

Effects of plant invasions on the species richness of abandoned agricultural land

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While exotic plant invasions are thought to lead to declines in native species, the long-term impacts of such invasions on community structure are poorly known. Furthermore, it is unknown how exotic plant invasions compare to invasions by native species. We present data from 40 yr of continuous vegetation sampling of 10 fields released from agriculture to examine the effects of invasions on species richness. The effects of both exotic and native species invasions on species richness were largely driven by variations among fields with most species not significantly affecting species richness. However, invasion and dominance by the exotics *Agropyron repens*, *Lonicera japonica*, *Rosa multiflora*, *Trifolium pratense* and the native *Solidago canadensis* were associated with declines in richness. Invasions by exotic and native species during old field succession have similar effects on species richness with dominance by species of either group being associated with loss of species richness. Exotic species invasions tended to have stronger effects on richness than native invasions. No evidence was found of residual effects of invasions because the impacts of the invasion disappeared with the decline of the invading population. When pooled across species, heavy invasion by exotic species resulted in greater loss of species richness than invasion by native species. Studies of invasion that utilize multiple sites must account for variability among sites. In our study, had we not included field as a factor we would have incorrectly concluded that invasion consistently resulted in changes in species richness.

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The widespread invasion of exotic plant species is a major concern from both the perspectives of conservation and ecological research. Exotic invasions are often associated with 1) declines in local plant diversity (Richardson et al. 1989, Woods 1993, Wyckoff and Webb 1996, McCarthy 1997, Hutchinson and Vankat 1997, Christian and Wilson 1999), 2) declines in forest regeneration (Thomas 1980, Woods 1993, Wyckoff and Webb 1996, Hutchinson and Vankat 1997) and 3) reductions in the productivity of agricultural land (Pimentel et al. 2000). In addition, exotic invasions often accrue the financial costs of biological or chemical control (Pimentel et al. 2000). Ecologists struggle to understand the factors that make species invasive

(Baker 1965, Bazzaz 1996, Rejmánek 1999), conditions that make communities subject to invasion (Peart and Foin 1985, Fox and Fox 1986, Kotanen et al. 1998, Stapanian et al. 1998, Knops et al. 1999) and the subsequent impact of invasions on community structure (Richardson et al. 1989, Hutchinson and Vankat 1997, McCarthy 1997, Woods 1997, Parker et al. 1999).

Three factors limit our understanding of the impacts of exotic species invasion into plant communities: 1) a lack of information comparing native and exotic species invasions, 2) the confounding effects of disturbance history, and 3) the limitations of correlational approaches. Most ecological studies of invasive plant species inadequately address these problems, potentially

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leading to the development of inappropriate conclusions and management practices.

An unresolved question facing ecologists is whether exotic and native plant species differ fundamentally in their function within plant communities. In experimental comparisons of native and exotic plants, exotic species are generally found to be competitively superior (D'Antonio and Mahall 1991, Dillenburgh et al. 1993, Fogarty and Facelli 1999, Hamilton et al. 1999, Marler et al. 1999), have faster and more plastic growth (Schierenbeck et al. 1994, Bazzaz 1996, Schweitzer and Larson 1999, Milberg et al. 1999) and higher reproductive capacities (Rejmánek 1989, Bazzaz 1996). Because these comparative studies focus on problematic exotic species, they may provide biased information on the relative performance of native and exotic plant species in general. Systematic comparisons of native and exotic species at a community-wide scope are needed to adequately compare these two groups.

The frequency and intensity of disturbance is one of the principal factors considered to regulate community invasibility (Fox and Fox 1986, Hobbs 1989, Kotanen et al. 1998). However, an association between disturbance and invasion makes it difficult to separate the effects of an exotic species from the effects of the disturbance that originally led to the invasion (Woods 1997). Because exotic plants commonly dominate abandoned agricultural land (Bard 1952, Pickett 1982, Rejmánek 1989, Bazzaz 1996, Bastl et al. 1997), successional studies, with continuous species invasions and losses, provide a unique opportunity to test the role of exotic species in determining community structure and dynamics under a known disturbance history.

The limited temporal duration of most studies constrains our understanding of the function of exotic species in plant communities (Lodge 1993, Fike and Niering 1999, Smith and Knapp 1999, Parker et al. 1999). Inferences about long-term impacts and population persistence based on short-term investigations may not accurately predict the influence of exotic invaders on plant communities. Ecologists have attempted to address the limitations of short-term studies through a chronosequence approach, where areas of differing levels of invasion are assumed to represent areas differing in time since invasion. Greater abundance of an invader indicates longer times since initial invasion. This approach often uses correlations to infer ecological impacts of the exotic species invasion (Thomas 1980, Richardson et al. 1989, Woods 1993, Hutchinson and Vankat 1997). Because of the long time spans involved in most successions, space-for-time substitutions are commonly used (Glenn-Lewin and van der Maarel 1992). Critical assumptions of the chronosequence approach are that 1) all sites will be, or have been subjected to similar processes, and that 2) the patterns among sites reflect temporal change (Pickett 1989, Glenn-Lewin and van der Maarel 1992). These assump-

tions may not be met and chronosequences may suggest quite different patterns from those revealed from long-term studies (Jackson et al. 1988, Pickett 1989). Patterns revealed in chronosequence studies may reflect associations caused by disturbance history or other site characteristics unrelated to invasion (Woods 1997). For this reason, long-term studies of permanent plots are far superior to chronosequence studies in verifying the potential impacts of exotic species on plant community structure.

