Exotic plant invasions over 40 years of old field successions: community patterns and associations

Scott J. Meiners, Steward T. A. Pickett and Mary L. Cadenasso

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While exotic plant species often come to dominate disturbed communities, long-term patterns of invasion are poorly known. Here we present data from 40 yr of continuous vegetation sampling, documenting the temporal distribution of exotic plant species in old field succession. The relative cover of exotic species decreased with time since abandonment, with significant declines occurring ≥ 20 yr post-abandonment. The number of exotic species per plot also declined with time since abandonment while field-scale richness of exotics did not change. This suggests displacement occurring at small spatial scales. Life history types changed from short-lived herbaceous species to long-lived woody species for both native and exotic plant species. However, shrubs and lianas dominated woody cover of exotic plants while trees dominated native woody cover. The species richness of exotic and native species was positively correlated at most times. In abandoned hay fields, however, the proportion of exotic plant cover per plot was inversely related to total species richness. This relationship suggests that it is not the presence, but the abundance of exotic species that may cause a reduction in community diversity. While the development of closed-canopy forest appears to limit most introduced plant species, several shade-adapted exotic species are increasing within the fields. These invasions may cause a reversal of the patterns seen in the first 40 yr of succession and may result in further impacts on community structure.

S. J. Meiners (cfsjm@eiu.edu), Dept of Biological Sciences, Eastern Illinois Univ., 600 Lincoln Ave., Charleston, IL 61920-3099, USA. – S. T. A. Pickett and M. L. Cadenasso, Inst. of Ecosystem Studies, Box AB, Milbrook, NY 12545-0129, USA.

The invasion of terrestrial communities by exotic plant species is a major concern for both ecologists and natural resource managers. With the increased speed of planned and unplanned movement of species throughout the world and greater rates of disturbance, exotic plants are becoming more important in regional floras (Mooney et al. 1986, Robinson et al. 1994). Furthermore, exotic species already cover vast areas of many community types and sometimes dominate local plant communities. These invasions affect both natural and agricultural systems and cause financial as well as biological problems in areas of heavy invasion (Pimentel et al. 2000). While there has been a heightened awareness of the problem of exotic invasive plant species, there

are few studies that examine plant invasions over long periods (Lodge 1993, Fike and Niering 1999).

Studies of exotic plant species have largely used an autecological perspective (Woods 1997). Many of these studies focus on the pattern of invasion of an exotic species in the landscape, examining factors that affect species movement, such as corridors (Benninger-Truax et al. 1992, Forman 1995), edges (Brothers and Spingarn 1992, Luken and Goessling 1995), and habitat connectivity (Forman 1995, Hutchinson and Vankat 1998). Once propagules arrive in a site, factors such as the level of disturbance (Fox and Fox 1986, Kotanen et al. 1998), resource availability (Fox and Fox 1986, Luken and Goessling 1995, Hutchinson and Vankat

1997), and species interactions (Fox and Fox 1986, Pyke 1990, Tilman 1997) may determine the success of an invasion.

Once in a community, exotics may suppress native species or prevent tree regeneration (Thomas 1980, Woods 1993, Wyckoff and Webb 1996, Hutchinson and Vankat 1997, Meiners et al. 2001). Vegetation sampling studies indicate that exotic plant species are often associated with a decrease in the number of species in natural communities (Richardson et al. 1989, Woods 1993, Wyckoff and Webb 1996, McCarthy 1997, Hutchinson and Vankat 1997, Christian and Wilson 1999). This suggests that invading exotic species do not merely fill vacant niches in natural communities (Tilman 1997, D'Antonio et al. 1998) or replace native species one-for-one, but that they displace species disproportionately from the community, lowering diversity. However, the mechanisms behind these patterns are largely unknown. Two-species competition experiments between native and exotic species often indicate that exotic species are highly competitive (D'Antonio and Mahall 1991, Dillenburgh et al. 1993, Hamilton et al. 1999, Marler et al. 1999). Unfortunately, it is not known whether exotic species are, in general, stronger competitors than native species. Additional mechanisms for the success of exotic species include adaptations for increased vagility, fecundity and resource acquisition relative to native species (Rejmánek 1989, Bazzaz 1996).

