuge in the western United States beginning 12,000 radiocarbon years ago, and it was the last tree taxon to arrive at study sites from British Columbia and Alberta to the Yukon Territory, reaching its present northern range limits in the Yukon in the last 500 years. Comparison of curves for increasing pollen accumulation rates (a proxy for population size) at sites across the region showed that estimated population doubling times ranged from 80 to 1100 years. Forests being invaded by lodgepole pine were similar at all sites, consisting of spruce (*Picea*), trembling aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). Rather than being governed by biotic interactions, differences in population growth rates of lodgepole pine were attributed by MacDonald and Cwynar (1991) to regional differences in topography and edaphic conditions. Population growth was slowest at sites with least

availability of suitable sites for establishment of lodgepole pine and with watersheds in which soils were most favorable for long-term persistence of the pre-existing community.

Many paleoecological studies demonstrate that, during the Holocene, temperate and boreal forests were invaded successfully as species spread northward (Watts 1973, Davis 1981, Huntley and Birks 1983, Delcourt and Delcourt 1987, Birks 1989, MacDonald and Cwynar 1991). These studies show that, overall, invasibility of resident forest communities is conditioned both by the intrinsic rate of increase of populations extending their range and by ambient environmental conditions that render resident communities more or less resistant to invasion. The latter factor is a form of biological inertia to invasion. In historic times, observational studies of temperate forest succession have shown that late-successional forests are relatively resistant to invasion by non-native plant species (Rejmánek et al. 1987, Rejmánek 1989, Gibson et al. 2000). At the stand level, invasibility is conditioned by the patchiness of the forest mosaic and the distribution of the invasible and resistant stands. Davis *et al.* (1998) described the pattern and process of hemlock extension into resident forest stands during the Holocene in the mixed conifer-northern hardwood region of the western Upper Peninsula of Michigan. In postglacial times, eastern hemlock (*Tsuga canadensis*) has been able to invade stands of eastern white pine but not pre-existing hardwood stands. Eastern hemlock seedlings are inhibited either by the thick leaf litter or the dense shade that occurs in oak- or maple-dominated stands. Thus, biological feedbacks prevent eastern hemlock from invading northern hardwood stands and constitute a form of biological inertia to invasion that is an outcome of microenvironmental conditions created by the long-lived resident species (Davis et al. 1998).

Prehistoric human disturbance and community invasibility

Prehistoric Native Americans played a role in changing the openness and composition of riparian communities in the deciduous forest region of eastern North America (Delcourt et al. 1986, Smith 1992). During the early Holocene, late-successional bottomland hardwood forests developed on floodplains of major rivers of the southeastern United States. After 4000 radiocarbon years ago, during the Archaic cultural period, Native Americans began to settle along stream banks of the lower Mississippi River and its tributaries, clearing local areas for establishment of villages (Smith 1992). The

paleoethnobotanical record documents that human-disturbed local clearings in the forest canopy became sites for the establishment of annual and perennial weedy plant species including chenopods (*Chenopodium berlandieri*), marshelder (*Iva annua*) and ragweed (*Ambrosia* spp.) that had been confined previously to marginal environments on gravel bars and stream banks (Marks 1983) but that became successful invaders into Native American old-fields (Delcourt et al. 1986). In the Little Tennessee River Valley (Delcourt et al. 1986), the ethnobotanical record shows a strong correspondence between increasing density of human occupation sites through the Archaic and Woodland cultural periods and the increasing representation of old-field species such as American cane (*Arundinaria gigantia*), red cedar (*Juniperus virginiana*), and pine (*Pinus virginiana*). Weed species that invaded old fields that were previously unable to penetrate closed bottomland forests may be an example of the resistant capabilities of forests to invasion, possibly owing to inertia. After A.D. 1250 to 1450, many floodplain agricultural sites were abandoned (Smith 1992) and underwent secondary succession to dense vegetation cover of wet prairie or dense canebrakes (Platt and Brantley 1997). Prehistoric human activities thus initially opened this landscape to invasion by native species extending beyond their previous habitats. Land abandonment was followed by establishment of new kinds of successional communities, such as canebrakes, that became highly resistant to subsequent biological invasion, persisting for centuries until burned and cleared by European farmers. Thus land clearance by Native Americans caused a resistant community (bottomland forest) to be replaced by an early-successional, open community including invasive weeds. Succession to dense, monospecific canebrakes once again converted the landscape to a resistant community.

Forest-stand simulation models and lag times for invasion

Long-term forest dynamics simulated by forest-stand models give insights into responses of species, including both lags in change of community composition because of biological inertia and because of hysteretic responses, or abruptly differential responses of a species to continuous trends in climate change, across important thresholds in physiological tolerance. Davis and Botkin (1985) examined the sensitivity of forest vegetation to climate change using the JABOWA model to simulate community response to different magnitudes and durations of temperature cooling (Botkin et al. 1972). They found that, across the

ecotone from northern hardwood to northern conifer forest in New England, climate cooling of 2° C lasting for several hundred years sufficed to shift dominance from sugar maple to spruce. This magnitude of climate change simulated that of the "Little Ice Age," which extended from about A.D. 1450 to 1850. Less climate cooling or shorter duration of climate fluctuation had less demonstrable effects on community composition unless accompanied by increased levels of exogenous disturbance. Heavily shaded sugar maple forest manifested resistance to invasion through inertia by conifer species both because of the longevity of this late-successional forest dominant and because of its local influence on seedling establishment. The study of Davis and Botkin (1985) demonstrated both thresholds and lags in response to climate change at the stand level, exacerbated by biological inertia.

Shugart *et al.* (1981) used the FORET (Forests of Eastern Tennessee) stand simulation model to look at forest dynamics under conditions of both climate warming and cooling. For a hypothetical stand composed of American beech (*Fagus grandifolia*) and tulip poplar (*Liriodendron tulipifera*), they performed multiple simulation runs to see how two species with different life-history characteristics would replace one another in response to a gradient of changing climate that slowly and systematically changed their competitive advantage. They found that at cooler temperatures the forest was dominated by beech and at warmer temperatures the forest was dominated by tulip poplar. Changes in dominance of the species, however, occurred abruptly across temperature thresholds that differed under warming *versus* cooling conditions. Shugart *et al.* (1981) attributed this hysteresis to differential lags in response to climate change depending on whether climate was favorable for seedling recruitment and growth of saplings (increasing temperature in the case of tulip poplar) or whether it was unfavorable, leading to dieback of canopy trees without subsequent regeneration (cooling temperature in the case of tulip poplar). The lag times for community replacement, owing to adult lifespans of species, are a form of biological inertia. These threshold responses can explain inertial changes of community structure, as individual life spans track climate changes differently.

