COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Propagule pressure-invasibility relationships: testing the influence of soil fertility and disturbance with *Lespedeza cuneata*

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Abstract Although invasion risk is expected to increase with propagule pressure (PP), it is unclear whether PP-invasibility relationships follow an asymptotic or some other non-linear form and whether such relationships vary with underlying environmental conditions. Using manipulations of PP, soil fertility and disturbance, we tested how each influence PP-invasibility relationships for *Lespedeza cuneata* in a Kansas grassland and use recruitment curve models to determine how safe sites may contribute to plant invasions. After three growing seasons, we found that the PP-invasibility relationships best fit an asymptotic model of invasion reflecting a combination of density-independent and density-dependent processes and that seeds were aggregated within the plant community despite efforts to uniformly sow seeds. Consistent with some models, community invasibility decreased with enhanced soil fertility or reduced levels of disturbance in response to changes in the fraction of safe sites. Our results illustrate that disturbance and soil fertility can be a useful organizing principle for predicting community invasibility, asymptotic models are a reasonable starting point for modeling invasion, and new modeling techniques—coupled with classic experimental approaches—can enhance our understanding of the invasion process.

Introduction

Understanding and predicting invasions remains a formidable challenge given the expansion of invaders and the continual introduction of new species. One approach to this problem is to determine how invasibility varies among communities. Community invasibility varies strongly among communities depending on differences in abiotic or biotic properties of the system or the combination of such factors (D'Antonio 1993; Lambrinos 2002; Mitchell et al. 2006). While such approaches are useful, they generally do not fully account for propagule pressure (PP), defined as the number of introductions or the immigration rate into a community (Drake and Lodge 2006; Lockwood et al. 2009; Simberloff 2009; Williamson 1996).

Consider for example, two communities that have different susceptibilities to invasion (i.e., invasibility; Fig. 1). Invasibility would be expected to increase with PP yielding different PP-invasibility relationships (Fig. 1A–B or C–D). If the PP differs between the two communities, it may appear that both communities have equal invasibility (Fig. 1A, D) which is clearly not true in this case. Furthermore, even if community invasibility is equal at one level of PP, a change in PP could lead to a very different outcome (Fig. 1A–C versus B–D) if the slopes of the PP-invasibility

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relationships differ among communities. Consequently, different PP-invasibility relationships may strongly influence the interpretation of community invasibility and these relationships are likely to vary with spatio-temporal differences in herbivory, disturbance, resource supply and competition, but such relationships are rarely quantified.

Although asymptotic PP-invasibility relationships are assumed, other relationships are also possible if invader traits or community characteristics lead to Allee effects (Drake and Lodge 2006; Taylor and Hastings 2005). For example, PP-invasibility relationships could be linear, unimodal or sigmoidal depending on the type of competition between resident species and the invader or the presence of herbivores. Different PP-invasibility functions will potentially lead to changes in the establishment probability, rate of spread, or the equilibrium densities of the invader. For example, a sigmoidal relationship would indicate that initial establishment rates are low until the PP exceeds a threshold after which establishment occurs very rapidly. Such sigmoidal relationships would explain why many invaders remain at low abundance over long time periods and then seem to quickly expand spatially or become locally dominant (Drake and Lodge 2006). Despite the potential importance of these PP-invasibility relationships to understanding and predicting invasion risk, there are few empirical tests over a sufficient range in PP to discriminate among non-linear relationships (Poulsen et al. 2007).

Currently, it is unclear what factors consistently influence the slope or shape of PP-invasibility relationships as community invasibility is a complex combination of abiotic conditions and biotic interactions (Mitchell et al. 2006). One potential approach to simplify this complexity for plant communities, is the conceptual model proposed by Huston (2004) in which soil fertility and disturbance are viewed as the two dominant environmental variables. Soil fertility can influence invasibility by altering growth rates of resident species and the competitive interactions among species. For example, in grasslands, higher soil fertility leads to increased plant density and higher aboveground biomass, which reduce light availability and the potential number of safe sites suitable for new colonists (Fowler 1988; Harper et al. 1961). Consequently, colonization of both native and non-native species decreases as soil fertility increases (Dickson and Foster 2008; Houseman and Gross 2011).