To address the three limitations outlined above, we utilized 40 yr of permanent plot data, determining the impacts of both native and exotic invasions on the structure of successional plant communities. Plot data were derived from 10 abandoned agricultural fields of known disturbance histories in the piedmont region of New Jersey, USA. All species abundant enough for analysis were included to provide an unbiased comparison of both the native and exotic assemblages. This study addresses the following questions. 1) How does invasion by native or exotic species affect richness in successional communities? 2) Are species effects on diversity consistent among fields? 3) Do native and exotic species invasions have different effects on species richness? 4) Do residual effects of species invasions persist after the invading population declines?

Methods

Data collection

Since 1958, the vegetation of abandoned agricultural fields at the Hutcheson Memorial Forest Center (HMFC) has been monitored with the use of permanent plots (Small et al. 1971, Pickett 1982). This study is known as the Buell-Small Succession Study (BSS), named for the project initiators (www.ecostudies.org/bss). Within each of 10 fields, 48 plots are arranged in a regular pattern that varies somewhat with the shape of the field. Most of these fields abut the old-growth forest of HMFC. Fields were abandoned as pairs in alternate years from 1958 until 1966. Since release, data collection occurred every year until 1979, when sampling was switched to alternate years. At each sampling, the percent cover of all species present in each permanently marked 0.5×2.0 m plot is recorded. These data represent the longest continuous data set on old field successional change known.

Statistical analyses

Data were summarized at two spatial scales in this study, the plot and field scale. To determine the temporal pattern of each species invasion, data were pooled across all fields. All subsequent analyses were con-

ducted at the plot scale within invaded fields. These analyses included field as a categorical variation to account for variation among fields. To determine the effects of plant invasion on species richness, the change in total species richness of plots was related to change in cover of the invading species.

For each species, the temporal pattern of plant cover summed across all fields was examined and a sampling period was chosen that approximated the initiation of the species invasion (t_{initial}) and extended to the peak cover of the invading species (t_{peak}). The value of t_{initial} was set at the time when cover of the invading species was $\approx 5\%$ or less, or at year 1 for species invading immediately after abandonment. The value of t_{peak} was set at the year of maximum cover for the invading species. When t_{initial} and t_{peak} were > 10 yr apart, t_{peak} was set as $t_{\text{initial}} + 10$ to limit changes in community structure that were external to the invasion. Only fields in which cover of the invading species at t_{peak} averaged $\geq 1\%$ per plot were included in the analyses. Within invaded fields, only those plots that were invaded at t_{peak} were included. This removes from comparison local areas that may not be suitable for invasion by a species or areas that have not received sufficient seed to result in an invasion (Treberg and Husband 1999), thereby focusing the analyses on the effects of invasion.

The increase in cover (C) of the invading species ($C_{\text{peak}} - C_{\text{initial}}$) and the change in species richness ($S_{\text{peak}} - S_{\text{initial}}$) was calculated for each plot. By calculating change in richness and cover over time, we account for successional changes in vegetation over time. Plots were separated into three invasion classes based on change in cover of the invading species: light (0.5–33% cover), moderate (33.5–66% cover) and heavy (66.5–100% cover). Plots that had a decrease in cover of the invading species from t_{initial} to t_{peak} were dropped from analysis. All species that had at least 5 plots representing each invasion class were analyzed for their impacts on species richness. The influence of invasion class on change in species richness was evaluated with ANOVA (Anon. 1989).

To compare the effects of native and exotic species invasions on community diversity, the average change in species richness from t_{initial} to t_{peak} was calculated in each invasion class for all plots within a field. This was done separately for each species within each field to account for differences among fields. These values were then analyzed with ANOVA with species nested within nativity (Anon. 1989).

Species that exhibited a pronounced decline in abundance within 10 yr of t_{peak} were further analyzed for the presence of residual effects of the invasion on species richness. A sampling time was selected that had a substantial decrease in cover of the invading species (t_{after}) but that was temporally as close to t_{peak} as possible to minimize external influences on richness. The value of t_{after} had at least a 50% decline in cover of

the invading species. The same invasion classes were used as in the previous analysis, substituting changes in species richness from t_{initial} to t_{after} as the response variable. Residual effects of the invasion on species richness were evaluated with ANOVA (Anon. 1989).

Results

The fields contained 117 exotic and 216 native species over the entire 40-yr span of data collection. A total of 12 exotic and 14 native species were sufficiently abundant to meet all criteria for analysis of their influences on species richness (Table 1). These species included a wide range of life forms from annuals to woody vines, and ranged temporally from immediately post-abandonment to 40 yr after release from agriculture. Invading species cover increased on average at least one order of magnitude from t_{initial} to t_{peak} . Fifteen species (9 exotic and 6 native) had sufficient population decreases to allow for analysis of residual effects of the invasion on species richness.