Kräuchi (1995) applied FORSUM, a forest successional model that incorporates climate change effects on forest dynamics and structure, to examine vegetation response to climate change at the Solling spruce site in Switzerland. Under climate warming of mean

annual temperature increase of 0.3°C/decade, *Picea abies* would disappear completely and be replaced by a *Luzulo Fagetum* forest type with *Acer platanoides*, *Quercus petraea* and *Fagus sylvatica* after 180 years. Without any warming effects and a discontinuation of logging, the forest would be dominated after 300 years by beech (*Fagus sylvatica*) and other tree species. The long time period before significant vegetation changes would occur was attributed to the acidic litter layer that favors *Picea* regeneration and the shading of germinating seedlings by the closed spruce canopy. Part of this example can be considered biological inertia, because the leaf litter produced by the canopy is changing the microclimate of germination sites to be conducive to spruce regeneration.

Incorporating Biological Inertia into Invasion Ecology

Toward a unified framework

Lodge (1993 a, b) hypothesized that ecological resistance to invading species consists of three elements: environmental resistance (temperature, water flow, chemistry, structure, and abiotic resources), biotic resistance (prey availability, competition, predation, disease, and parasites), and demographic resistance of the invasive species (numbers introduced, ability to increase when rare). Environmental resistance contributes to the time lag in establishment of invasive species populations; biotic and demographic resistances are important influences in the integration of invasive species into the community (Figure 1; (Moyle and Light 1996). Biological inertia is a force that acts mainly to limit invasions by maintaining biological control over some elements of the environment. It can be due to environmental resistance created by biotic factors, as well as to biotic resistance simply because the residents continue to occupy space, and this influence can last for long periods of time, owing to the lifespan of long-lived trees. Because of the lag time inherent in eliminating resident species after environmental conditions become suitable for invasion by immigrating species, we propose that biological inertia is yet another important factor in the establishment of invasive species and is therefore an additional component of ecological resistance that has not been generally considered in invasion ecology (Figure 1).

We believe that biological inertia may be involved in other factors found to influence invasibility, including environmental changes (Davis and Botkin 1985), the proximity of the

community to critical ecotones (Gosz 1992), the heterogeneity of the landscape near ecotone boundaries (Neilson et al. 1992), stochastic events that constitute the disturbance regime (Kowarik 1995, Cadenasso and Pickett 2001), and facilitation by other species (Simberloff and Von Holle 1999). We propose that biotic inertia may play a part in resistance to invasion, along with these other factors. The interrelationship between biological inertia and the lag time for the invasion of non-native species is further complicated by the potential for multiple equilibrium points for communities and species hysteretic responses to climate change (Shugart et al. 1981). These multiple equilibrium points are achieved when communities near the extremes of their natural distributions are replaced by different communities, following a disturbance. These communities may have very different invasibilities and inertial properties. Additionally, resident species that track climate changes differently can have differential effects on invading species.

Late-successional forests exhibiting biological inertia to non-nonindigenous plant invasion

Most of the field experimental research that has explored the diversity-invasibility question was conducted in open-canopy biomes, including grasslands (Tilman et al. 1996, Knops et al. 1997, Crawley et al. 1999) and old fields (Palmer and Maurer 1997, Lavorel et al. 1999). The property of biological inertia acting in concert with ecological resistance may not be as apparent in these systems. One of Crawley's (Crawley 1987) two predictors of an easily invaded community is a community with low levels of plant cover. Native communities that 'create' their own microenvironments (*e.g., Tsuga canadensis* stands) tend to inhibit the establishment of new species (Davis et al. 1998).

We propose that biological inertia is more prevalent in closed communities (*e.g.*, forests), where the vegetation has more control over abiotic conditions (such as light, temperature, and soil chemistry) than in open communities (*e.g.*, prairies). Rejmánek (1996) compiled a worldwide list of 42 woody species that invade at least one area of primary tropical forest. Twenty-one of these are invasive only on islands. Of the other 21 species that invade continental primary tropical forest, 8 of these are found only in gaps. Simberloff et al. (2002, in press) censused native forest reserves on an Argentinian island that surrounded several abandoned forestry experiments. Seventy-three conifer and 62 broad-

leaved species (totaling over 100, 000 individuals of varying ages) were planted from 1926-1940 in discrete areas. Simberloff et al. (2002, in press) found that only 13 species invaded the surrounding intact, native forest and 36 individuals grew to heights greater than 10m after 61-75 years of abandonment. The biological inertia exerted by these late-successional stands that surround the forestry plantations may have acted to inhibit establishment of most of the non-natives, with the exception of a few shade-adapted species.

There are examples of intact late-successional forests with intact historical disturbance regimes that have been invaded successfully by one or more shade-tolerant species. *Lonicera tatarica* invades relatively undisturbed, old-growth, temperate northeastern United States habitat (Woods 1993). Webb et al. (2000) described *Acer platinoides*, *Lonicera japonica*, *Alliaria petiolata*, *Berberis thunbergii*, and *Wisteria floribunda* invasion into a relatively undisturbed, secondary, 18 ha forest tract in New Jersey. Garlic mustard has spread through high-quality forests in northern Illinois with flooding disturbance (Nuzzo 1999). *Tibouchina herbacea*, a sub-shrub native to South America, is invading undisturbed, closed canopy wet forests of Hawaii and Maui (Almasi 2000). Rejmánek (1989) provides a list of 60 species from 40 families that invade natural or seminatural communities worldwide. This list appears especially diminutive, considering the magnitude of nonindigenous species present worldwide. Lockwood et al. (2001) indicated that only 5.8%, 9.7%, and 13.4% of all nonindigenous species naturalized in California, Florida and Tennessee, respectively, invade natural areas. Thus, although some nonindigenous species can penetrate closed-canopied native forests, it appears that only a few shade-tolerant species are able to do this in any particular region and that natural areas effectively preclude most non-native invaders. We believe that intact closed-canopy forests exhibit inertia to biological invasion because of the microenvironmental influences of the stands and the sheer time it takes to replace resident adults with invasive exotic species.

