Invasion impacts diversity through altered community dynamics

KATHRYN A. YURKONIS, SCOTT J. MEINERS and BRENT E. WACHHOLDER

Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920, USA

Summary

1 Invading plant species often alter community structure, composition and, in some instances, reduce local diversity. However, the community dynamics underlying these impacts are relatively unknown.

2 Declines in species richness with invasion may occur via displacement of resident species and/or reduction of seedling establishment by the invader. These two mechanisms differ in the demographic stage of the interaction.

3 We document turnover dynamics using long-term permanent plot data to assess the mechanism(s) of invasion impacts of four exotic species on a mixed community of native and exotic species. These mechanisms were evaluated at both the neighbourhood (1-m^2 plot) and population (individual species) scales.

4 During invasion, species richness declined with increasing invader cover for three of the four invaders. All invaders reduced colonization rates, but had no effect on extinction rates at the neighbourhood scale. Populations differed in their susceptibility to invasion impacts, with significant reductions in colonization for 10 of 25 (40%) species and increases in extinction for only 4 of 29 (14%) species.

5 At neighbourhood and population scales, influences of invasion on community dynamics were essentially the same for all invaders regardless of life-form. While individual resident species had some increase in extinction probability, community richness impacts were largely driven by colonization limitation.

6 The consistency of invasion impacts across life-forms suggests establishment limitation as a general mechanism of invasion impact. This common causal mechanism should be explored in other systems to determine the extent of its generality.

Key-words: colonization rates, community dynamics, extinction rates, exotic species, invasion impacts, species turnover

Introduction

Exotic species invasion is a biological disturbance affecting ecosystems worldwide, and in some cases invasion can have large effects. Invading species can affect the trajectory of invaded vegetation by altering natural disturbance regimes (Mack & D'Antonio 1998) and reducing diversity (Meiners *et al.* 2001). In addition, invasion can affect plant communities by altering resource dynamics (Vitousek *et al.* 1987; Ehrenfeld 2003) and interspecific interactions (D'Antonio *et al.* 1998; Christian & Wilson 1999). However, not all

species have these impacts; only a select few cause large changes within invaded communities (Williamson 1996; Levine *et al.* 2003). Despite the magnitude of invasions occurring across the world, the mechanisms underlying invasion impacts are not well understood (Blossey 1999; Parker *et al.* 1999; Byers *et al.* 2002; Levine *et al.* 2003).

Invasive species are often noted for their tendency to alter species richness within invaded communities (Rejmánek & Rosén 1992; Hager & McCoy 1998; Parker *et al.* 1999; Meiners *et al.* 2001). Proposed mechanisms explaining invader effects on community diversity can be divided according to the demographic stage that is impacted by the invasion. The invader can either affect resident species established within the community

Correspondence: Scott J. Meiners (tel. +1 217 581 3425; fax +1 217 581 7141; e-mail sjmeiners@eiu.edu).

(species displacement), inhibit the establishment of new individuals (establishment limitation), or both.

Resident species displacement, where plant invaders reduce local diversity by displacing established species, has been the most widely suggested mechanism of invasion impacts (Hager & McCoy 1998; Parker *et al*. 1999; reviewed in Levine *et al*. 2003). Such displacement may occur through resource competition where the invader more readily secures limiting resources (Schoener 1983; Tilman 1997), exhibits allelopathic effects that suppress neighbouring species (Callaway & Aschehoug 2000), or develops antagonistic soil microbial feedbacks (Bever 2003; Callaway *et al*. 2005).

Invasion can also affect the community via establishment limitation by reducing colonization success of resident species (Crawley *et al*. 1999; Cahill 2003; Seabloom *et al*. 2003; Hager 2004; Yurkonis & Meiners 2004). This may result from site saturation by invader propagules (Brown & Fridley 2003), which take up available germination sites, reducing establishment rates of other species. Similarly, reductions in resource availability have also been shown to reduce local establishment. Communities with relatively low levels of available resources are often resistant to the establishment of new colonists (Tilman 1993; Burke & Grime 1996; Knops *et al*. 1999; Davis *et al*. 2000; Symstad 2000; Cahill 2003; Cleland *et al*. 2004). However, increased resource availability has also been shown to decrease colonization rates (Stevens *et al*. 2004) through increasing stem density. Where competitive interactions shape community structure, invasion may more strongly inhibit colonization of species within the same functional group as the invader (Prieur-Richard *et al*. 2000; Symstad 2000; Fargione *et al*. 2003) due to more similar resource requirements. These potential effects of invasion may become magnified in systems already limited via dispersal of native seed (Seabloom *et al*. 2003), in highly fertile sites (Cleland *et al*. 2004; Stevens *et al*. 2004) or those recovering from disturbance events (Stampfli & Zeiter 2004) where re-colonization is limited.