Invasions by most species did not reduce the species richness of plots. In this study, the vast majority (90% exotic, 94% native) of species did not attain sufficient abundance within the community to have testable influences on diversity. Of those that became abundant, only 5 species (1.5% of the total species pool) were associated with significant declines in species richness once site factors were accounted for. In this survey, 97% of exotic plant invasions did not result in a measurable effect on species richness in these communities.

Exotic species generally elicited a decrease in $S_{\text{peak}} - S_{\text{initial}}$ with increasing severity of invasion (Fig. 1). Most of these invasions (8 of 12) resulted in a net loss of species over the course of the invasion, with the most species lost from the high invasion class. ANOVA results indicate that only four of these species had significant effects of invasion class when differences among fields were accounted for (Table 2). Field was generally the most important factor in the analysis. When variation among fields in invasion and species richness was not accounted for, the invasion class often became significant. The relationship between change in species richness and plant invasion was generally consistent among fields. Two species, *Barbarea vulgaris* and *Chrysanthemum leucanthemum*, were exceptions, with a significant invasion \times field interaction. Both of these species had invasions associated with decreases in species richness in some fields and increases in others.

Native species had more varied responses of species richness to their invasion than did exotic species (Fig. 2). Most species (8 of 14) show some effects of invasion on change in species richness, with the high invasion class having the most species lost or the fewest species

gained. These effects became non-significant with the inclusion of field in the ANOVA (Table 2). Only one species, *Solidago canadensis*, had a significant effect of invasion class on richness change, with plots containing moderate invasions losing 4 species on average while the other two classes gained a species. Differences among fields accounted for the majority of the variation, and again accounts for most of the invasion effects seen in Fig. 2. Two species, *Aster pilosus* and *Eupatorium rugosum*, had a significant invasion \times field interaction. For both species, half of the fields had invasions associated with increases in species richness and the other half had invasions associated with decreases in species richness.

Native and exotic species have similar effects on change in species richness over successional time (Table 3, Fig. 3), with species richness decreasing with increasing invasion class. However, invasion by exotic species had an overall larger effect on change in species richness than invasion by native species (a significant nativity effect). The invasion class of both native and exotic species had similar effects on species richness as seen by the non-significant interaction term.

There is no evidence that the invasion of plots by either native or exotic species has any long-term effects on species richness (Table 4, Fig. 4). As in the previous analyses, field identity accounted for the majority of the variation within the data. Once the effects of field were accounted for in the ANOVA, invasion class became non-significant for all species. *Chrysanthemum leucanthemum* had a significant invasion \times field interaction, with one field showing a positive association between invasion and richness and another field a negative association. The other four fields did not have significant relationships.

Discussion

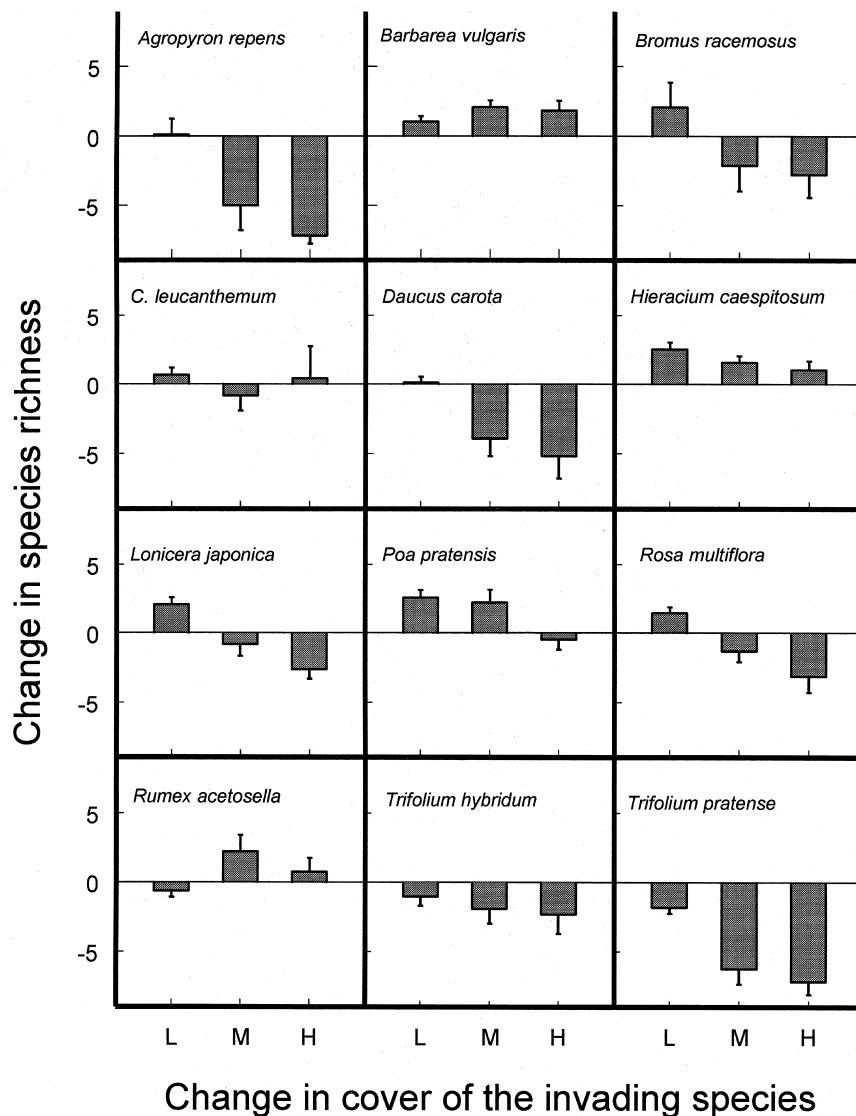
Invasion effects on richness

Invasions by most species in this post-agricultural succession did not have a significant influence on species richness (Williamson and Fitter 1996). However, a few species had very strong effects on community richness. This result is in contrast to most field studies, which find significant negative associations between exotic