A major confounding factor in the study of the effects of exotic species on plant communities is the role of disturbance. Exotic plant invasions are frequently associated with disturbances in plant communities (Fox and Fox 1986, Hobbs 1989, Luken and Goessling 1995, Kotanen et al. 1998). Disturbance by itself may also lead to changes in community composition and dynamics (Pickett and White 1985). For this reason, it is difficult, if not impossible, to differentiate the effects of the exotic species on the plant community from the effects of the disturbance that lead to the initial plant invasion (Woods 1997). The prevalence of heavily invaded, disturbed plant communities in the landscape makes this an important area of study.

The effects of scale are evident in published studies of plant invasions. At regional scales, the relationship between exotic and native species richness is often a positive one (Stohlgren et al. 1998, 1999, Lonsdale 1999, Stadler et al. 2000). While at smaller scales within sites, the same communities may show a negative correlation between exotic plants and native species richness (Stohlgren et al. 1998, 1999). Scale must be explicitly included in studies of exotic species to adequately assess patterns. Without direct consideration of scale, mechanistic interpretation of patterns is difficult and comparison of studies impossible.

While successional processes following disturbance have been well described in the eastern deciduous forest region (Bard 1952, Bazzaz 1968, Peet and Christensen 1980, Pickett 1982), the role of exotic species in these processes has not been characterized. From chronosequence studies, the importance of exotic species appears to decrease with successional time (Bard 1952, Pickett 1982, Inouye et al. 1987, Rejmánek 1989, Bazzaz 1996, Bastl et al. 1997). This generalization requires statistical testing of long-term data to evaluate its validity. If succession leads to communities with fewer exotic plants, then management that encourages later successional communities may reduce regional levels of invasion. This type of approach may be a sustainable alternative to time and resource intensive control efforts.

Since 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. Despite the interest in exotic plant invasions, a lack of described patterns from natural systems limits our ability to understand these invasions. The temporal patterns in species abundance and diversity, as well as changes in life history characteristics and the dynamics of native and exotic species over successional time are poorly described, plagued with the problems previously discussed, or anecdotally suggested. We quantify these basic community level patterns to generate testable hypotheses about exotic species in successional systems.

This study utilized 40 yr of continuous vegetation data from a series of 10 old fields of differing disturbance histories to evaluate changes in exotic species abundance and diversity over successional time. We also evaluated the relationships of exotics to other basic measures of plant community structure. The analyses were used to answer the following questions: 1) Does the species richness and cover of exotic species decrease over successional time? 2) How do these patterns compare to those of native species? 3) How does the scale of observation affect successional patterns of exotics? 4) Do the life history characteristics of the exotic community differ from those of the native community? 5) What is the relationship between exotic plants and measures of diversity? and 6) How does previous agricultural use affect these relationships?

Methods

Data collection

Since 1958, fields at the Hutcheson Memorial Forest Center (HMFC) have been abandoned from agriculture and the successional patterns of the vegetation monitored with the use of permanent plots (Small et al.

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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 to 1966. The fields differed in season of abandonment (autumn or spring), final crop (hay field or row crops) and soil treatment (plowed or intact vegetation). Since release, data collection occurred every year until 1979, when sampling switched to alternate years. At each sampling, the percent cover of all species present in each permanently marked 0.5×2.0 m plot was recorded. These data represent the longest continuous data set on successional change known. Nomenclature follows Gleason and Cronquist (1991).

Data analyses

We standardized age of field as time since release. Total exotic cover and percent exotic cover were calculated on a per plot basis only. Species richness of exotic and native species and percent exotic species were calculated at two scales, as plot and field totals. These calculations were done every year for the first 5 yr, then every 5 yr until year 40. Because not all fields were sampled every year at the beginning of the study, and because of limited replication in the oldest fields, repeated measures analysis was done for data from years 1, 2, 4, 10, 15, 20, 25 and 30 (Anon. 1989). These analyses evaluated change over time for exotic cover, species richness and proportion exotic species. Field identity and the time × field interaction were also included in the analysis. Proportional data were arcsin-square root transformed prior to analysis. Nativity status and life history form were obtained from Gleason and Cronquist (1991).