Collectively, invasion impacts on communities, through any mechanism, have been documented with few species and mostly anecdotal evidence (Parker *et al*. 1999; Levine *et al*. 2003). In order to properly assess invasion impacts, local turnover dynamics in relation to changes in species richness must be examined within a system. Within communities, species richness is a balance between colonization and extinction rates (MacArthur & Wilson 1967) barring speciation events. Therefore, if an invading species causes a change in local species richness, this change must reflect a change in the balance between local colonization and extinction rates, and the turnover rates of individual species (Levins 1969; Ouborg 1993; Husband & Barrett 1996; Blomqvist *et al*. 2003).

By identifying how community dynamics change with invasion, we can then isolate the demographic stage of the interactions driving invasion impacts. Increased extinction rates reflect invasion interactions

with resident species and indicate that species displacement mechanisms drive invasion impacts. Decreased colonization rates reflect limitations on local establishment and indicate that invader–seedling interactions drive invasion impacts. Overall, the impact of invasion on community dynamics reflects net displacement and establishment limitation effects. Therefore even simple community associations may result from more complex underlying species interactions.

In this study we examined species turnover dynamics associated with four exotic species invasions to explicitly determine the mechanism(s) of invasion impacts on species richness. We calculated turnover dynamics based upon 46 years of vegetation data from a series of abandoned agricultural fields in the New Jersey Piedmont region. We used these data to determine: (i) Does invasion relate to changes in community species richness? (ii) If so, does invasion primarily change colonization and/or extinction rates? (iii) Do similar trends occur at the neighbourhood and population scales in the impact of invasion?

Methods

STUDY SYSTEM

We used data collected on the invasion of four exotic species into abandoned agricultural land in the Piedmont region of New Jersey, USA (40°30′ N, 74°34′ W) as part of the Buell-Small Succession Study (BSS). Initiated in 1958, the study consists of 10 agricultural fields abandoned in pairs over a period of 8 years (Buell *et al*. 1971; Pickett 1982). Fields differed in season of abandonment, last crop and final ploughing regime to assess the impact of different disturbance legacies on succession (Myster & Pickett 1990). Within each field, 48 permanently marked 0.5×2.0 m plots were established immediately after abandonment (Pickett 1982). In each year (alternate years since 1979), the percentage cover of all species present in each plot was recorded. As plants often have overlapping canopies, total plant cover may greatly exceed 100% within each plot. These data represent the longest continuous data set on post-agricultural successional change known. Nomenclature follows Gleason & Cronquist (1991).
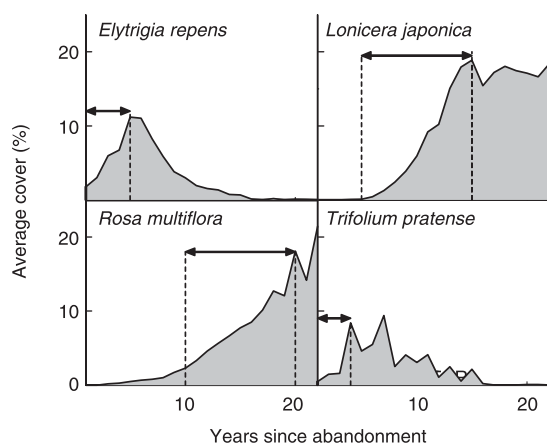
The successional dynamics of this system are well characterized. Of the 342 species identified within the study, 222 (65%) are native. Despite the variation in pre-abandonment conditions, the general successional trajectories of all fields are remarkably similar, though composition often varied dramatically as did the rate of successional change (Myster & Pickett 1990, 1994). While the fields accumulated species over successional time, the number of species in each 1-m² plot remained constant at about 13 species (Meiners *et al*. 2002). Interestingly, the total number of exotic species found in the fields also decreased over time. Because the majority of exotic species within the site are ruderals characteristic of agricultural systems, the abundance of exotic

species was initially high (> 50% relative cover) but has declined through succession to approximately 30% relative cover (Meiners *et al*. 2002).

