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Spatial interplay of plant competition and consumer foraging mediate plant coexistence and drive the invasion ratchet

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Indirect effects may play an important role in structuring plant communities. Using a spatially explicit model of consumer foraging and plant competition, we demonstrate how the relationship between the spatial area over which plants compete and the spatial scale of consumer behaviour can determine the outcome of competition when one plant species provides a refuge for mobile consumers (i.e. refuge-mediated apparent competition). Once an initial population of the invader is established, complete invasion may be inevitable because of an ever-advancing invasion front ratchets forward driven by a feeding front of mobile consumers. Because the spatial extent of apparent competition determines the area available for colonization, consumers may also dictate the rate at which an invasion occurs. We find that, as long as refuge-mediated apparent competition is sufficiently localized, invasion is possible even in systems characterized by low overall levels of consumer pressure. Moreover, we show that a stable equilibrium can result in which both resident and invading plants coexist, suggesting that spatial heterogeneity created by refuge-mediated apparent competition may be important in mediating coexistence in plant communities. The spatial interplay of consumer behaviour and plant competition may be an underappreciated mechanism affecting the composition, diversity and spatial pattern of plant communities.

Keywords: behaviour; biological invasions; consumers; refuge-mediated apparent competition

1. INTRODUCTION

Apparent competition, whereby plants compete indirectly by changing the density of a shared consumer (Holt 1977), is an indirect mechanism of competition that may be important in many plant communities (Connell 1990; Chaneton & Bonsall 2000; Noonburg & Byers 2005). Research on apparent competition among plants typically focuses on changes in the density of consumers (e.g. Holt 1977; Connell 1990; Chaneton & Bonsall 2000) or changes in the short-term foraging preferences of consumers (Holt & Kotler 1987), in effect concentrating solely upon trophic links among species. Indeed, evidence for the importance of consumer-foraging behaviour in plant population and community dynamics is widespread (e.g. Atsatt & O'Dowd 1976; McNaughton 1978; Palmer *et al.* 2003; Baraza *et al.* 2006), as the effect of consumers on a target species often depends upon neighbouring plants, ranging from positive (associational resistance; e.g. Hambäck *et al.* 2003) to negative consumer effects (associational susceptibility; e.g. White & Whitham 2000). As described by Connell (1990), apparent competition may also occur when plants affect consumer behaviour by providing a refuge, which subsequently increases consumer pressure on other nearby plants (e.g. Caccia *et al.* 2006; Orrock *et al.* 2010). The refuge may take the form of a favourable microclimate,

a preferred nesting or roosting habitat, or an area where consumers are less likely to fall prey to predators.

Many empirical examples suggest that refuge-mediated apparent competition may be an important component of plant community dynamics; i.e. provision of a shelter may be a common cause of differential consumer effects in both aquatic and terrestrial systems (Connell 1990; Bell *et al.* 1991; Menge 1995). For example, vertebrate consumers seeking refuge in chapparal contribute to the well-known, conspicuous 'bare zones' of vegetation at the chapparal/grassland boundary (Bartholomew 1970; Connell 1990) and establishment of a native grass is most limited by consumers near dense stands of an invasive exotic plant (Orrock *et al.* 2008; Orrock & Witter 2010). Similarly, native rodents are more abundant in the dense cover of an exotic beach grass and thus have larger impacts on native plants (Boyd 1988; Dangremond *et al.* in press), consumers seeking cover in bamboo-dominated habitats create spatial variation in consumption of tree seeds and seedlings (Caccia *et al.* 2006, 2009), and beetles that find refuge beneath nurse plants alter seedling recruitment beneath nurse plants as well as in an adjacent habitat (Chaneton *et al.* 2010). In essence, the ability of consumers to focus their foraging near refuges can lead to strong spatial variation in the strength of the interaction between consumers and plants, which can in turn drive plant community dynamics.

Motivated by these empirical examples, we develop a spatially explicit model of apparent competition that incorporates the non-trophic effect that arises when one plant provides a refuge for foraging consumers. In light

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of a recent, spatially implicit model that illustrates how refuge-mediated apparent competition may occur (Orrock *et al.* 2010), the model described in this paper is intended to evaluate whether the explicit consideration of spatial interactions among plants and consumers alters the dynamics of plant invasion and persistence. Spatially implicit and explicit models and analyses may yield very different insights (e.g. Dytham 1994; Veldtman & McGeogh 2004). Spatial variation in the strength of refuge-mediated apparent competition is likely to arise from spatially varying consumer-foraging behaviour, as empirical observations demonstrate that the distance to a refuge can play a key role in consumer-foraging activity (Caro 2005; Stankowich & Blumstein 2005). Spatial dynamics in plant communities arise because plants disperse and compete over finite (and often distinct) distances (Huston & DeAngelis 1994; Nathan & Muller-Landau 2000). Importantly, the consumers that generate apparent competition could also operate on spatial scales quite different from the scales at which local plants interact and disperse. This can lead to spatial variation in the strength of apparent competition among plants, with the potential to alter opportunities for coexistence or exclusion, and setting up the opportunity for travelling waves (Lambin *et al.* 1998) and other forms of spatially explicit phenomena.