To determine the influence of scale on the temporal patterns of native and exotic species, the above analyses were repeated for measures of species richness and percent exotic species, using plot averages for each field and combined totals for each field. Contrasts with year 1 were calculated to determine significant changes from initial conditions. When the time × scale interaction was significant, these contrasts were calculated for each scale separately.

We compared native and exotic communities in two ways, as relative cover in each life history form and as proportion of species in each life history form. The proportion of cover in each life history class was calculated for native and exotic communities over the 40-yr sampling regime. Proportions were calculated yearly for the first 20 yr, then every other year to reflect the change in sampling interval. Differences between natives and exotics in relative cover of life history classes

were evaluated with a Cochran-Mantel-Haenszel test (Anon. 1989). To test for differences between the exotic and native species pool, the proportion of species in each life history class was also calculated for all native and exotic species present over the 40-yr sampling period. Differences between native and exotic species pools were evaluated with a χ^2-test. For both sets of analyses, woody and herbaceous vines were combined into one life history class. There was only one herbaceous vine species in both the native and exotic communities, which attained $< 0.1\%$ relative cover.

To determine the effects of site history on the role of exotics in influencing community structure, the data were separated into fields that were last in row crops vs those that were last used for hay. Similar analyses were done for the effects of season of abandonment and final soil treatment. However, analyses did not show strong effects of the season and soil treatments and the results are not presented here. The relationships among exotic species richness and native species richness, and proportion exotic cover and total species richness were calculated as Spearman rank-sum correlations (Anon. 1989). Significance criteria were Bonferroni-adjusted to account for multiple comparisons. To determine whether patterns increased or decreased in strength, the absolute values of the correlation coefficients were correlated with time since abandonment. Positive correlations indicate increasing strength of relationship, while negative correlations indicate decreasing strength.

Results

Diversity and abundance of exotics through succession

The absolute and relative cover of exotic species declined with succession (Fig. 1, Table 1). Total exotic cover varied dramatically for the first 10 yr, generally decreasing after year 10. The proportion of exotic cover in the plots varied within the first 5 yr after retirement and decreased sharply in years 10–40. Fields varied significantly in their response to time since abandonment, but had the same general temporal patterns. Total exotic cover was significantly different from initial conditions in years 2, 10 and 20–30 (contrasts with year 1, $p < 0.05$). Similarly, the decline in proportion of exotic cover remained significant $10+$ yr after abandonment (contrasts with year 1, year 4, $p > 0.05$; years 2 and 10–30, $p < 0.01$).

There was great variation among fields in the richness of native and exotic species as well as the proportion of exotic species over successional time (Fig. 2, Table 1). The number and proportion of exotic species per plot tended to decrease with time since abandonment, while the number of native species gradually increased. Fields that were originally used for hay
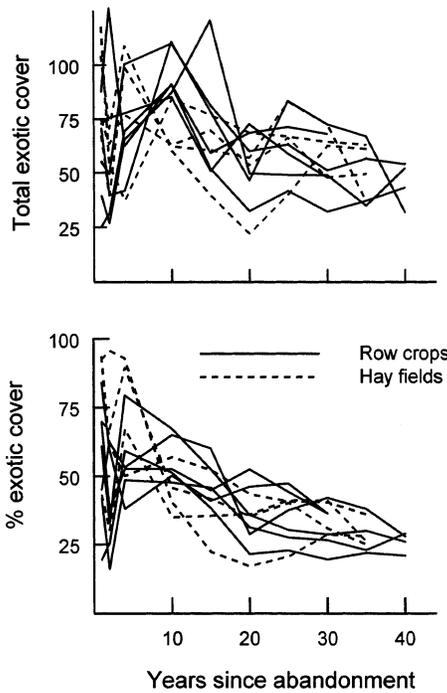
Fig. 1. Changes in total and relative exotic plant cover in each of 10 fields over 40 yr of succession. Lines represent the mean for each field in that period. Because cover is summed across overlapping species canopies, total cover may exceed 100%.

production were not visibly different that those previously in row crop agriculture.

