

Trophic Interactions during Primary Succession: Herbivores Slow a Plant Reinvasion at Mount St. Helens

William F. Fagan^{1,2,*} and John G. Bishop^{3,4}

1. Department of Biology, Arizona State University, Tempe, Arizona 85287;
2. Department of Zoology, University of Washington, Seattle, Washington 98195;
3. School of Biological Science, Washington State University—Vancouver, Vancouver, Washington 98686;
4. Department of Botany, University of Washington, Seattle, Washington 98195

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ABSTRACT: Lupines (*Lupinus lepidus* var. *lobbii*), the earliest plant colonists of primary successional habitats at Mount St. Helens, were expected to strongly affect successional trajectories through facilitative effects. However, their effects remain localized because initially high rates of reinvasive spread were short lived, despite widespread habitat availability. We experimentally tested whether insect herbivores, by reducing plant growth and fecundity at the edge of the expanding lupine population, could curtail the rate of reinvasion and whether those herbivores had comparable impacts in the older, more successional advanced core region. We found that removing insect herbivores increased both the areal growth of individual lupine plants and the production of new plants in the edge region, thereby accelerating the lupine's intrinsic rate of increase at the front of the lupine reinvasion. We found no such impacts of herbivory in the core region, where low plant quality or a complex of recently arrived natural enemies may hold herbivores in check. In the context of invasion theory, herbivore-mediated decreases in lupine population growth rate in the edge region translate into decreased rates of lupine spread, which we quantify here using diffusion models. In the Mount St. Helens system, decreased rate of lupine reinvasion will result in reductions in rates of soil formation, nitrogen input, and entrapment of seeds and detritus that are likely to postpone or alter trajectories of primary succession. If the type of spatial subtleties in herbivore effects we found here are common, with herbivory focused on the edge of an expanding plant population and suppressed or ineffective in the larger, denser central region (where the plants might be more readily noticed and studied), then insect herbivores may have stronger impacts on the dynamics of primary succession and plant invasions than previously recognized.

Keywords: primary succession, herbivory, invasion, colonization, lupine, Mount St. Helens.

Primary succession—the formation of biological communities in locations lacking a biological legacy—has been an important focus of ecological research for at least a century (Cowles 1899; Lawrence 1958; Connell and Slatyer 1977; Vitousek et al. 1987; Morris and Wood 1989; Vitousek and Walker 1989; del Moral 1993; Miles and Walton 1993; Chapin et al. 1994). Ecologists have identified the rate of abiotic amelioration, the proximity of propagule sources, and competitive and facilitative interactions among plant species as the factors that most govern the pace of revegetation during primary succession (Connell and Slatyer 1977; Vitousek et al. 1987; Vitousek and Walker 1989; del Moral 1993; Miles and Walton 1993; Chapin et al. 1994). Generally lacking from studies of terrestrial primary succession, however, has been attention to how consumer-resource dynamics influence colonization and invasive spread of early successional plant species. Though few in number, investigations of the impacts of insect herbivory on plant succession (Brown 1984, 1985; Bach 1994) provide evidence that invertebrate herbivory can influence the pace and trajectory of successional dynamics. In contrast to terrestrial systems, experimental manipulations of grazer densities in marine habitats consistently demonstrate that consumers strongly affect successional pathways (e.g., Lubchenco 1978, 1983; Sousa 1979; Buschmann 1990; Hixon and Brostoff 1996).

Primary succession is an inherently spatial process because successful early colonists give rise to local patches of vegetation that facilitate further colonization via dispersal of their progeny. The gradual, upstream colonization of moraines following glacial retreat is one example of such a spatial progression of successional dynamics (Chapin et al. 1994). Consequently, parallels exist between successional spread and the spread of exotic, invading species (e.g., Lewis 1997; Shigesada and Kawasaki 1997). However, research investigating herbivore-plant interactions in such an explicitly spatial context is scarce. Notable

* E-mail: bfagan@asu.edu. The authors contributed equally to this work.

Table 1: Characteristics of core and edge regions of the lupine population at Mount St. Helens during 1993

	Patches surveyed	Quadrats surveyed	Total area censused (m ²)	Total extent (km ²)	Median (range)			
					Lupine density (m ⁻²)	Median nearest-neighbor distance (m)	Percentage cover of lupine	Percentage cover of all other plants
Core region	4	44	29.5	.5	73.0 (1.5–1100)	.04 (.00–.14)	44 (4–92)	31.8 (.00–108.8)
Edge region	50	NA	4,560	2.5	.13 (.007–7.5)	.48 (.10–6.78)	.03 (.004–.15)	.12 (.00–1.90)

Note: Medians and ranges of descriptive variables are calculated across sampled patches within the edge region and across sampled quadrats within the core region. For nearest neighbor distances, we present the medians and ranges (taken across patches or quadrats) of median within-patch or within-quadrat nearest-neighbor distances.

exceptions such as Louda (1982), Louda and Rodman (1996), and Root (1996) identify ways in which herbivore-plant interactions can vary through space and illustrate how consideration of such spatial variation can provide a more complete picture of overall plant-herbivore dynamics. Similarly, Maron and Harrison's (1997) investigation of insect interactions within a bush lupine system show that spatial aspects of consumer-resource dynamics can be critical to understanding mechanisms underlying ecological pattern formation.

Here we adopt a spatial perspective afforded by ecological invasion theory to investigate the impacts of insect herbivores on the dynamics of a plant, *Lupinus lepidus*, that is colonizing primary successional habitat at Mount St. Helens, Washington. Predictions from an array of theoretical models (e.g., Skellam 1951; Moody and Mack 1988; Shigesada and Kawasaki 1997) indicate that dynamics in the edge regions of an expanding population can often determine the rate of invasive spread. Classical invasion theory maintains that edge regions are important to invasion dynamics because they are primary sources for dispersers into as-yet unpopulated habitat and because edges typically lack high densities that can reduce per capita reproduction (but see Kot et al. 1996; Clark et al. 1998). We present experimental evidence that insect herbivores reduce plant growth and reproduction at the edge of a reinventing wave of lupine, thereby reducing the rate of reinvasion. Such herbivore impacts on lupine population growth are absent at the older, more successional advanced core of the population. Because lupines are a nitrogen-fixing species that accelerates primary succession in this system (e.g., Morris and Wood 1989; Halvorson et al. 1992; del Moral 1993; Titus and del Moral 1998), our data indicate that insect herbivores are directly influencing the pace and pattern of revegetation at Mount St. Helens.