Biological inertia exerted by late-successional stands is further supported by evidence from studies of plant succession. Rejmánek (1989) demonstrated that the relative number and cover of invading species in three successional sequences from central Europe declined exponentially with old-field successional stage. Gibson et al. (2000) found that the herbaceous understory vegetation in Illinois mesic forests shifted from non-native to native

dominance during succession. The confounding factor for this study and all successional studies is that propagule pressure of non-natives may be reduced during successional progression, given that human influences may be less likely to dominate later stages. A study of flooded forests eliminated this confounding factor, as stream deposition across all forest stages resulted in even propagule pressure across all stages (Rejmanek et al., 1987). Rejmánek et al (1987) found that nonindigenous species richness declined with successional stage, with Japanese climbing fern (*Lygodium japonicum*) the only nonindigenous species left in forests greater than 50 years old. This finding agrees with the premise of Grime (1979) that progression of successional stages appears to increase inertia to biological invasion. The resistance of late-successional forests may be due to environmental and biotic resistances or biological inertia. However, the environment of the site stays the same during successional time. The biota changes during succession, and with it biological inertia and biotic resistance to invasion. Thus one or both of these two latter factors are responsible for the lack of invasion of late-successional forests. Biological inertia is the long time it takes for trees to die and the microenvironmental influence of these trees and biotic resistance is the direct effect of the trees on the invading plants, such as shading and root competition. Even though the components of ecological resistance are interdependent and can act simultaneously, based on the evidence that we provide for biological inertia, we believe that inertia is the more important force in invasibility into late-successional forests.

Paleoecological and forest stand simulation studies show that disturbance frequency and duration appear to be two of the largest predictive factors in invasibility of some plant communities (Watts 1973, Davis and Botkin, 1985). Disturbances such as windfall that open stands to increased sunlight and thereby increase their invasibililty may be viewed as agents that remove stand inertia. To predict the success of invasion into inertial communities, both the frequency of disturbance and the life strategy exhibited by the potentially invasive species should be considered.

The mechanisms for resistance of late-successional forests are usually attributed to light levels and distance from invasion source (biotic and demographic factors). DeFarrari and Naiman (1994) found that number and cover of non-natives were significantly negatively correlated with patch age and canopy density in a variety of upland and riparian

habitats of the Olympic peninsula, Washington, USA. In their study of invasibility of southwestern Ohio forests, Hutchison and Vankat (1997) found high light levels and proximity to an abundant seed source increased forest invasibility to Amur honeysuckle (*Lonicera maackii*).

While there are always species capable of invading older stands, the richness and cover of non-natives generally decrease with stand age and canopy coverage (Rejmánek et al. 1987, Rejmánek 1989, Deferrari and Naiman 1994, Gibson et al. 2000). We are not claiming that inertial communities are entirely resistant to the huge suite of nonindigenous species that bombard modern forests today. It is possible that non-natives can establish footholds and a metapopulation structure in areas where there are canopy openings. However, the overall richness of non-natives will be lower in inertial communities, as the interiors of late-successional forests largely disallow 'ruderal' species invasion, which are adapted to high-light, disturbed conditions at the forest edge (Rejmánek 1989).

Certain nonindigenous species exhibit biological inertia

Contrary to Elton's (1958) notion of biological resistance as an inhibiting factor in species invasions (Simberloff 1986), there are many examples of nonindigenous species that readily invade an area and support monospecific populations, precluding further invasion of other species into the understory. Thus a species-poor community can be highly resistant to further invasion. In Crawley's list of the twenty most invasive alien plant species in Britian, the most noteworthy attribute possessed by the majority of the species is their "tendency to form dense thickets where regeneration by other plants is precluded" (Crawley 1987). It is not known whether these plant species (especially the short-lived species) are allelopathic (Rice 1984). Johnstone (1986) described monospecific stands of riparian weeds (*Typha* or *Sporodanthus*) as "invasion-proof." *Miconia calvescens*, a tree introduced into many Pacific Islands (e.g. Tahiti, Hawaii), is a noxious weed that forms monospecific stands and produces a dense shade with its overlapping, broad leaves, precluding native understory species (Meyer 1996). Seventy to 100 native plant species are directly threatened by invasion of *M. calvescens* into native Tahitian forests (Loope 1997). Hydrilla, *Hydrilla verticillata*, was introduced into Florida and became a vegetative scourge of the freshwater flora and fauna (Schmitz et al. 1983). This species forms dense canopies in the upper portion of the water column, thus

reducing light penetration, altering oxygen-transfer dynamics, and reducing water circulation (Schmitz et al. 1997). Not only low levels of dissolved oxygen but also significant changes in turbidity, color, chlorophyll, pH, specific conductivity, and phosphorous are common under the canopy of this species (Schmitz et al. 1997). The above cases are not examples of environmental resistance because the environment is created by the exotic species themselves. However, the "invasion-proof" aspect of these stands may be attributed to either or both biotic resistance and inertia. All of these examples indicate that species can invade an area and reduce the habitat availability for native species not adapted to the substantial change in the environmental conditions by the monospecific stands. Once established and incorporated into the community, the invasive nonindigenous species thus may introduce a new source of biological inertia to further community change.

Conclusions

Research needs

The characteristics of communities and landscapes that have not been invaded by nonindigenous species have not been thoroughly researched. Vermeij (1996) suggested that tests investigating the attributes of recipient biotas or regions that make them susceptible to invasion are a top priority for conservation biology. Additionally, the primary objective of these experiments "... should be ... not to exclude explanations, but to rank them or to explore their interdependence" (Vermeij 1996, p.8). In order for us to understand the relationship of biological inertia to ecological resistance better, more studies of the diversity-invasibility relationship, structure of the recipient communities, and specific life history features of invading species must be undertaken in closed-canopy systems to better evaluate these processes. Additionally, manipulative experiments would be helpful to explore the importance of the different elements of ecological resistance (Von Holle and Simberloff 2000). Much of the theory that depicts species richness of the recipient community as the sole contributor to a non-invasible system is mistaken if biological inertia, abiotic, and demographic factors are not considered as well.

