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LETTER

Invasion impacts local species turnover in a successional system

Kathryn A. Yurkonis and Scott J. Meiners*
Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920 USA
**Correspondence: E-mail: cfsjm2@eiu.edu*

Abstract

Exotic plant invasions are often associated with declines in diversity within invaded communities. However, few studies have examined the local community dynamics underlying these impacts. Changes in species richness associated with plant invasions must occur through local changes in extinction and/or colonization rates within the community. We used long-term, permanent plot data to evaluate the impacts of the exotic vine *Lonicera japonica*. Over time, species richness declined with increasing *L. japonica* cover. *L. japonica* reduced local colonization rates but had no effect on extinction rates. Furthermore, we detected significant reductions in the immigration of individual species as invasion severity increased, showing that some species are more susceptible to invasion than others. These findings suggest that declines in species richness associated with *L. japonica* invasion resulted from effects on local colonization rates only and not through the competitive displacement of established species.

Keywords

Community dynamics, diversity, exotic species, *Lonicera japonica*, population dynamics, preemptive competition, species turnover.

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INTRODUCTION

Invading species alter plant community structure and composition through influences on ecosystem processes (Vitousek *et al.* 1987), alteration of disturbance regimes (Mack & D'Antonio 1998) and interspecific interactions (D'Antonio *et al.* 1998). In some instances, invasion results in reduced local diversity (Rejmánek & Rosén 1992; Meiners *et al.* 2001). Declines in diversity are typically thought to occur through direct competitive displacement of established resident plants by the invader (Parker *et al.* 1999). Alternatively, inhibition of seedling germination and establishment by a resident invader may reduce diversity (Crawley *et al.* 1999). However, these mechanisms have not been evaluated because of limited long-term data on the impacts of invasion on community dynamics (Parker *et al.* 1999; Byers *et al.* 2002). This is the first study to directly assess the mechanisms of invasion impacts through local community dynamics.

Species richness at any scale is maintained through a balance between colonization and extinction rates (MacArthur & Wilson 1967). Therefore, reductions in diversity following invasion must result from changes in colonization and/or extinction rates at community (MacArthur & Wilson 1967; Ouborg 1993) and population scales (Levins 1969; Ouborg 1993). However, this dynamic perspective has not been applied to invasion studies, preventing the mechanism(s) of invasion impacts from being determined (Byers *et al.* 2002).

To address this critical need, we quantified local turnover dynamics during invasion of a successional system by *Lonicera japonica* Thunb. *L. japonica* is a highly competitive vine introduced from Asia in the mid-1800s that has spread throughout the eastern and central United States and appears to affect community structure (Friedland 1982; Dillenburg *et al.* 1993; Meiners *et al.* 2001). We used long-term data on community dynamics to ask the following questions: (1) Does local species richness decrease in association with *L. japonica* invasion?, (2) How does invasion affect local colonization and extinction rates? and (3) Do the impacts of invasion fall evenly across all common species? We pose this study as a potentially useful protocol for assessing invasion impacts in a mechanistic manner.

METHODS

Data collection

We used data collected on *L. japonica* invasion of abandoned agricultural land in the Piedmont region of NJ, USA

(40°30′ N, 74°34′ W) as part of the Buell–Small Succession Study (BSS), initiated in 1958. The study site consists of 10 agricultural fields abandoned in pairs from 1958 to 1966 that varied in the season of abandonment, last crop and plowing regime (Myster & Pickett 1990). Within each of the 10 fields, 48 permanently marked 0.5 × 2.0 m plots were established immediately after abandonment (Pickett 1982). In each year (alternate years since 1979), the percent cover of all species present in each plot was recorded. Because cover was assessed for each species individually, total cover within a plot often exceeds 100%, reflecting overlapping plant canopies. Therefore a plot with 100% *L. japonica* is completely covered by the invader, but could also contain several other species, particularly ones that are supporting the vine. These data represent the longest continuous data set on post-agricultural successional change known. Nomenclature follows Gleason & Cronquist (1991).

Data analyses

To evaluate vegetation dynamics in response to invasion, we looked at changes in plot composition occurring between time of the initial invasion (5 years post abandonment: T_5) and peak of *L. japonica* cover (15 years post abandonment: T_{15}) based on coverage across the site (Table 1). We used the change in *L. japonica* cover in each plot ($T_{15}-T_5$) as a measure of invasion magnitude. Analyses were limited to invaded plots to eliminate confounding effects of species richness on invasibility (Meiners *et al.* 2004).

