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

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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 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 aboveground biomass and rooting structure type. 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 assessed success of an invasion by plant survivorship and growth. We analyzed survivorship of functional groups with loglinear models for the analysis of categorical data in a 4way table. There was a significant interaction between functional groups removed in a plot and survivorship in the functional groups added to that plot. 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 these functional groups in this plant community; however, composition of the recipient community is a significant factor in community assembly.

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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 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 (Gleason 1926, 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 predictable cohorts 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 is divided into functional or taxonomic groups

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(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 to determine the role and importance of functional groups in plant community 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 on 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 functional groups of rodents in 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, a contention rejected by Brown et al. (2002). Assembly rules for plants have proven harder to demonstrate (Wilson 1995). Wilson and colleagues have tested for 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 (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 40-mm² 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. Symstad (2000) experimentally tested differential invasion by functional groupings (classified by resource acquisition types) that had their functional groups removed, without replacement, from 4×8 m plots at the Cedar Creek Natural History Area in Minnesota, USA. She found weak evidence that C_3 graminoids repelled functionally similar invaders in addition to C_4 graminoids. Our experiment differs fundamentally from Symstad's (2000), as we assembled communities to simulate otherwise natural, undisturbed communities in the "unfavored state" described by Fox and Brown (1993). These "unfavored states" are assemblages where sizes of functional groups differ by more than one species. We attempted to simulate a natural, undisturbed community by maintaining the original plot biomass with the replacement of biomass of the removed community members and by not disturbing the soil after the "invasion".

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 and resistance to flooding. We use the term "functional group" in this paper; related terms include guild (Simberloff and Dayan 1991), lifeform (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 that community. The central question is: do invaders from a functional group that has been removed or whose size has been reduced perform better than those whose functional groups have not been manipulated? We pose three specific hypotheses to address this central issue:

- 1) When a functional group has been removed, a community will become 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.
- 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 closed-canopy, forested 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 of forest understory plants and introducing invaders into these manipulated plots. Our functional groups were established a priori using the deductive method (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 aboveground biomass and rooting structure type. These morphological characteristics differentiate a plant's use of space and resources: large aboveground biomass plants have different resource (including space) requirements than small plants and taprooted species have different resource use patterns than adventitious and fibrous rooted (non-taprooted) species in the soil matrix (Fig. 1). The horizontal structure of plants is a determinant of their ability to use resources that are heterogeneously distributed in space (Pitelka and Ashmun 1986). Rooting architecture is determined by degree of branching, balance of primary and adventitious roots, and branching plasticity (Fitter 1987). This architecture may be important for storage and anchorage and is important for resource use (Fitter 1987). Thus, plant morphology has been found to influence resource acquisition directly. Our root classification rested solely on whether the total root structure (including primary and adventitious roots) was primarily taprooted or not. 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 < 1/2 m tall will not be in its adult state). Shrub and vine species in the genera Smilax, Parthenocissus and Rubus generally have low biomass in this acidic, low nutrient, forested habitat in comparison to the trees and shrubs that comprise the large-biomass groupings. Thus, they were placed in the small-biomass groups. Although they may not presently be in the adult state that confers the functional group status, these groupings have different predictors for total dry weight (Table 1) at the < 1/2 m state. The functional groups are small aboveground biomass, non-taprooted structure (SN); small aboveground biomass, taproot (ST); large aboveground biomass, non-taprooted structure (LN); and large aboveground biomass, taproot (LT) (Appendix 1 and Fig. 1). Functional groups were classified by descriptions

provided by Gleason and Cronquist (1991), combined with field observations.