Table 1. Summary information on the populations of exotic and native species used in the analysis of invasion effects on species richness. Cover values based on invaded fields and plots only (see text for invasion criteria). t_x is years since release from agriculture. Life form abbreviations: A = annual, AG = annual grass, B = biennial or short-lived perennial, P = perennial, PG = perennial grass, S = shrub, V = woody vine. Nomenclature, life form and nativity status follows Gleason and Cronquist (1991).

	Life form	Number of fields	Initial conditions		Peak of invasion		After invasion	
			t_{initial}	Cover (%)	t_{peak}	Cover (%)	t_{after}	Cover (%)
Exotic species								
<i>Agropyron repens</i>	PG	3	1	3.5	5	39.0	10	0.8
<i>Barbarea vulgaris</i>	B	8	1	4.4	2	27.7	4	1.4
<i>Bromus racemosus</i>	AG	1	4	1.0	10	52.8	–	–
<i>Chrysanthemum leucanthemum</i>	P	6	2	0.9	6	24.0	10	5.1
<i>Daucus carota</i>	B	8	1	0.5	4	16.7	10	3.4
<i>Hieracium caespitosum</i>	P	10	4	5.4	10	41.2	15	15.4
<i>Lonicera japonica</i>	V	10	5	0.2	15	41.8	–	–
<i>Poa pratensis</i>	PG	8	4	2.0	10	44.2	15	22.1
<i>Rosa multiflora</i>	S	10	10	2.5	20	32.7	–	–
<i>Rumex acetosella</i>	P	7	1	0.9	3	20.0	10	0.9
<i>Trifolium hybridum</i>	P	2	1	1.1	4	25.3	10	0.6
<i>Trifolium pratense</i>	B	4	1	1.2	4	29.2	10	1.4
Native species								
<i>Ambrosia artemisiifolia</i>	A	5	1	13.5	2	48.9	5	0.5
<i>Aster pilosus</i>	B	8	2	0.1	10	23.8	15	12.1
<i>Calystegia sepium</i>	P	8	1	0.9	6	14.5	–	–
<i>Erigeron annuus</i>	A	8	1	2.1	2	22.1	5	5.9
<i>Eupatorium rugosum</i>	P	2	30	2.6	40	27.6	–	–
<i>Euthamia graminifolia</i>	P	9	4	2.0	10	24.3	–	–
<i>Fragaria virginiana</i>	P	9	4	0.9	10	32.9	20	8.2
<i>Parthenocissus quinquefolia</i>	V	8	10	1.1	20	19.4	–	–
<i>Plantago rugelii</i>	P	6	1	12.8	3	33.6	5	8.3
<i>Potentilla simplex</i>	P	3	3	1.1	10	40.6	15	2.3
<i>Solidago canadensis</i>	P	9	10	0.7	20	16.1	–	–
<i>Solidago juncea</i>	P	9	5	0.4	15	18.5	–	–
<i>Solidago rugosa</i>	P	6	10	1.7	20	30.6	–	–
<i>Toxicodendron radicans</i>	V	10	10	0.9	20	21.5	–	–

Fig. 1. Change in species richness in association with invasion by exotic plant species. Data for invaded plots only. Sampling times for each species listed in Table 1. Change in cover of invading species classes are: L = light, M = moderate, H = heavy.



species and community richness (Richardson et al. 1989, Woods 1993, Wyckoff and Webb 1996, McCarthy 1997, Hutchinson and Vankat 1997, Christian and Wilson 1999, Meiners and Pickett 1999, but see Wisser et al. 1998, Treberg and Husband 1999). This difference is probably caused by the focus of field studies on species that are thought a priori to have strong impacts on plant communities. Community-wide studies should show much lower incidence of impacts (e.g. Myster and Pickett 1992, this study).

The effects of the invasion generally increase with increasing cover of the invading species. This pattern is seen in both the native and exotic species studied. This suggests that ecological impacts of invasions are more dependent on the dominance in cover of a patch by a species rather than the presence of the species (Richard-

son et al. 1989, Woods 1993, Morgan 1998). One difficulty in comparing our result to those in the ecological literature is the variation in methodologies used. Studies that use cover or dominance of exotic species to assess invasion impacts tend to find negative associations between invasion and diversity (Richardson et al. 1989, Woods 1993, Hutchinson and Vankat 1997, Christian and Wilson 1999, but see Treberg and Husband 1999). In contrast, studies that relate species richness of exotics to species richness of native species tend to find positive associations (Stohlgren et al. 1998, Lonsdale 1999, Smith and Knapp 1999). Analyses based on cover of the invader seem more appropriate for assessing the impacts of invasions because they incorporate estimates of the abundance of the invader rather than presence alone.