In addition, disturbances also impact invasibility and are likely to interact with soil fertility (Huston 2004). Here we refer to either abiotic or biotic sources of disturbance that occur periodically and lead to a reduction of the dominant species. Contrasting low- and high-disturbance environments, which reflect either the intensity or frequency of disturbance, represents the potential extremes for the combination of soil fertility and disturbance. In high soil fertility environments, disturbances may mitigate the competitive
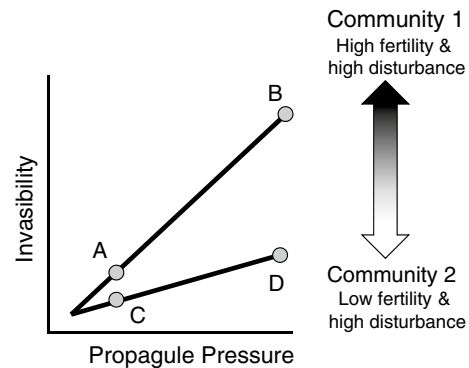

Fig. 1 Hypothetical propagule pressure (PP)-invasibility relationships for two communities that fall at opposite ends of a fertility gradient and experience high disturbance. Under equal PP, invasibility is dictated by the interaction between soil fertility and disturbance that alter opportunities for colonization, plant growth rates, and mortality (see "Introduction" for more details). Two communities may appear to have equal invasibility because of differences in PP (*A* vs. *D*) despite differences under equal PP (*B* vs. *D*). Furthermore, understanding the PP-invasibility relationships (*slopes*) is needed to determine the level of PP necessary for differences in invasibility to be manifested (*A–C* vs. *B–D*) particularly if the relationships are non-linear

advantage of resident species by increasing the number of safe sites and the availability of light and soil resources for new invaders (Davis et al. 2000). Consequently, invasibility rates may increase in high soil fertility communities if the disturbances are of sufficient intensity. Conversely, at low soil fertility growth rates may be so slow that invaders may be unable to establish or reproduce before disturbance leads to invader mortality (Fig. 1).

The generality of the disturbance and soil fertility model is a major area of interest in invasion ecology yet does not account for variability in PP-invasibility relationships (e.g., Fig. 1). Differences in disturbance and soil fertility are likely to alter PP-invasibility relationships by changing microsite availability and altering plant growth and mortality rates. Under an asymptotic model, PP-invasibility relationships may be linear over much of the range in PP so that differences in the slopes reflect important environmental differences among systems (Fig. 1). In this case, difference among slopes leads to an increasing sensitivity to changes in PP. For example, at low PP even systems with moderately large differences in the PP-invasibility relationships will have similar invasibility. However, as PP increases, differences in invasibility become clear. On the other hand, seed predation at low density or allelopathic effects from seed (Dudley and Fick 2003) may generate sigmoidal-shaped or unimodal PP-invasibility relationships complicating the interpretation when PP is not known.

Despite the potential importance of PP for understanding community invasibility, few studies incorporate PP over a

sufficient range to adequately discriminate between asymptotic and other non-linear models (Poulsen et al. 2007). Here we use invasion of *Lespedeza cuneata* into grasslands of the Great Plains as a model system to test PP-invasibility relationships in environments where disturbance and soil fertility were experimentally controlled. *L. cuneata* is a legume introduced to North America from Asia for erosion control and forage but has become a problem in native North America where it suppresses native species (Brandon et al. 2004; Silliman and Maccarone 2005; Wong et al. 2012). Seeds of *L. cuneata* can be dispersed by wind and animals (G. R. Houseman, W. H. Fick, unpublished data) and a single plant can produce in excess of 6,500 seeds/plant, which is five times that of native congeners (Woods et al. 2009). This high seed production coupled with both short- and long-distance modes of dispersal is likely to create large variation in PP across landscapes.

We hypothesized that invasion by *L. cuneata* depends on PP, site soil fertility, and disturbance inherent in grasslands of the Great Plains. In this region, most grasslands are under some form of management that may include grazing, native hay production, or other low-impact activities. For hayed systems, aboveground biomass is harvested once per year generally mid-way through the growing season so that grassland plants recover from biomass removal prior to winter. Grazed systems include foraging by cattle which not only removes plant biomass, but creates physical disturbances to plants and soil during grazing activities. These types of land management represent an increasing gradient of disturbance intensity that can be ordered as undisturbed < hayed < grazed. Along this disturbance gradient, differences in disturbance may increase light availability or colonization sites in the plant community that may increase community invasibility; however, it is possible that high-intensity disturbances may increase invader mortality and thereby decrease invasibility.

In addition to disturbances associated with management activities, grasslands exist across a range of soil fertility—which are typically limited by precipitation, N and P—depending on soil type, topography, climatic conditions and animal inputs. For example, in addition to removal of plant biomass and soil disturbance, cattle alter nutrient dynamics through urine and feces deposition creating a complex soil fertility-disturbance effect that can increase colonization by subordinate species (Bakker and Olff 2003). This variation in soil fertility is also likely to interact with disturbance to alter patterns of invasibility, but a comparison of such systems requires control of PP.

Although asymptotic PP-invasibility relationships might be assumed, our focal species may exhibit sigmoidal-shaped PP relationships. Because *L. cuneata* is known to produce organic compounds (Langdale and Giddens 1967) that may have allelopathic effects on competing species

(Dudley and Fick 2003), the probability of establishment may increase exponentially above some threshold density yielding sigmoidal relationships.

