Applied Vegetation Science 12: 45–53,

On a level field: the utility of studying native and non-native species in successional systems

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Abstract

Questions: How do successional systems contribute to our understanding of plant invasions? Why is a community-level approach important in understanding invasion? Do native and non-native plant species differ in their successional trajectories within communities?

Location: Northeastern United States, in the Piedmont region of New Jersey. Previously farmed since the 1700s, ten fields were experimentally retired from agriculture beginning in 1958.

Methods: Fifty years of permanent plot data were used to quantify the population demographics of the 84 most abundant species during succession. These measures were then used to compare native, non-native and non-native invasive species' population dynamics in succession.

Results: Once basic life-history characteristics were accounted for, there were no differences in the population dynamics of native, non-native, and non-native invasive plant species. However, the species pool in this study was biased towards ruderal species, which largely constrained non-native species to early succession.

Conclusion: Successional systems are crucial to our understanding of invasions as they constrain all species to the role of colonizer. By focusing on the whole community, rather than on individual problematic species, we found no systematic differences between native and non-native species. Thus, knowing simple life-history information about a species would be much more useful in setting management priorities than where the species originated.

Keywords: Community structure; Long-term study; Plant invasions; Population dynamics; Succession.

Introduction

Succession is one of the longest-studied ecological phenomena and has developed over time from early descriptive work (e.g., Cowles 1899; Clements 1916; Gleason 1927) to contemporary mechanistic and experimental studies (e.g., Hils & Vankat 1982; Tilman 1985; Carson & Pickett 1990; Larson & Siemann 1998; Wilson & Tilman 2002). This long interest in succession is based on the expectation that by understanding the processes that regulate succession, we will better understand the factors that determine community structure, assembly, and dynamics. While successional communities serve as useful model systems to address fundamental community drivers common to all plant communities, they are also particularly useful in guiding restoration efforts (Luken 1990; Cramer & Hobbs 2007; Walker et al. 2007). The purpose of this paper is to specifically focus on the unique contribution of successional systems to our understanding of invasion biology and to the remediation of such invasions.

Successional communities as model systems

Several factors make successional communities ideal model systems to understand plant invasions. Most important of these is that successional systems constrain all species to the role of colonizer. In most invasions, a new species moves into an established plant community with an existing resident plant population. When comparing the dynamics of two species in different phases of population growth (expansion vs. maintenance), it is not surprising that the colonizing species often exhibits different population dynamics than resident species. In contrast, successional systems place all species, native and non-native alike, in the same phase of population expansion. Therefore, comparisons between species of differing origin can be made on an equivalent basis.

Focusing on successional dynamics also alleviates the confounding factors generated by comparing sites of varying disturbance regimes, where the patterns of invasion may reflect direct species interactions, differential response to disturbances, or a combination of the two (Hobbs 1989; Sax & Brown 2000; Huston 2004). Successional systems are also valued as model systems because of their relatively rapid rates of community turnover compared to other community types (Prach et al. 1993; Myster & Pickett 1994). While preservation of disturbed systems is not generally a conservation concern, successional systems will provide information within reasonably short time spans that can be applied to the management of other plant communities of more conservation value. This application will be especially important for plant communities that would be slow to show the impacts of invasion because of low rates of turnover.

Finally, successional systems are useful in the study of invasions because of the global ubiquity of post-agricultural and other disturbed landscapes. By understanding the role of invasions in successional systems, we learn about a sizeable and growing land area. Successional communities are also characteristically heavily colonized by non-native species (Rejmánek 1989; Robertson et al. 1994; Kotanen et al. 1998; Stapanian et al. 1998). The dominance of non-native species is particularly evident early in succession, as the abundance of non-native species often declines with time (Inouye et al. 1987; Bastl et al. 1997; Meiners et al. 2002). The availability of a diverse assemblage of native and non-native taxa provides a powerful research context for understanding the role of non-native species within communities, particularly with the presence of dominant non-natives.