The negative association between exotic plants and community diversity has been used to suggest that invading exotic species do not merely fill vacant niches in natural communities (Tilman 1997), or replace native species one-for-one, but that they displace species disproportionately from the community, lowering diversity. This mechanism is often cited in field studies of invasive exotic plants, either as correlational or as anecdotal information, but has not been experimentally tested. Problematic exotic species are generally found to be competitively superior to native species in two-species competition experiments (D'Antonio and Mahall 1991, Dillenburgh et al. 1993, Marler et al. 1999). However, it is not known whether exotic species are on average competitively superior to native plant species, which would be necessary to result in lowered diversity within a community. The competitive displacement of native plant species is often used as justification for the eradication of individual exotic species, although the perceived relationship with diversity has not been demonstrated (Anderson 1995, Hager and McCoy 1998, Treberg and Husband 1999). Most exotic species have only trivial impacts on community structure, becoming minor components of the plant community, increasing local species diversity (Williamson and Fitter 1996, Parker et al. 1999, this study, Meiners et al. unpubl.).

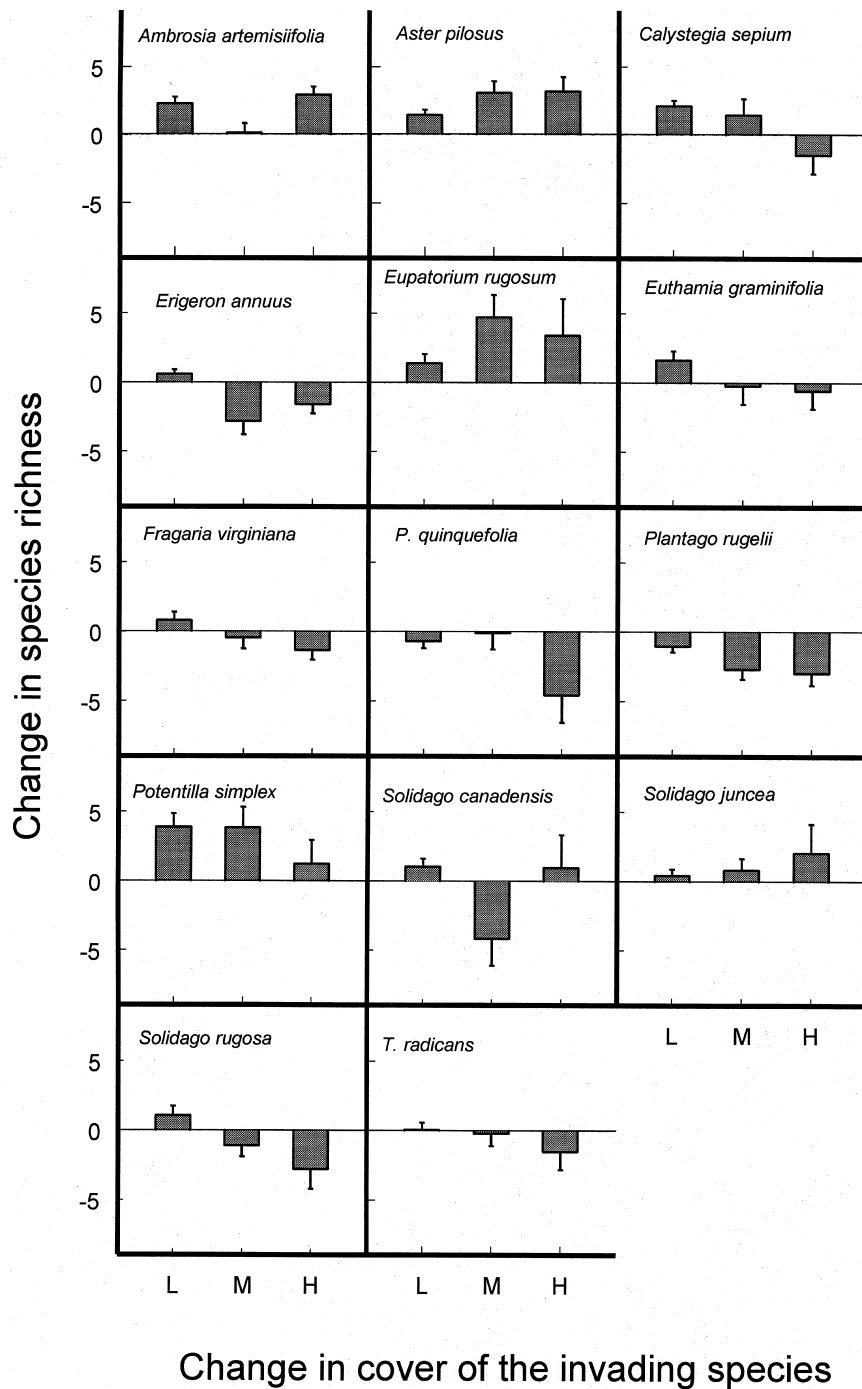
Species characteristics

The species with significant effects on richness ranged across most of the life histories tested in this study. Four of the 5 species are long-lived perennial herbaceous or woody species that have become problematic weeds of agricultural or natural areas. The exception to this is *Trifolium pratense*, a biennial to short-lived perennial species that is widely planted because of its nitrogen fixation capabilities. *Agropyron repens* is a weed of agricultural land throughout North America and Europe that spreads rapidly in pastures (Palmer and Sagar 1963). *Lonicera japonica* and *Rosa multiflora* are widespread woody species of Asian origin that dominate disturbed land in the eastern United States (Thomas 1980, Amrine and Stasny 1993). *Solidago canadensis*, a native North American species, has become a problematic weed in European agricultural areas (Weber 1997). All of these species are widespread, have high reproductive capacities, are capable of forming monospecific patches, and are associated with agricultural practices. While these characteristics are similar to those of many successful exotic invasions (Baker 1965, Rejmánek 1989, Bazzaz 1996), there is no characteristic that would differentiate these species a priori from the larger pool tested. The only generalization about life history characteristics that can be made is that annuals do not appear problematic in this system.

Table 2. Summary of 2-way ANOVAs on the effects of exotic and native species invasion on change in species richness ($S_{\text{peak}} - S_{\text{initial}}$) in old fields. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	Invasion (I)	Field (F)	I × F	Model R ²