In addition to testing for different PP-invasibility relationships, we examined the relative contributions of density-dependent and density-independent processes by modeling recruitment curves under the experimentally controlled environmental conditions. For example, Poulsen et al. (2007) ascribe density-independent processes to the linear (ascending) slope of the PP-establishment curve while density-dependent processes control the asymptote. Building on this approach, Duncan et al. (2009) developed a mechanistic model of recruitment curves based on the premise that invasibility is limited by the availability of safe sites in which new seedlings can establish (Fowler 1988). Both approaches potentially increase the insight that can be gleaned from invasion studies by allowing the shapes of PP-establishment relationships to indicate the type and relative strength of ecological processes with which they are consistent.

Although a number of studies have addressed PP (Eckberg et al. 2012; Eschtruth and Battles 2011; Von Holle and Simberloff 2005), few have tested for different PP-invasibility relationships particularly under different environmental conditions. The objective of this study was to quantify the shape of the PP-invasibility relationship for *L. cuneata*, to test whether these patterns vary with experimentally controlled effects of soil fertility and disturbance, and to apply recruitment curve models to this experimental system to determine what parameters potentially account for invasion success.

Materials and methods

Experimental design

The experiment was conducted at the University of Kansas Field Station in northeastern Kansas, USA (Jefferson County, 39°03′N, 95°12′W). The site was formerly under hay production but had shifted back to prairie dominated by indian grass (*Sorghastrum nutans*) in response to natural immigration and germination from the seedbank. Prior to the experiment, *L. cuneata* was absent from the experimental area. The experiment was a factorial design that included three levels of disturbance and two levels of fertilization crossed with PP accomplished with *L. cuneata* seed additions (0, 32, 60, 124, 252, 500, 752, 1,000, 5,000, and 10,000 seeds· m^{-2}) applied to 0.75 × 0.75-m plots arranged in a randomized, complete block design. For the undisturbed and simulated grazing treatments, we also had an additional treatment in which we experimentally increased reproduction (seed) of the resident species (*S. nutans*) to

test whether competition for establishment sites might alter community invasibility. However, we found little evidence of recruitment from resident seed and subsequently ignored this factor and pooled replicates with the other factors in the analysis. This resulted in either one (haying) or two replicates (undisturbed or grazing) per block for a total of 300 plots.

In addition to the plots described above, 54 plots were designated as ancillary plots in which environmental variables could be measured in response to disturbance and fertilization. These plots did not receive seed and were arranged in a randomized complete block design with three replicates of each treatment.

Seed of *L. cuneata* was hand collected from three, naturally occurring populations found within 40 km of the experimental site in November and December 2006. Whole plants were collected from each site and seeds removed from plants were thoroughly mixed among all populations. Seed mass-number relationships were determined by weighing various subsamples of seed material and counting the intact seeds. From these relationships, the mass of seed material was used to obtain the target seed density for each replicate. Seeds were hand sown in late winter of 2007. To manipulate plot soil fertility, 16 g N m^{-2} (NPK 24-2-11; Lesco, Cleveland, OH) was added to fertilization treatments in May of 2007–2009. At this site both N and P can limit production so a complete fertilizer was utilized as the goal was to increase plant productivity rather than test the effects of a particular limiting nutrient. For the simulated haying treatments, biomass was cut at a height of ~5 cm with a weed whip in mid-July of 2007 and 2008 and, to the extent possible, all cut biomass was removed from the plots. Simulated grazing treatments were designed to represent a rotational grazing scheme by removing the upper 50 % of the standing vegetation in early June, July and August of 2007 and 2008. Because large grazers affect soil as well as plant production, we disturbed soil in the grazing treatments by vigorously scratching the soil surface with a hoe in a patch of approximately 15 cm diameter. At each time period, the location of these simulated soil disturbances was changed so that the soil disturbance was ephemeral. Because simulated haying and grazing included biomass removal, we did not apply disturbances in the third year so that we could obtain the full potential density, biomass, and flowering of *L. cuneata*.

Data collection

We quantified differences in light availability below the plant canopy but above the litter among the various fertilizer and disturbance treatments in the ancillary plots. Light (photosynthetic photon flux density) was measured using a AccuPAR LP-80 light ceptometer (Pullman, WA) at five positions equispaced within each plot over the first growing season.

After the third growing season, we quantified stem density in the central 0.5 × 0.5-m area of each plot. Because *L. cuneata* is capable of slow clonal spread, we counted both individual stems and "potential" plants when multiple stems appeared to originate from the same root crown.

Data analysis

Differences in light availability was tested with mixed-model repeated-measures ANOVA with disturbance and soil fertility as main effects and time as a repeated measure using SAS version 9.2 (SAS Institute, Cary, NC).