Community dynamics

To document *L. japonica* impacts on local community structure, we related changes in species richness to the magnitude of *L. japonica* invasion for each plot (Meiners *et al.* 2001). Although fields accumulated species over this time period there was no change in the average species richness per plot (Meiners *et al.* 2002). We calculated net change in species richness as the difference between richness at T_{15} and T_5 within each plot. The relationship between magnitude of invasion and change in species richness was analyzed using an ANCOVA using field identity as a categorical variable. Colonization and extinction rates were calculated for each plot as the number of new species gained or lost between T_5 and T_{15}. Because of the timing of data collection (mid summer) and our inability to follow individuals, we cannot separate seedling germination from establishment processes. These data are representative of the majority of successful colonizations because new germinants are mostly well established by the time of mid-summer vegetation sampling. Although multiple colonization and extinction events may have occurred over the invasion time period, our measures of colonization and extinction reflect net changes in community composition. The utility of this approach is that it would tend to only include successful colonizations (or extinctions) rather than including all unsuccessful events. As before, ANCOVA was used to simultaneously evaluate field identity and *L. japonica* impacts.

Table 1 Average cover and number of plots invaded by *Lonicera japonica* at the beginning, (5 years post abandonment) and end of the observation period (15 years post abandonment), within the 10 fields of the Buell–Small Succession study. Each field contains 48 plots

	% Cover (plots)	
Field	T_5	T_{15}
C3	0.0 (0)	23.1 (27)
C4	0.8 (5)	31.8 (33)
C5	0.1 (1)	37.0 (46)
C6	0.0 (0)	2.0 (5)
C7	0.0 (0)	4.3 (17)
D1	<0.1 (1)	30.8 (32)
D2	<0.1 (1)	4.4 (6)
D3	0.0 (0)	17.0 (22)
E1	<0.1 (1)	27.0 (24)
E2	0.0 (0)	21.7 (17)

Population dynamics

Colonization rates were also determined for *individual* species. Species that colonized 100 or more of the 480 plots during the study period were selected as commonly colonizing species. This selection was based upon a natural break in the frequency of plot colonization. Although potentially important to assessing local response to invasion, species with lower colonization frequencies were not assessed within this study because of the low statistical power associated with these comparisons. Local colonization rates were determined individually for the 13 species that met this criterion. Logistic regression was used to relate species colonization probability to change in *L. japonica* cover in each plot. Relationships with individual species extinction rates were not examined because *L. japonica* impacts were only found for colonization events at the community level.

RESULTS

Community dynamics

Local species richness declined with *L. japonica* invasion intensity ($F_{1,207} = 4.118$; $P = 0.044$; $R^2 = 0.433$; Fig. 1). Average plot richness remained constant over the invasion period at 13 species, but varied greatly with invasion. Plots

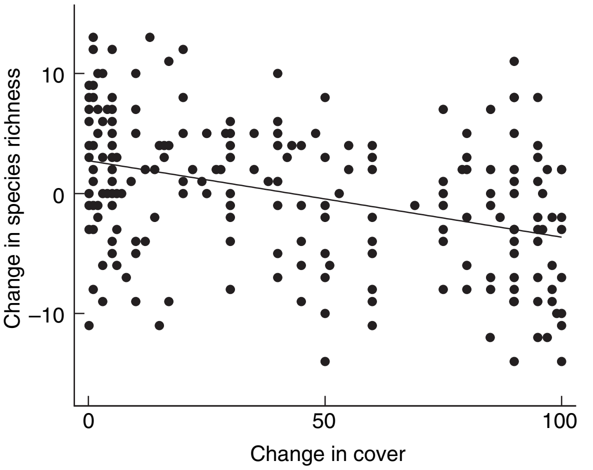

Figure 1 Net change in species richness with increase in *Lonicera japonica* cover.

with limited *L. japonica* invasion gained on average three species over the invasion period, while heavily invaded plots lost an average of three species. This represents a net decline of six species (46%) over the invasion period in heavily invaded plots relative to minimally invaded counterparts. There was no interaction with invasion and field identity ($F_{9,207} = 1.208$; $P = 0.291$). However, field significantly influenced change in species richness ($F_{9,207} = 6.667$; $P < 0.001$) within this model.

Local colonization rates were affected by both field identity ($F_{9,207} = 3.592$; $P = 0.0004$) and *L. japonica* invasion ($F_{1,207} = 5.958$; $P = 0.015$) with no interaction ($F_{9,207} = 1.208$; $P = 0.292$; model $R^2 = 0.319$; Fig. 2). Local extinction rates were also influenced by field identity ($F_{9,207} = 2.937$; $P = 0.003$) but were independent of *L. japonica* invasion ($F_{1,207} = 2.682$; $P = 0.103$), and their interaction ($F_{9,207} = 0.940$; $P = 0.492$; model $R^2 = 0.234$; Fig. 2). Thus local colonization rates decreased with *L. japonica* invasion while local extinction rates remained constant over the 10-year invasion period.