Description of the Study Site and Focal Species

The 1980 eruption of Mount St. Helens, Washington, created a 60-km² region of primary successional habitat, prin-

cipally on the volcano's north slope, and extirpated all plant and animal species from the area (del Moral and Bliss 1993; del Moral et al. 1995). Outside this zone, disturbance intensity decreased with increasing distance from the volcano. Remnant individuals of many species survived in isolated and sheltered pockets in these outer zones. In 1981, a species of lupine (Fabaceae: *Lupinus lepidus* var. *lobbii*, a native perennial herb) colonized the otherwise barren north slope of Mount St. Helens from remnant populations elsewhere on the volcano. For the next several years the lupine population spread rapidly outward from this initial invasion focus (del Moral et al. 1995) and was the most successful colonist on pumice and rock substrates (which encompass most available habitats; del Moral and Bliss 1993). By 1990, the lupine population on the north slope of Mount St. Helens involved a large, central core region of extremely high lupine density surrounded by numerous, low-density edge patches up to 2 km from the core (table 1; del Moral et al. 1995; Bishop 1996). Low-density, patchily distributed lupine also typifies intervening areas between the edge and core regions as well as the expanding fringes of core patches. By 1992, population growth rates in recently founded, low-density lupine patches (typical of the edge region) had dropped to levels far below the prodigious rates observed during the early stages of colonization (fig. 1; del Moral et al. 1995; Bishop 1996), contributing to surprisingly slow rates of spread in recent years.

At Mount St. Helens, *L. lepidus* has received substantial attention from researchers seeking to understand its population biology, ecophysiology, and population genetics and its contributions to soil formation, soil fertility, and successional dynamics (e.g., Wood and del Moral 1987; Morris and Wood 1989; Halvorson et al. 1991, 1992; del Moral 1993; del Moral and Wood 1993; Bishop and Schemske 1998; Titus and del Moral 1998; Braatne and Bliss 1999; J. G. Bishop, unpublished manuscript; C. M. Crisafulli, W. M. Childress, E. J. Rykiel, Jr., and J. A. MacMahon, unpublished manuscript). Numerous studies

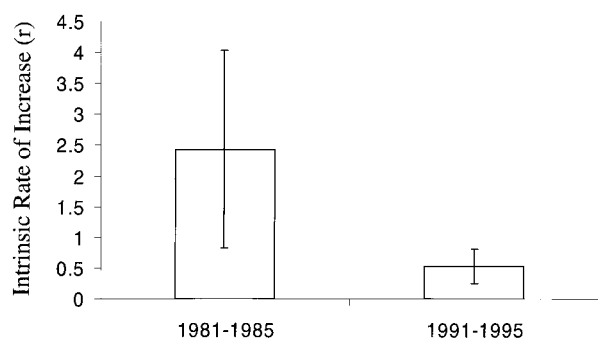


Figure 1: Mean ($\pm 95\%$ confidence interval) intrinsic rate of increase ($r = \ln \lambda$) of low-density lupine patches at the beginning of lupine colonization and 10 yr later. Data for 1981–1985 are for the initial point of colonization in the core region and are provided courtesy of C. M. Crisafulli, W. M. Childress, E. J. Rykiel, Jr., and J. A. MacMahon (unpublished manuscript); confidence intervals across years are calculated via the method of Heyde and Cohen (1985). For the 1991–1995 transitions, data are mean growth rates of 13 edge-region lupine patches. Detailed descriptions of data for 1991–1995 are in Bishop (1996). Lupine growth rates differ significantly between the two time periods ($t_{16} = 2.62$, $P = .009$).

demonstrate lupines' ability to ameliorate physical conditions and influence subsequent successional dynamics. For example, *L. lepidus* can fix >7 kg nitrogen $\text{ha}^{-1} \text{yr}^{-1}$, compared with background rates of only 2 kg $\text{ha}^{-1} \text{yr}^{-1}$, and dramatically increases organic matter accumulation by trapping detritus (Kerle 1985; Halvorson et al. 1991, 1992). Live lupines can suppress invading ruderals, whereas dead lupines facilitate these same species (Morris and Wood 1989; del Moral and Bliss 1993). Overall, however, the net effect of lupines on species richness, biomass production, and primary succession is facilitative (Morris and Wood 1989; Wood and Morris 1990; del Moral and Wood 1993; Tsuyuzaki et al. 1997; Titus and del Moral 1998; C. M. Crisafulli, W. M. Childress, E. J. Rykiel, Jr., and J. A. MacMahon, unpublished manuscript). Decreased rate of lupine spread thus diminishes the impact of lupines on community development (Halvorson et al. 1992; del Moral and Bliss 1993).

Several Plausible Hypotheses Do Not Explain Lupine's Decreased Rates of Population Growth and Spatial Spread

Several mechanisms could potentially account for the dramatic decrease in lupine's intrinsic rate of increase (r) under low-density conditions (fig. 1), which, we will argue, reduced lupine's rate of spread. We argue that all but one of these mechanisms are unlikely explanations for the observed decrease in lupine population growth rate.

A first potential mechanism is intraspecific resource competition, which can regulate population growth in plants (Crawley 1989). In fact, high conspecific density and ensuing competition for soil resources are known to reduce per capita reproduction and population growth in *L. lepidus* (Bishop 1996). However, lupine densities sufficient to cause such competitive effects (typically >50 plants m^{-2} , based on a regression of D_{t+1}/D_t vs. D_t for 44 core region quadrats sampled each year for 5 yr, where D_t is $\ln[\text{lupine density}]$ in year t) are restricted to the core region. Extensive surveys in 1993 of core and edge region patches show that, in contrast to the high lupine densities characterizing the core region, densities in the edge region did not exceed 7.5 plants m^{-2} (table 1). Median percentage lupine cover in the edge region was roughly three orders of magnitude lower than in the core region (table 1), and median within-patch nearest-neighbor distance in the edge region was over 10 times greater than the corresponding measure for the core region (table 1). Consequently, intraspecific competition appears unlikely to be responsible for the reductions in lupine growth rate.

Population growth rate also may be regulated by resource competition among plant species, and competitive displacement is a common mechanism of successional species replacement (e.g., Connell and Slatyer 1977). On a local scale, a variety of plants appear to exclude lupines competitively (C. M. Crisafulli, W. M. Childress, E. J. Rykiel, Jr., and J. A. MacMahon, unpublished manuscript). However, such species only occur in substantial densities in the core region and a few other locations (table 1). Nonlupine plant species, nearly all ruderals (e.g., *Hypochaeris radicata*, *Anaphalis margaritacea*, and *Epilobium angustifolium*), covered a mere 0.16% of the surface area in the typical edge lupine patch during the 1993 survey and never exceeded 2% cover (table 1). Consequently, interspecific competition is unlikely to be responsible for the reduced lupine growth rates.