Experimental design

Community manipulation

A randomized block design was employed across four plots to test hypotheses 1 and 2 (Fig. 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 70×10 m area. Each of these areas had four rows with 1 m between rows. Each sub-plot was 1.5×1.5 m. 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 sub-plots, was censused and manipulated in 1999. The second pair of plots, each with 28 subplots, were censused and manipulated in 2000 (Fig. 2). 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). We designed this treatment to ascertain whether one functional group member could represent an entire functional group, which would imply that 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 and that plot was dropped from the total pool of plots. 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 biomass 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



Fig. 1. Representative species in each functional group: a) small aboveground biomass, non-taprooted structure (SN) – *Diphasiastrum digitatum*; b) large aboveground biomass, non-taprooted structure (LN) – *Amelanchier arborea*; c) small-aboveground biomass, taproot (ST) – *Rubus* sp.; and d) large aboveground biomass, taproot (LT) – *Quercus rubra*. These plants are commonly found in our study site. Average total biomass of the plants in the large biomass functional groups is significantly greater than that of the plants in the small-biomass functional groups by one-way student's t-test [t = 4.05, p = 0.0002. Average biomass (g) ± standard error (n); large = 1.40 ± 0.43 (16), small = 0.21 ± 0.04 (38)].

Table 1. Functional group characteristics that most significantly predict total biomass. The dependent variable was total dry biomass and the independent variables were all plant characters listed in the first column. Independent variables exhibiting multicollinearity were removed. 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, SN total biomass = 0.8708 - 0.39 SD+0.10 IL -0.08 NOL; ST total biomass = -0.26 + 0.30 SD+0.01 CL; LN total biomass = -16.09 - 1.68 CL+4.46 CW; LT total biomass = -1.209 + 0.37 SD+0.025 PH -0.081 CW+0.371 NOL.

Plant character	Functional group					
	SN	ST	LN	LT		
Stem diameter	*	*		*		
Canopy length		*	*			
Canopy width			*	*		
Internode length	*					
Plant height				*		
No. of leaves	*			*		
Model R ² and p-value	0.6764, p = 0.4437	0.7713, p < 0.0001	0.9359, p = 0.0041	0.9176, p = 0.0193		

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. Biomass was maintained to simulate a natural, undisturbed community in the "unfavored state" of Fox and Brown (1993).



Fig. 2. Experimental design for the invaders placed in the 138 sub-plots sampled in this study. Numbers in parentheses indicate number of replicates, or sub-plots. The boxes with the functional groups indicated (SN, ST, LN, LT) are the number of sub-plots that have those functional groups manipulated for each treatment above. For the "one representative species" treatment, SN (small aboveground biomass, non-taprooted structure), LN (large aboveground biomass, taproot), ST (small aboveground 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, SN, LN, LT, and ST indicate eliminated functional groups in those plots. The 138 sub-plots were divided among 4 larger plots, having 1X and 2X treatments, and further split by site location. 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 LN and LT removed (indicated in bold) and a total of 56 plots.

The control plots were left with the original complement of species. All manipulated plants were shorter than 0.5 m.

Invader input

After a two-week period to allow for rerooting of plants, these 1.5×1.5 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 (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, added in 1999 and 2000, respectively. 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 (Fig. 2). The "one representative species" and "lack of functional group" treatments within the 1X treatment had only two functional groups manipulated, LN 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 strongest (Vermeij 1996). The establishment phase of invasion might have very different community dynamics and yield different 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% nonindigenous, and .009% unknown provenance. Average biomass of large invaders was greater than that of small invaders (Fig. 1).

Trait measurement

Our proxy measure for each functional group's aboveand belowground 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 1). The traits were measured in the field, in situ, as follows:

- Stem diameter: measured at ground level, using calipers. For grasses, the entire clump of leaves was measured, rather than a single culm.
- 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.
- 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 its survival (Table 1, Fig. 3). All the traits that most significantly predict 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



Fig. 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. Median functional group survivorships are: SN > LN > 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.

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 2).

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 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 pvalues (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 for all three invader sets. Each invader addition was tested separately, unless specified below. Neither site, location nor flooding condition of the sub-plots had significant effects on the functional-group-removed-by-functional-group-invaded interaction, so we combined all plots, regardless of whether they were streamside, non-streamside, flooded, or non-flooded 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). These analyses (PROC LOGISTIC of SAS) were performed with logistic regression with survivorship (dead or alive) as 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 (SN & ST) and large (LN & LT) and root classes: non-taprooted (SN & LN) 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 were removed.