A preliminary study of 14 native and 12 exotic taxa that became abundant during succession found only five species whose invasions were associated with declines in species richness (Meiners *et al*. 2001). These species included four exotics of Eurasian origin: *Elytrigia repens* (L.) Nevski. (perennial grass), *Lonicera japonica* Thunb. (liana), *Rosa multiflora* Thunb. (shrub), and *Trifolium pratense* L. (leguminous short-lived perennial herb), with only a single native species, *Solidago canadensis* L. (perennial herb). More detailed analyses, however, found no influence of *S. canadensis* on species richness, community colonization/extinction dynamics, or any individual resident species (K. A. Yurkonis, unpublished data). The current study therefore specifically focuses on the four exotic invaders to determine the mechanism(s) that generated their community-level impacts.

DATA ANALYSES

To evaluate community dynamics in response to invasion, we determined changes in plot composition between the time of the initial invasion ($T_{initial}$) and peak of invader cover (T_{peak}) based on average coverage and frequency across all invaded fields (Fig. 1). We then used change in invader cover ($T_{peak} - T_{initial}$) as a measure of invasion magnitude in each plot (Meiners *et al*. 2001; Yurkonis & Meiners 2004). The time of initial invasion represents when low frequency and cover of the invader was observed across the site, rather than, necessarily, the time of initial invasion within individual plots. Because fields varied in abandonment over an 8 calendar-year period, time was measured as years since abandonment. Study periods ($T_{initial}$ to T_{peak}) for each invader are as follows: *Elytrigia repens* 1–5 years since abandonment, *Lonicera japonica* 5–15 years since abandonment, *Rosa multiflora* 10–20 years since abandonment and *Trifolium pratense* 1–4 years since abandonment (Fig. 1).

While this results in differing sample periods for each invader, the resulting time periods closely match the life span and turnover of the resident species dominant during each invasion (Von Holle *et al*. 2003). Early invaders *E. repens* and *T. pratense* invaded systems dominated by short-lived species with relatively rapid turnover (5 years or less), while the later invaders *R. multiflora* and *L. japonica* invaded systems dominated by longer lived species with slower turnover (> 10 years). *Elytrigia repens* and *T. pratense* invaded four of the 10 fields while *L. japonica* and *R. multiflora* invaded all fields across the site. Because diversity is often associated with plot invasibility in this system (Meiners *et al*. 2004), analyses were limited to invaded plots for each species.

Analyses were conducted at two ecological scales, neighbourhood and population, to determine the mechanism(s) that generate invasion impacts within these successional fields. The neighbourhood scale, hereafter defined as the local community within each plot, is the scale at which species interact to generate invasion impacts. The neighbourhood scale was used to assess impacts of invaders on species richness, colonization rates and extinction rates. To determine the mechanism(s) responsible for neighbourhood level dynamics, population scale analyses were conducted. At the population scale, we examined species–species interactions to determine the influence of invasion on the colonization and extinction dynamics of individual resident species based on plot occupancy.

NEIGHBOURHOOD DYNAMICS

To document impacts of each invader on neighbourhood dynamics, we related the change in species richness ($S_{peak} - S_{initial}$) to the magnitude of invasion for each plot (Meiners *et al*. 2001; Yurkonis & Meiners 2004). The relationship between magnitude of invasion and change in species richness was analysed with ANCOVA using field identity as a categorical variable and invasion magnitude as a continuous one. Neighbourhood colonization and extinction rates were calculated for each plot as the number of new species gained or lost between $T_{initial}$ and T_{peak}. Although multiple colonization and extinction events may have occurred over invasion study periods, our measures of colonization and extinction reflect net changes in composition. The utility of this approach is that it would tend to only include successful colonizations (or extinctions) rather than including minor fluctuations. As before, ANCOVA was used to simultaneously evaluate field and invader impacts on dynamics. Analyses of the residuals for all comparisons did not indicate the need for any data transformations.