Exotic species				
<i>Agropyron repens</i>	3.43*	8.83***	0.01	0.60
<i>Barbarea vulgaris</i>	1.07	7.71***	2.15*	0.40
<i>Bromus racemosus</i>	0.11	—	—	0.13
<i>Chrysanthemum leucanthemum</i>	0.13	17.64***	3.50**	0.56
<i>Daucus carota</i>	0.09	12.27***	0.91	0.50
<i>Hieracium caespitosum</i>	2.67	15.20***	0.72	0.43
<i>Lonicera japonica</i>	10.25***	6.86***	1.23	0.46
<i>Poa pratensis</i>	0.90	5.40***	0.94	0.32
<i>Rosa multiflora</i>	8.73***	1.96*	1.42	0.29
<i>Rumex acetosella</i>	1.23	9.05***	0.77	0.46
<i>Trifolium pratense</i>	10.89***	7.70***	1.30	0.37
<i>Trifolium hybridum</i>	0.11	1.08	—	0.03
Native species				
<i>Ambrosia artemisiifolia</i>	1.89	9.32***	1.71	0.48
<i>Aster pilosus</i>	2.77	17.88***	2.10*	0.50
<i>Calystegia sepium</i>	0.14	20.10***	0.19	0.53
<i>Erigeron annuus</i>	0.82	9.08***	1.72	0.30
<i>Eupatorium rugosum</i>	2.10	8.14**	3.52*	0.21
<i>Euthamia graminifolia</i>	0.49	6.35***	1.08	0.39
<i>Fragaria virginiana</i>	1.68	5.08***	1.00	0.41
<i>Parthenocissus quiquefolia</i>	1.58	3.91***	1.05	0.25
<i>Plantago rugelii</i>	0.08	27.82***	0.49	0.48
<i>Potentilla simplex</i>	0.58	0.58	1.36	0.19
<i>Solidago canadensis</i>	3.29*	1.96	0.54	0.20
<i>Solidago juncea</i>	0.23	6.86***	0.85	0.40
<i>Solidago rugosa</i>	1.30	1.31	0.42	0.19
<i>Toxicodendron radicans</i>	0.39	0.81	1.49	0.23

Fig. 2. Change in species richness in association with invasion by native plant species. Data for invaded plots only. Sampling times for each species listed in Table 1. Change in cover of invading species classes are: L = light, M = moderate, H = heavy.



Differences among fields

While the fields of the Buell-Small Succession Study are adjacent to each other, the differences in pre-abandonment history have resulted in the development of dramatically different vegetation (Myster and Pickett 1990). This variation in vegetation and disturbance history resulted in the dominance of site effects in all

analyses. Analyses across fields often resulted in significant negative associations between species richness and invasion, even though there was no pattern evident within each field. The common practice of evaluating invasion effects by comparing sites differing in level of invasion may also lead to such incorrect conclusions. This problem is analogous to the drawbacks found in

Table 3. Nested ANOVA summarizing the influence of nativity and invasion class on the impacts of invasion on plot species richness.

	DF	MS	F	p
Field	9	114.23	9.30	0.0001
Species (nativity)	24	31.90	2.60	0.0001
Invasion class	2	131.74	10.72	0.0001
Nativity	1	93.34	7.60	0.0061
Invasion class × nativity	2	19.49	1.59	0.2062
Error	378			

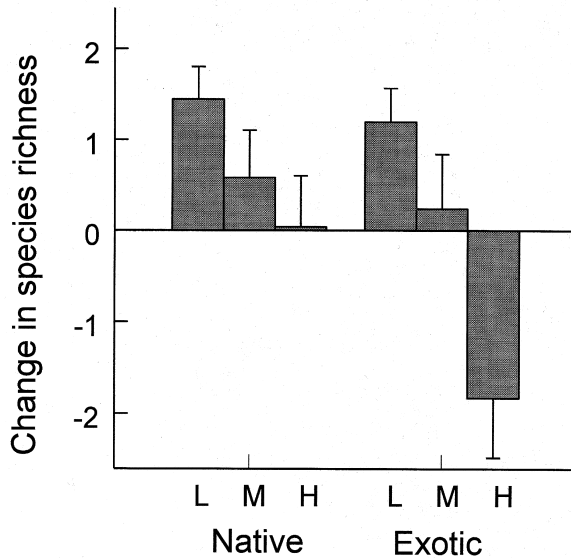


Fig. 3. Summary of change in species richness in association with plant invasion by native and exotic species. Invasion classes are: L = light, M = moderate, H = heavy.

using space for time substitutions in studying successional processes through time (Pickett 1989).