The degree of persistence of functional groups three years after planting was 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 identified 46, 51, 38 and 32 species in the SN, ST, LN and LT groupings, respectively, using the nomenclature and species descriptions of Gleason and Cronquist (1991) supplemented by field observations and experiments (Appendix 1, experiment described under Methods, "Trait measurement"). There are 14, 19, 1, and 1 non-indigenous species in these groupings, respectively. Specimens were pressed and catalogued in the Univ. 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 first invader addition of 1X-planting).

There were no significant differences in survivorship of 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). Additionally, there were no differences in overall invader survivorship between the one representative species and lack of functional group treatments. Lastly, there were no differences in invader survivorship 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 (Table 2, 3). 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 2A), species in the SN 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



Fig. 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.

Table 2. 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 0.0016. 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 sample sizes of these tests are in parentheses, following the p-values.

(A) 2 Weeks

Functional group removed	Invading functional group				
	LN	LT	SN	ST	
LN	0.04 (6)	0.47 (20)	0.01 (39)	0.02 (69)	
LT SN	0.03 (15) 0.91 (14)	$0.18(10) \\ 0.11(18)$	0.04 (56) 0.35 (24)	0.02 (57) 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 group removed	Invading functional group				
	LN	LT	SN	ST	
LN LT SN ST	0.65 (8) 0.26 (20) 0.17 (16) 0.08 (7)	0.15 (11) 0.34 (10) 0.0002 (19) 0.18 (12)	0.09 (45) 0.19 (58) 0.39 (28) 0.25 (10)	0.68 (72) 0.008 (61) 0.009 (85) 0.22 (97)	

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

the second year of the treatment when SN was removed than when any other functional group was removed (p = 0.0002, n = 19, Table 2B). The second census of the 2X, second invader addition treatment had a significant overall functional-group-removed-by-functional-groupinvaded interaction. However, none of the tests of specific functional group invading and specific functional group removed were significant after adjustment for multiple tests (Table 3).

Following the second hypothesis, we expected to find that invaders in the functional group that was eliminated from a plot were more likely to succeed because that

Table 3. 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 0.0016. 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 sample sizes of these tests are in parentheses, following the p-values.

(A) 2 Weeks

Functional group removed	Invading functional group				
	LN	LT	SN	ST	
LN LT SN ST	() (9) 0.92 (24) 0.79 (13) () (15)	() 0.51 (1) () 0.69 (1)	0.65 (57) 0.93 (62) 0.81 (58) 0.83 (54)	0.65 (95) 0.94 (74) 0.81 (93) 0.82 (90)	

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

(B) 1 Year

Functional group removed	Invading functional group				
	LN	LT	SN	ST	
LN LT SN ST	0.4243 (9) 0.6269 (24) 0.8121 (12) 0.4358 (14)	(\dots) (\dots) (\dots) (\dots)	0.0129 (50) 0.1273 (61) 0.0992 (54) 0.0137 (53)	0.0856 (94) 0.0250 (73) 0.6171 (84) 0.8256 (90)	

Overall functional-group-removed-by-functional-group-invaded p-value = 0.0185, n = 626

particular soil horizon and aboveground space was less occupied 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 (Table 2-4). 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 growths of the 17 most abundant invaders in the two invader additions of the 2X treatment (1999 and 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 5).