A third potential explanation is that lupines occupied most high-quality sites early on in the reinvasion and are now relegated to colonizing areas in which they fare poorly. Several lines of evidence indicate that this is an unlikely explanation. *Lupinus lepidus* is characteristic of high-altitude pumice communities and resource-poor moraine substrates at the fringes of alpine glaciers (Franklin and Dyrness 1973; Kruckeberg 1983). Following the eruption, lupines colonized substrates 200–600 m below preruleption elevations. At these lower elevations, which are similar to those in our study sites, decreased drought stress and longer growing seasons are known to increase lupine growth rate, size, and fecundity relative to plants at preruleption elevations (Braatne 1989; Braatne and Bliss 1999). Bishop (1996) transplanted 328 lupines into 41 widely spaced uncolonized sites in the edge area, chosen

without regard to microhabitat. Nearly two-thirds of the plants survived, and 38 of 41 patches have persisted for six growing seasons. Population growth in these patches has been highly variable, but in some years growth rates approach those observed shortly after the eruption, and years of low population growth are highly correlated with insect damage (Bishop 1996; J. G. Bishop, unpublished manuscript). Other studies in the edge area demonstrate very high survival rates of lupine seedlings (Tsuyuzaki et al. 1997). These observations indicate that edge sites represent typical lupine habitat and that site quality alone is unlikely to explain the recent decrease in lupine growth rates.

A potential cause of reduced spatial spread (but not locally reduced population growth) is dispersal limitation (i.e., lupines have not been able to reach areas beyond their current range). Lupines possess relatively large seeds, which decrease the frequency of long-range dispersal to good-quality sites (Wood and del Moral 1987; del Moral and Wood 1993). Yet a few edge patches were highly isolated (at least 2 km from a seed source), and seed traps located many meters away from seed sources regularly recruited lupine seeds (Wood and del Moral 1987; del Moral and Wood 1993). Consequently, dispersal ability alone is unlikely to explain the decreased lupine spread rates. However, weak dispersal ability coupled with decreased production of seeds could contribute to slower spread rates.

The above mechanisms appear inadequate as explanations of the pronounced decrease in lupine population growth rates under low-density conditions (fig. 1). Consequently, we sought to test experimentally whether an alternative mechanism, one that focused on the colonization of primary successional habitats at Mount St. Helens by several species of insect herbivores, could be responsible. Substantial herbivore populations were first recorded from the core region in the mid-1980s (C. M. Crisafulli, W. M. Childress, E. J. Rykiel, Jr., and J. A. MacMahon, unpublished manuscript) and probably reached the edge region around 1990 (Bishop 1996). Detailed observational data indicate that insect herbivory in edge region patches is strongly correlated with decreased lupine survival, seed production, and population growth (J. G. Bishop, unpublished manuscript) and has caused the local extinction of entire lupine patches (J. G. Bishop and W. F. Fagan, unpublished data). These results indicate that insect herbivores are at least partially responsible for decreased lupine population growth rates, but establishing herbivory as the causal mechanism requires experimental study.

During short 3-mo growing seasons, lupines at Mount St. Helens endure a suite of native insect herbivores, chiefly lupine-specific lepidopterans that are divisible into two

functional groups. The first group, which consists of univoltine folivorous leaf miners and caudex borers (Tortricidae: *Hystricophora paradisae*; Noctuidae: *Euxoa* spp.), causes plant damage that is immediately obvious on visual inspection (either as a complete yellowing of leaves bound up in webbing and then mined out or as a distinctive gray pallor on plants whose vascular tissues have been attacked). The evidence of such herbivory persists throughout the growing season. The second important group of herbivores destroys lupine seeds before explosive dehiscence of the fruits. This second group includes larvae of several species (Lycaenidae: *Plebejus icariodes montis*; Noctuidae: *Schinia sueta*; Anthomyiidae: *Crinurina* sp.). Impacts of these species on lupines are subtle and must be assessed through careful examination of lupine fruits for holes and hollowed-out seeds.

Methods

Experimental Methods

To evaluate herbivore impacts on lupine population dynamics and how such impacts vary across the density gradient associated with spatial expansion, we designed a balanced two-way factorial experiment, demarcating 16 experimental census plots: eight near the center of the lupine population (core sites) and eight in satellite patches near the edge of the expanding lupine population (edge sites). Plots measured 4 m² in the edge region and 0.1–0.5 m² in the core region to contain comparable sample sizes. On four plots in each region, we sprayed the broad-spectrum, short-lived (1–2 d half-life on foliage, 15–90 d half-life in soil; Walker and Keith 1992; J. Stark, personal communication), topical, synthetic pyrethroid insecticide esfenvalerate (Asana, DuPont; in aqueous solution, 6 mg m⁻² active ingredient) on June 22, 1995, and again on July 17, 1995. Control plots received comparable volumes of water. Greenhouse studies indicated esfenvalerate did not enhance plant growth or survivorship. This absence of effect is consistent with the high C:N ratio and absence of other critical nutrients in esfenvalerate and with studies of its close chemical relative, fenvalerate, which also find no effects on plant growth and reproduction (discussed in Root 1996). No insecticide was applied during the 1996 and 1997 growing seasons.

Census Methods

During 1995, we censused all plots four times, recording plant size, infructescence and fruit production, herbivore leaf damage (scored as percentage of leaves bound together and/or eaten), and arthropod counts by taxa for each of ~1,100 plants. For clarity we use the term “folivore and

caudex borer prevalence” to refer to the percentage of plants attacked by the folivore/caudex borer guild (i.e., *Euxoa*, *Hystricophora*, or both). Censusing occurred immediately before each insecticide application and twice later in the season (August 4, 1995, and August 17, 1995). Phenological studies indicate this sampling scheme effectively assesses growth, reproduction, and summer mortality for lupines (Bishop and Schemske 1998). Laboratory dissections of all fruits from at least five infructescences per plot collected on each of the last three census dates provided estimates of seeds per fruit and seed damage. We collected infructescences for dissection from like-treated regions just outside the plot boundaries to minimize the demographic consequences of our sampling. All plots were again censused on August 27, 1996, and edge plots only were censused on August 3, 1997.

To allow extrapolation of our experimental results to landscape-level processes, we assessed spatial patterns of damage by the most prominent edge-region herbivore, the folivorous leaf miner *Euxoa*, in 1998. We estimated percentage damage by *Euxoa* by quantifying percentage ground surface covered by lupine and percentage of lupine surface area bound up in *Euxoa* webs, in circles of 5–10-m radius, at 100-m intervals along four transects ≥ 1 km long. Transects ran from the center of high-density core regions to low-density edge regions. We also surveyed four additional core sites to increase our sample size under conditions of high lupine cover.