Overall, the average number of exotic species per field changed little with succession, with no significant

Table 1. Results of repeated measures analysis of changes in exotic species over time. Sources containing time (time since abandonment) or interactions with time are within subject tests and report an F-test using Pillai's Trace.

| Source of variation	DF	F	p
Total exotic cover			
Field	9,454	10.49	0.0001
Time	7,448	40.04	0.0001
Time × field	63,3178	15.58	0.0001
Percent exotic cover			
Field	9,454	23.75	0.0001
Time	7,448	131.23	0.0001
Time × field	63,3178	18.71	0.0001
Exotic species richness			
Field	9,454	48.45	0.0001
Time	7,448	119.68	0.0001
Time × field	63,3178	14.84	0.0001
Native species richness			
Field	9,454	13.31	0.0001
Time	7,448	155.45	0.0001
Time × field	63,3178	20.27	0.0001
Percent exotic species			
Field	9,454	37.44	0.0001
Time	7,448	285.83	0.0001
Time × field	63,3178	12.25	0.0001
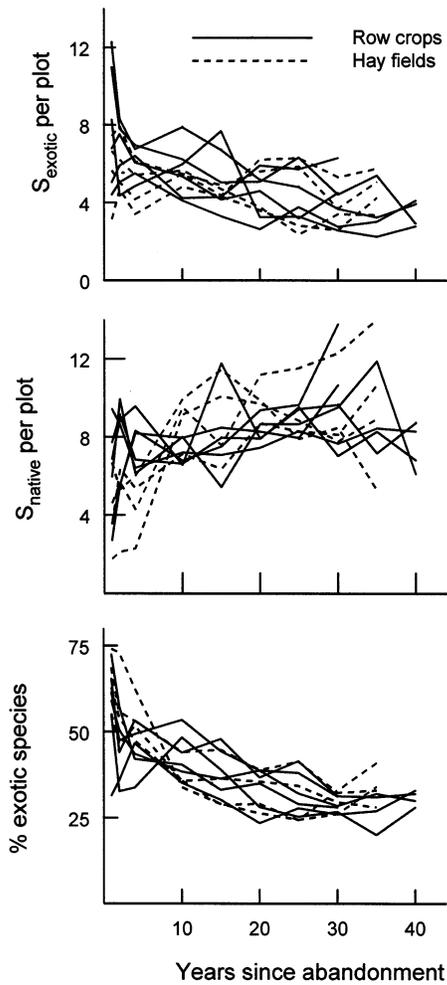
Fig. 2. Temporal changes in the richness and relative percentage of native and exotic species in each of 10 fields over 40 yr of succession. Lines represent the mean for each field in that period.

changes from year 1 (Fig. 3, Table 2). This is in contrast to plot-scale species richness of exotics, which decreased significantly from initial values in years 4–30 (all $p \leq 0.02$). Species richness of native species increased during succession at field scale but changed little within plots. Field-scale richness of native species increased significantly from year 1 in years 4–30 (contrasts with year 1; all $p < 0.002$). Time, scale and the scale × time interaction were significant in the repeated measures analysis for both native and exotic species. While native and exotic species richness per plot changed with succession, the total species richness per plot did not change over the course of this study ($p > 0.05$). In contrast, total species richness at the field scale shows a gradual accumulation of species, with significant changes from year 1 in years 4–30 (contrasts with year 1; all $p < 0.01$).

The proportion of exotic species declined sharply with time since abandonment (Fig. 3). There was no effect of scale or a scale × time interaction (Table 2) but time since abandonment was significant. Proportion of exotic species showed an immediate drop after the first year of succession at both scales (years 2–30, p ≤ 0.0011).