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 introduced 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 (taprooted or non-taprooted) of the second invader addition of the 2X treatment, one year later, had decreased survivorship (p = 0.048, chi-

Table 5. 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 $\alpha = 0.0046$. 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 Aster divaricatus *Cerastium vulgatum Desmodium sp. *Duchesnia indica Aster sp. A Hamamalis virginiana Maianthemum	LN ST SN ST ST LN SN	$\begin{array}{c} 0.3120 \ (19) \\ 0.7418 \ (13) \\ (\ldots) \\ 0.2243 \ (12) \\ 0.6879 \ (11) \\ 0.1312 \ (22) \\ 0.1783 \ (12) \\ 0.5617 \ (11) \end{array}$	() 0.3515 (12) 0.2636 () () () () 0.7552 (25)
canadense Mitchella repens Oxalis stricta Parthenocissus quinquefolia Potantilla canadansis	SN ST ST	0.7304 (29) () 0.4758 (18)	() 0.1675 (7) ()
Potentila canadensis Potentilla simplex *Prunella vulgaris *Rosa multiflora *Veronica officinalis Viola septentrionalis	ST ST LN SN ST	$\begin{array}{c} (\dots) \\ (\dots) \\ 0.0994 \ (39) \\ (\dots) \\ (\dots) \\ 0.1220 \ (28) \end{array}$	$\begin{array}{c} 0.0139 (16) \\ 0.2929 (20) \\ 0.0976 (12) \\ 0.4795 (3) \\ 0.1031 (15) \\ 0.1895 (24) \end{array}$

square = 3.91). There were no significant size-removedby-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 a significant difference in survivorship of the first invader addition of the 2X treatment, across three years. Median survivorship, after

Table 4. 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 sample sizes of these tests are in parentheses, following the p-values.

(A) 2 Wee

Functional group removed	Invading functional group				
	LN	LT	SN	ST	
LN LT	0.24 (103) 0.43 (89)	() (3) () (11)	0.10 (11) 0.38 (17)	0.09 (39) 0.87 (42)	

Overall functional-group-removed-by-functional-group-invaded p-value of 0.18, n = 336 (B) 1 Year

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

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

being planted, of species in the different functional groups, was in the order: SN = 27.5 months > LN = 18.87 months > ST = 12.68 months > LT = 11.33 months after planting, respectively (Fig. 3). Because more than half of the SN 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 report assembly rules for both plants and animals, and many studies fail to detect them (Weiher and Keddy 1995, Gotelli and Graves 1996). It has been suggested that the presence of assembly rules is so well established that future research should turn to establishing what the assembly rules are and how they vary along gradients and among taxa (Weiher and Keddy 1995). However, Wilson (1995) argued that field experiments to test plant community structure have been burdened with several methodological 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 among 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 in this system.

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 we compared the p-values to Bonferroni-adjusted alpha values. It is possible that relay floristics (Egler 1954) are occurring here, where the environmental conditions at a site are made more or less amenable by the cooccurence of species or functional groups. Connell and Slayter (1977) described several observational and experimental studies that demonstrate relay floristics, in which 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 (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 see 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 have been 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 have allowed 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 (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-groupremoved-by-functional-group-invaded interactions. Invaders without taproots (SN, then LN) 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 environmentallydisturbed 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.

Aboveground 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 architecture, 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). This is an early attempt at identifying functional groups for forest communities. Other functional classifications such as different clonal growth forms (Gough et al. 2001), canopy stratification (Wilson 1989b), shade tolerance (Hubbell and Foster 1986), woody vs herbaceous plants (Reich et al. 2003), pollination mode (Faegri and van der Pijl 1979), or rooting depths might have yielded very different results. Additionally, our view of resource gathering may be quite different from that of an autotrophic organism (Simberloff and Dayan 1991).

This is the clearest 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 these functional groups in 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. However, other functional classifications of these plants in this system might have yielded different results.