Invader stem density after 3 years was quantified as a function of seed addition (*s*) in the first year. Values for *s* were between 0 and 2,500 seeds/0.25 m^2 reflecting the number of seeds sown within the 0.5 × 0.5-m area in which plant establishment was quantified. Preliminary analysis demonstrated that there was no difference between the two measures so we present only the individual stem data as there is less risk of error due to personal interpretation. We compared different models describing this function using maximum likelihood to determine the best-fit parameters and likelihood ratio tests to compare pairs of nested models in a classic frequentist framework (Bolker 2008).

First we analyzed the general shape of the relationship. A linear function with a zero intercept was compared with a saturating function

$$f_1(s) = \frac{bs}{a + s} \tag{1}$$

where *b* is the maximum stem density at high levels of seed addition and *a* is the seed density at which stem density is halfway to *b*. The saturating function was compared to a Hill function, which is a sigmoid-shaped function

$$f_k(s) = \frac{bs^k}{a^k + s^k}. \tag{2}$$

For example, a familiar example of a Hill function, with $k = 2$, is the Holling type III functional response.

In addition, the importance of density-dependent and density-independent components was investigated. The density-dependent component was quantified by using the above comparison of a saturating model to a non-saturating, linear model (and a zero intercept) *bs* (2007). In contrast, we compared a full saturating model (Eq. 1) to a saturating model which assumes complete seedling establishment at small seed densities, $b = 1$ (Poulsen et al. 2007). This later comparison examines the importance of a density-independent component, fractional germination and establishment regardless of density, in a model with an overriding density-dependent process (Poulsen et al. 2007).

Finally, a comparison among saturating models (all of which have density-dependent and density-independent components), can provide insight into the way in which seeds compete for resources and the spatial distribution of those seeds. Functional forms have been derived from first principles which describe how seed addition might be related to establishment (Duncan et al. 2009). Data consistent with a given model provide support for a given mechanism, with the caveat that unexamined models may be equally or more strongly supported. The most general saturating function is the Brännström–Sumpter function

$$g_\lambda(s) = bn \left(1 - \frac{\lambda^\lambda}{(\lambda + s/n)^\lambda}\right), \tag{3}$$

where the number of available microsites is n and an index of seed aggregation is λ (Brännström and Sumpter 2005). The number of propagules established under contest competition (Nicholson 1954) at a microsite with at least one propagule is b, which can be interpreted as the net combination of seed viability and microsite viability. When λ approaches infinity, the Skellam function emerges

$$g_\infty(s) = bn(1 - e^{-s/n}) \tag{4}$$

which assumes independent distribution of establishment probability across microsites. When $\lambda = 1$, Eq. 3 collapses to the Beverton–Holt

$$g_1(s) = \frac{bs}{1 + s/n} \tag{5}$$

which can be derived from a clumped distribution of seeds across microsites as modeled by a negative binomial distribution (derived similarly in Eager et al. 2012). Practically, the combination of b and n determines the initial slope of establishment and the saturating number of established propagules, while λ controls the sharpness with which the rising establishment function approaches the asymptote for established propagules. Mathematically, Eq. 5 is a reparameterization of Eq. 1.

The distribution of propagules among microsites is indicated by λ in the Brännström–Sumpter function, but the distribution of established propagules among quadrats and the degree of dispersion in that distribution is an additional parameter that is fit to the data during maximum likelihood estimation. All estimations presented here utilized a negative binomial distribution as the error structure, which was strongly supported for these data by Akaike's information criteria (AIC) as compared to the normal and Poisson distribution. The comparison of saturating functional forms, as well as the importance of density-dependent and density-independent components, was calculated with the full interaction of the disturbance and soil fertility treatments in b and n. Subsequently, the significance of treatments and interactions were determined by backwards elimination,
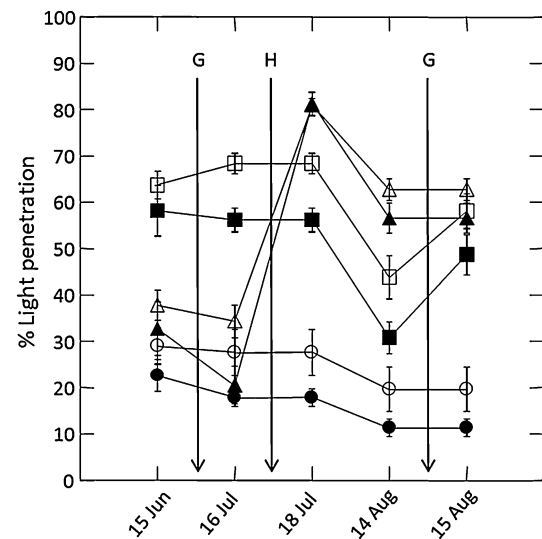

Fig. 2 Light penetration (mean ± 1 SE) through the plant canopy in response to undisturbed (*circles*), simulated haying (*triangles*), or simulated grazing (*squares*) under either unfertilized (*open symbols*) or fertilization (*filled symbols*) that led to a three-way interaction between time, fertilization, disturbance ($F_{8,\ 220} = 2.7$, $P = 0.004$). Note that the dates are not equispaced and that light data were not collected prior to the first grazing event (G). *H* Haying event

comparing the relevant nested models via likelihood ratio tests. We used the statistical program R (http://www.r-project.org/) and the library mle2 for the above analysis.