Statistical Methods

All experimental data were analyzed via two-way ANOVA with site (core vs. edge) and treatment (insecticide vs. control) as factors. In addition, even though no significant pretreatment differences existed between insecticide and control plots in either the core or the edge region, we included initial lupine cover as a covariate in our analyses to account for variance introduced by the potential presence of subtle pretreatment differences among plots. For analyses of population growth rate based on changes in plant densities, we substituted initial lupine density for initial lupine cover as a more appropriate covariate. Before introducing either covariate into the statistical model, we tested for homogeneity of covariation slopes across treatments (Sokal and Rohlf 1995; Systat 1998). Subsequent to the ANCOVAs, we conducted selected post hoc pairwise comparisons that we corrected for multiple tests using sequential Bonferroni adjustments. Data expressed as proportions were arcsine square-root transformed before analysis.

We calculated the intrinsic rate of increase (r) for lupine in each experimental replicate as $r = \ln(N_{t+1}/N_t)$, where N_t and N_{t+1} are the number of lupines present at consec-

utive annual censuses (Caswell 1989). The only exception to this procedure was our r_{1995} calculations, which are for the growing season only, not a complete annual transition. In addition, because lupines’ functional importance (i.e., effects on soil development) may scale with plant area, we also calculated r by substituting lupine surface area at each census for numbers of individuals.

Invasion Speed Formulae, Intrinsic Rate of Increase, and Diffusion Coefficient

Spatial spread of reinvading organisms can often be approximated as a simple reaction-diffusion process (Skellam 1951; Okubo 1980; Andow et al. 1990), with invasion speed

$$c = 2\sqrt{rD}, \quad (1)$$

where r (yr^{-1}) is the intrinsic rate of population increase and D ($\text{m}^2 \text{yr}^{-1}$) is the diffusion coefficient, a measure of spatial spread rate. We will use data from our edge insecticide plots as an estimate of what lupine r would be in the absence of herbivory.

If one envisions lupine colonization as a two-step process made up of preherbivore and herbivore stages, it is possible to quantify an herbivore-induced reduction in invasion speed using a different formulation of the diffusion process. Specifically, the time-averaged lupine invasion velocity since herbivore arrival approaches

$$c = \frac{\sqrt{4Dr_2 + 4D(r_1 + r_2)t_1/t_2 + 4Dr_1t_1^2/t_2^2}}{\sqrt{4Dr_1t_1^2/t_2^2}}, \quad (2)$$

where r_1 and r_2 are lupine population growth rates before and after herbivore arrival at the population’s edge, t_1 (years) is the duration of the prior herbivore-free period, and t_2 (years) is the time since herbivore arrival (see appendix for derivation). Relying on preherbivore estimates of lupine population growth (fig. 1), we set $r_1 = 2.4$. Our experimental data (i.e., control plots in the edge region) will provide an estimate of r_2 . Finally, because severe herbivore impacts first reached portions of the edge region around 1990 (Bishop 1996), we use $t_1 = 9$ (i.e., 1990–1981 [the population’s founding date]) and $t_2 = 9$ to quantify average lupine invasion speed after the 1998 growing season.

We used nonlinear regression to characterize lupine dispersal via the redistribution kernel method (Kot et al. 1996). This entailed mapping the locations of a total of 1,821 first-generation progeny of 43 parental patches throughout the edge region during 1992–1997. Each parental patch contained one to three reproductives in a 1-

m² area, with extremely low plant density between patches, which allowed tracking of progeny up to ~20 m from parent patches. We estimated the coefficient of diffusion (D) from these data because local-scale lupine redistribution kernels approximated the normal distribution governing diffusive spread (Kot et al. 1996). We have no evidence that postdispersal seed predation alters the shape of lupine redistribution kernels and have observed extremely few postdispersal seed predators (e.g., ants or birds) in edge-region patches. Instead, we focus on the ways in which insect herbivory alters the lupine's rate of increase and, as a consequence, spread rate.

Results

First a couple of general statistical comments concerning our experimental analyses. In our ANCOVAs, covariates (initial lupine density or initial lupine cover) were significant in only one of eight analyses but were retained in all analyses because they helped to explain a portion of the residual variance. In those cases when ANCOVA identified a significant effect of either the region or treatment factor (or their interaction), but the covariate was non-significant, omitting the nonsignificant covariate and re-doing the analysis never resulted in loss of significance of the main effect or interaction. For only one response variable (percentage seed damage) did the test for homogeneity of slopes indicate a significant departure from the assumptions of ANCOVA. For this case, we substituted initial lupine density for initial lupine cover as the covariate in our statistical model (density passed the slope test) and reran the analysis. For clarity, we have aggregated F statistics and P values from our analyses in table 2.

Dramatic differences in lupine density and percentage cover between core and edge study plots were typical of core and edge regions as a whole. For example, during the June 1995 census, mean (\pm 95% confidence interval [CI])

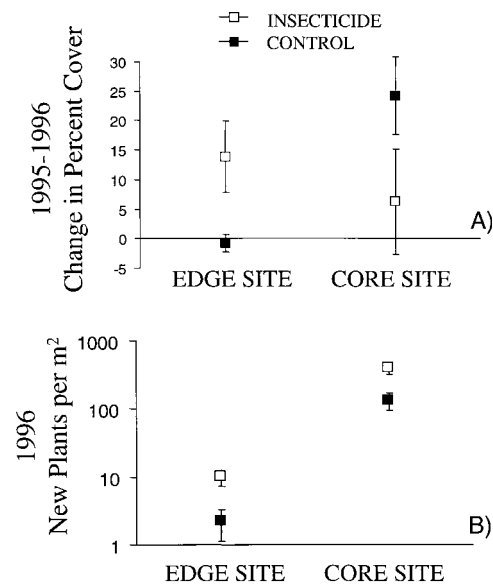


Figure 2: Mean (\pm SE) change in percentage lupine cover (A) and production of new plants (B) as of August 27, 1996, two full growing seasons postmanipulation. Note that a significant region \times treatment interaction in B is obscured by the logarithmic axis.

lupine density in the core plots was 324 (\pm 55) plants m⁻² but only five (\pm 2) plants m⁻² in the edge region (compare with table 1). In contrast to these obvious regional differences, we found no significant premanipulation differences between edge control and edge insecticide plots or between core control and core insecticide plots.

