

NATIVE AND EXOTIC PLANT SPECIES EXHIBIT SIMILAR POPULATION DYNAMICS DURING SUCCESSION

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Abstract. A growing body of literature has led to the debate in invasion biology whether exotic species perform within communities differently than native taxa due to inherent advantages. To address this issue, the population dynamics of native and exotic plant species were assessed from a 48-year record of permanent plot data from the Hutcheson Memorial Forest Center (New Jersey, USA) to determine rate of increase, lag time, maximum frequency, and the year of peak frequency. Overall, native and exotic species exhibited very similar population dynamics. Rates of increase and length of lag times were similar between native and exotic taxa but were strongly influenced by plant life form. Short-lived species were characterized by rapid population growth rates and short lag times. Growth rates decreased and lag times increased with species longevity. Overall, correlations between population metrics were the same in native and exotic taxa, suggesting similar trade-offs in life history patterns. The one difference observed was that, in native species, peak frequency was negatively associated with the year of peak frequency (i.e., early-successional species tended to become more abundant), while there was no relationship in exotic species. These analyses show that exotic species behave in essentially the same way as native taxa within dynamic communities. This suggests that abundant native and exotic plant species are exploiting the same range of ecological strategies resulting in similar roles within communities.

Key words: *exotic species invasions; growth rates; population dynamics; successional dynamics.*

INTRODUCTION

The global homogenization of biotic communities has led to widespread investigation of exotic species invasions and comparisons with native taxa. One generality to emerge from these studies is that exotic plant species often outperform native taxa within recipient communities. However, this generalization may be biased by the selective study of particularly problematic exotic plant species. As most invasions do not result in the establishment of widespread populations (Williamson 1996, Sax and Brown 2000), these selective results may not be representative of the vast majority of exotic plant species. Before the general utility of these case studies can be evaluated, comparative studies must focus on the entire suite of abundant exotic plant invaders and compare them to a range of native plant species.

The success of exotic plant species relative to native taxa has been explained through numerous hypotheses. Exotic invaders may have escaped the natural enemies that limited them in their native ranges (Keane and Crawley 2002, Wolfe 2002), resulting in an advantage over native taxa that possess intact herbivore and pathogen communities. This release from the selective pressures that maintain defenses may subsequently

result in selection towards allocation to growth and reproduction, increasing competitive ability (Blossey and Notzold 1995). Another major explanation for the success and impacts of invading species is that the invader possesses individual traits or a combination of traits that are unique to or underrepresented in the recipient community, allowing the invader to exploit resources or opportunities unutilized by the native community (Vitousek et al. 1987, Fargione et al. 2003). Other explanations of exotic success include competitive superiority (Collins and Wein 1993, Daehler 2003), avoidance of seed predation (Pyke 1990), increased phenotypic plasticity (Schweitzer and Larson 1999), faster growth rates (Milberg et al. 1999), and greater dependence on disturbance (Mack 1989, King and Grace 2000) among others. However, generalizations are difficult in that studies often focus on particularly problematic species, which may not be representative of the exotic plant community as a whole.

Another prominent view is that native and exotic species draw from the same pools of potential traits (Huston 1994, Thompson et al. 1995, Smith and Knapp 2001). More importantly, these traits are governed by the same underlying energetic constraints and trade-offs (Grime 2001). These universal “rules” lead to native and exotic species pools that are essentially the same from a functional perspective. If this is true, an individual exotic species may possess characteristics (such as those listed above) that allow it to succeed in a particular recipient community, but native and exotic species, as a whole,

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should not differ in these functional characteristics. Based on this hypothesis, we would expect the vast majority of exotic species to become residents within native communities and to behave similarly to native species (Ortega and Pearson 2005).

The issue of whether successful exotic species differ from successful natives is a fundamental question in invasion biology. If exotic species are in general superior to native species, as suggested by much of the ecological literature, then this superiority, however derived, should lead to differences in population dynamics within communities: increased growth rates, abundance, and so on. However, if these two groups are drawn from the same pool of traits, then exotic and native taxa should show largely similar population dynamics within communities. Despite the focus on comparing native and exotic species, entire communities composed of interacting native and exotic species have not been systematically examined to determine whether the population dynamics of these two groups fundamentally differ.