Fig. 1 Average plot cover of each invader through time in the Buell-Small succession study fields. Times of initial and peak invasion used within the study (invasion window) for each invader are denoted by arrows.

POPULATION DYNAMICS

Colonization and extinction rates were also determined for individual species, regardless of nativity, in

association with each invader. As successional systems are typically heavily invaded by exotic species (Bard 1952; Inouye *et al.* 1987; Rejmánek 1989; Bazzaz 1996), many of the residents examined are themselves naturalized exotics. This holistic approach generates a more realistic view of invader impacts than focusing solely on natives and ignoring Eurasian species that have become common constituents of the community. However, this model system may not provide results applicable to exotic invasions into previously uninvaded communities.

All species that colonized or went extinct in 100 or more of the 480 ($\geq 21\%$) plots during each invasion were selected for analysis. Species selection was based upon the natural break in frequency of plot colonization and extinction. Species below this break tended to invade or go extinct in relatively few plots. Less-frequent species, although potentially important in neighbourhood response to invasion, were not assessed within this study because of the weak statistical power associated with lower frequencies. Colonization/extinction rates were then determined individually for each species that met this criterion.

Colonization and extinction rates were calculated for each plot as the number of new species gained or lost between $T_{initial}$ and T_{peak} for each of the invaders. Although multiple colonization and extinction events may have occurred over the invasion period, our measures of colonization and extinction reflect net changes in community composition because we examined the endpoints only. The utility of this approach is that it would tend to only include successful colonizations (or extinctions) rather than including all unsuccessful events. Logistic regressions were used to relate probability of colonization/extinction for each species to invasion intensity in each plot. A Dunn-Sidák correction for multiple comparisons was used to adjust the significance criterion and results are reported at the $P = 0.10$ and $P = 0.05$ level. As these population patterns are used to explain dynamics at the neighbourhood scale, the lower significance criterion are included to identify potential interactions that generate net invasion impacts.

Results

NEIGHBOURHOOD RESPONSES TO INVASION

Neighbourhood species richness declined with invasion intensity for three of the four invaders (Fig. 2). *Trifolium pratense* ($F_{1,120} = 6.29$, $P = 0.013$, $R^2 = 0.471$), *Lonicera japonica* ($F_{1,207} = 4.12$, $P = 0.044$, $R^2 = 0.433$) and *Rosa multiflora* ($F_{1,180} = 6.91$, $P = 0.009$, $R^2 = 0.201$) all showed significant associations with declines in neighbourhood species richness during their invasions. There were no interactions between invasion intensity and field for any of the invaders. However, field was a significant determinant of change in neighbourhood richness during the *E. repens* ($F_{3,79} = 5.31$, $P = 0.002$,

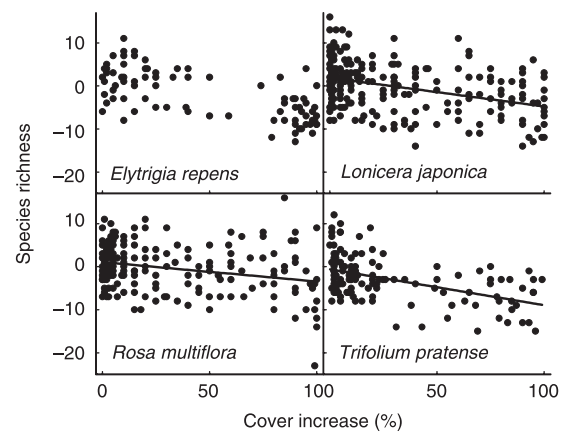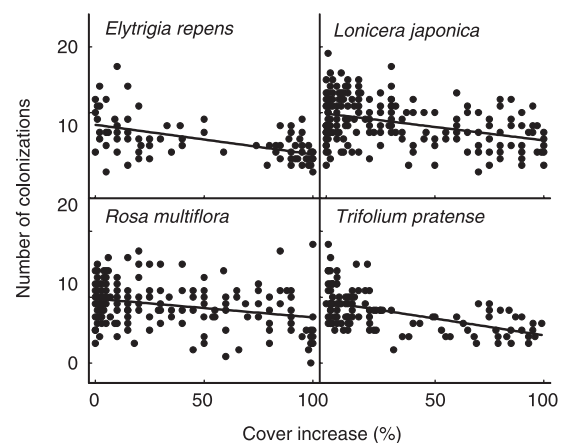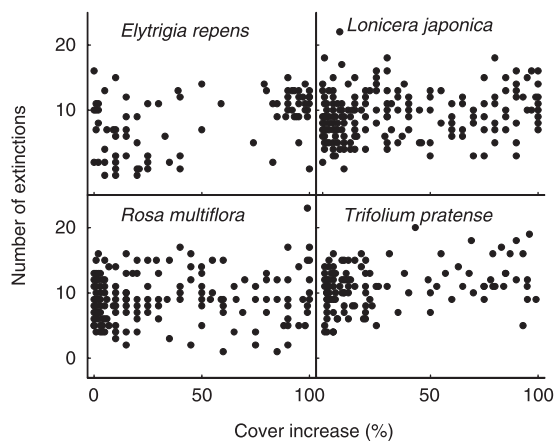**Fig. 2** Net change in species richness with increase in invader cover.