A few species showed inconsistency of effects among sites, as shown by a significant field × invasion interac-

tion. While the effects of invasion class were non-significant, these results illustrate the importance of among-site variation in determining the influence of an invasion on community structure. Not all sites and species invasions will result in similar community-wide effects. The identity of the invading species and the composition of the existing community are both important in determining the success and impact of the invasion (Lodge 1993).

Native vs exotic invasions

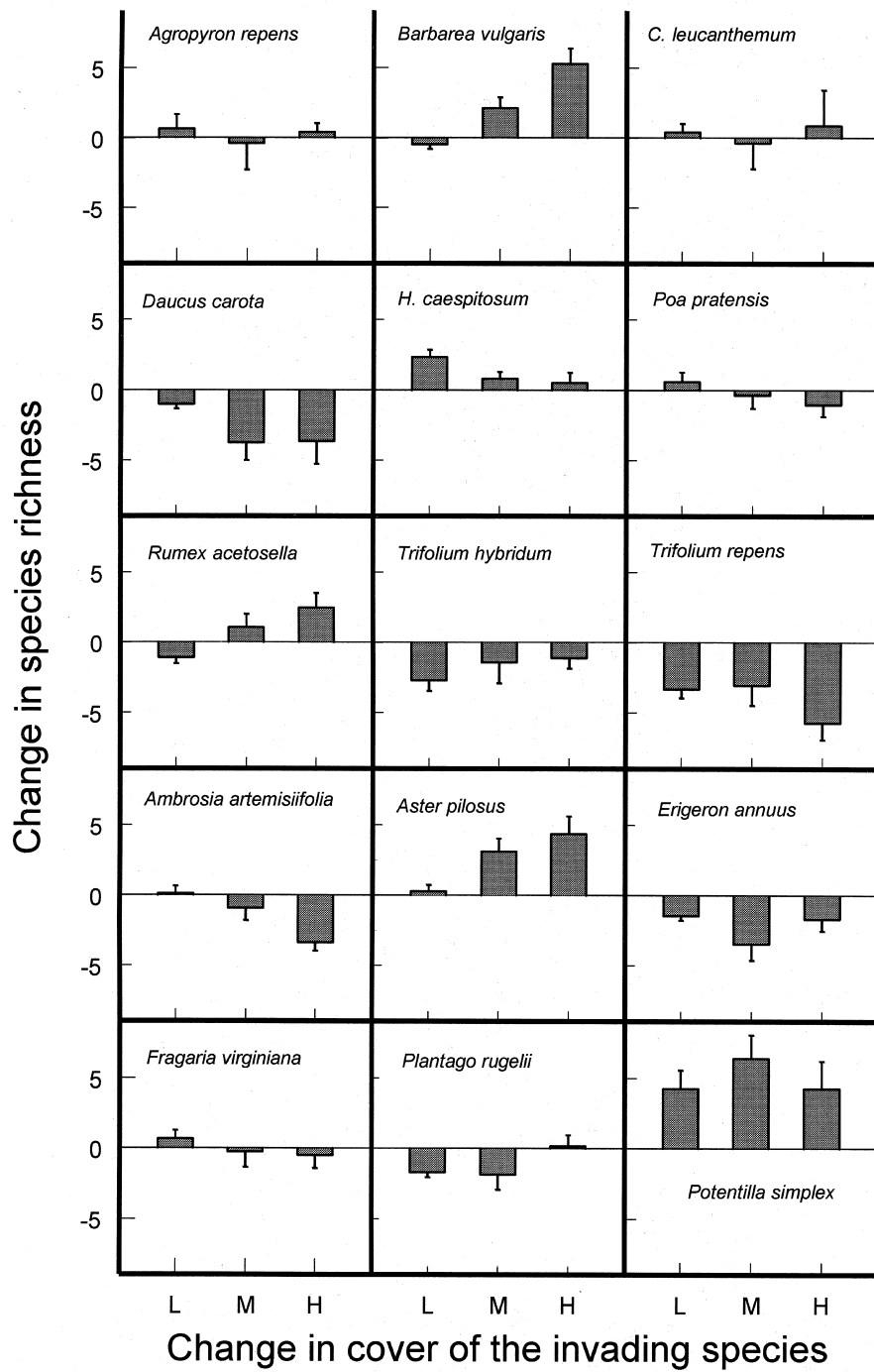
Native and exotic species appear to function in similar ways within plant communities, exhibiting similar influences on species richness in this system. However, the magnitude of the depression of species richness was greater for exotic than for native invasions. The greater impact of exotics within this study may be indicative of an overall competitive superiority of dominant exotics in comparison to dominant native species as is suggested by competition experiments (D'Antonio and Mahall 1991, Dillenburg et al. 1993, Marler et al. 1999). The evolutionary history of the exotic species in eastern North America may explain these differences in competitive ability. Many of these species are adapted to persistence in highly disturbed Eurasian agricultural systems and generally have much stronger impacts on agricultural productivity than native agricultural weeds (Pimentel et al. 2000). Native species, in contrast, largely evolved in persistent openings within forest communities (Marks 1983).