Research is also needed into the spatial patterning of invasion of native communities by nonindigenous species, particularly focusing on invasibility as a function of scale of

disturbance relative to the extent of intact native habitat. For managed forests, invasibility may be enhanced by fragmentation. Invasion ecologists need to ask what are the critical thresholds beyond which a resident community that, when closed, has high biological inertia will become vulnerable to invasion by non-natives because of changes in landscape heterogeneity and fragmentation into a more open system (Franklin and Forman 1987). Further, we need to evaluate the degree to which fragmented landscapes generated by land use history now exhibit inertia by conversion to more closed systems ("pattern inertia" of Wallin et al. [1994]).

Many ecological studies are of such short duration (Tilman 1988) that they are unable to detect evidence of biological inertia. Tilman (1988, p.151) suggested that, "the longer that an experiment proceeds, the more its results represent a response to the average climatic conditions that exist in a geographic region." The extreme events that could break down inertia are less likely to be witnessed in short time periods characteristic of most ecological studies. Thus, the many studies that attribute 'resistance' to such factors as climate mismatch or biological interactions might also, if carried out for a long enough time, document vegetational inertia as a biotic mechanism that is mediated through abiotic means and confers resistance.

Management needs

Both prehistoric and historic human habitat use have fragmented previously closed communities, rendering them less resistant to invasion by both native and nonindigenous species. Thus, it is possible that biological inertia is a factor that is ignored in modern studies of population dynamics, because it is obscured by anthropogenic disturbance. Smith (1965) proposed that human activity is able to tip the balance of vegetational inertia towards vegetational change. Disruption of inherent biological inertia to invasion is a consequence of human activities that has important implications for conservation and management of natural biological communities. To diminish the vulnerability of biological communities to invasion by nonindigenous species, late-successional forests should be kept intact with their historical disturbance regimes. To this end, land acquisition patterns can focus on retaining communities that are likely to maintain themselves while rejecting weedy native and nonindigenous species. A landscape mosaic containing these types of communities could

be designed to surround and thus better protect parks (Cadenasso and Pickett 2001). Buffer zones that spatially reduce the contrast between late-successional, inertial, interior communities and intensively managed land would further limit the spread of nonindigenous species from human-dominated systems (Ambrose and Bratton 1990).

Summary

Natural range extension is a well studied process that can be extended to understand invasion by nonindigenous species. Biological inertia has been shown in paleo-ecological, simulation and successional studies to be a significant factor that precludes establishment of invading plant species. Inertia constitutes an additional property of ecological resistance to biological invasion that should be considered in future studies. Additionally, these kinds of inertial properties of late-successional vegetation can be extended to landscape-scale management for non-native invasions.

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References

Almasi, K. N. 2000. A non-native perennial invades a native forest. Biological Invasions **2**:219-230.

Ambrose, J. P., and S. P. Bratton. 1990. Trends in landscape heterogeneity along the borders of Great Smoky Mountains National Park. Conservation Biology **4**:135-143.

Birks, H. J. B. 1989. Holocene isochrone maps and patterns of tree-spreading in the British Isles. Journal of Biogeography **16**:503-540.

Botkin, D. B., J. R. Wallis, and J. F. Janak. 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology **60**:849-&.

Cadenasso, M. L., and S. T. A. Pickett. 2001. Effect of edge structure on the flux of species into forest interiors. Conservation Biology **15**:91-97.

Clark, J. S. 1998. Why trees migrate so fast: Confronting theory with dispersal biology and the paleorecord. The American Naturalist **152**:204-224.

Cole, K. 1985. Past rates of change, species richness, and a model of vegetational inertia in the Grand Canyon, Arizona. The American Naturalist **125**:289-303.

Crawley, M. J. 1987. What makes a community invasible? Pages 429-453 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, Succession, and Stability. Blackwell Scientific.

Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters **2**:140-148.

Crone, E. E. 1997. Delayed density dependence and the stability of interacting populations and subpopulations. Theoretical Population Biology **51**:67-76.

Crooks, J. A., and M. E. Soulé. 1999. Lag times in population explosions of exotic species: causes and implications. *in* O. T. Sandlund, P. J. Schei, and A. Viken, editors. Invasive Species and Biodiversity Management. Kluwer.

Cwynar, L. C., and G. M. MacDonald. 1987. Geographical variation of lodgepole pine in relation to population history. The American Naturalist **129**:463-469.

Davis, M. A., K. Thompson, and J. P. Grime. 2001. Charles S. Elton and the dissociation of invasion ecology from the rest of ecology. Diversity and Distributions **7**:97-102

Davis, M. B. 1981. Quaternary history and the stability of forest communities. Pages 132-153 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest Succession: Concepts and Application. Springer-Verlag, New York, New York.

Davis, M. B. 1987. Invasions of forest communities during the Holocene: beech and hemlock in the Great Lakes Region. Pages 373-393 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, Succession and Stability. Blackwell Scientific, Oxford, UK.

Davis, M. B., and D. B. Botkin. 1985. Sensitivity of cool-temperate forests and their fossil pollen record to rapid temperature change. Quaternary Research **23**:327-340.

Davis, M. B., R. R. Calcote, S. Sugita, and H. Takahara. 1998. Patchy invasion and the origin of a hemlock-hardwoods forest mosaic. Ecology **79**:2641-2659.

Deferrari, C. M., and R. J. Naiman. 1994. A Multiscale Assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. Journal of Vegetation Science **5**:247-258.

Delcourt, P. A., and H. R. Delcourt. 1987. Long-term Forest Dynamics of the Temperate Zone. Springer-Verlag, New York, NY.

Delcourt, P. A., H. R. Delcourt, P. A. Cridlebaugh, and J. Chapman. 1986. Holocene ethnobotanical and paleoecological record of human impact on vegetation in the Little Tennessee River Valley, Tennessee. Quaternary Research **25**:330-349.

Du Rietz, G. E. 1949. Huvudenheter och huvudgränser i svensk myrvegetation. Svensk bot. Tidskr. **43**:274-309.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen, London.

Ewel, J. J., D. J. O'Dowd, J. Bergelson, C. C. Daehler, and C. M. D'Antonio. 1999. Deliberate introductions of species: Research needs. BioScience **49**:619-630.

Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology **1**:5-18.

Gibson, D. J., E. D. Adams, J. S. Ely, D. J. Gustafson, D. McEwen, and T. R. Evans. 2000. Eighteen years of herbaceous layer recovery of a recreation area in a mesic forest. Journal of the Torrey Botanical Society **127**:230-239.

Gorham, E. 1957. The development of peat lands. Quarterly Review of Biology **32**:145-166.