Fig. 3 Response of community colonization rates to change in invader cover. Rates calculated as the number of species gained or lost over respective invasion windows.

$R^2 = 0.684$) and *L. japonica* ($F_{9,207} = 6.67$, $P < 0.001$) invasions. The invasion of *E. repens* was not related to changes in species richness.

Neighbourhood colonization rates declined with increased invasion intensity for all species (Fig. 3; *Trifolium pratense*, $F_{1,120} = 4.15$, $P = 0.044$, $R^2 = 0.377$; *Elytrigia repens*, $F_{1,79} = 15.01$, $P < 0.001$, $R^2 = 0.739$; *Lonicera japonica*, $F_{1,207} = 5.96$, $P = 0.015$, $R^2 = 0.319$; *Rosa multiflora*, $F_{1,180} = 10.76$, $P = 0.001$, $R^2 = 0.154$). Field was a significant determinant of colonization rate in association with *E. repens* ($F_{3,79} = 29.51$, $P < 0.001$) and *L. japonica* ($F_{9,207} = 3.59$, $P < 0.001$) invasions though there were no interactions between invasion intensity and field for any of the exotic species. In contrast, neighbourhood extinction rates were not affected by any of the invasions (Fig. 4) and were solely determined by field (*Trifolium pratense*, $F_{3,120} = 2.81$, $P = 0.042$, $R^2 = 0.428$; *Elytrigia repens*, $F_{3,79} = 26.62$, $P < 0.001$, $R^2 = 0.770$; *Lonicera japonica*, $F_{9,207} = 2.94$, $P = 0.003$, $R^2 = 0.234$; *Rosa multiflora*, $F_{9,180} = 2.51$, $P = 0.010$, $R^2 = 0.271$).

Fig. 4 Response of community extinction rates to change in invader cover. Rates calculated as the number of species gained or lost over respective invasion windows.

POPULATION RESPONSES TO INVASION

Invasion was associated with declines in colonization rates for 10 of 25 (40%) common species (Table 1), following the neighbourhood level pattern. Invasions of *Lonicera japonica*, *Rosa multiflora* and *Trifolium pratense* were also associated with increased extinction rates for 4 of 29 (14%) species (Table 2). *Elytrigia repens* showed no effects on population extinction rates. All impacts, regardless of significance level, were negative and we found no facilitative interactions with invasion. Species affected by invasion either through decreased colonization rates or increased extinction rates primarily consisted of a variety of wind-dispersed perennials. Multiple invaders were found to influence turnover dynamics of individual resident species.

Discussion

Within this system, field was consistently important but did not confound invasion effects on community dynamics. Field effects on community dynamics most likely reflect legacies from different abandonment regimes and successional trajectories that lead to variation in composition across the site (Myster & Pickett 1990; Meiners *et al*. 2002). Despite variation among fields, we found no field × invasion interactions, suggesting that invasion impacts on community dynamics were consistent across fields.