We present a model of refuge-mediated apparent competition that incorporates explicit spatial dynamics, which arise when consumers seek refuge in one habitat and consume plants nearby, and when plants compete over a finite distance. Our spatially explicit model reveals several insights that build on the results in our previous, spatially implicit model (Orrock *et al.* 2010): inferior competitors can expand into an existing plant community behind a front of consumer pressure; the rate of invasion hinges upon the spatial concordance of consumer pressure and plant competition; and spatial segregation of consumer pressure can create novel opportunities for coexistence that may be widespread in terrestrial and aquatic systems.

2. A SPATIALLY EXPLICIT MODEL OF REFUGE-MEDIATED APPARENT COMPETITION

Our model assumes spatially explicit competition for space between two annual plant species, and consumption by a herbivore preferring one of them. As with other theoretical studies of invasion (Levine *et al.* 2006), we consider a one-dimensional, linear habitat initially composed of a common resident annual plant species and a rare and spatially localized invading annual plant species (see electronic supplementary material, figure S1); in effect, the initial condition we examine assumes that a small population of the invader species has just established in a small area, as might occur owing to local disturbance or a pulse of mortality of the resident. As described below, competition for space is modelled as a lottery (Chesson & Warner 1981) with the spatial scale of lottery dynamics determined by the size of the interaction neighbourhood, which we assume represents the scale of both local competition and plant dispersal. We assume that consumers already present within the system, or those nearby that are attracted to the refuge, set a level of consumption that is spatially focused by the refuge-providing plant, but experienced by the

refuge species. For simplicity, the landscape has reflecting boundaries and contains S_T total sites.

(a) Interactions among plants

Each site in the model landscape is occupied by a single adult plant of type i (i.e. either a resident or invading plant, so the landscape is saturated), and the number of sites occupied by type i at time t is $S_{i,t}$ (electronic supplementary material, figure S1a). At the beginning of each model time step, plants have a specific amount of per-site biomass, B_i (electronic supplementary material, figure S1a). Plants produce seeds as a product of their biomass remaining after consumption (see §2b; electronic supplementary material, figure S1b) and their fecundity per unit biomass, F_i (electronic supplementary material, figure S1c). These seeds are evenly dispersed (i.e. a uniform dispersal kernel) across a fixed number of neighbouring sites in the model landscape (electronic supplementary material, figure S1d), which defines the interaction neighbourhood within which competition occurs (Eppstein & Molofsky 2007). The interaction neighbourhood that is relevant to interactions between species is centred on the boundary between resident and invading plants, and extends D units (or $S_{i,t}$ units if $S_{i,t} < D$) in each direction from the boundary (electronic supplementary material, figure S1d), where D is measured as a number of contiguous sites (i.e. individual plants in the domain of competition) in the simulated landscape. This formulation assumes equal dispersal distances and generation times for the two plant types, i.e. both are annual plants with similar dispersal strategies. We assume that, given large enough population sizes ($S_{i,t} \geq D$), each plant species contributes an equal number of sites to the interaction neighbourhood, i.e. $D = D_R = D_I$. If $S_{i,t} < D$, as may occur when the invader first arrives and is rare, or when an invasion is almost complete and the resident is rare, then plant i contributes $S_{i,t}$ sites to the interaction neighbourhood. In other words, the number of sites occupied by species i within the interaction neighbourhood at time t is $N_{i,t} = \min(S_{i,t}, D)$.

Competition among seeds for sites is modelled as a lottery (Chesson & Warner 1981), where the proportion of sites occupied in the interaction neighbourhood in the next generation is determined simply by the relative proportion of seeds produced by each species in the interaction neighbourhood in the current generation (the area occupied in the next generation is generated by a deterministic rule, i.e. there are no stochastic dynamics).

(b) Consumer foraging

We assume that consumers forage exclusively on resident plants, but enjoy some protection because of the refuges provided by the invader. A general rule of thumb is that consumers forage to minimize risk (μ) and maximize harvest rate (h), i.e. the ' μ/h rule' (Gilliam & Fraser 1987). We assume higher harvest rates for resident plants ($h_I < h_R$) and a lower risk : harvest ratio when foraging on residents ($\mu_R/h_R < \mu_I/h_I$; a limiting case considered below is when there is no foraging at all on the invaders). A common empirical observation is that consumers forage up to a specific distance from refuge

habitats (Caro 2005; Stankowich & Blumstein 2005), because they are capable of fleeing to the refuge when danger threatens. We capture this behaviour in our model by assuming that a portion of the resident habitat within a specific distance to the refuge shares the value of μ associated with the refuge; we call this distance the 'risk shadow', R (electronic supplementary material, figure S1b).