To address this fundamental issue of invasion biology, the performance of exotic and native plant species was compared within a successional sequence. Successional communities are useful model systems for studying invasions because (1) they are abundant globally, (2) they are typically heavily invaded, and (3) the population dynamics of component species occur over relatively short time periods. Furthermore, successional systems place all species in the role of invader, avoiding the bias associated with comparing established resident native species with establishing populations of exotics. The purpose of this study was to use long-term permanent plot data to determine basic measures of population dynamics for a range of species and to assess whether appreciable differences exist between native and exotic taxa.

METHODS

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), known as the Buell-Small Succession Study (BSS). Within each of 10 contiguous fields, 48 plots are arranged in a regular pattern that varies somewhat with the shape of the field. The agricultural history of each field was experimentally manipulated by varying time of abandonment (spring or fall), final crop (row crops or *Dactylis glomerata* hay) and final soil treatment (plowed or unplowed). Fields were abandoned as pairs in alternate years from 1958 until 1966. Variation in year of abandonment in conjunction with manipulation of pre-abandonment treatment generated large compositional variation among the fields (Myser and Pickett 1990). Since abandonment, 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

with the aid of a sampling frame. These data represent the longest continuous data set on old field successional change known.

The data contain a total of 110 exotic and 194 native species, reflecting the heavily invaded nature of most successional systems. To assess the population dynamics for native and exotic taxa within the BSS, the 25 most frequent native and exotic species were selected for analysis. These taxa represent the most common species throughout succession and cover a variety of life forms (Appendix). These 50 species represent a total of 86.2% and 86.9% of all exotic species occurrences and cover respectively, and a total of 13.6% and 76.3% of all native species occurrences and cover. Frequency (the number of plots occupied by a species) was used as the basis for all comparisons to allow equivalent analyses to be done across a suite of species that included large variation in total plant size. For each species, the temporal pattern of plot occupancy was determined and the following metrics calculated:

- 1) Maximum rate of increase: the largest single-year increase in the percentage of occupied plots by a species in each field. This is used as a functional estimate of each species' population growth rate, though it would also include some aspect of a species' dispersal ability.

- 2) Lag time: the length of time in years between when a species first invades a field and when it first exceeded 5% frequency (>2 plots) in that field. Fields in which a species was never found in more than 2 plots were not included in the analysis for that species.

- 3) Maximum frequency: the maximum percentage of plots occupied by a species in each field.

- 4) Year of population peak: the number of years since abandonment that a species attained its maximum frequency across the site.

Both the maximum rate of increase and population lag time could be influenced by the ability of a species to spread within a site since the metrics are based on plot occupancy and not numbers of individuals. Therefore, these two metrics are not completely independent, but they both capture different variation in the data. Analyses were conducted on the average value across fields for each species, except for year of population peak, which was determined for all fields pooled together. Each species was assigned into one of three life-form categories (annual or biennial/short-lived perennial, perennial, and woody) following Gleason and Cronquist (1991).

Each population metric was analyzed with ANOVA using origin and life form as categorical variables. Life form was included to remove potential bias of species introduction (e.g., exotic species are disproportionately composed of short-lived species in these data), and to account for relatively simple differences in life history among species. To conform to normality assumptions of ANOVA, population growth rate data were log transformed and lag time data were rank transformed. Maximum frequency and year of population peak data

TABLE 1. ANOVA of the influence of species origin and life form on population dynamics.