Results

Environmental conditions

In general, both soil fertility and disturbance influenced light penetration to the soil surface (Fig. 2). However, the consistency of these effects was dependent upon the timing of measurement during the growing season as indicated by a three-way interaction among time, disturbance and fertilization ($F_{8,\ 174} = 2.98$, $P = 0.0038$). Following the initial grazing event in June, light availability in grazed plots was nearly double that of undisturbed or hayed treatments. These light differences between grazed and undisturbed plots were maintained throughout the growing season as the repeated grazing events compensated for plant growth ($F_{1,\ 174} = 7.75$, $P < 0.0001$). In contrast, light availability in the hayed plots, which were similar to undisturbed plots early in the growing season, increased substantially following the haying treatment in July and exceeded that of the grazed plots ($F_{1,\ 174} = 7.3$, $P < 0.0001$). Likewise, when averaged over all time periods, fertilization decreased light penetration to the soil surface by increasing resident community biomass compared to unfertilized controls
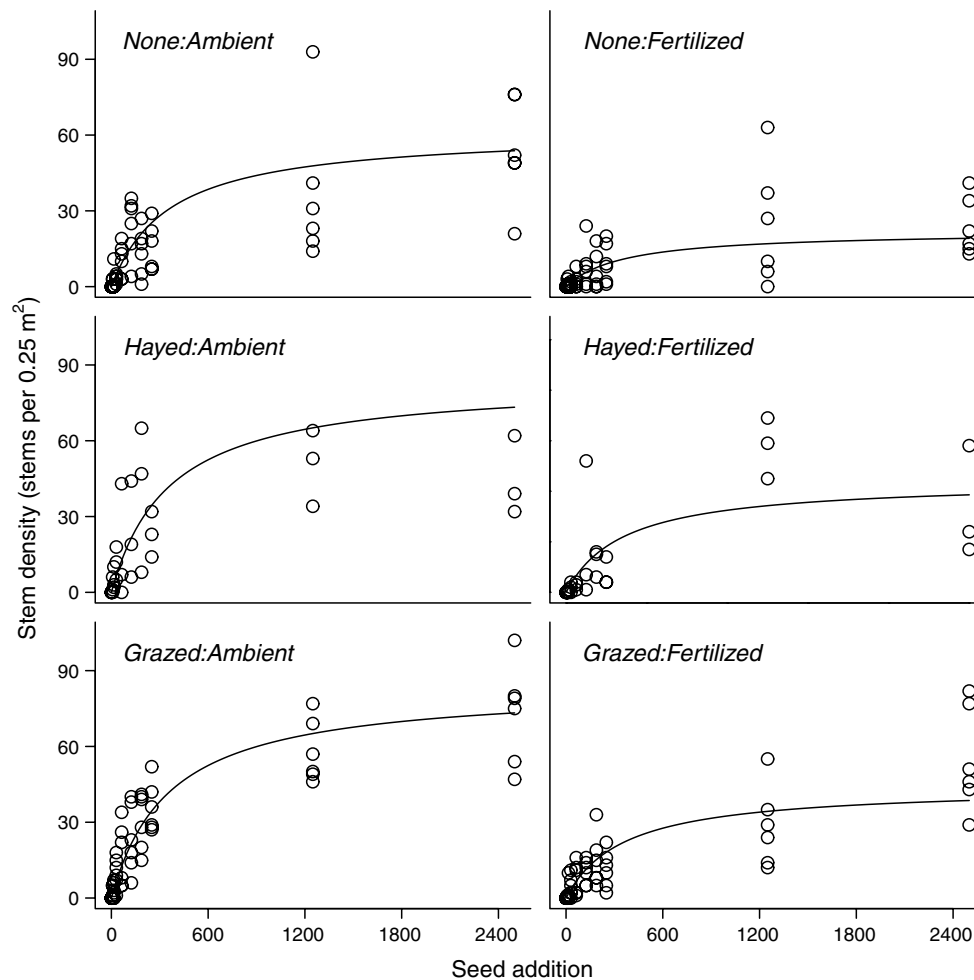
Fig. 3 Establishment of *Lespedeza cuneata* under experimentally controlled seed sowing, disturbance (none, hayed, grazed in the rows), and soil fertility [ambient (*left panels*) or fertilized (*right panels*)] and after three growing seasons. This illustrates the main effect of disturbance on the saturation level of the PP-invasibility relationship. Fertilization decreased the fraction of viable sites ($\chi^2 = 55.7$, $df = 1$, $P < 0.0001$), and disturbance increased the fraction of viable sites ($\chi^2 = 24.2$, $df = 2$, $P < 0.0001$)