Population dynamics

Of the 13 commonly colonizing species, six showed significant declines in probability of local colonization as *L. japonica* invasion increased (Fig. 3). Species that responded to invasion included the native forbs *Achillea millefolium* (Wald $\chi^2 = 9.248$; 1 d.f.; $P = 0.002$), *Aster pilosus* (Wald $\chi^2 = 6.684$; 1 d.f.; $P = 0.010$), *Euthamia graminifolia* (Wald $\chi^2 = 5.076$; 1 d.f.; $P = 0.024$), *Oxalis stricta* (Wald $\chi^2 = 9.261$; 1 d.f.; $P = 0.002$), and *Solidago rugosa* (Wald $\chi^2 = 8.661$; 1 d.f.; $P = 0.003$) and the exotic shrub *Rosa multiflora* (Wald $\chi^2 = 6.650$; 1 d.f.; $P = 0.010$). Additional species analyzed that were not affected by invasion included: herbaceous perennials – *Fragaria virginiana* and *Solidago juncea*, lianas – *Parthenocissus quinquefolia* and *Toxicodendron radicans*, a grass – *Poa compressa*, and exotic forbs – *Daucus carota* and *Hieracium caespitosum*.

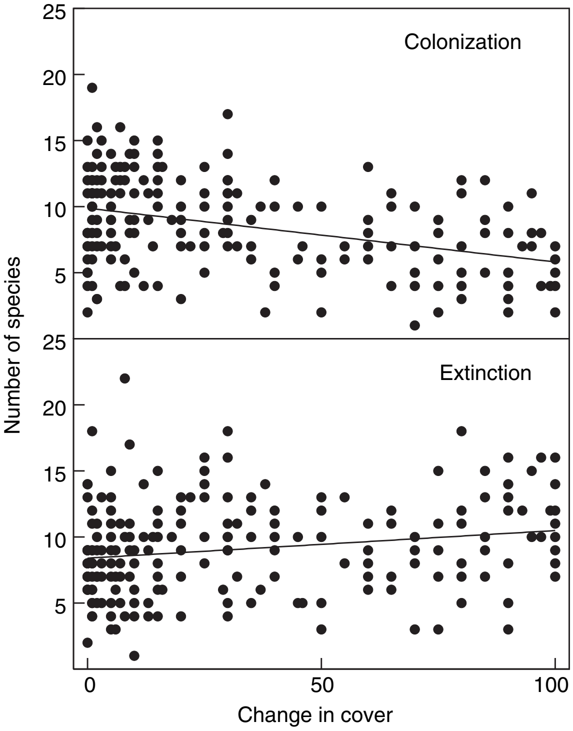

Figure 2 Response of community colonization and extinction rates to change in *Lonicera japonica* cover. Rates calculated as the number of species gained or lost over the 10-year time frame of *L. japonica* invasion.

DISCUSSION

In this study, *L. japonica* was clearly associated with reductions in local diversity. However, this did not occur through increased extinction rates, but through decreased colonization rates – suggesting that pre-emptive competition limiting immigration was the primary mechanism controlling invasion effects on local diversity (Schoener 1983; Crawley *et al.* 1999). While *L. japonica* probably competes with other resident species for resources, we found no evidence that interactions with residents altered local dynamics.

Site was consistently a strong determinant of local dynamics within these models. These site differences can be explained by variation in successional trajectories as a result of differences among the fields in initial abandonment conditions and agricultural histories (Myster & Pickett 1990). These differences resulted in compositional differences and internal dynamics that persisted throughout the

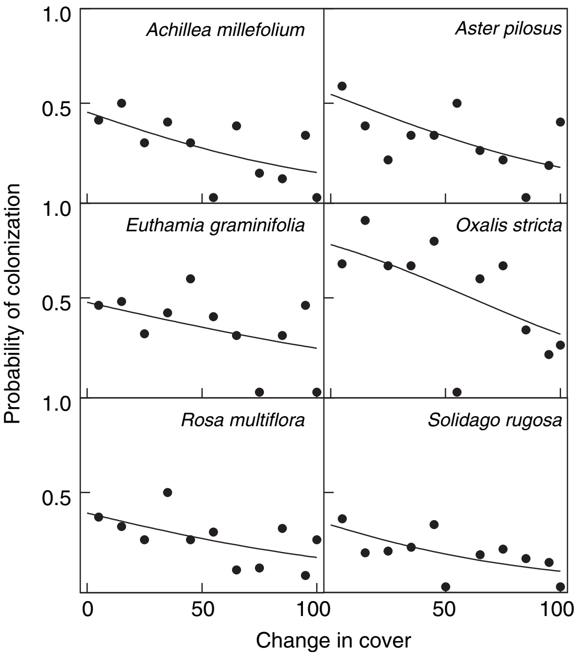

Figure 3 Response of population colonization rates to change in *Lonicera japonica* cover. Rates calculated as the number of plots colonized by each species over the 10-year time frame of *L. japonica* invasion. Lines represent model predictions from logistic regressions. Points represent the proportion of plots colonized summarized in 10% cover increments. Only those species with significant relationships are shown.

time period analyzed in this study. Most importantly, site had no interactions with *L. japonica* invasion suggesting that impacts were consistent across these divergent fields.