Model term	df	MS	F	P	R ²
Maximum rate of increase					
Origin	1	0.063	1.86	0.180	0.49
Life form	2	0.589	17.35	<0.001	
Origin × life form	2	0.070	2.06	0.140	
Error	44	0.034			
Lag time					
Origin	1	64.5	0.49	0.488	0.44
Life form	2	1694.4	12.84	<0.001	
Origin × life form	2	99.0	0.75	0.478	
Error	44	131.9			
Maximum frequency					
Origin	1	614.8	1.88	0.177	0.19
Life form	2	390.0	1.20	0.312	
Origin × life form	2	787.8	2.41	0.101	
Error	44	326.4			
Year of population peak					
Origin	1	38.5	0.80	0.376	0.74
Life form	2	2304.1	47.89	<0.001	
Origin × life form	2	54.2	1.13	0.333	
Error	44	48.1			

did not require transformation. Relationships among population measures were analyzed with Spearman rank-sum correlations. These correlations were conducted both across all species, and for native and exotic taxa separately to look for variation in life history trade-offs. All analyses were conducted with SPSS version 13.0 (SPSS, Inc., Chicago, Illinois, USA).

RESULTS

The analyses revealed nearly identical population dynamics for native and exotic plants during succession. Species origin was not significant in any of the ANOVA models. However, life form tended to explain much of the variation in population metrics. The maximum rate of population increase did not differ between native and exotic plant species (Table 1, Fig. 1) but decreased dramatically from short-lived to long-lived life forms. The rate of population increases ranged from an absolute increase of nearly 50% of plots per year in native annuals to a maximum increase of 10% for native woody species. Similarly, population lag times went from less than one year on average for short-lived annuals and biennials, to an average of four or more years for woody species, but did not vary between native and exotic taxa of the same life form. For both of these analyses, each life form was statistically distinguishable from all others.

Peak frequency was not significantly associated with origin or life form and ranged from 88% to 27% across all species. The year of peak frequency followed typical patterns expected in secondary succession. Annuals and biennials/short-lived perennials reached their population peaks before 10 years after abandonment, perennial herbaceous species peaked slightly later near year 15, and woody species reached peak abundance nearly 30

years post abandonment (Table 1, Fig. 1). There was no effect of origin on the time of population peak as these were nearly identical within each life form.

Measures of population dynamics were correlated with each other showing largely expected patterns (Fig. 2). Plants with rapid rates of population increase tended to have short time lags and peak early in succession

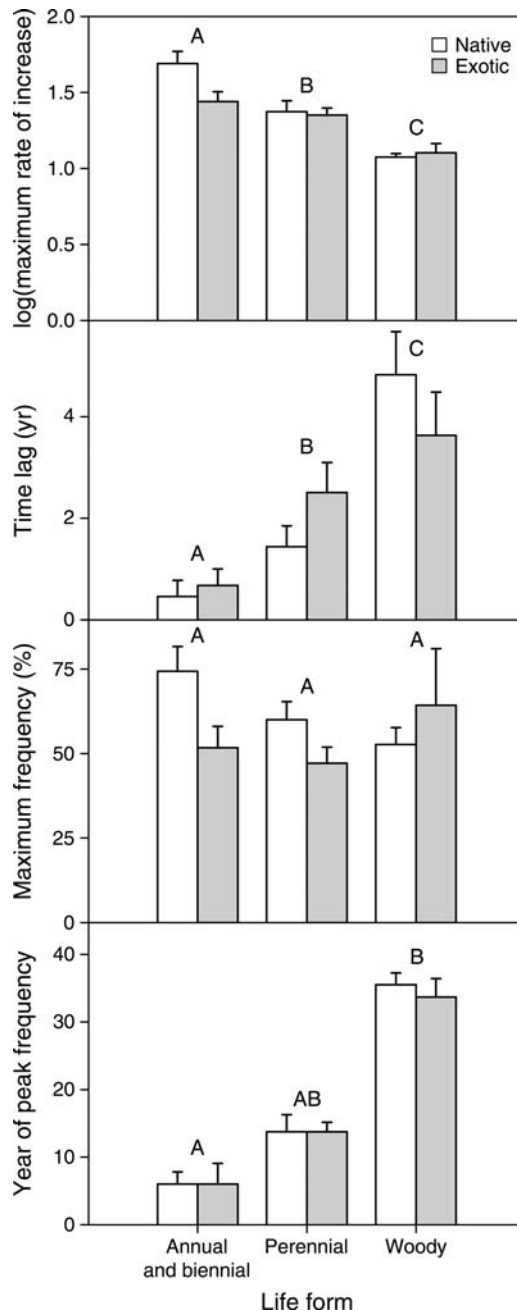


FIG. 1. Influence of life form and species origin on population parameters for the 25 most frequent native and exotic species within the Buell-Small succession study (BSS). Life forms sharing the same letter are not statistically different based on a Duncan's post hoc test. Data plotted are means + SE.