The utility of a whole-community approach to invasion

While most studies of non-native plants focus on one or a few problematic species, there is a real need to examine invasion from a whole-community approach. There have been many studies that compare the performance of native and non-native species, often based on species co-occurrence within communities or on congeneric pairs (e.g., Hamilton et al. 1999; Bossdorf et al. 2004; Huston 2004; Vilà & Weiner 2004). One generality to emerge from these studies is that non-native plant species often outperform native taxa within recipient communities. However, this generalization may be biased by the selective study of particularly problematic non-native plant species (Vilà & Weiner 2004). By focusing research efforts on those non-native species that we perceive to be threats to existing plant communities, we may bias results towards highly successful species that are not characteristic of the majority of the non-native community. The potential for this bias can be seen in studies that have attempted to look at a much broader suite of species where differences between native and non-native species are not apparent (Thompson et al. 1995; Daehler 2003).

In looking at the entire assemblage of species present within a community, it is also necessary to compare ecologically similar species. As species within a life form share the same broad life-history characteristics and tradeoffs (Grime 2001), focusing analyses on variation within such groupings should yield ecologically meaningful results. For example, ruderal species are often broadly distributed and over-represented in non-native floras because of their association with agricultural practices and disturbance (Chocholouskova & Pyšek 2003). While comparing an entire suite of species would likely show net differences between native and non-native assemblages, the appropriate comparison would be between native and non-native ruderal species. Since plant communities are often challenged by multiple species of invaders, it is logical to study invasion at a similar ecological scale. Also, a whole-community approach is more likely to yield information important to land managers, particularly for species new to a region (Parker et al. 1999; Byers et al. 2002).

Are native and non-native species similar?

Whether non-native species differ functionally from natives is a fundamental question in invasion biology that has been present in the ecological literature since the earliest comments on species invasions. The success of non-native plant species relative to native taxa has been explained through numerous hypotheses including: escape from natural enemies (Keane & Crawley 2002; Wolfe 2002), evolution of increased competitive ability (Blossey & Notzold 1995), possession of unique physiological attributes (Vitousek et al. 1987; Sala et al. 1996; Fargione et al. 2003), competitive superiority (Collins & Wein 1993; Daehler 2003), phenotypic plasticity (Schweitzer & Larson 1999; Hulme 2008), and faster growth rates (Milberg et al. 1999) among others. If non-native species are generally superior to native species, then these advantages should lead to differences within communities such as increased growth rates or relative abundance.

In contrast to focusing on the differences between native and non-native species is the view that both groups draw from the same pools of traits and population limitations (Thompson et al. 1995; Smith & Knapp 2001; Huston 2004), and are governed by the same underlying ecological tradeoffs (Grime 2001). Based on this perspective, we would expect overall similarity between native and non-native assemblages and for most non-native species to become innocuous residents within native communities (Ortega & Pearson 2005). To address these contrasting views, we will first explore a conceptual framework of successional change and its utility in organizing our understanding of invasion; second, provide a brief overview of the Buell-Small Succession Study, the source of the data that will be utilized to address these questions; third, compare the population dynamics of native and non-native species; and finally, place our result in a restoration context to point out management opportunities.

Community change

To understand invasion in the context of succession, it is necessary to conceptually organize the various drivers of community change. Here, we employ a hierarchical conceptual model of community change (Pickett & McDonnell 1989; Pickett & Cadenasso 2005) consisting of three ecological levels: (1) site conditions and history, (2) differential species availability, and (3) differential species performance (Pickett et al. this issue). Within this model framework, each level constrains the processes that occur at lower ecological levels. The first level within this framework, site conditions and history, sets the base conditions for all dynamics that occur within a system. In succession, this level encompasses the timing and conditions of abandonment, the agricultural history of the site (particularly soil fertility and structure), and the environmental conditions at the time of abandonment.

The site conditions and history set the stage for the propagules persisting in and arriving to the site. The next level, differential species availability, determines which species will be present within the community. Species availability is determined by the location of reproductive individuals within the landscape, the vagility of dispersing propagules, the timing of reproduction, and the persistence of propagules in the soil. Once the species pool is set, the ecological sorting of species may begin. At this third ecological level, differential species performance determines the internal dynamics of the system and generates the species turnover characteristic of succession. These processes include, but are not limited to, competition, variation in life histories, herbivory, and chemical interactions among plants. As we are interested in understanding whether native and non-native species function similarly within successional communities, we will focus predominantly on differential species performance in this study. However, we will also need to explicitly deal with the constraints imposed by the species pool.