Community dynamics

Reduced local colonization rates in association with *L. japonica* invasion may be caused by a variety of environmental and demographic factors that control seedling germination and establishment. These controls include reductions in light or nutrient availability to levels that inhibit seed germination and establishment (Tilman 1993; Knops *et al.* 1999; Symstad 2000) or the development of thick litter layers that form a barrier to emerging seeds (Tilman 1993). Declines in species richness may also be caused by the saturation of available microsites for establishment by propagules of the invading species (Brown & Fridley 2003).

The most probable mechanisms of *L. japonica* impacts are those controlling resources available for colonizing species. Light and soil resource availability (Tilman 1993; Burke & Grime 1996; Knops *et al.* 1999; Cahill 2003) have been shown to regulate colonization success in many systems. As seedlings would be the demographic stage most susceptible to limiting resources, small changes in available resources may dramatically decrease establishment (Crawley *et al.* 1999; Cahill 2003). Thus changes in resource availability with invasion should have a greater effect on colonizing species than resident species. Other mechanisms of invasion impacts seem much less likely to be important in this system. *L. japonica* does not produce a thick litter layer that would function as a barrier to colonizing species, although it may function as a trap for litter of other species. *L. japonica* seed set is severely limited by pollinator availability, constraining this species to largely spread vegetative (Larson *et al.* 2002). Consequently, safe sites for seedling establishment should not be saturated, allowing the colonization of other species. At a larger scale, *L. japonica* does not appear to impact the reproductive effort of *Solidago rugosa* when in direct competition (Friedland 1982), suggesting that it may have few effects on overall propagule availability.

Population dynamics

The impacts of *L. japonica* invasion do not fall evenly across the community – only six of the 13 commonly colonizing species had decreased local colonization rates. There does not seem to be any pattern that determines which species were impacted. *Parthenocissus quinquefolia* and *Toxicodendron radicans* are functionally similar to *L. japonica*, both are prostrate or climbing woody plants that have relatively large, bird-dispersed seeds. Interactions between similar species are predicted to be stronger than those among species from other functional groups (Prieur-Richard *et al.* 2000; Symstad 2000). However, we find no evidence of *L. japonica* inhibiting establishment of these functional counterparts. The most probable explanation for differential impacts is that species vary in sensitivity to competition while seedlings (Cahill 2003).

Alternatively, colonizing species may have been locally dispersal limited (Tilman 1997; Levine 2000) resulting in decreased colonization rates. Species limited in distribution across the BSS could experience declining local colonization rates independent of invasion impacts. However, this seems unlikely since the species examined were, by definition, common across all BSS fields and no plot should have been far from a potential seed source.

CONCLUSIONS

Exotic species impacts on local dynamics are relatively unknown, yet have been identified as a valuable area of study to mitigate the effects of invasive species (Parker *et al.* 1999; Prieur-Richard *et al.* 2000; Byers *et al.* 2002). Temporally limited studies of invasion, however, have prevented adequate assessment of these questions (Parker *et al.* 1999;

Byers *et al.* 2002). This is the first study to specifically examine local species turnover dynamics in plant communities as a function of exotic species invasion and has resulted in two unexpected findings.

First, we find that the conventional mechanism of exotic species impacts – interactions between established plants and a new invader is not consistent with local dynamics in this system. Exotic species impacts were more subtle, affecting new species colonization, while leaving resident extinction dynamics unaltered. This suggests that studies investigating direct interactions between mature resident and invader species may not reveal invasion impacts. However, we do not rule out interactions with resident species as a mechanism of invasion impacts for other invaders or in other systems, particularly those strongly structured by competition. Second, we found no apparent linkage between the traits of locally colonizing species and whether they were affected by invasion. This suggests that it may be difficult or impossible to *a priori* determine which species in a community may be impacted by exotic species invasion.

We pose this analysis, directly linking invasion to local dynamics, as a useful protocol for assessing invasion impacts in any system. This analysis suggests probable mechanisms of impacts that can be directly assessed in experimental systems and that are critical to the development of functional mitigation programs. Furthermore, to adequately address the ubiquity of the invasion impacts on local dynamics seen in this study, these methods must be applied to long-term data from other systems.

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