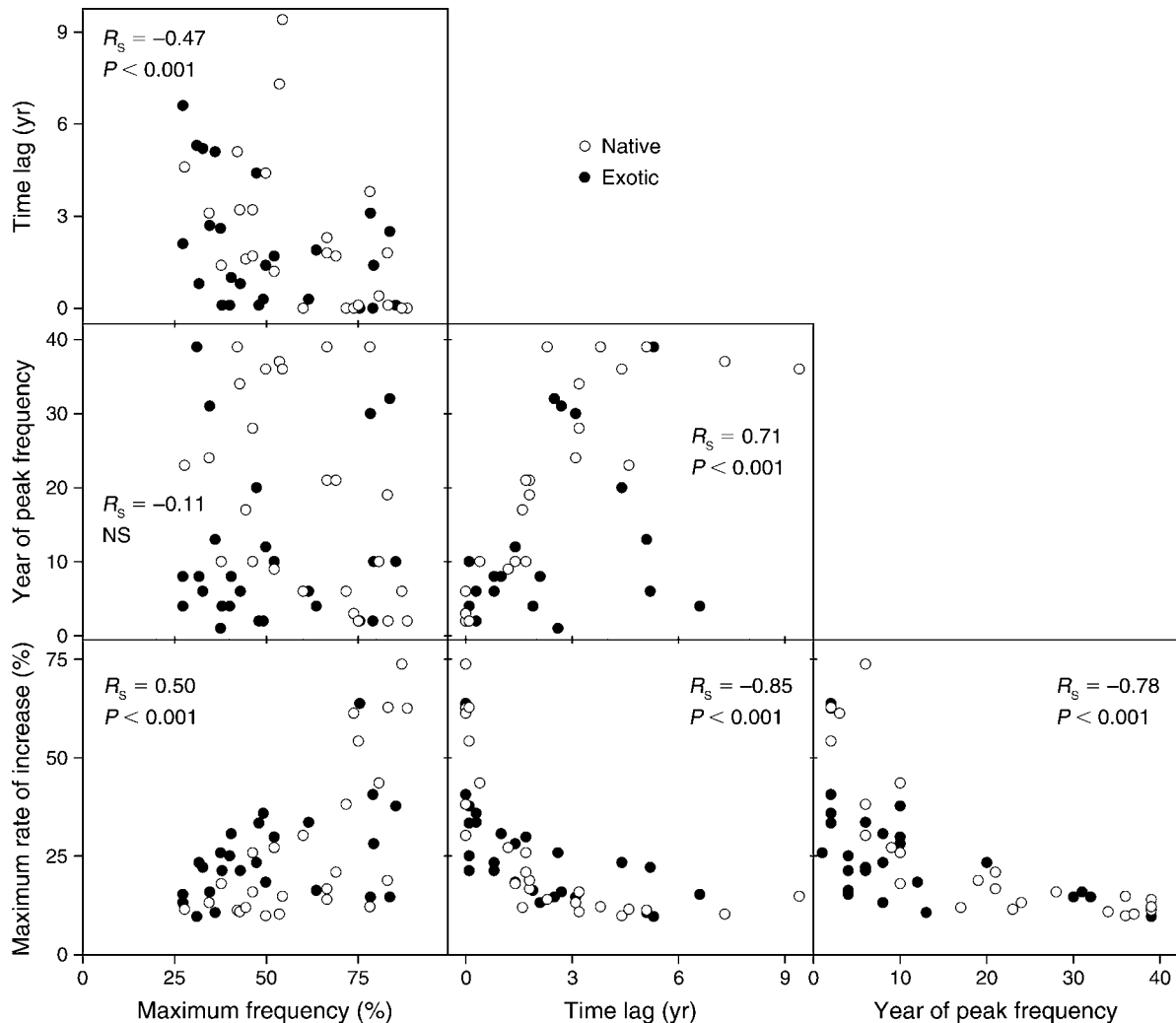


FIG. 2. Correlations between measures of population dynamics. Correlation coefficients reported within each graph are Spearman rank-sum correlations calculated using native and exotic species combined; "NS" indicates that the correlation was not significant.