Attacks by folivorous and caudex-boring insect herbivores decreased both the vegetative growth of individual lupine plants and the production of new plants in the edge region (fig. 2). Factorial ANCOVA (see "Methods") revealed a region \times treatment interaction for the 1995–1996 change in percentage lupine cover and a main effect of

Table 2: Statistical analyses from factorial ANCOVA for the experiment investigating herbivore impacts on lupines in core and edge regions of Pumice Plains at Mount St. Helens, Washington

Response variable	Region \times treatment interaction		Region		Treatment	
	F	P	F	P	P	F
Change in percentage lupine cover (1995–1996)	10.10	$P < .01$	8.73	$P = .01$...	NS
New plant production m ⁻² (1996)	10.24	$P < .01$	28.9	$P < .001$	$P < .01$	$F = 11.44$
Lupine intrinsic rate of increase (1995–1996, numbers)	5.82	$P < .04$...	NS	...	NS
Lupine intrinsic rate of increase (1995–1996, surface area)	15.01	$P < .005$...	NS	...	NS
Total seed production (1995)	9.24	$P = .01$...	NS	...	NS
Prevalence of folivores and caudex borers (1995)	3.43	$P < .10$	3.20	$P < .10$	$P < .005$	$F = 13.56$
Percentage leaf damage (1995)	...	NS	24.88	$P < .001$	$P < .01$	$F = 10.58$
Percentage seeds damaged (1995)	28.07	$P < .001$	51.59	$P < .0001$	$P < .001$	$F = 21.40$

Note: All F statistics have one numerator and 11 denominator degrees of freedom.

region (core > edge). Post hoc comparisons indicated that percentage lupine cover in edge insecticide plots was greater than in edge control plots ($P < .03$), but change in percentage lupine cover in core insecticide and core control plots were not different ($P > .08$). After two growing seasons, percentage lupine cover in insecticide-treated edge plots had increased by 13% (fig. 2A) but exhibited no change over premanipulation levels in untreated edge plots.

For new plant production per meter squared (fig. 2B), we found a region \times treatment interaction and main effects of region (core > edge) and treatment (insecticide > control). Post hoc pairwise comparisons with Bonferroni protection indicated that the nearly fivefold increase in new plant production per meter squared in the edge insecticide plots was significantly greater than in edge control plots ($P < .02$). New plant production per meter squared in the core insecticide was also greater than in the core control plots ($P < .01$). In contrast to these effects on lupine growth and reproduction, we found no significant impacts of herbivory on lupine survivorship.

Overall, herbivore impacts curbed the lupine's intrinsic rate of increase at the front of the lupine reinvasion such that an increase in the intrinsic rate of increase was evident at the end of the 1996 growing season (i.e., after two seasons of growth) in the insecticide-treated edge plots, while control populations, with natural levels of herbivory, continued to decline (fig. 3A). Analyses revealed a region \times treatment interaction for lupine intrinsic rate of increase over the 1995–1996 period. Pairwise comparisons indicated that lupine population growth rates were greater in edge insecticide plots than in edge control plots ($P < .01$) but that lupine population growth rates in core insecticide and core control plots were comparable ($P > .08$). Because our experimental herbivore removal was only short term, lupine populations in edge insecticide plots resumed their decline during 1997, the third growing season of our study (fig. 3A). Calculating lupine r by substituting lupine surface area at each census for numbers of individuals yielded analogous results throughout (fig. 3B), with the region \times treatment interaction being even more pronounced.

Because of effects of plant density and age structure, total seed production per meter squared during 1995 was over 60 times greater in untreated core sites than in untreated edge sites (fig. 4A). In the edge region, experimental reduction of herbivores increased total seed production per meter squared threefold (post hoc Bonferroni pairwise comparison: $P = .01$) and nearly quadrupled the number of undamaged seeds per meter squared. In contrast, in the core region, herbivore reduction did not alter total seed production ($P = .88$; fig. 4A).

For 1995, analyses of the prevalence of folivorous and

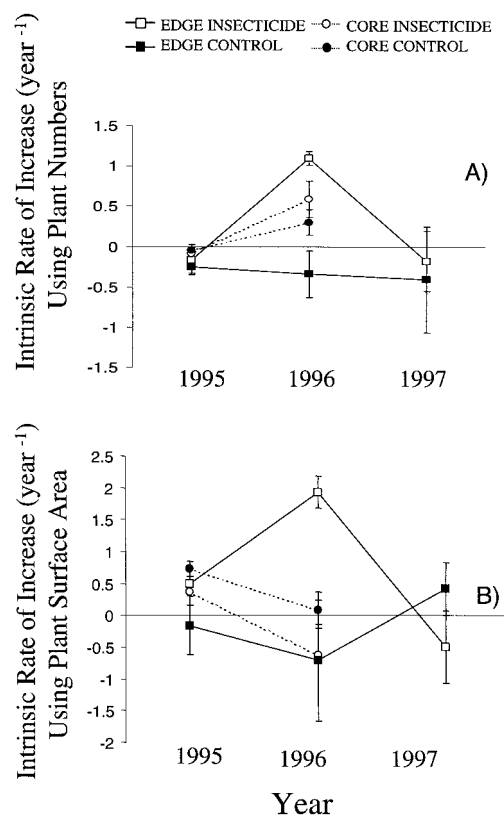


Figure 3: Mean (\pm SE) intrinsic rate of increase for lupine, calculated after each year's end-of-season census (see "Methods"), using numbers of plants (A) and lupine surface area (B).

caudex-boring caterpillars (fig. 4B) indicated a marginal interaction effect and both a treatment effect (control > insecticide) and a marginal effect of region (edge > core). (Omitting initial lupine cover as a covariate here [it was nonsignificant, $P > .65$] leads to a significant [$P < .01$], rather than marginal, effect of region.) Post hoc pairwise comparisons with Bonferroni protection further revealed that caterpillar prevalence in the edge control plots was greater than in core control plots ($P < .03$) and that caterpillar prevalence in edge insecticide plots was less than in edge control plots ($P < .02$). However, caterpillar prevalence in core insecticide and core control plots were comparable ($P > .07$). In all, prevalence of folivorous and caudex-boring caterpillars was over seven times greater in untreated edge plots than in untreated core plots (fig. 4B). These caterpillars inflicted substantial leaf damage on lupines in some treatments (fig. 4C). We found a significant region effect (edge > core) and a significant treatment effect (control > insecticide). Post hoc comparisons indicated that over twice as much leaf damage occurred on control lupines in the edge region as on control lupines