Gosz, J. 1992. Ecological functions in a biome transition zone: translating local responses to broad-scale dynamics. Pages 55-75 *in* A. J. Hansen and F. d. Castri, editors. Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag, New York, NY.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, Chichester.

Gurney, W. S. C., S. P. Blythe, and R. M. Nisbet. 1980. Nicholson blowflies revisited. Nature **287**:17-21.

Huntley, B., and H. J. B. Birks. 1983. An atlas of past and present pollen maps for Europe: 0-13000 years. Cambridge University Press, Cambridge, UK.

Hutchinson, T. F., and J. L. Vankat. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. Conservation Biology **11**:1117-1124.

Johnstone, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. Biological Review **61**:369-394.

Knops, J. M. H., D. Tilman, S. Naeem, and K. M. Howe. 1997. Biodiversity and plant invasions in experimental grassland plots. ESA Bulletin **78**:125.

Kot, M. 2001. Elements of Mathematical Ecology. Cambridge University Press, Cambridge.

Kowarik, I. 1995. Time lags in biological invasions with regard to the success and failure of alien species. Pages 15-38 *in* P. Pyšek, K. Prach, M. Rejmánek, and M. Wade, editors. Plant Invasions-General Aspects and Special Problems. SPB Academic Publishing, Amsterdam, The Netherlands.

Krauchi, N. 1995. Application of the model Forsum to the Solling spruce site. Ecological Modelling **83**:219-228.

Lavorel, S., A.-H. Prieur-Richard, and K. Grigulis. 1999. Invasibility and diversity of plant communities: from pattern to processes. Diversity and Distributions **5**:41-49.

Lockwood, J. L., D. Simberloff, M. L. McKinney, and B. Von Holle. 2001. How many, and which, plants will invade natural areas? Biological Invasions **3**:1-8.

Loope, L. L. 1997. Hawaiian Ecosystems at Risk (HEAR) project's Harmful Non-Indigenous Species (HNIS) report on *Miconia calvescens*. Haleakala National Park Field Station, USGS/BRD.

MacDonald, G. M., and L. C. Cwynar. 1991. Post-glacial population growth rates of *Pinus contorta* ssp. *latifolia* in Western Canada. Journal of Ecology **79**:417-429.

Marks, P. L. 1983. On the origin of the field plants of the northeastern United States. American Naturalist **122**:210-228.

Meyer, J. Y. 1996. Status of *Miconia calvescens* (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). Pacific science **50**:66-76.

Moyle, P. B., and T. Light. 1996. Biological invasions of fresh water: empirical rules and assembly theory. Biological Conservation **78**:149-161.

Neilson, R. P., G. A. King, R. L. DeVelice, and J. M. Lenihan. 1992. Regional and local vegetation patterns: the responses of vegetation diversity to subcontinental air mass. Pages 129-149 *in* A. J. Hansen and F. d. Castri, editors. Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag, New York, NY.

Nuzzo, V. 1999. Invasion pattern of the herb garlic mustard (*Alliaria petiolata*) in high quality forests. Biological Invasions **1**:169-179.

Palmer, M. W., and T. Maurer. 1997. Does diversity beget diversity? A case study of crops and weeds. Journal of Vegetation Science **8**:235-240.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Karieva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: towards a framework for understanding the ecological effects of invaders. Biological Invasions **1**:3-19.

Pearsall, W. H. 1959. The ecology of invasion: ecological stability and instability. New Biology **29**:95-101.

Platt, S. G., and C. G. Brantley. 1997. Canebrakes: An ecological and historical perspective. Castanea **62**:8-21.

Rejmánek, M. 1989. Invasibility of plant communities. Pages 369-388 *in* J. A. Drake, H. A. Mooney, F. d. Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M.

Williamson, editors. Biological Invasions: a Global Perspective. John Wiley and Sons, Chichester, UK.

Rejmánek, M. 1996. Species richness and resistance to invasions. Pages 153-172 *in* G. H. Orians, R. Dirzo, and J. H. Cushman, editors. Biodiversity and Ecosystem Processes in Tropical Forests. Springer-Verlag, Berlin Heidelberg.

Rejmánek, M., C. E. Sasser, and J. G. Gosselink. 1987. Modeling of vegetation dynamics in the Mississippi River deltaic plain. Vegetatio **69**:133-140.

Rice, E. L. 1984. Allelopathy, 2nd edition. Academic Press, New York.

Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions **6**:93-107.

Schmitz, D. C., J. D. Schardt, A. J. Leslie, J. F.A. Dray, J. A. Osborne, and B. V. Nelson. 1983. The ecological impact and management history of three invasive alien aquatic plant species in Florida. Pages 173-194 *in* B. N. McKnight, editor. Biological Pollution: The Control and Impact of Invasive Exotic Species. Indiana Academy of Sciences, Indianapolis, Indiana.

Schmitz, D. C., D. Simberloff, R. H. Hofstetter, W. Haller, and D. Sutton. 1997. The ecological impact of nonindigenous plants. Pages 39-62 *in* D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. Strangers in Paradise: Impact and Management of Nonindigenous Species in Florida. Island Press, Washington, DC.

Shrader-Frechette, K.S., and E.D. McCoy. 1993. Method in Ecology: Strategies for Conservation, Cambridge University Press, Cambridge.

Shugart, H. H., D. C. West, and W. R. Emanuel. 1981. Patterns and dynamics of forests: an application of simulation models. Pages 74-94 *in* D. C. West, H. H. Shugart, and D. B. Botkin, editors. Forest Succession, Concepts and Application. Springer-Verlag, New York, NY.

Simberloff, D. 1986. Introduced Insects: A biogeographic and systematic perspective. Pages 3-24 *in* H. A. Mooney and J. A. Drake, editors. Ecology of Biological Invasions in North America and Hawaii. Springer-Verlag, New York.

Simberloff, D., M. A. Relva, and M. Nuñez. in press. Gringos en el Bosque: Introduced tree invasion in a *Nothofagus/Austrocedrus* forest. Biological Invasions.

Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? Biological Invasions **1**:21-32.

Smith, A. G. 1965. Problems of inertia and threshold related to post-Glacial habitat changes. Proceedings of the Royal Society of London series B. Biological Sciences **161**:331-342.

Smith, B. D. 1992. Rivers of change: essays on early agriculture in eastern North America. Smithsonian Institution Press, Washington, D.C.