NEIGHBOURHOOD RESPONSES TO INVASION

We found consistent impacts across life-forms of invaders. Invasion of an exotic grass, short-lived perennial, liana and shrub all yielded similar neighbourhood responses within this successional system. Neighbourhood species richness declined with increased invasion intensity as a result of decreased colonization rates, suggesting that most invasion impacts occur as new species become established. Although interactions with

Table 1 Results of logistic regression of colonization rates of common species with invasion intensity for four exotic species. Of all the species assessed, only species with significant associations are shown. Colonization rates and invasion intensity were assessed on a plot-by-plot basis for the invasion window selected for each species. Each term is associated with 1 d.f. Nativity and life-forms are indicated in parentheses following each species: N = native, E = exotic, A = annual, B = biennial/short-lived perennial, G = grass, L = liana, P = perennial, S = shrub, T = tree

Invader	Species	β	Wald χ^2
Trifolium pratense[1]	*Aster pilosus* (NB)	−0.026	7.893*
	Hieracium caespitosum (EP)	−0.038	8.396*
	Rumex acetosella (EP)	−0.021	6.756†
Elytrigia repens[2]	*Aster pilosus* (NB)	−0.029	8.774*
	Daucus carota (EB)	−0.027	7.251*
Lonicera japonica[3]	*Achillea millefolium* (NP)	−0.017	9.248*
	Oxalis stricta (NP)	−0.021	9.261*
	Solidago rugosa (NP)	−0.017	8.661*
Rosa multiflora[4]	*Juniperus virginiana* (NT)	−0.017	7.583†
	Poa compressa (EG)	−0.013	7.452†
	Solidago juncea (NP)	−0.017	12.157*

*Dunn-Sidák corrected *P* = 0.05; †Dunn-Sidák corrected *P* = 0.10.
Tested but non-significant species:
[1]*Acalypha rhomboidea* (NA), *Aster ericoides* (NP), *Calystegia sepium* (NP), *Daucus carota* (EB), *Erigeron annuus* (NA), *Oxalis stricta* (NP) and *Taraxacum officinale* (EB).
[2]*Acalylpha rhomboidea* (NA), *Aster ericoides* (NP), *Aster lanceolatus* (NB), *Calystegia sepium* (NP), *Erigeron annuus* (NA), *Hieracium caespitosum* (EP), *Oxalis stricta* (NP), *Rumex acetosella* (EP) and *Solanum carolinense* (NP).
[3]*Aster pilosus* (NB), *Daucus carota* (EB), *Euthamia graminifolia* (NP), *Fragaria virginiana* (NP), *Hieracium caespitosum* (EP), *Parthenocissus quinquefolia* (NL), *Poa compressa* (EG), *Rosa multiflora* (ES), *Solidago juncea* (NP) and *Toxicodendron radicans* (NL).
[4]*Euthamia graminifolia* (NP), *Fragaria virginiana* (NP), *Lonicera japonica* (EL), *Oxalis stricta* (NP), *Parthenocissus quinquefolia* (NL), *Rubus alleghiensis* (NS), *Solidago canadensis* (NP), *Solidago rugosa* (NP) and *Toxicodendron radicans* (NL).

established resident species appear much less important (Crawley *et al*. 1999; Cahill 2003; Yurkonis & Meiners 2004), this does not rule out species displacement as a mechanism of community-level change. Species such as *Trifolium pratense*, with marginal effects on neighbourhood extinction rates and impacts on individual species, may have stronger impacts in other systems.

A variety of environmental and demographic factors may be limiting establishment with invasion. These factors include reductions in light or nutrient availability to levels that inhibit seed germination and establishment (Tilman 1993; Knops *et al*. 1999; Symstad 2000; Cahill 2003; Brandon *et al*. 2004) or the development of thick litter layers that form a barrier to emerging seeds (Facelli & Pickett 1991; Tilman 1993). Reduced colonization rates may also be caused by the saturation of available microsites for establishment by propagules of the invading species (Brown & Fridley 2003). However, several

Table 2 Results of logistic regression of extinction rates of common species with invasion intensity for four exotic species. Of all the species assessed, only species with significant associations are shown. Extinction rates and invasion intensity were assessed on a plot-by-plot basis for the invasion window selected for each species. Each term is associated with 1 d.f. Nativity and life-forms indicated as in Table 1