While there may be a negative relationship between exotic species invasion and diversity at small scales (Stohlgren et al. 1998, 1999, this study), at larger scales native and exotic species are often positively associated (Stohlgren et al. 1998, 1999, Wisser et al. 1998, Lonsdale 1999, Levine and D'Antonio 1999, Smith and Knapp

Table 4. Summary of 2-way ANOVAs on the residual effects of exotic and native species invasion on change in species richness after decline of the population ($S_{\text{after}} - S_{\text{initial}}$). * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	Invasion (I)	Field (F)	I × F	Model R ²
Exotic species				
<i>Agropyron repens</i>	0.44	7.96***	0.47	0.23
<i>Barbarea vulgaris</i>	1.31	15.85***	0.42	0.48
<i>Chrysanthemum leucanthemum</i>	0.44	22.04***	2.67*	0.60
<i>Daucus carota</i>	0.25	9.15***	1.40	0.33
<i>Hieracium caespitosum</i>	1.14	15.12***	0.98	0.43
<i>Poa pratensis</i>	0.31	4.47***	1.28	0.27
<i>Rumex acetosella</i>	0.14	5.82***	0.05	0.32
<i>Trifolium hybridum</i>	0.38	0.80	—	0.02
<i>Trifolium pratense</i>	0.69	4.98**	1.14	0.14
Native species				
<i>Ambrosia artemisiifolia</i>	0.50	19.02***	0.90	0.61
<i>Aster pilosus</i>	0.29	16.93***	1.54	0.55
<i>Erigeron annuus</i>	2.75	12.24***	0.73	0.28
<i>Fragaria virginiana</i>	0.14	4.49***	1.24	0.37
<i>Plantago rugelii</i>	0.09	7.62***	0.63	0.21
<i>Potentilla simplex</i>	1.00	11.01***	0.41	0.43

Fig. 4. Change in species richness following the decline of exotic and native species invasions. Data for invaded plots only. Sampling times for each species listed in Table 1. Change in cover of invading species classes are: L = light, M = moderate, H = heavy.



1999). This may indicate that the diversity of exotic and native species is controlled by similar mechanisms, such as habitat heterogeneity (Lonsdale 1999), disturbance (Stohlgren et al. 1998), or soil characteristics (Harrison 1999). Because ecological interactions occur at small spatial scales within plant communities, the small-scale

negative association between diversity and exotic invasion is probably indicative of competitive interactions. In contrast, diversity at regional scales is less determined by species interactions and more the result of large changes in abiotic factors (Rosenzweig and Abramsky 1993, Tilman and Pacala 1993).

Overall, native and exotic species may not be as dissimilar as comparisons to problematic exotics would indicate (Levine and D'Antonio 1999). Over the broad range of species' life histories and successional ages investigated in this study, our general conclusion is that both native and exotic species show the same low incidence of effects on species richness.

Residual effects of invasions

We found no evidence for invasion effects that persist beyond the decline of the species during succession. Species that change soil nutrient status or other soil chemical properties would be expected to have long-lasting effects on the community (Vitousek et al. 1987, Walker and Smith 1997). The only species in this analysis capable of nitrogen fixation were the legumes *Trifolium hybridum* and *T. pratense*. While the strong declines in species richness associated with *T. pratense* during the invasion may result from the alteration of local nutrient levels, these effects do not persist beyond the time span of the population in the community. Allelopathy has been implicated for several herbaceous species in old fields, including *Solidago canadensis* (Jackson and Willemssen 1976, Fisher et al. 1978, Boser and Reader 1995). If allelopathic chemicals are present, they appear to have short residence times in the soil or to have only weak effects on species richness. Clearly, exotic species with much stronger effects on soil chemistry than those studied, may exhibit prolonged residual effects. Our analysis of post-invasion effects is conservative, as only two of the species that had significant effects on richness (*Agropyron repens* and *Trifolium repens*) could be analyzed for residual effects.

Exotic species removals generally result in an increase in the abundance and diversity of native species (McCarthy 1997, Pickart et al. 1998). Such removal treatments may duplicate the consequences of a natural population decline or may prevent the development of an alternative plant community (Fike and Niering 1999). Our results suggest that, in this system, invasive control by species removal would be successful in alleviating any effects of the invasion. Alternatively, in cases where species removal is inappropriate or impractical, management practices that lead to the successional replacement of an invader should have similar beneficial effects on diversity. This type of management may be more sustainable and cost-efficient, and should not incur any long-term effects on community structure.

Conclusions

While plant invasion certainly alters plant community composition, the direct effects on patterns of diversity are largely unquantified. From our survey, most inva-

sions will have little to no effect on the diversity of plant communities. Although invasions by exotic species have stronger effects on community structure, native and exotic invasions appear to have similar overall effects. Long-term data are necessary to adequately evaluate the impacts of invasions without the problems associated with analyses across sites.

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