Thompson, K., J. G. Hodgson, and T. C. G. Rich. 1995. Native and alien invasive plants: More of the same? Ecography **18**:390-402.

Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, N.J.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature **379**:718-720.

Turchin, P. 1990. Rarity of density dependence or population regulation with lags. Nature **344**:660-663.

Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time-series. Ecology **73**:289-305.

Von Holle, B., and D. Simberloff. 2000. Ranking the components of ecological resistance to biological invaders in a southeastern riparian forest. Pages 351 *in* Ecological Society of America, 85th Annual Meeting, Snowbird, Utah.

Wallin, D. O., F. J. Swanson, and B. Marks. 1994. Landscape pattern response to changes in pattern generation rules - land-use legacies in forestry. Ecological Applications **4**:569-580.

Watts, W. A. 1973. Rates of change and stability in vegetation in the perspective of long periods of time. Pages 195-205 *in* H. J. B. Birks and R. G. West, editors. Quaternary Plant Ecology. Blackwell, Oxford.

Webb, S. L., M. Dwyer, C. K. Kaunzinger, and P. H. Wyckoff. 2000. The myth of the resilient forest: Case study of the invasive Norway maple (Acer platanoides). Rhodora **102**:332-354.

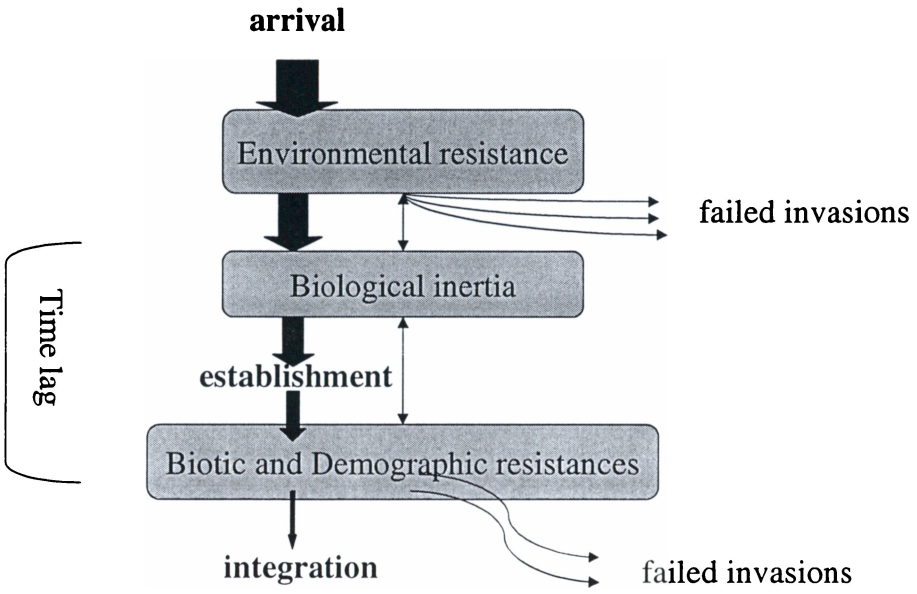
Williamson, M. 1996. Biological Invasions. Chapman & Hall, London.

Woods, K. D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in 4 New England forests. American Midland Naturalist **130**:62-74.

Appendix

Figure 1. A conceptual model of the process of integration of a biological invader into a local area. The elements of ecological resistance are in boxes going from the top to the bottom of the figure and the phases of establishment are in plain text. The different elements of ecological resistance are listed top-down in order of importance. Biological inertia is second in importance to environmental resistance in the establishment of exotic species. The elements of biological inertia, and biotic and demographic resistances, add to time lag effects. Adapted from Moyle and Light, 1996.

Figure 1.


arrival
Environmental resistance
failed invasions
Biological inertia
Time lag
establishment
Biotic and Demographic resistances
integration
failed invasions

CONCLUSION

Ranking the Components of Ecological Resistance to Biological Invaders: An Experimental Manipulation in a Southern Appalachian Riparian Forest

Introduction

Both (Part **I, II**) of my explorations of biotic resistance revealed that biotic interactions did not have a large influence on invader survivorship, relative to demographic and environmental factors. Additionally, species of some functional groups were better at invading these forested areas than species of others. These results are promising for further exploration of indentification of functional groups as potential invaders of habitat types and of possible facilitations among species.

These indirect interactions are clearly influenced by the disturbance regime (Part **II**). The two different kinds of stresses imposed on the plants had two totally different results (Part **III**). Non-indigenous species and smaller species survived transplanting better than natives and larger species, respectively. The fact that natives and larger species better survived flooding and the range of environmental and biotic influences after one year implies that these plant types are better at invading natural systems of this sort. Additionally, the fact that non-indigenous species did not outperform natives in the highly flooded areas implies that results of previous observational studies that revealed high invasibility of flooded areas (Deferrari and Naiman 1994, PlantyTabacchi et al. 1996, Hood and Naiman 2000) may have been due to increased propagule import that accompanied the anthropogenic or natural disturbance regimes.

The additional, fourth component of ecological resistance to biological invasion, inertia, may cast further light on invasibility (Part **IV**). This will be an additional component in future ecological resistance ranking studies. I predict that the environmental and biotic resistance influences on invader survivorship relative to propagule pressure will be low on a yearly basis but will have great cumulative impact over long periods of time. I also expect these influences to change with time. I expect that it will take longer than this experimental time frame to accurately monitor all three influences on invasibility.

I have tested a number of factors that relate to ecological resistance and uncovered patterns within each component of ecological resistance. I have suggested a new component of ecological resistance to invasion. Consequently, there are a number of hypothesis that I would like to test regarding resistance in the future.

Results and Discussion

Fox's assembly rule does not apply to this system (Part I)

There was a significant interaction between functional groups removed from the plot and survivorship in the functional groups added to those plots. However, survivorship of species in functional groups introduced into the plots with their respective functional group removed did not differ from survivorship when any other functional group was removed. Additionally, growth of each of the most abundant species did not differ significantly among plots with different functional groups manipulated. Specifically, species did not fare better in those plots that had representatives of their own functional group removed. Fox's assembly rule does not hold for this plant community; however, resident composition was found to affect community assembly.