Invader	Species	β	Wald χ^2
Trifolium pratense[1]	*Ambrosia artemisiifolia* (NA)	0.052	18.993*
Elytrigia repens[2]	–	–	–
Lonicera japonica[3]	*Rumex acetosella* (EP)	0.051	9.973*
Rosa multiflora[4]	*Daucus carota* (EB)	0.016	8.107†
	Oxalis stricta (NP)	0.019	10.069*

*Dunn-Sidák corrected *P* = 0.05; †Dunn-Sidák corrected *P* = 0.10.
Tested but non-significant species:
[1]*Acalyphya rhomboidea* (NA), *Barbarea vulgaris* (EB), *Chenopodium album* (EA), *Digitaria sanguinalis* (EG), *Mollugo verticillata* (EA), *Portulaca oleracea* (EA), *Raphanus raphanistrum* (EA), *Setaria faberii* (EG) and *Verbascum blattaria* (EB).
[2]*Acalypha rhomboidea* (NA), *Ambrosia artemisiifolia* (NA), *Barbarea vulgaris* (EB), *Chenopodium album* (EA), *Digitaria sanguinalis* (EG), *Mollugo verticillata* (EA), *Plantago rugelii* (NP), *Portulaca oleracea* (EA), *Raphanus raphanistrum* (EA), *Setaria faberii* (EG) and *Verbascum blattaria* (EB).
[3]*Acalypha rhomboidea* (NA), *Allium vineale* (EP), *Ambrosia artemisiifolia* (NA), *Aster ericoides* (NP), *Aster pilosus* (NB), *Calystegia sepium* (NP), *Dactylis glomerata* (EG), *Daucus carota* (EB), *Erigeron annuus* (NA), *Plantago lanceolata* (EP), *Plantago rugelii* (NP), *Silene latifolia* (EB) and *Solanum carolinense* (NP).
[4]*Acalypha rhomboidea* (NA), *Ambrosia artemisiifolia* (NA), *Aster ericoides* (NP), *Aster pilosus* (NB), *Calystegia sepium* (NP), *Cerastium vulgatum* (EP), *Erigeron annus* (NA), *Hieracium caespitosum* (EP), *Oenothera biennis* (NB), *Plantago lanceolata* (EP), *Poa pratensis* (EG), *Rumex acetosella* (EP).

of these factors can be discounted in this system. We do not find abundant seedlings of the invaders (S. J. Meiners, personal observations), suggesting propagule pressure is not influencing colonization dynamics and, with the possible exception of the grass *Elytrigia repens*, the invaders also do not produce a heavy litter layer that would inhibit seed germination (Bosy & Reader 1995). Finally, the common species studied do not appear to be dispersal limited and have the potential to colonize all open microsites (Seabloom *et al.* 2003; Yurkonis & Meiners 2004).

The most probable mechanism of impact is therefore invader control over available resources for colonizing species. Light and soil resource availability (Tilman 1993; Burke & Grime 1996; Knops *et al.* 1999; Davis *et al.* 2000; Cahill 2003; Stevens *et al.* 2004) have been shown to regulate colonization success in many systems. As seedlings would be the demographic stage most susceptible to limiting resources (Fenner 1987), small changes in available resources may dramatically decrease seedling establishment (Crawley *et al.* 1999; Cahill 2003) without affecting mature individuals.

Invasion impacts on population dynamics are similar to those on neighbourhood dynamics. Invasion was related to a decline in immigration for 40% of common species, while only 14% showed evidence of displacement with invasion. Although individual species showed displacement effects, these were not strong enough to influence the neighbourhood scale pattern. Individual population responses mechanistically explained neighbourhood dynamics and showed that the net impacts of an invasion may be generated primarily by establishment limitation rather than extinction (Levins 1969; Ouborg 1993; Blomqvist *et al.* 2003).