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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, non-taprooted (SN)

SMALL SHRUB Epigaea repens Gaultheria procumbens Mitchella repens FERNS Botrychium virginianum Dennstaedtia punctilobula Osmunda cinnamomea Polystichum acrostichoides Thelypteris noveboracensis

FERN-ALLIES Diphasiastrum digitatum Equisetum arvense Lycopodium obscurum

Large biomass, non-taprooted (LN)SHRUBSCAlnus serrulataEAmelanchier arboreaGAsimina trilobaGCastanea pumilaECeanothus americanusECornus alternifloraECornus sericeaECorvlus americanaK

Large biomass, taproot (LT) TREES <u>Acer negundo</u> <u>Acer pensylvanicum</u> <u>Acer spicatum</u> <u>Acer rubrum</u> <u>Aesculus flava</u> <u>Betula lenta</u> Carpinus caroliniana Carya cordiforms

Small biomass, taproot (ST) HERBACEOUS DICOTS

*Achillea millefolium Anemone arborea Anemone lancifolia Anemone virginiana Aster divaricatus Boykinia acontifolia *Brassica rapa *Brassica nigra Chimaphila maculata *Chrysanthemum leucanthemum *Cichorium intybus Desmodium sp. *Duchesnia indica HERBACEOUS DICOTS Aristolochia macrophylla *Cerastium viscosum *Daucus carota *Glecoma hederacea Hexastylis sp. *Lysimachia nummularia *Thymus serpyllum *Veronica officinalis

HERBACEOUS MONOCOTS <u>Amianthium muscaetoxicum</u> <u>Arisaema triphyllum</u> <u>*Commelina communis</u>

Corylus cornuta Euonymus americanus Gaylussacia baccata Gaylussacia ursina <u>Hamamelis virginiana</u> <u>Hypericum densiflorum</u> <u>Ilex montana</u> <u>Ilex opaca</u> Ilex verticillata Kalmia latifolia Lindera benzoin

Carya glabra Carya ovata Crataegus crus-galli Crataegus coccinea *Eleagnus umbellata Fraxinus pennsylvanica Liriodendron tulipifera Magnolia tripetala

Erigeron annuus Fragaria virginiana Galax aphylla *Galinsoga quadriradiata Galium aparine Galium pilosum Galium triflorum *Geranium pusillum Goodyera pubescens *Hieracium caespitosum Hieracium paniculatum Lobelia cardinalis *Medicago lupulina *Mollugo verticillata Dioscorea villosa Luzula echinata Maianthemum canadense Medeola virginiana Sisyrinchium sp. Symplocarpus foetidus Streptops roseus Trillium sp.

GRAMINOIDS

Agrostis hyemalis Carex laxiflora Carex radiata *Dactylis glomerata

Pyrularia pubera Quercus prinoides Rhododendron calendulaceum Rhododendron maximum Rhus glabra Ribes sp. *Rosa multiflora Salix nigra Salix eriocephala

<u>Nyssa sylvatica</u> Oxydendrum arboreum Pinus rigida <u>Pinus strobus</u> Populus grandidentata Prunus pensylvanica Prunus serotina Quercus alba

Oxalis stricta Parnassia asarifolia Pedicularis canadensis *Plantago major Plantago rugelli Podophyllum peltatum Potentilla canadensis Potentilla simplex *Potentilla recta *Prunella vulgaris *Rumex acetosella Salvia lyrata Scutellaria serrata Sedum ternatum Danthonia compressa *Festuca eliator *Holcus lanatus Panicum boscii *Phleum pratense *Poa compressa *Poa pratensis Digitaria filiformis

VINES <u>Smilax glauca</u> Smilax hispida Smilax rotundifolia

Salix sericea Sassafras albidum Spiraea alba Spiraea tomentosa Vaccinium arboreum Vaccinium erythrocarpum Vaccinium stamineum Vaccinium pallidum Viburnum sp.

Quercus coccinea Quercus muenlenbergii Quercus prinus Quercus rubra Quercus velutina Robinia pseudoacacia Tsuga canadensis Ulmus americana

Senecio aureus *Taraxacum officinale Thalictrum clavatum *Urtica dioica *Verbascum thapsus Viola rotundifolia Viola sororia

SHRUBS/VINES

Parthenocissus quinquefolia *Rubus idaeus Rubus spp.