Biological resistance to invaders exists in the form of canopy and understory functional group composition (Part II)

The most significant biotic influences on invader survivorship in this system of flooded and non-flooded plots were the overstory of *Rhododendron maximum* and the understory functional group composition. Invader survivorship increased with distance from *R. maximum* and with richness of the understory SB functional group. Survivorship was positively correlated with recipient community species richness and plot light availability and negatively correlated with recipient plot density. However, the diversity-invasibility relationship differed in more flooded areas with a negative relationship between plot richness and invader survivorship. Density is an important factor that should be analyzed simultaneously with richness of recipient plots, in order to disentangle their separate contributions to invasion resistance. Full understanding of Elton's notion of biotic resistance requires a further exploration of the role of disturbance regimes.

Natural disturbance enhances resistance to biological invaders (Part III)

Non-indigenous species survived transplanting better than natives and native species survived a year of the ambient environmental and biotic stresses better than non-indigenous species. Surviving non-indigenous species had significantly greater canopy length and width growth than did surviving natives in the non-flooding plots. Native species had higher survivorship than non-indigenous species in both flooding conditions. Large aboveground biomass, branching-rooted (LB) plants had higher survivorship than those in other functional groups after one year, across flooding treatments. According to Elton's (1958) original biotic resistance theory, non-indigenous invaders should have been better invaders of these low diversity, highly disturbed stream habitats than natives. The fact that the opposite trend was observed suggests that natural disturbance (flooding) inhibits invasion by most non-indigenous species in this system.

Biological inertia as a fourth component of ecological resistance (Part IV)

I propose that biological inertia within the resident community is a fourth component of ecological resistance to invasion, because of the lag time inherent in eliminating resident species after environmental conditions become suitable for invasion by immigrating species. Microclimatic conditions created by the existing vegetation that are favorable for the existence of the present community or population promote the continuity of the present community. This is a form of biological inertia to invasion that reflects the life-history characteristics of the resident species. Biological inertia is hypothesized to vary with (1) the magnitude, duration, direction, rate, and variability of climate or other environmental changes; (2) proximity of the community to critical ecotones; (3) heterogeneity of the landscape near ecotone boundaries; and (4) changes in the natural or anthropogenic disturbance regime.

Open questions

This was the first simultaneous experimental exploration of biotic and environmental resistance. Among questions that arose as I explored these factors of ecological resistance were:

What role does biological inertia play in ecological resistance to invaders?

As I investigated the relative roles of the factors of ecological resistance to invaders, I realized how different this system is relative to other systems that have been used to test biotic resistance experimentally. This study was conducted in a closed-canopy forest, which exerts a strong influence on the type of organism that can successfully invade. Both the invaders and the community types are very different from those explored previously, which are open-canopied habitats, such as grasslands and old fields (Part **IV**). Exactly how great an influence micro-environmental conditions that are generated by the forest canopy have on the success of an invading non-indigenous species, relative to the original three proposed factors, is of interest. Mechanisms such as light, soil chemistry and root competition can be explored to understand this influence. The influence of the overstory composition on invader survivorship is fascinating because this influence was clearly not only due to light availability (Part **II**). Exploring the other factors that may be responsible for this canopy influence, such as water availability or root competition, would be an interesting research project.

Does ecological resistance have a greater influence on the germination stage of invader establishment?

This thesis explored the mechanisms of ecological resistance to biological invaders during the establishment phase of an invader. The establishment dynamics might be very different for germinating seeds than for transplanted individuals. In fact, I hypothesize that ecological resistance would be a stronger influence at the germination stage. I did not use seeds in this experiment because I did not want to distribute non-indigenous seeds downstream. The ideal system in which to explore the germination hypothesis would be a system that does not pair propagule pressure with the disturbance, such as a fire-disturbed ecosystem.

Do other natural disturbance regimes inhibit invasion by non-indigenous species?

It is interesting to me that natural disturbance had a greater influence on the success of invaders than the biotic components. I was surprised to learn that the diversity-invasibility relationship changed across flooding regimes. I would like to explore the mechanisms of the

influence of disturbance regimes on the diversity-invasibility relationship, and whether other natural disturbances inhibit rather than facilitate invasion by non-indigenous species.

Conservation implications

Riparian systems are diversity hotspots, experience great human impact, and have the largest effects on landscape processes (Chapin et al., 1997). In an age when riparian habitat is increasingly encroached upon by human development, management of this resource is vital to conserving biodiversity. Riparian plant species are very sensitive to hydrological change (Tabacchi 1995), with the implication that species composition changes in response to human manipulation of the hydrological regime. Studying a naturally disturbed riparian system and identifying demographic and environmental factors that contribute to invasion will help with the management of rivers and streams.

Effects of non-native species are a great hazard to global biodiversity, second only to habitat destruction (Glowka et al. 1994, Wilcove et al. 1998). To make informed management decisions, we must know how plant communities resist invasion. Studies such as this will equip time-limited natural area managers with the ability to prioritize habitats they should monitor most intensively for invasive species to retain the highest native diversity. Currently, the United States spends $3.6 to 5.4 billion a year in total direct costs for non-indigenous plant weeds (U.S. OTA 1993). These costs may be defrayed if the mechanisms of resistance to invasions were better understood.

References

Deferrari, C. M., and R. J. Naiman. 1994. A multiscale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. Journal of Vegetation Science **5**:247-258.

Glowka, L., F. Burhenne-Guilmin, and H. Synge. 1994. A Guide to the Convention on Biological Diversity. IUCN, Gland.

Hood, W. G., and R. J. Naiman. 2000. Vulnerability of riparian zones to invasion by exotic vascular plants. Plant Ecology **148**:105-114.

PlantyTabacchi, A. M., E. Tabacchi, R. J. Naiman, C. Deferrari, and H. Decamps. 1996. Invasibility of species rich communities in riparian zones. Conservation Biology **10**:598-607.

Tabacchi, E. 1995. Structural variability and invasions of pioneer plant communities in riparian habitats of the middle Adour River (SW France). Canadian Journal of Botany-Revue Canadienne de Botanique **73**:33-44.

United States Congress. 1993. Harmful Non-Indigenous Species in the United States. Office of Technology Assessment, Washington, D.C.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience **48**:607-615.

APPENDIX

Appendix 1. Plant species in study site, listed by functional group. Underlined species were those used as invaders. Nomeclature follows that of Gleason and Cronquist (1991). Non-indigenous species are marked with a '*'. Species in bold are annuals and were removed from all analyses after the first census year.