Life histories of exotic and natives

The successional changes in life history of both native and exotic species showed changes from relatively short-lived species to perennial woody species over time (Fig. 4). However, exotic species contributed little cover as trees. Lianas and shrubs dominated the woody cover of exotics. These differences between native and exotic communities were statistically significant (Cochran-Mantel-Haenszel test p = 0.001). The distribution of

Table 2. Results of repeated measures analysis of the influence of sampling scale on changes in native and exotic species richness over time. Sources containing time (time since abandonment) or interactions with time are within subject tests and report an F-test using Pillai's Trace.

Source of variation	DF	F	p
Exotic species richness			
Scale	1,18	886.73	0.0001
Time	7,12	12.96	0.0001
Time × scale	7,12	13.39	0.0001
Native species richness			
Scale	1,18	655.57	0.0001
Time	7,12	33.43	0.0001
Time × scale	7,12	19.94	0.0001
Percent exotic species			
Scale	1,18	0.06	0.8128
Time	7,12	41.53	0.0001
Time × scale	7,12	2.40	0.0796
Total species richness			
Scale	1,18	1108.80	0.0001
Time	7,12	9.30	0.0005
Time × scale	7,12	8.74	0.0007

species among life forms also differed between native and exotic communities for the total species pool ($\chi^2 = 26.6$, 5 DF, p = 0.001). The exotic assemblage comprised more annual and biennial species while the native species pool contained more perennial, shrub and tree species.
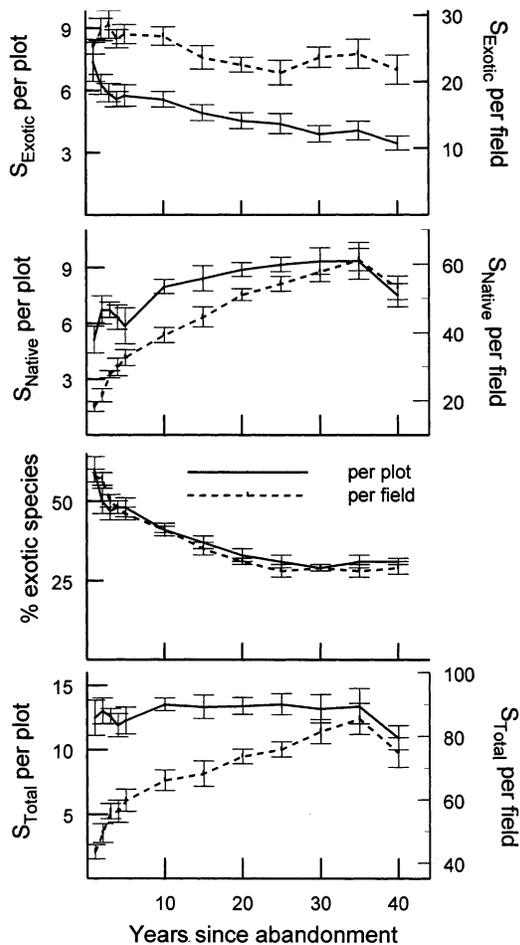
Fig. 3. Effects of sampling scale (field vs plot) and time since abandonment on the species richness of exotic and native species and on the percentage of exotic species over 40 yr of succession. Points represent mean ± 1 SE of all fields sampled in that period.
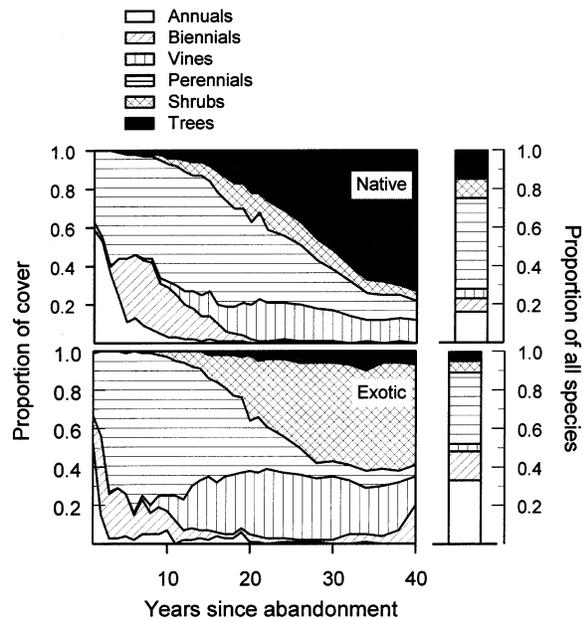
Fig. 4. Change in life history characteristics of the native and exotic plant assemblages over 40 yr of succession. Panels on the left depict the change in proportion of total cover in each life history class with time since abandonment. Panels on the right show the proportion of species in each life history class from the total species pool.