Buell–Small Succession Study (BSS)

A permanent-plot study of old field succession was initiated by Murray Buell, Helen Foote Buell, and John Small in the Piedmont region of New Jersey, USA. This landmark study has continued uninterrupted for 50 years, making it the longest continuous study of post-agricultural secondary succession. The study consists of ten fields, each containing 48 permanently marked 1-m^2 plots. The fields were abandoned over an 8-year span and with a variety of pre-abandonment agricultural treatments. Fields were sampled every year until 1979, when sampling was switched to alternate years, with half of the fields sampled each year. At each sampling, the percentage cover of all species present in each plot is recorded. While variation in pre-abandonment conditions resulted in some differences in early successional dynamics (Myster & Pickett 1990; Myster & Pickett 1994), the close proximity of all ten fields minimizes the importance of site conditions and history in determining invasion within the BSS. Similarly, the species pool dispersing to the individual fields should be relatively homogeneous across the site. Specific details of the study and the site may be found elsewhere (Buell et al. 1971; Pickett 1982; Meiners et al. 2007).

The successional transitions within the BSS represent a fairly typical successional trajectory for the eastern deciduous forests of the Eastern United States (Fig. 1a). Early stages are dominated by short-lived, herbaceous species, which are quickly replaced by perennial herbs. After 20 years of successional change, woody species (shrubs, lianas, and trees) were the dominant life forms, with trees becoming dominant by 30 years after abandonment. As the BSS fields have nearly completed the transition from open agricultural land to a young forested system, the species present also represent a broad range of species. Similarly, the population dynamics of these species represent responses to the full range of conditions present within succession. This diversity of species and ecological strategies is critical, as any whole-community study must include as wide a range of variation as possible to avoid selection bias and to increase the generality and robustness of conclusions.