while plants that increased more slowly tended to peak later. Plants with rapid rates of increase also tended to become more abundant within the successional fields, though typically for only a brief window of time. When analyzed separately, native and exotic taxa had qualitatively similar trade-offs in population dynamics, though correlation coefficients were consistently higher for native taxa. The one difference identified was that maximum frequency and the year of peak frequency was not correlated in exotic taxa ($R_s = 0.013$, $P = 0.95$), while native taxa had a negative correlation, with later successional species tending to peak at lower frequencies ($R_s = -0.48$, $P = 0.015$).

DISCUSSION

Life forms

Not surprisingly, life form was consistently a strong predictor of population dynamics. Variation among life

forms largely reflects variation in lifespan with short-lived annual and biennial species exhibiting fast population growth rates and short population lag times. These species were also largely restricted to early successional habitats. One clear exception was the exotic biennial *Alliaria petiolata*, an invader typically found only in forest understory communities, which reached peak frequency 31 years after abandonment. This species had high population growth rates and short lag times like other annual and biennial species. *Alliaria petiolata* is considered a problematic invader throughout the northeastern United States, particularly because of its ability to quickly spread and dominate a site (Cavers et al. 1979, Nuzzo 1999).

Woody species represent the opposite end of the gradient of ecological strategies from the short-lived species. Woody species grow much more slowly, allocating resources to growth of woody support tissue



PLATE 1. The young forest in field C6 of the Buell-Small Succession Study, photographed after 43 years of succession. This field, one of ten replicates, was last used in the production of *Dactylis glomerata* hay and was abandoned in 1964. Species common at the time the photograph was taken include the exotics *Alliaria petiolata*, *Lonicera japonica*, and *Rosa multiflora* and the natives *Acer rubrum*, *Cornus florida*, and several *Vitis* species. Photo credit: S. Meiners.

and delaying reproduction (Grime 2001). In line with this strategy, woody species spread much more slowly within the fields and exhibited relatively long lag times in population growth. These species also dominated the later stages of succession documented in this study. The woody exotics included in these analyses, *Celastrus orbiculatus*, *Lonicera japonica*, and *Rosa multiflora*, are all considered regionally problematic invasive species because of their dominance and impacts on richness and diversity of native communities (Robertson et al. 1994, Fike and Niering 1999, Yurkonis et al. 2005). However, even these species, which are among the most widespread and aggressive invaders, exhibit population dynamics nearly identical to the less abundant native early- and mid-successional woody species at the site.

Species origin

Origin was not a significant predictor of population growth and spread in any of the analyses performed. Like other studies that have examined a broad suite of species (Thompson et al. 1995, Daehler 2003), this study finds no evidence for systematic differences in native and

exotic species. While individual exotic species may behave differently than ecologically similar native species, the characteristics of successful exotic species as a whole cannot be separated from the range seen within native taxa. It is important to note that the majority of exotic species examined here are not recent invaders, but have been established within the region for more than 100 years. If naturalization leads to changes in population dynamics over time, then more recent invaders may exhibit differences from similar natives. However, the influence of naturalization on invading plant populations is not clear. Evolutionary changes may lead to increased allocation to competitive ability (Blossey and Notzold 1995) leading to increased performance with time since invasion. Alternatively, if evolutionary changes within herbivore communities lead to shifts in diet, then invading populations may become less successful as they accumulate natural enemies.