Table 3. The effects of agricultural history on the correlation between species richness of native and exotic species across all fields. Data shown are Spearman correlation coefficients. Sample size varies with the number of fields sampled in a given time period. Bonferroni-adjusted significance criteria for each column is p = 0.004 for an overall α = 0.05.

Age	Hay fields			Row crops		
	n	R	p	n	R	p
1	192	0.53	0.0001	272	0.14	NS
2	192	0.45	0.0001	272	0.09	NS
3	144	0.38	0.0001	272	−0.01	NS
4	192	0.58	0.0001	288	0.17	0.0034
5	144	0.16	NS	288	0.06	NS
10	192	0.32	0.0001	288	0.28	0.0001
15	192	0.38	0.0001	288	0.40	0.0001
20	192	0.37	0.0001	288	0.53	0.0001
25	192	0.40	0.0001	288	0.52	0.0001
30	192	0.54	0.0001	288	0.66	0.0001
35	192	0.52	0.0001	192	0.51	0.0001
40	–	–	–	192	0.55	0.0001

Site history effects on relationships with exotics

In sites that had been last farmed as hay fields, the species richness of native species was positively associated with the species richness of exotic species (Table 3). This relationship was not initially present in fields previously used for row crops, but developed 4 yr post-abandonment. This relationship disappeared for both types of fields in year 5, reappearing in years ≥ 10. The strength of the correlation did not change with time since abandonment in hay fields ($r_S = -0.009$; p = 0.98), but increased in row crop fields ($r_S = 0.85$; p = 0.0004).

The proportion of exotic cover in a plot was negatively associated with total species richness in hay fields (Table 4). The strength of this relationship declined with time since abandonment ($r_S = -0.87$; p = 0.0005),

Table 4. The effects of agricultural history on the correlation between the proportion of exotic cover and total species richness across all fields. Data shown are Spearman correlation coefficients. Sample size varies with the number of fields sampled in a given time period. Bonferroni-adjusted significance criteria for each column is p = 0.004 for an overall α = 0.05.

	Hay fields			Row crops		
Age	n	R	p	n	R	p
1	192	−0.71	0.0001	272	−0.42	0.0001
2	192	−0.50	0.0001	272	0.13	NS
3	144	−0.60	0.0001	272	0.06	NS
4	192	−0.65	0.0001	288	−0.15	NS
5	144	−0.54	0.0001	288	0.04	NS
10	192	−0.27	0.0001	288	0.09	NS
15	192	−0.24	0.0007	288	−0.15	NS
20	192	−0.04	NS	288	0.06	NS
25	192	−0.19	NS	288	0.09	NS
30	192	−0.21	0.0025	288	0.12	NS
35	192	−0.12	NS	192	0.18	NS
40	–	–	–	192	0.16	NS

disappearing in years 20, 25 and 35. In row crop fields, this negative association between exotic cover and species richness only appeared in year 1 (Table 4). This association was only found in the two fields that were abandoned in the spring, with no relationship in autumn-abandoned fields. The spring-abandoned fields had less than half of the perennial cover of autumn-abandoned fields (4 vs 9% cover per plot), leaving an abundance of annual and biennial species. The strength of the association between exotic cover and species richness did not change over time for row crop fields ($r_S = 0.09$; p = 0.77).

Discussion

Diversity and abundance of exotics through succession

This study found significant declines in the abundance and richness of exotic species ≥ 20 after abandonment without management intervention. The analyses presented here provide a quantitative and statistical test of earlier observations of changes in exotic species through succession. The invasions in this study were initially severe, with exotic species comprising over 50% of the cover and species in each field. Declines from this heavily invaded state suggest that many exotic plant invasions may be self-limiting in areas where succession is allowed to proceed. While exotic species in this study declined, the number of native species increased, leading to the maintenance of diversity in these fields.