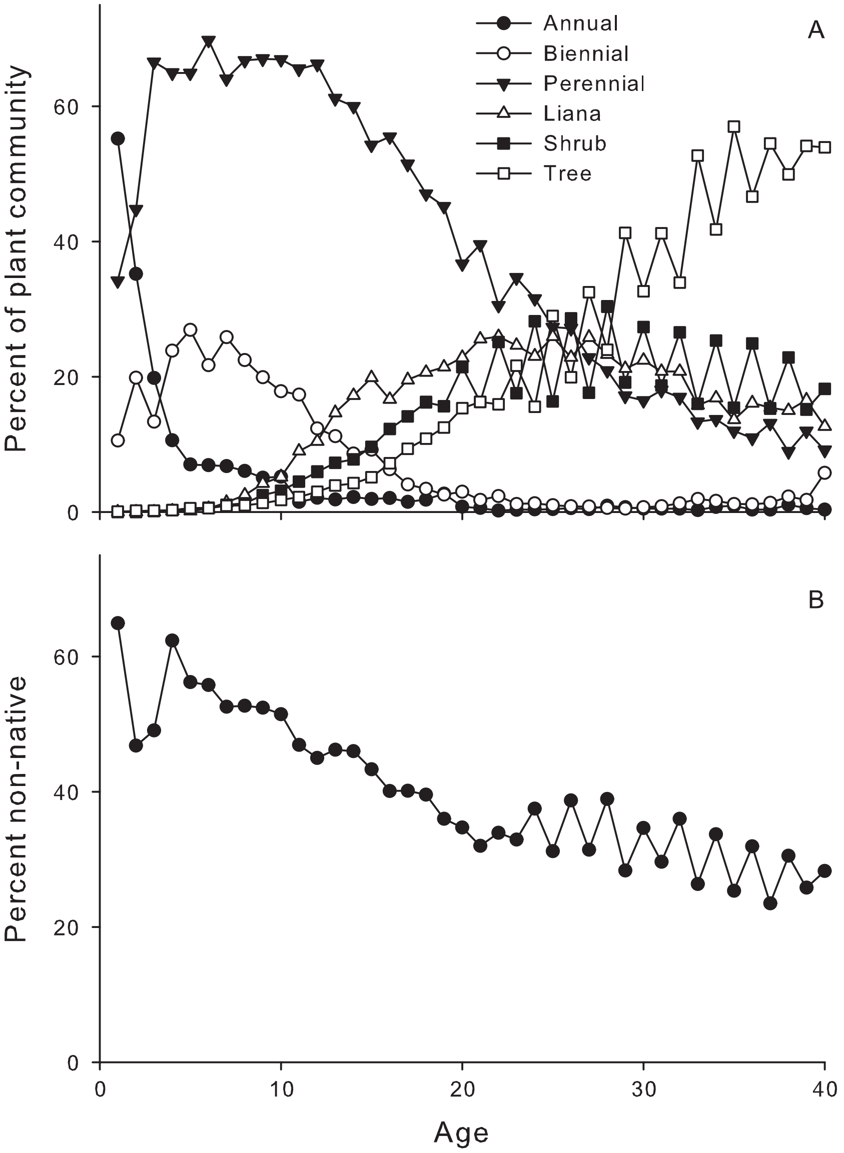

Fig. 1. Changes in life form (**a**) and relative abundance of non-native species (**b**) over 40 years of succession. Data presented are cover values summarized across all ten fields of the Buell–Small Succession Study. Oscillations past year 20 result from the switch to alternate year sampling.

The large transitions in the structural composition of the community also result in large changes in species origin during succession (Fig. 1b). Early stages were dominated by non-native species. During succession, the relative abundance of non-native taxa declined dramatically, showing a nearly 50% reduction over the first 40 years of succession. While the data presented here are based on cover estimates, there were similar declines in non-native species as a percentage of the species pool (Meiners et al. 2002). This decline in non-native taxa with succession is largely due to the dominance of the ruderal portion of the species pool by non-native taxa.

The species pool of the BSS is also depauperate in non-native woody species. Two non-native species, the shrub *Rosa multiflora* and the liana *Lonicera japonica*, contributed large amounts of cover to the system. However, there were no non-native tree species abundant enough to quantify their population dynamics. The lack of late-successional woody species further contributes to the decline of non-native species with succession. Because of the agricultural history of the site and the surrounding landscape, the majority of non-native species were dependent on open site conditions and benefit from the continual disturbance associated with agriculture. This agricultural context skewed the species pool available for later successional stages towards native taxa. However, the decline in the abundance of non-native species does not represent differential performance between native and non-native taxa. Instead, this transition is a constraint on dynamics imposed by species availability within the landscape. As large shifts in life form occur during succession, the bias in the species pool makes it even more important to compare differential performance within similar species groups.

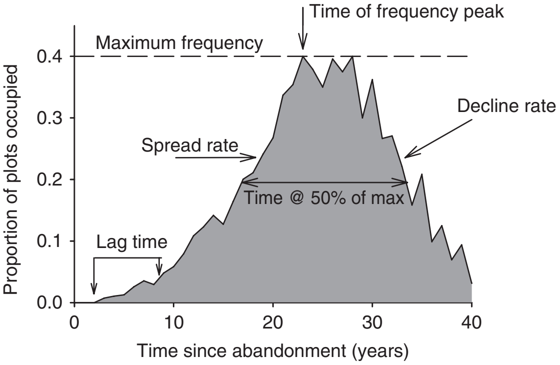

Fig. 2. An example of the metrics used to describe population dynamics using *Solidago canadensis*. The same metrics were also calculated using plot cover. Two other measures, peak dominance (total cover/total frequency) and the time of peak dominance, were also calculated.

Comparisons of native and non-native species

In order to directly assess differential species performance, we used the BSS permanent-plot data to document the population dynamics of all species that became abundant enough to generate quantifiable dynamics. This yielded a selection of 84 (32 non-native; 52 native) species that were abundant during all stages of old field succession. Fourteen of the non-native species were further characterized as invasive based on a composite list of species invasive within the US (http://www.plants.usda.gov, accessed 05.2008). The population dynamics of these species were described using 14 metrics based on species frequency and cover (Fig. 2 and Table 1; for details of analysis see Meiners 2007). These data were then analyzed using a principal components analysis to condense the population dynamics down to a few axes. The first two axes of this analysis explained 41 and 30% of the variation in population dynamics, respectively.