Small biomass, branching, rhizmatous. (SB)			
SMALL SHRUB	*Lycopodium obscurum*		GRASSES
Epigaea repens		**Lysimachia nummularia*	*Agrostis hyemalis*
Gaultheria procumbens	HERBS	*Maianthemum canadense*	*Carex laxiflora*
Mitchella repens	*Amianthium muscaetoxicum*	*Medeola virginiana*	*Carex radiata*
	Arisaema triphyllum	*Sisyrinchium* sp.	**Dactylis glomerata*
FERNS	*Aristolochia macrophylla*	*Symplocarpus foetidus*	*Danthonia compressa*
Botrychium virginianum	****Cerastium viscosum***	*Smilax glauca*	**Festuca eliator*
Dennstaedtia punctilobula	**Cerastium vulgatum*	*Smilax hispida*	**Holcus lanatus*
Osmunda cinnamomea	****Commelina communis***	*Smilax rotundifolia*	*Panicum boscii*
Polystichum acrostichoides	**Daucus carota*	*Streptops roseus*	**Phleum pratense*
Thelypteris noveboracensis	*Dioscorea villosa*	**Thymus serpyllum*	**Poa compressa*
FERN-ALLIES	**Glechoma hederacea*	*Trillium sp.*	**Poa pratensis*
Diphasiastrum digitatum	*Hexastylis* sp.	**Veronica officinalis*	*Digitaria filiformis*
*****Equisetum arvense***	*Luzula echinata*		
Large biomass, branching, rhizmatous. (LB)			
(SHRUBS)	*Corylus cornuta*	*Pyrularia pubera*	*Salix sericea*
	Euonymus americanus	*Quercus prinoides*	*Sassafras albidum*
Alnus serrulata	*Gaylussacia baccata*	*Rhododendron calendulaceum*	*Spiraea alba*
Amelanchier arborea	*Gaylussacia ursina*	*Rhododendron maximum*	*Spiraea tomentosa*
Asimina triloba	*Hamamelis virginiana*	*Rhus glabra*	*Vaccinium arboreum*
Castanea pumila	*Hypericum densiflorum*	*Ribes* sp.	*Vaccinium erythrocarpum*
Ceanothus americanus	*Ilex montana*	**Rosa multiflora*	*Vaccinium stamineum*
Cornus alterniflora	*Ilex opaca*	*Salix nigra*	*Vaccinium pallidum*
Cornus amomum	*Ilex verticillata*	*Salix eriocephala*	*Viburnum sp.*
Cornus sericea	*Kalmia latifolia*		
Corylus americana	*Lindera benzoin*		

Appendix 1, Continued

Large biomass, taproot (LT)			
(TREES AND SMALL TREES)			
Acer negundo	*Carya glabra*	*Nyssa sylvatica*	*Quercus coccinea*
Acer pensylvanicum	*Carya ovata*	*Oxydendrum arboreum*	*Quercus muenlenbergii*
Acer spicatum	*Crataegus crus-galli*	*Pinus rigida*	*Quercus prinus*
***Acer rubrum*	*Crataegus coccinea*	*Pinus strobus*	*Quercus rubra*
Aesculus flava	**Eleagnus umbellata*	*Populus grandidentata*	*Quercus velutina*
Betula lenta	*Fraxinus pennsylvanica*	*Prunus pensylvanica*	***Robinia pseudoacacia*
Carpinus caroliniana	*Liriodendron tulipifera*	*Prunus serotina*	*Tsuga canadensis*
Carya cordiforms	*Magnolia tripetala*	*Quercus alba*	*Ulmus americana*
Small biomass, taproot (ST)			
(HERBS)	*Desmodium* sp.	***Medicago lupulina***	**Rubus idaeus*
**Achillea millefolium*	**Duchesnia indica*	*Melanthium parviflorum*	*Rubus spp.*
Anemone arborea	*****Erigeron annuus***	***Mollugo verticillata***	**Rumex acetosella*
Anemone lancifolia	***Fragaria virginiana*	***Oxalis stricta*	*Salvia lyrata*
Anemone quinquefolia	*Galax aphylla*	*Parnassia asarifolia*	*Scutellaria serrata*
Aster divaricatus	**Galinsoga quadriradiata*	*Parthenocissus quinquefolia*	*Sedum ternatum*
Boykinia acontifolia	*****Galium aparine***	*Pedicularis canadensis*	*Senecio aureus*
****Brassica rapa***	*Galium pilosum*	**Plantago major*	**Taraxacum officinale*
****Brassica nigra***	*Galium triflorum*	***Plantago rugelli*	*Thalictrum clavatum*
Chimaphila maculata	****Geranium pusillum***	*Podophyllum peltatum*	****Trifolium* sp.**
**Chrysanthemum leucanthemum*	*Goodyera pubescens*	*Potentilla canadensis*	**Urtica dioica*
**Cichorium intybus*	**Hieracium caespitosum*	***Potentilla simplex*	**Verbascum thapsus*
	Hieracium paniculatum	**Potentilla recta*	*Viola rotundifolia*
	Lobelia cardinalis	**Prunella vulgaris*	*Viola sororia*

VITA

Betsy Von Holle was born in Milwaukee, Wisconsin on July 23rd, 1972. She attended public schools in Livermore, California, the Alameda County public school system, where she graduated from Granada High School in June, 1990. She entered the University of California, at San Diego, during September of 1990 where in December, 1994 she received a Bachelor of Science in Ecology, Behavior and Evolution. She completed an internship studying the impact of an invasive hydroid on the northern Chesapeake Bay benthic community after a year at the Smithsonian Environmental Research Center (SERC) in Edgewater, Maryland. She then held a four-month internship studying invertebrate behavior at the Mitrani Center for Desert Ecology, in Sde Boker, Isreal. She returned to SERC after this experience and worked as a research assistant for a marine invasion biology project for an additional year. In August of 1997, she entered the Ph.D. program in Ecology and Evolutionary Biology at the University of Tennessee, Knoxville. The doctoral degree was received August, 2002.

She is presently working on disturbance histories of Cape Cod National Seashore as determinants of invasive plant distribution for her postdoctoral studies. She is a National Parks Ecological Research fellow at Harvard Forest, Harvard University. This fellowship was granted from the Andrew Mellon Foundation, the National Parks Service, and the Ecological Society of America.