($F_{1,\,46} = 121$, $P < 0.001$). This reduction in light was significant ($P < 0.05$) at each measured time period for each disturbance type except for 15 June in grazed plots and 15 June, 18 July, and 14 and 15 August for hayed plots. In general, the lack of an effect of fertilization on light penetration at these specific time periods was due to a large amount of biomass removed by the haying or grazing treatments.

Establishment

Stem density of the invader had a saturating relationship with invader seed density (Fig. 3), which was a significantly better fit than a linear relationship ($\chi^2 = 116.0$, $df = 6$, $P < 0.0001$). The sigmoid-shaped relationship (Eq. 2) was not supported when compared to the more parsimonious saturating relationship (Eq. 1) ($\chi^2 = 1.17$, $df = 1$, $P = 0.30$).

Because the saturating relationship was a significantly better fit than a linear relationship, there was an important density-dependent component to the PP-invasibility function. At the same time, the full saturating relationship was a better fit than the density-dependent-only relationship ($\chi^2 = 188.23$, $df = 6$, $P < 0.0001$), indicating that both density-independent and density-dependent factors are critical components to the PP-invasibility function.

Comparing the mechanistically derived saturating functions, the more complex Brännström–Sumpter function (with a best fit $\lambda = 7.0$) was not a significantly better fit than the simpler Beverton–Holt ($\chi^2 = 1.95$, $df = 1$, $P = 0.16$) nor simpler than the Skellam ($\chi^2 = 1.74$, $df = 1$, $P = 0.19$). The Beverton–Holt and the Skellam functions cannot be compared using a likelihood ratio test because they are not nested, therefore we used AIC for this one comparison (Burnham and Anderson 2002). The
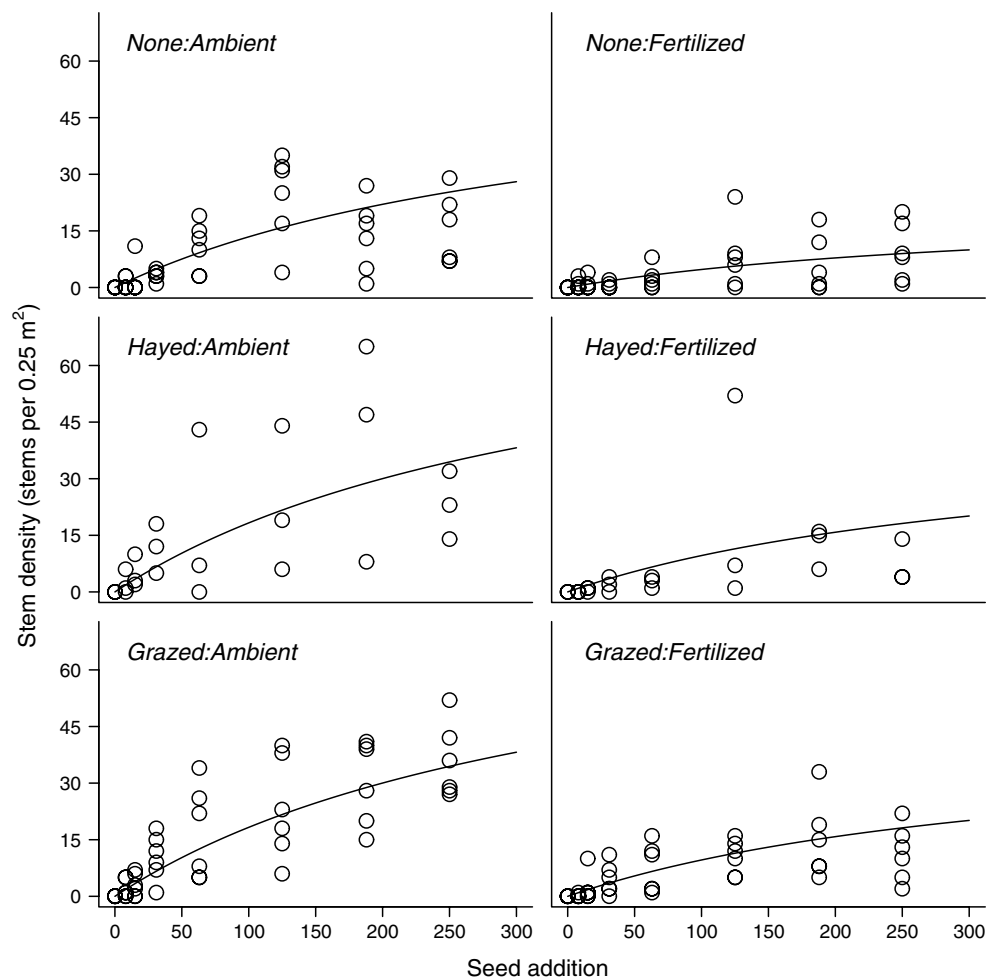
Fig. 4 Establishment of *L. cuneata* over low to moderate seed densities under experimentally controlled disturbance (none, hayed, grazed in the rows), and soil fertility [ambient (*left panels*) or fertilized (*right panels*)] after three growing seasons. This illustrates the main effect of fertilization on the slope of the PP-invasibility relationship (Δ Akaike's information criteria = 61.3, $df = 1$, $P < 0.0001$)