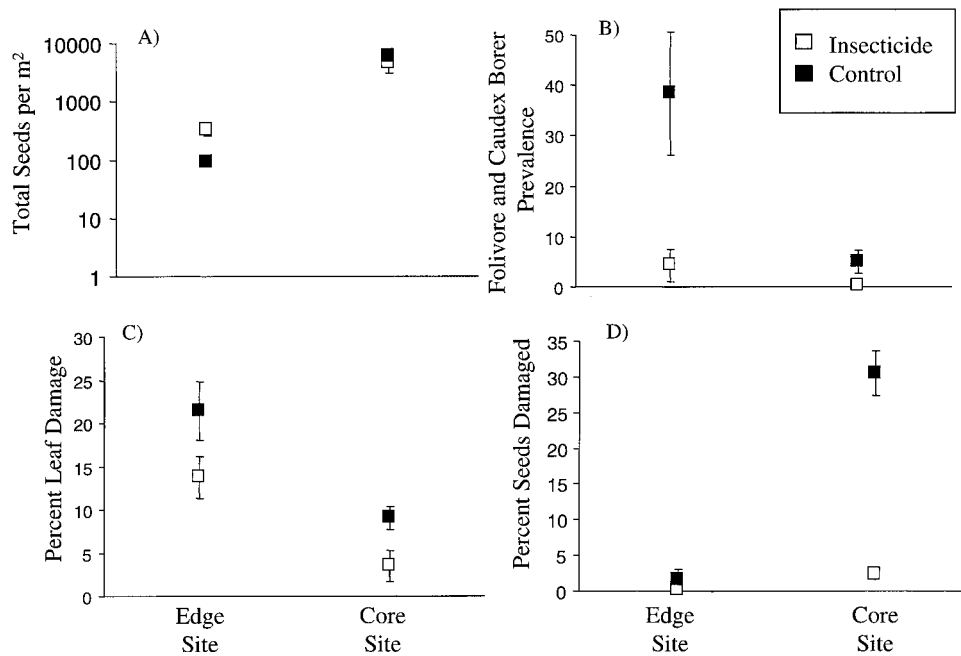


Figure 4: Mean (\pm SE) lupine seed production (A), prevalence of (i.e., the percentage of plants attacked by) folivorous and caudex-boring caterpillars (B), leaf damage (C), and seed damage from cryptic seed predators (D) by the end of summer 1995, the season in which we removed insect herbivores from treatment plots using an insecticide.

in the core region (post hoc Bonferroni pairwise comparison: $P = .01$; fig. 4C). The 35% (relative percentage) decrease in leaf damage in edge insecticide plots compared with edge control plots was significant ($P = .056$).

In contrast to the folivore guild, the other guild of lupine herbivores (caterpillar and fly seed predators) had more pronounced effects in the core region, where this different group of herbivores inflicted predispersal damage on nearly one-third of all seeds produced (fig. 4D). For seed damage, we found a region \times treatment interaction and main effects of region (core > edge) and treatment (control > insecticide). Post hoc pairwise comparisons indicated that seed damage was lower in edge control plots than in core control plots ($P < .001$) and lower in core insecticide plots than in core control plots ($P < .001$) but comparable in edge insecticide and edge control plots ($P = .25$).

Extensive transect surveys of folivore damage in 1998 indicated that foliage damage shows strong negative density dependence, with high levels of damage throughout the edge region and virtually no damage in the core region (fig. 5).

We estimated the coefficient of diffusion (D) as $1.51 \text{ m}^2 \text{ yr}^{-1}$ (Wald 95% CI: 1.45–1.58). Substituting this estimate of spread rate and estimates of the lupine's intrinsic rates of increase without and with herbivores ($r = 1.10$ and

$r_2 = -0.34$, respectively, calculated using numbers of plants; fig. 3A) into equations (1) and (2) indicates that by the end of the 1998 growing season, the concentrated impacts of herbivory at the population's edge had reduced the lupine's average invasion speed by 54% (fig. 6). Such impacts translate into a pronounced decrease in the estimated spatial extent of a typical lupine patch (fig. 6).

Discussion

Core and edge sites differed strongly in both the type and intensity of herbivore impacts on plant population dynamics. At edge sites, leaf damage from folivorous and caudex-boring caterpillars (fig. 4C) resulted in dramatic reductions in leaf photosynthetic area and, consequently, decreased plant growth (fig. 2A) and seed production (fig. 4A). Because 96% of *Lupinus lepidus* seeds germinate the first year and edge patches suffered >40% seed predation in 1994 (Bishop 1996), increased new plant density at the edge in 1996 (fig. 2B) was directly attributable to herbivore removal.

In contrast, folivores and caudex-boring caterpillars were virtually absent from the core (fig. 4B), where predispersal seed predators were the predominant herbivores. Although insecticide application in the core region decreased seed damage (fig. 4D), there was no significant

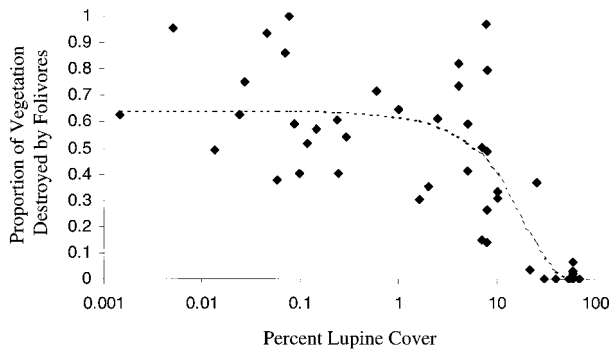


Figure 5: Damage from folivorous caterpillars (*Euxoa* sp.) as a function of percentage lupine cover during 1998. Dashed line is best fit curve from logistic regression.

effect on population growth rate (fig. 3A) because there was no increase in seed production (fig. 4A). This result indicates that soil resources limit both seed production and population growth in the core region. Because lupines, like many plants (Crawley 1989, 1990), appear limited at high densities by postgermination competition rather than seed production (Bishop 1996; J. G. Bishop, unpublished manuscript), high levels of seed predation may be unimportant for local rates of increase in the core. Nonetheless, this seed loss may affect spatial spread and rates of increase at low-density margins of core areas.

Extensive observational data indicate that core-edge differences in folivore and caudex borer prevalence are both widespread and consistent between years. Our landscape-level survey in 1998 showed that percentage damage by *Euxoa* folivores averaged across the edge region was ~60% (fig. 5). Longer-term data indicate that prevalence of this herbivore averaged between 25% and 50% in the years 1993–1995 versus peak prevalence of ~8% in the center of core areas, and the prevalence of caudex borers reached 77% in edge patches in 1994 (Bishop 1996). In contrast, between 1990 and 1996, seed predation averaged about 35% in both regions but fluctuated tremendously between years (Bishop 1996; Bishop and Schemske 1998). These observational results extend the conclusions of our removal experiment: herbivores reduce rates of population increase throughout the edge region and have done so for a substantial portion of the posteruption colonization period. These data also indicate that cumulative effects of both herbivore guilds could well be more severe in the edge region than revealed by our experiment, which did not completely eliminate herbivores from treatment plots.