To compare ecologically similar groups of species, the data were separated into short-lived herbaceous (annual and biennial), perennial herbaceous, and woody (liana, shrub, and tree) species. While there were large differences among groups, within each of these groups the range of population dynamics was nearly identical for native and non-native species (Fig. 3). Despite the presence of the regionally invasive woody species – *Rosa multiflora* (shrub), *Celastrus orbiculatus* and *Lonicera japonica* (lianas) – the range of population dynamics in woody species was wholly contained within the range seen for equivalent native taxa. Similarly, within short-lived herbaceous species, two invasive species

Table 1. Variation in population dynamics among life forms. See Fig. 2 for explanations of the various metrics. Data presented are mean (SE).

Population metric	Annuals and biennials	Herbaceous perennials	Shrubs, trees, and lianas
Cover-based metrics			
Rate of increase (% cover/year)	4.5 (0.9)	2.5 (0.4)	5.7 (1.3)
Lag time (years)	1.7 (0.7)	2.7 (0.6)	10.7 (1.2)
Max. cover (%)	6.3 (1.2)	6.4 (1.1)	12.8 (2.8)
Year of cover peak	7.5 (2.3)	12.1 (1.6)	28.6 (2.0)
Span at 50% of max. (years)	3.1 (0.5)	8.0 (0.8)	13.3 (1.4)
Rate of decline (% cover/year)	3.9 (0.7)	2.5 (0.4)	6.7 (1.7)
Frequency-based metrics			
Rate of increase (plots/year)	24.2 (3.7)	13.6 (2.1)	16.3 (1.8)
Lag time (years)	1.5 (0.7)	2.0 (0.5)	8.6 (1.1)
Max. frequency (% of plots occupied)	40.0 (4.1)	36.6 (3.3)	41.9 (5.6)
Year of frequency peak	8.0 (2.4)	15.4 (1.9)	34.8 (1.3)
Span at 50% of max. (years)	6.1 (1.0)	16.9 (1.4)	16.8 (1.6)
Rate of decline (plots/year)	18.9 (2.1)	11.2 (0.8)	18.5 (1.9)
Dominance measures			
Max. dominance (%cover)	20.9 (2.8)	23.4 (2.5)	47.7 (5.3)
Year of dominance peak	9.5 (2.3)	12.1 (1.7)	26.8 (2.5)

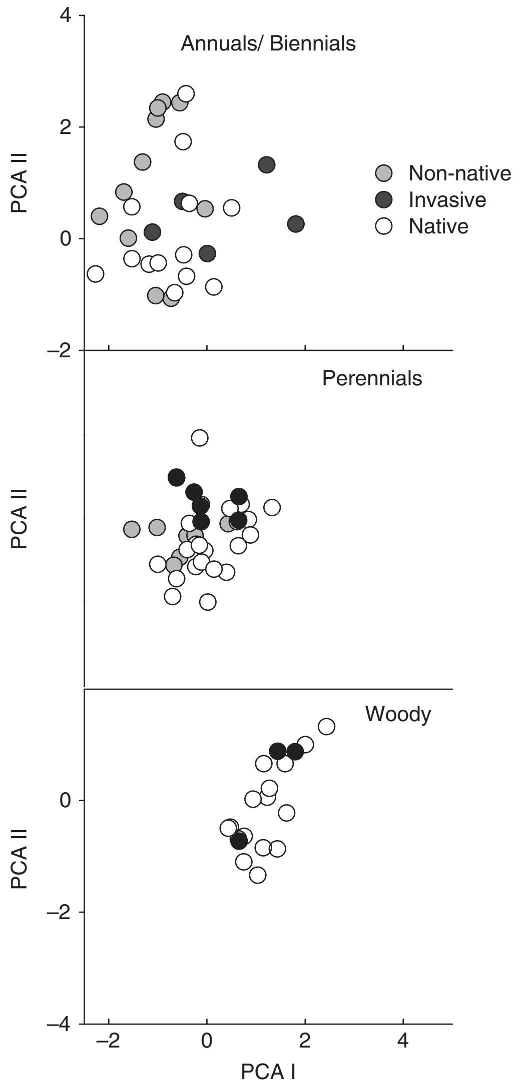

Fig. 3. Influence of species origin on the population dynamics of the 84 most common species within the BSS. Non-native species were subdivided into invasive and non-invasive taxa**.** Ordination plots of the 14 population metrics separated into life form groups from a principal components analysis.

characteristic of forested environments, *Alliaria petiolata* and *Microstegium vimineum*, had remarkably similar population dynamics to other short-lived herbs, except that they occurred later in succession (shifted to the right on axis 1). Within perennial herbaceous species, taxa categorized as invasive were separated slightly from non-invasive taxa, but were still within the range of population dynamics found in native species.