One explanation for differences between neighbourhood and population dynamics lies in the characteristics of the species that were assessed. Most of the species that exhibited increased extinction rates were short-lived ruderal species whose population dynamics are characterized by high extinction and recolonization rates (Grime 2001). It is possible that increased extinction rates for such species actually reflect decreased colonization rates within this system. If invasion inhibits resident species recolonization from source populations (rescue effect *sensu* Brown & Kodric-Brown 1977), absence of replacement is likely to lead to increased extinction being observed.

Individual species responses to invasion cannot be understood without assessing potentially obscured invasion impacts. Contrary to the preliminary study, we did not see declines in neighbourhood richness with *Elytrigia repens* invasion. However, this invader created significant changes in neighbourhood and population colonization rates. In this case, neighbourhood and population level effects did not translate into an overall change in species richness. Hence, the lack of a pattern in vegetation may erroneously suggest a lack of impact.

Most studies of invasion impacts do not account for the impacts of several invaders to determine the net effects of invasion on a system, although many systems are challenged with multiple invasions (Simberloff & Von Holle 1999). Within our analyses, we found relationships between multiple invaders and both native and exotic resident species. For example, invasion by each of the early invaders depressed colonization of *Aster pilosus* Willd., a common early successional species. Similarly, colonization rates of *Rumex acetosella* L. were depressed by *Trifolium pratense* while extinction rates were increased by *Lonicera japonica*. Species interacting with multiple invaders would likely experience greater impacts within the system than those affected by only one invasion. Thus, in order to fully assess a resident species' status, invasion studies need to consider the impact of several invaders on resident populations.

We expected invasion to result in stronger effects on species of similar functional characteristics as a result of intense interactions among similar species (Prieur-Richard *et al.* 2000; Symstad 2000; Fargione *et al.*

2003). However, resident species in the same functional group (shrub, liana, etc.) were not disproportionately affected by invasion within this system. For example, *Lonicera japonica* had no effect on the colonization rates of other lianas (*Parthenocissus quinquefolia* (L.) Planchon. and *Toxicodendron radicans* (L.) Kuntze.) and Rosa *multiflora* had no effect on the other common shrub (*Rubus allegheniensis* T. C. Porter.). *Trifolium pratense* reduced colonization of *Aster pilosus* while showing no impacts on *Daucus carota* L. and *Taraxacum officinale* Webber ex. Wiggers., all biennials/short-lived perennials. The one significant interaction does not suggest systematically stronger interactions within functional groups.

An explanation for the lack of strong functional group interactions is that the invader could be colonizing sites unoccupied by the same functional group (Elton 1958; Fox 1987; Mack 2003). However, there is no evidence for this type of control on invasion within this system as invasions of the exotic species discussed here were not regulated by their functional counterparts (Meiners *et al.* 2004), as found by Von Holle & Simberloff (2004). Differences between our results and those in the literature are most likely attributable to differences in the dynamic nature of this study system. In successional systems species interactions tend to be over shorter periods and resource limitation shifts over time from soil nutrients to light availability (Tilman 1985).

Conclusions

We found a general mechanism for invasion impacts resulting from invader–seedling interactions. This result was consistent across several life-forms of invaders. We argue that using changes in species richness alone as a method of impact assessment will not adequately predict or describe the effects of invasion. Community level impacts may not reflect important impacts on dynamics of individual species. Furthermore, mitigation efforts must consider that population dynamics do not necessarily translate to community processes and vice versa. If invasion impacts are dominated by establishment limitation, mitigation efforts should be focused on maintaining establishment opportunities for resident species populations. While we specifically focused on the impacts of exotic species in this system, invading species that become dominant in other systems may also show these impacts regardless of nativity.

Invasions must be assessed at both neighbourhood and population scales to fully assess impact. However, most studies refrain from this multiscale approach of invasion and either focus on overall community level effects or individual species competitive responses to invasion (Blossey 1999; Parker *et al.* 1999; Byers *et al.* 2002; Levine *et al.* 2003). Examination of invasion at the former scale may miss significant individual species interactions, while studies at the latter scale cannot determine the effect of the invader on multiple species.

We propose this method as a new standard to determine invader impacts on a community by directly linking impacts with the underlying community dynamics that result in altered community structure. Mechanistic approaches such as this are necessary to depict and manage the impacts of invasion and should be applied to other systems to assess the ubiquity of these dynamics in explaining invasion impacts.

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