Beverton–Holt function was the best-fit saturating function as it had greater support in the data than the Skellam function ($\Delta AIC = 3.7$, Akaike weight 0.86 vs. 0.14).

Using the mechanistically based Beverton–Holt function (Eq. 5) to investigate recruitment, we found there was no interaction between soil fertility and disturbance in n, the number of microsites ($\chi^2 = 1.58$, $df = 2$, $P = 0.45$), as well as no main effect of soil fertility (($\chi^2 = 2.01$, $df = 1$, $P = 0.16$) or disturbance ($\chi^2 = 0.71$, $df = 2$, $P = 0.702$). In other words, n was uniform across all treatments with an expected mean of $n = 358.1$. There was no interaction between soil fertility and disturbance in b, the viable fraction given at least one seed ($\chi^2 = 3.19$, $df = 2$, $P = 0.20$). However, there was a main effect of fertilization decreasing the fraction of viable sites (additive decrease of -0.11, $\chi^2 = 55.7$, $df = 1$, $P < 0.0001$). In addition, disturbance increased the fraction of viable sites ($\chi^2 = 24.2$, $df = 2$, $P < 0.0001$), with no difference between grazing

and haying ($b_{\text{grazing/haying}} = 0.23$, $b_{\text{none}} = 0.17$; $\chi^2 = 0.29$, $df = 1$, $P = 0.59$). The best-fit dispersion parameter in the negative binomial distribution was $k = 1.88$. When using the Eq. 1 parameterization of the saturating function, fertilization resulted in a shallower slope (Fig. 4) of the PP-invasibility relationship ($\chi^2 = 63.3$, $df = 1$, $P < 0.0001$), while grazing and haying increased the maximum stem density at high PP ($\chi^2 = 26.8$, $df = 2$, $P < 0.0001$).

Discussion

Non-linearities and PP-invasibility relationships

Current understanding of species invasions is limited by the lack of information characterizing the shape of PP-invasibility relationships particularly in differing ecological contexts. In this system, we found that PP-invasibility

relationships conformed to an asymptotic relationship regardless of the type of disturbance or soil fertility examined. Such patterns are predicted by some theoretical models (Drake and Lodge 2006; Duncan et al. 2009) but are not commonly demonstrated in experimental studies (Clark et al. 2007; Poulsen et al. 2007). The absence of sigmoidal or unimodal patterns suggests that linear-saturating models might be utilized in future models and empirical studies to compare differences among management regimes. However, it remains unclear whether the observed responses can be applied to a wide array of plant species or environmental contexts because so few studies have included a sufficient range in seed density to determine how the PP-invasibility pattern changes at high density.

Over a large range of *L. cuneata* seed densities, disturbance and soil fertility influenced the slope and maximum density of these relationships. These differences are driven by environmental conditions and highlight the importance of accounting for PP when assessing system invasibility (Fig. 1). For example, our data suggest that undisturbed communities had lower invasibility than grazed communities under equal PP. However, in our system undisturbed communities would have the same invasibility as grazed communities if the PP was 58 % higher in undisturbed than grazed communities. Likewise a 130 % increase in PP in fertilized communities would lead to similar invasibility as that of communities under ambient soil fertility. Such differences in PP are very likely to occur due to variations in size, distance, and density of source populations. Consequently, PP is an important component for modeling species invasions (Eckberg et al. 2012; Eschtruth and Battles 2011; Lockwood et al. 2005; Tanentzap and Bazely 2009).