While species did not separate based on origin, there was a clear separation among life forms in their population dynamics (Table 1). In general, short-lived annual and biennial species peaked earlier in succession, were dominant for a relatively brief time period, and spread quickly throughout the fields with little to no population lag time. The population dynamics of woody species were much different, with slower rates of spread and lag times averaging 10 years. However, these species peaked much later in succession and dominated the communities for much longer time periods. Herbaceous perennial species were mostly intermediate between the short-lived herbs and the woody species.

Overall, we could find no systematic differences in how native and non-native species performed within this successional community. However, the species pool was selectively biased towards early successional non-natives based on the agricultural history of the site and the surrounding landscape. Separating out influences of differential species availability from differential species performance was critical in understanding invasion in this system, as this bias would have translated to non-native species as a whole having population dynamics more similar to ruderal species. Of course, sites with different histories of species introduction may have non-native species pools that are biased in different ways. For example, areas where the main pathway for invasion has been via horticultural spread of ornamental plants would not be expected to have high abundances of ruderal species, but would instead be biased towards perennial and woody species. It is imperative that all large-scale comparisons of native and non-native taxa take into account basic variation among life forms to ensure comparison of equivalent species.

Lessons for restoration

As succession and restoration have long been thought to be tightly linked processes (Clements 1949), increased understanding of the behavior of non-native species in successional systems should also generate information applicable to system management. The following lessons for restoration emerge from this summary of species within the BSS data.

Similarity of population dynamics

While individual species, native or non-native, may have unique combinations of traits that make them more successful than other similar species, these differences were not prevalent enough to generate systematic differences based on origin. This is not to say that all species were functionally the same, as there was much variation within each life form. The ecological similarity of native and non-native species also results in similar successional roles. Even the most invasive species in this survey, the shrub *Rosa multiflora* and the liana *Lonicera japonica*, appear constrained to mid-successional habitats. Both species peaked about 20 years post-abandonment and have been decreasing in abundance for the last decade, as would be expected for shade-intolerant woody species. Management interventions in successional systems should be reserved for species that prevent successional transitions or have the ability to persist in late successional habitats.

Life form variation in population dynamics

One clear pattern seen in the population dynamics data is that life forms differ in consistent and predictable ways. While variation among life forms is not unexpected, it does provide a mechanism for assessing management priorities when other information on invasiveness is lacking. Annual and biennial species should always be high management priorities, even when they first appear within a site. Rapid spread will make these species difficult to contain if they pose management issues. In contrast, the slower spread of woody species in combination with the longer lag times of their populations will allow managers at least a few years to assess the potential risk posed by the invasion.

Primacy of the species pool

We can see clear influences of the regional species pool in this study. The BSS has an over-representation of shade-intolerant, early successional species, as would be expected in a primarily agricultural system. This bias in the species pool largely constrained the non-natives to early and mid-successional roles. Land managers must be aware not only of the species within their management area, but also of species in the surrounding landscape and those that may be introduced.

Conclusions

As successional systems are globally common and often heavily invaded, they are critical to our understanding of invasion. Successional systems provide key situations to compare native and non-native taxa without selection bias. Furthermore, successional systems are unique in that they constrain all species to the role of colonizer. This simple fact allows comparisons of equivalent processes to be generated. By exploiting the distinctive benefits of successional systems, we show remarkable similarity between native and non-native taxa in their population dynamics. From a theoretical perspective, these results argue for the overall equivalency of native and non-native taxa and that mechanisms of dominance should be common to all plant species. The issue of similarity between native species and their introduced counterparts is not a new one, nor is it likely to be resolved soon. However, it is an issue central to invasion biology that must be addressed.

Acknowledgements. P. Frey, L. Ladwig, N. Morris, B. Nott and N. Pisula provided valuable comments on previous versions of this manuscript. This research was supported by NSF grant DEB-0424605 and both the Council on Faculty Research and the Graduate School of Eastern Illinois University.

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Received 12 February 2008;
Accepted 2 June 2008
Co-ordinating Editor: M. Cadenasso.