The loss of exotic species appears to be related to canopy closure within the sites. As woody cover increased in the fields, herbaceous species, particularly annuals and biennials became much less abundant. Many of these species were exotics that dominated the plant community early in succession. While decreases in light associated with canopy closure may lead to declines in abundance for some exotic species (Robertson et al. 1994), this mechanism will only function for shade-intolerant species.

Some shade-tolerant species are increasing in the site and may present the next invasion challenge to the plant community. *Alliaria petiolata*, an exotic biennial, has become abundant in forested portions of the fields in sufficient amounts to cause an increase in biennial cover in the last few sampling years. This species is associated with declines in understory diversity (McCarthy 1997). Shrub honeysuckles (*Lonicera maackii* and *L. tartarica*) are increasing in abundance and have been associated with decreases in native species diversity elsewhere (Hutchinson and Vankat 1997). These shrubs may further invade the site as gaps form from the death of early successional trees, as has been shown with *L. maackii* (Luken and Goessling 1995). Norway maple *Acer platanoides* has invaded the old growth

forest at HMFC (Ambler 1965), but has not established in the sampling plots. This species has successfully invaded many forests in New Jersey, resulting in declines in understory diversity and tree regeneration (Wyckoff and Webb 1996). Other potentially increasing species in the site include *Microstegium vimineum* and *Berberis thunbergii*, both of which are spreading in northeastern forests (Fairbrothers and Gray 1972, Ehrenfeld 1997). Invasions by shade-tolerant species may reverse the patterns seen in the first 40 yr of succession, leading to increases in exotic plant cover and potentially to declines in native plant diversity.

Interactions within the plant community may drive early changes in species composition as well. The drop in species richness of exotics in years 2–3 is reflected by an increase in native species per plot (Fig. 2) resulting in a brief decrease in the percentage of exotic species. The changes in richness reflect a large decrease in exotic annual species, which appears to allow an invasion of native species into the plots. These annual exotic species may be inhibiting the establishment of native species (Connell and Slatyer 1977) in the first year. However, in an experimental test of this hypothesis, inhibitive interactions were not found in an early successional plant community in Ohio (Hils and Vankat 1982). It may be that the exotic annual species are saturating all available niches, preventing the invasion of other species in the first year (Tilman 1997, but see Zobel et al. 2000).

Further evidence for species saturation comes from changes in species richness through time. Throughout the 40 yr of this study, plot-scale species richness has remained constant while field-scale richness has continued to increase. Furthermore, as the number of exotic species in each plot declined, the number of native species increased, maintaining constant plot diversity. In California grasslands, variation in exotic species invasion and soil fertility results in constant total species richness (Harrison 1999). This response may indicate competitive or inhibitive interactions between native and exotic species for limited niche space. These data suggest that plots are saturated with species and that species sorting occurs during succession with native species eventually displacing exotics.

The temporal consistency in species richness per plot is similar to the spatial consistency in species richness reported by Gross et al. (2000). They found that herbaceous-dominated communities had an average of 8–15 species m^{-2}, despite large variation in productivity among sites. This rather limited range of species richness at the 1 m^2 scale may indicate some overall limitation to small-scale species richness (Gross et al. 2000)

Life histories of exotic and natives

The species pools of natives and exotics differ dramatically. The exotic species pool is disproportionately composed of short-lived species, reflecting the abundance of agricultural weeds in the flora. The exotic community also has few woody species. Though both shrub and vine species in the exotic community have low species richness, they contribute relatively large amounts of cover to the community. The lack of woody species in the exotic community reflects the abundance of exotic open-adapted herbaceous species.

The abundance of short-lived, open-adapted species in the exotic plant community explains their decline as native tree cover increases in the fields. Canopy closure appears to prevent most invasions from persisting over long periods (Robertson et al. 1994). This also shows the potential for shade-tolerant exotic species to invade and expand within these sites. For example, *Alliaria petiolata* has invaded forested portions of several fields in years ≥ 30 of the study. With continued invasion and spread by shade-tolerant exotic species, community structure may shift to a forest canopy dominated by native species with an herbaceous understory dominated by a few exotic species. This pattern is beginning to develop in some portions of HMFC.