Effect of disturbance and soil fertility on invasibility

Our results demonstrate that, under equal PP, invasibility increases with disturbance. Both simulated haying and grazing increased the establishment of *L. cuneata* into grassland compared to undisturbed plots by almost doubling maximum stem density. The fact that light penetration also increases with disturbance is consistent with the idea that these disturbances alter community structure, which consequently alters the establishment curve. Based on the Duncan model, this increased invasibility could be due to an increase in the number of safe sites created by a reduction in resident species biomass. This inference is consistent with several models of invasion (Davis et al. 2000; Huston 1994), as well as other observational (Eschtruth and Battles 2009; Wiser et al. 1998) and experimental studies (Dickson and Foster 2008; Duggin and Gentle 1998; Renne et al. 2006; Thompson et al. 2001). Although we incorporated two types of disturbances that vary in disturbance intensity (one versus three biomass removal events and the latter with soil disturbance), we found little difference in invasibility between the two, potentially because both disturbance create an equivalent number of safe sites.

In contrast to disturbance, increased soil fertility reduces the invasibility of *L. cuneata* in this grassland system (Brandon et al. 2004; Sanders et al. 2007). Based on the Duncan model, increased fertilization decreased the slope of the PP-invasibility relationship by reducing the number of safe sites, which is consistent with several experimental studies (Dickson and Foster 2008; Houseman and Gross 2006, 2011) and supports the view that increased plant biomass or increased resident plant density reduces the opportunity for invaders to germinate or proceed to adult life stages. Although fertilizer application could potentially suppress N-fixing legumes either by changing N or P availability (Vitousek et al. 2002), a preliminary greenhouse experiment did not support this hypothesis (Coykendall, unpublished data). Additionally, Sanders et al. (2007) also report very low *L. cuneata* establishment at low light availability (below 10 % of full light in June) suggesting that increased soil fertility limits *L. cuneata* by reducing light availability.

In contrast to our results, reports from other systems indicate that invasibility can increase with plant productivity (Duggin and Gentle 1998; Lake and Leishman 2004; Siemann et al. 2007; Thompson et al. 2001). These divergent responses may reflect several potential explanations. First, the effect of increased soil fertility may depend on ambient soil fertility and the traits of the invader. For example, community invasibility may increase following fertilizer addition if the initial conditions are near the low end of a productivity gradient while invasibility may decrease if the initial conditions fall between moderate to high productivity prior to the increase in soil fertility. Second, the importance of co-varying factors may determine whether increased soil fertility increases or decreases invasibility (e.g., disturbance discussed below). Third, invaders may respond differently to enhanced soil fertility than native species if invaders are N-fixers or possess unique traits that increase invasibility in comparison to native species (Callaway and Ridenour 2004). Fourth, it may be difficult to predict the effect of soil fertility on community invasibility without species trait-environment information.

Although some models (Huston 2004) and empirical studies (Duggin and Gentle 1998; Thompson et al. 2001) suggest that disturbance may counteract the negative effects of enhanced soil fertility on invasibility, we found that increased soil fertility consistently reduced invasibility regardless of the disturbance regime. Similar results have been reported by others (Dickson and Foster 2008; Renne et al. 2006). These cases where disturbance and soil fertility have independent effects on invasibility may occur because there is an insufficient range in soil fertility for the interaction to be expressed. In our case, the range in fertility is

representative of intermediate- to high-productivity grass-lands in our region, but reversals predicted by invasion models may require a greater range in fertility. Additionally, the potential for disturbance-soil fertility interactions on invasibility may vary among native and non-native species particularly if successful invaders have characteristics not common to native species as suggested by the novel weapons hypothesis (Callaway and Ridenour 2004).

Although disturbance and soil fertility had different effects on invasibility, all treatments were best fit by the Beverton–Holt relationships suggesting that increased PP leads to spatial clustering of seeds and contest competition during establishment (see "Materials and methods"). This clustering might occur if seed dispersal is influenced by the spatial pattern of resident species. There is growing evidence that resident plant species are aggregated within communities (Purves and Law 2002 and references therein) and, because of differences in plant growth form, seeds may not have an equal chance to arrive in all gaps (safe sites). For example, some species such as caespitose grasses naturally create gaps between clumps so that seeds that fall between clumps are much more likely to survive than those that fall within a clump. Consequently, the spatial pattern of establishment is aggregated even if seed arrival is relatively uniform. In our experiment, we tried to uniformly sow seeds, yet evidence for spatial aggregation of established plants emerged. Although this view fits with the model and observations in the field, it should be noted that other biological mechanisms could produce a similar pattern in the recruitment function and additional experiments would be needed to determine if sowing itself partially contributes to spatial clustering.

Our results illustrate that disturbance and soil fertility influence community invasibility and can be a useful organizing principle for predicting invasions in grassland systems. Additionally, our experimental evidence supports the view that asymptotic PP-establishment models are a reasonable starting point for modeling the initial steps of the invasion process. Finally, this work illustrates how combining new modeling approaches with classic experimental work can enhance our understanding of plant invasions.

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