One possible explanation for differences in herbivory between core and edge patches is compensatory growth of core plants; that is, perhaps the core region was somehow better for lupines than the edge region (e.g., increased

soil moisture), such that lupines in the core could recover from herbivory while those in the “harsher” edge region could not. However, because attacks by *Euxoa* and *Hystriophora* incur permanent and immediately recognizable damage to lupine vegetative tissues, we would have recorded these species had they occurred there. Thus, there simply was no substantial herbivory of this type to compensate for in the core region (figs. 4, 5). An important related hypothesis, which remains to be investigated, is that herbivore prevalence was higher in edge sites because plants there constitute a higher-quality food resource for herbivores.

A third hypothesis, for which there is some evidence, is that decreased prevalence and impacts of folivorous and caudex-boring lepidopterans in the core (figs. 4B, 4C, 5) are linked to successional changes in the arthropod predator assemblage, which may in turn be linked to increased productivity there (Oksanen et al. 1981; Fraser and Grime 1997). In comparison with the edge region, the core region features increased densities of generalist arthropod predators (e.g., spiders, beetles, true bugs; fig. 7), many of which were among the first species to colonize Mount St. Helens (Edwards 1986; Edwards and Sugg 1993; Crawford et al. 1995). We have observed crab spiders (*Xysticus* sp.) feeding on adult moths in the core region, and perhaps more importantly, the core region also harbors a large population of a more recent arrival, the tachinid

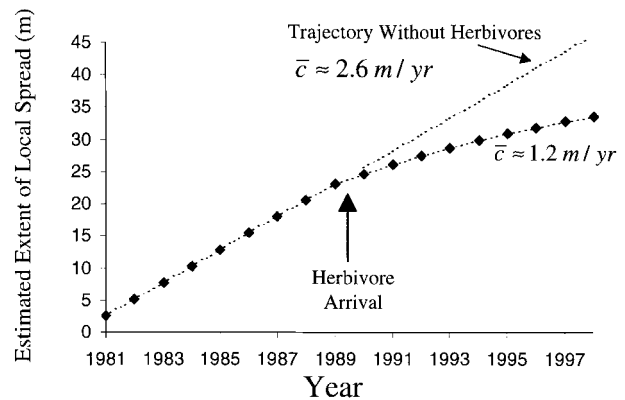


Figure 6: Estimated impacts of herbivores on local scale dynamics of the lupine invasion. The variable \bar{c} denotes the time-averaged lupine reinvasion speed as of 1998 as a function of herbivore presence, calculated using experimental data on population growth rates and supplemental data on local rates of spread. The local extent of lupine spread in a typical lupine patch is a linear function of time before herbivore arrival, but following the herbivore arrival, the extent of spatial spread of the lupine population is a slowly decelerating curve that, with present parameters, will reach a maximum of 42 m in the year 2016 before decreasing. Estimates of spread speed and extent do not include the effects of long-distance patch-forming dispersal events. See “Methods” for details.

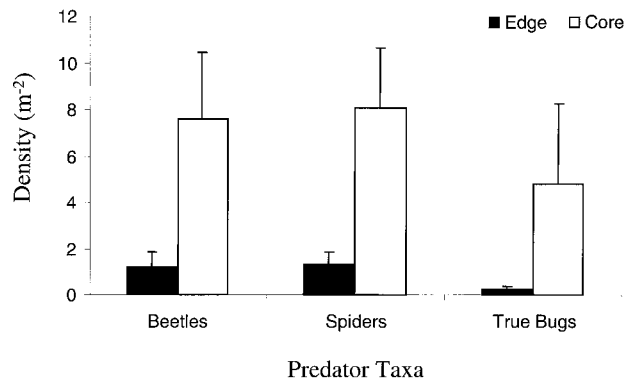


Figure 7: Mean (\pm SE) densities of generalist arthropod predators in core and edge regions of the lupine populations. Beetles chiefly include carabids and tenebrionids; spiders primarily include lycosids, gnaphosids, and thomisids; true bugs mainly include nabids, predatory lygaeids, and a few reduviids. All data are from August 1995 (control plots only). Similar qualitative trends in predator spatial distribution existed throughout the course of the project.

parasitoid *Peleteria malleola*, which specializes on large-bodied noctuids (e.g., *Euxoa*) as hosts (J. Edwards, unpublished manuscript). We found these tachinids to be absent from the edge region during extensive surveys in 1994. We hypothesize that folivore impacts are currently so weak in the core region because of the combined impacts of the generalist predators and the parasitoid. In contrast, in the edge region where the generalist predators are less abundant and the tachinids remain scarce or absent, the folivores are more common and have stronger effects on the lupines. Thus, from this perspective, we propose that arthropod colonization dynamics contribute to a tritrophic invasion in which the folivore populations that only recently colonized the core of the lupine population (and then spread outward) may themselves be undergoing colonization by a third trophic level (the parasitoid).

Long-term demographic studies of Mount St. Helens' lupines have documented extreme levels of herbivory—and accompanying depression of population growth rate—in some portions of the lupine population since 1986 and in the edge of the lupine population since 1990 (Bishop 1996; Bishop and Schemske 1998; C. M. Crisafulli, W. M. Childress, E. J. Rykiel, Jr., and J. A. MacMahon, unpublished manuscript). In the context of classical theories of biological invasions, herbivore-mediated decreases in lupine population growth rate in the edge region would translate into decreased rates of lupine spread across the landscape, which we have quantified here using diffusion models (fig. 6). We emphasize that our calculations reflect local-scale spread rates only; the pres-

ence of many well-separated lupine patches in the edge region indicates that long-distance dispersal of lupine seeds occurs (del Moral 1993), and thus our calculations underestimate the rate of large-scale spread (Kot et al. 1996). We also note as a caveat that, if the rate of lupine reinvasion is actually governed by rare, long-distance dispersal of seeds from the core region as opposed to seed dispersal from edge patches (see, e.g., a recent discussion the role of long-distance dispersal in invasion dynamics, Clark et al. 1998), we could be overestimating the impacts of herbivory on lupine colonization. However, because lupines are a heavy-seeded species (Wood and del Moral 1987; del Moral and Wood 1993), we suspect that the vast majority of patch-forming events in the edge region are the result of seeds dispersed from other edge region patches rather than from the much more distant core region. Because patch-forming dispersal events, like local spread rates, depend critically on seed availability, such events should be also be affected by herbivory that reduces seed availability in the edge region.