In many studies, exotic species limit forest regeneration (Thomas 1980, Woods 1993, Wyckoff and Webb 1996, Hutchinson and Vankat 1997). While this has not happened in the fields of the BSS study, the potential exists for an alternative plant community to develop, which does not include a closed-canopy forest (Fike and Niering 1999). Without the shading effects of a closed canopy, many shade-intolerant exotic plant invasions may persist, exerting continued influences on plant community structure and diversity.

Site history effects on relationships with exotics

Previous agricultural use had strong effects on the relationship between native and exotic species richness. In fields previously used to grow row crops, the positive association between native and exotic species developed over the first 4 yr of succession. Species richness in the first few years was probably a function of the chance occurrence of dispersal into a plot (Pickett et al. 1987, Tilman 1997, Wiser et al. 1998) and subsequent spread throughout the field. Once species accumulate, competitive or other interactions within the local plant assemblage result in sorting to produce the observed pattern (Pickett et al. 1987, Wiser et al. 1998, Meiners et al. 2001). Hay fields differed from row crop fields in that the association between native and exotic richness was present immediately post-abandonment. This suggests that the pattern had developed previously in the perennial crop community. The disappearance of the pattern in year 5 probably reflects a resorting of species following the loss of exotic annuals and biennials. An invasion of perennial species followed this period, resulting in the restoration of the previous association. The

positive spatial association between species richness of natives and exotics throughout succession suggests that the same general factors that regulate local diversity of native species regulate diversity of exotic species (Levine and D'Antonio 1999). Based on this finding, exotic and native species do not appear intrinsically different.

Agricultural history also affected the relationship between exotic cover and total plot species richness. Fields used to grow row crops showed a negative association between exotic cover and total richness only in the first year. This appears to be related to the lack of perennials in spring-abandoned row crop fields. Thereafter, there does not appear to be any detrimental effect of exotic cover on community diversity. In contrast, hay fields showed a negative association between exotic cover and total richness for the first 15 yr of succession. The dominance of hay fields by perennial exotic crop and weed species, which prevent the establishment of native species, may cause this association. Woody exotics replace the perennial community in years 20–25, during which the association disappears. The negative association between exotic cover and species richness resumes in year 30, as exotic shrubs come to dominate the site. With the loss of shrubs after canopy closure of native trees, the association breaks down again. This cyclic change in community associations with changes in dominant life forms is analogous to cycles of heterogeneity in old field succession proposed by Armesto et al. (1991).

Implications for the management of exotic species

As most invasions in this study declined dramatically with the establishment of a closed-canopy forest, management strategies that aim to encourage tree growth should help to control levels of many exotic species. For several exotic species, older forests support smaller populations than younger, more open forests (Robertson et al. 1994). However, canopy closure will only reduce populations of open-adapted exotic species. Areas of heavy invasion by shade-tolerant exotic species will require other methodologies.

Agricultural practices may also influence the future impacts of exotics. The frequent plowing associated with row crop agriculture prevents the accumulation of exotic perennial cover. When these sites are abandoned, both natives and exotics start invading at the same time, resulting in a plant community that does not show significant effects of exotic species. In contrast, agricultural practices with repeated biomass removals such as hay fields, meadows and grazing result in perennial exotic communities that resist invasion by other species (Mack 1989). These effects may persist for 15 yr or more. One-time plowing was not sufficient to reduce the impacts of these species on community development in these sites.

It is important to note that it is not the invasion of an exotic plant, per se, that reduces species richness but the dominance of a patch by exotic species that may result in reduced species richness. Species richness of natives and exotics are positively associated, showing no effects of exotic invasion on native species richness. However, when exotic plants make up a large proportion of the total cover of a plot, we observed reductions in community richness (Meiners et al. 2001). Therefore, managers should focus control efforts on species that have the potential to dominate local plant communities.

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