These data show remarkably little separation between native and exotic taxa even when examining exotic species with apparently unique dynamics. For example, *Alliaria petiolata* was the only abundant biennial species

that peaked once canopy closure had occurred across most of the fields. While *A. petiolata* appears to vary dramatically from other native and exotic short-lived species, this alternative strategy is also seen in native forest annuals such as *Impatiens capensis* and *Pilea pumila*. While these species were not common enough to be included within this study, they are common understory species throughout the eastern deciduous forest. Similarly, the two most abundant exotic species at the site, *Lonicera japonica* and *Rosa multiflora*, are clearly strong invaders (*sensu* Ortega and Pearson 2005) and have been shown to reduce local species richness and impact resident plant populations within the BSS (Yurkonis and Meiners 2006). However, as canopy closure has occurred, both of these species, like other native shrubs and vines, have experienced dramatic declines in frequency and cover (Meiners et al. 2002).

Trade-offs

The analysis of correlations between measures of population dynamics allows the direct comparison of strategies in a continuous fashion without artificially separating species into discreet groupings. Like the previous analyses, these correlations also show little separation between native and exotic taxa. The data show the trade-offs that are expected within a successional system (Grime 2001), where species with fast growth rates peak early in succession and have relatively brief population lag times. The positive correlation between growth rates and peak frequency most likely reflects the ability of species to disperse and capitalize on ephemeral resource pulses, such as those immediately following abandonment or after drought (Yurkonis and Meiners 2006).

The one difference between native and exotic species was in their relationship between maximum frequency and the year of peak frequency. While exotic species had no correlation, native species showed a negative correlation. Native species that dominate later in succession in the BSS data tend to be more patchily distributed among fields, leading to an overall decrease in the average peak frequency. In contrast, exotics that dominate later in succession tend to be just as widespread as those of early successional environments (e.g., *Alliaria petiolata* and *Rosa multiflora*). This difference may be caused by dispersal limitation in some native tree species (e.g., *Acer rubrum* and *Cornus florida*) or dependence on gaps in native lianas (e.g., *Toxicodendron radicans* and *Vitis* spp.; see Plate 1). While the sample size of exotics that peak late in succession is admittedly small, the apparent lack of dispersal limitation or habitat specificity in those exotics represents a biologically important difference that may exist between native and exotic species.

Conclusions

Despite the prevalence of mechanisms explaining the spread and success of exotic species within the ecological

literature, this study was not able to document substantial differences in the population dynamics of native and exotic plant species. While individual species may benefit from competitive superiority, escape from natural enemies, or other mechanisms that facilitate their success, these advantages do not appear sufficiently widespread to generate overall differences in population dynamics. Alternatively, these mechanisms may play a role, but are not sufficiently strong to influence population dynamics when part of a diverse and dynamic plant community. In either case, the overall similarity of the dynamics and life-history trade-offs indicates that native/exotic status has little influence on the performance of species in communities. These findings support the argument that native and exotic species are essentially drawing from the same pool of traits and therefore function within communities based on the same ecological rules (Huston 1994). Again, these conclusions are based on exotic species, which are largely naturalized within this system. Studies focusing on new invaders into systems may reveal differences not seen here.

These results have several implications for the study of exotic species invasions. First, it argues that the separation of invasion biology from the study of native species is artificial. Research should focus specifically on separating out the characteristics and conditions under which species become successful, as these are likely to be the same suite of conditions for species regardless of origin. Second, it calls into question attempts to form general explanations of invasions based on experimental study of a few species. The mechanisms determined from case studies of particularly problematic species will explain the success of a single species, but may shed little light on the process of invasion in general. Studies focusing on factors that allow the establishment and spread of species within communities, e.g., the fluctuating resource hypothesis (Davis et al. 2000), will allow researchers to determine where invasions of native or exotic species may occur. Complementary to this approach are studies that systematically examine determinants of performance across an entire community (e.g., the prevalence of negative biofeedbacks [Klironomos 2002]). Such studies will identify characteristics that have the potential to lead to species dominance within intact communities. Invaders that possess these or superior characteristics, regardless of origin, may then have the ability to invade and disrupt communities.

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APPENDIX

The 25 most frequent native and exotic species within the Buell-Small Succession Study (BSS) data used for all analyses (*Ecological Archives* E088-068-A1).