If herbivore impacts continue at their present rates, then an extrapolation of spread extent beyond 1998 (using progressively larger values for t_2 in eq. [2]; see fig. 6) indicates that a typical lupine patch would start to contract spatially around the year 2016 after reaching a maximum radius of 42 m. By 2062, the model predicts complete collapse and extinction of such a patch. Clearly predictions like these based on simple theoretical models of spatial spread must be kept in perspective, but they do help reinforce the importance of herbivory in this system. In addition, such calculations help illustrate a key point. Namely, even strong herbivore impacts on plant reproductive rate like those documented in this study ($\Delta r = -1.44$; fig. 3A) may not result in an immediate collapse of an invading population. In a sense, the model indicates that the lupine population built up a considerable “invasion momentum” during the herbivore-free years 1981–1990 that requires a prolonged bout of intense herbivory to overcome. Whether herbivory will remain intense enough to have such profound effects may well depend on the growth and spread of the predator and parasitoid populations. Such invasion momentum may be partly an artifact of our use of a linear model that allows high population levels to build up before the onset of herbivory. However, if this were more generally true, “invasion momentum” of this type would have important applied implications concerning the control of invasive species: delays of even a few years in the application of control methods against an invasive pest species could take years of dogged management efforts to surmount.

In the edge region, just a few weeks respite from the onslaught of folivorous and caudex-boring insect herbivores resulted in lasting, dramatic impacts on lupine pop-

ulation growth and spread. Such effects have rarely been documented in well-established plant populations (Louda 1982; Louda and Potvin 1995; Strong et al. 1995) or colonizing, successional ones (Brown 1984; Bach 1994; Strong et al. 1995). In contrast, herbivore removal in the high-density core region did not result in increased population growth, indicating that both seed availability (edge) and intraspecific competition (core) can drive dynamics in different portions of a plant population, a result that contrasts with recent syntheses (Crawley 1989, 1990). If such spatial subtleties in herbivore effects are common, with herbivory focused on the edge of an expanding plant population and suppressed or ineffective in the larger, denser central region (where the plants might be more readily noticed and studied), then insect herbivores might have stronger impacts on the dynamics of primary succession and plant invasions than previously recognized.

Farrell (1991) presents a model of consumer-driven succession wherein the effect of consumers depends on the model of succession (e.g., tolerance, inhibition, or facilitation). According to this view, consumers of pioneer species will increase rates of succession when the pioneers inhibit later successional species, but consumers will decrease rates of succession when early species facilitate later ones. Because living *L. lepidus* can temporarily inhibit other plant species (e.g. Morris and Wood 1989), consumers may cause local increases in rates of succession.

However, because dead lupines facilitate subsequent colonists (e.g., Morris and Wood 1989; Titus and del Moral 1998), only on consideration of larger-scale dynamics—in particular the spatial expansion of successional communities—does it become apparent that the overwhelming effect of consumers at Mount St. Helens may be to decrease successional rates. Even if herbivores merely slow the lupine invasion, concomitant reductions in rates of soil formation, nitrogen input, and entrapment of detritus and seeds (Halvorson et al. 1991, 1992; Titus and del Moral 1998) are likely to postpone or alter successional trajectories.

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APPENDIX

Herbivore Impacts on Invasion Dynamics

Mark Lewis (Department of Mathematics, University of Utah) generously provided the following derivation of equation (2). Consider a situation in which a point release of N individuals takes place at time $t = 0$. As discussed in the introduction, classical “Fisher-type” models for invading species predict that the rate of spread of such an invading population is governed by the leading edge of the invasion wave when population levels are low and, thus, nonlinear growth terms are negligible. We thus consider the case where the invader’s population dynamics are governed by a linear partial differential equation of the form

$$\begin{aligned} u_t &= Du_{xx} + ru, \\ u(x, 0) &= N\delta(x), \end{aligned} \tag{A1}$$

where $u(x, t)$ is the population density (m^{-2}) at spatial position x and time t , D is a diffusion coefficient ($\text{m}^2 \text{yr}^{-1}$), and r is an intrinsic rate of increase (yr^{-1}). Next, assume that the population’s growth rate is impacted by a consumer species starting at time T such that for $0 < t \leq T$, $r = r_1 > 0$, but for $t > T$, $r = r_2 < 0$. For $0 < t \leq T$, the exact solution to equation (A1) is then

$$u(x, t) = N \frac{e^{r_1 t - x^2/4Dt}}{\sqrt{4\pi Dt}}. \tag{A2}$$

Setting $u(x, t) = u_c$, a threshold level below which the species cannot be detected, the average velocity of the invasion since $t = 0$ is, after some algebra,

$$\frac{x}{t} = \sqrt{4r_1D - \frac{4D}{t} \ln \left(\frac{u_c}{N} \sqrt{4\pi Dt} \right)}. \quad (\text{A3})$$

The argument of the square root in equation (A3) will be positive providing the detection threshold is sufficiently small. Notice that, as $t \rightarrow \infty$, the average speed of the invasion since time $t = 0$ approaches $x/t = c = 2\sqrt{r_1D}$, as in equation (1). For $t > T$, we solve equation (A1) with $t_2 = t - T$, $r = r_2$, and initial conditions

$$u(x, 0) = N \frac{e^{r_1T - x^2/4DT}}{\sqrt{4\pi DT}}, \quad (\text{A4})$$

yielding

$$u(x, t_2) = N \frac{e^{r_1T + r_2t_2 - x^2/4D(t_2+T)}}{\sqrt{4\pi D(t_2+T)}}. \quad (\text{A5})$$

Setting $u(x, t_2) = u_c$ and solving for the average velocity of the invasion since T gives

$$\frac{x}{t_2} = \sqrt{4Dr_1(t_2+T) \frac{T}{t_2^2} + 4Dr_2 \frac{(t_2+T)}{t_2} - \frac{4D(t_2+T)}{t_2^2} \ln \left[\frac{u_c}{N} \sqrt{4\pi D(t_2+T)} \right]}. \quad (\text{A6})$$

Now, multiplying both sides of equation (A3) by $t = T$ yields $x(T)$, the extent of spread of the invasion by time T . Subtracting $x(T)/t_2$ from both sides of equation (A6) yields

$$\begin{aligned} \frac{x(t_2) - x(T)}{t_2} &= \sqrt{4Dr_1(t_2+T) \frac{T}{t_2^2} + 4Dr_2 \frac{(t_2+T)}{t_2} - \frac{4D(t_2+T)}{t_2^2} \ln \left[\frac{u_c}{N} \sqrt{4\pi D(t_2+T)} \right]} \\ &\quad - \frac{T}{t_2} \sqrt{4r_1D - \frac{4D}{T} \ln \left[\frac{u_c}{N} \sqrt{4\pi DT} \right]}, \end{aligned} \quad (\text{A7})$$

which is the average velocity of the invasion since T . As T and t_2 become large, equation (A7) simplifies to equation (2) after making the notational substitution $t_1 = T$. Using our parameters and assuming a lupine detection threshold of 0.1 m^{-2} , equation (2) overestimates the average invasion velocity predicted by equation (A7) by <10%.

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