During each time step of the model (analogous to a single growing season), consumers forage according to the μ/h rule, collectively consuming a total amount of biomass (C_T) necessary to meet their total energy requirements. Given our assumption that $h_I < h_R$ and $\mu_I < \mu_R$, consumers always begin foraging on resident plants within the risk shadow (i.e. in the refuge habitat), because $\mu_I/h_R < \mu_R/h_R$ and $\mu_I/h_R < \mu_I/h_I$. Consumers will only forage on resident plants beyond the risk shadow if all of the resident biomass within the risk shadow has been consumed (invasion is also possible when consumers switch before complete patch depletion; see §4). In particular, given our assumption that $\mu_R/h_R < \mu_I/h_I$, once the risk shadow is devoid of biomass, consumer foraging shifts to the non-refuge resident patch, as this is the patch with the next lowest value of μ/h . This condition also allows us to formulate the model solely in terms of consumption of resident plants, because invaders will only be consumed once all resident plant biomass has been consumed, i.e. given consumption of species i at each site x , $C_{i,x} \sum_x C_{R,x} \leq C_T$. We assume that the value of C_T is fixed; consumers consume enough biomass to maintain a constant population size, and there are no changes in the total consumer population size because of immigration or emigration (i.e. as might occur with short-term apparent competition). This assumption is realistic for cases where consumer dynamics are much slower than the plant dynamics, as might be the case with annual plants when compared with long-lived vertebrate grazers.

(c) Consumer effects on plant competition

Prior to the introduction of the new species (i.e. the invader), consumption will be spread among all sites occupied by the resident. After the invader is introduced, the availability of a refuge concentrates consumption near the invader (see electronic supplementary material, figure S1). Mathematically formalizing the above dynamics, the site occupancy for species i in a new generation, $S_{i,t+1}$, is the number of total sites currently occupied by i beyond the interaction neighbourhood ($S_{i,t} - N_{i,t}$, with $N_{i,t} = \min(S_{i,t}, D)$ in the interaction neighbourhood) plus the number of sites it is expected to occupy in the interaction neighbourhood based on its seed production relative to the other species. This production is determined by the fixed number of seeds produced by each plant per unit biomass, F_i , multiplied by the post-consumption plant biomass (the species- (i) and site- (x) dependent consumption $C_{i,x}$ subtracted from the per-site pre-consumption biomass B_i). Each species captures a portion of the interaction neighbourhood (a total of $N_{i,t} + N_{j,t}$ sites) based upon the relative proportion its seeds comprise of the total seed pool in the interaction neighbourhood; although seeds are randomly mixed in the interaction neighbourhood, the sites captured by

each species are assumed to remain contiguous for mathematical convenience (i.e. sites won by resident species are adjacent to the resident side of the interaction neighbourhood). This assumption essentially treats the outcome of plant competition in a specific, spatially implicit fashion; future studies that consider these dynamics in an explicit spatial context will be informative. We note that, as long as the fraction of sites captured by one species is greater within the interaction neighbourhood, the outcome of invasion is not affected by this simplification. The assumption that the area won by a species in the interaction neighbourhood is near the source population of that species is consistent with empirical dispersal kernels, as many seeds fall near parent plants (Nathan & Muller-Landau 2000). With these assumptions, the iteration for the number of sites occupied by species i competing with species j is:

$$S_{i,t} + 1 = (S_{i,t} - N_{i,t}) + \frac{(N_{i,t} + N_{j,t}) \sum_{x=1}^{N_{i,t}} (B_i - C_{i,x}) F_i}{\sum_{x=1}^{N_{i,t}} (B_i - C_{i,x}) F_i + \sum_{x=N_{i,t}+1}^{N_{i,t}+N_{j,t}} (B_j - C_{j,x}) F_j}, \quad (2.1)$$

In essence, each plant is capable of producing a fixed number of seeds per unit biomass, and consumers affect the realization of this seed production potential by reducing plant biomass. The assumption of reflecting boundaries allows analytical tractability when the interaction neighbourhood is less than two-dimensional sites owing to either species being rare, i.e. when $S_{i,t}$ or $S_{j,t} < D$ (use of absorbing boundaries would probably decrease the potential for invasion of a rare invader). Given the iteration in equation (2.1), invaders increase in frequency ($S_{i,t+1} > S_{i,t}$) when:

$$\frac{\sum_{x=1}^{N_{i,t}} (B_i - C_{i,x}) F_i}{N_{i,t}} > \frac{\sum_{x=N_{i,t}+1}^{N_{i,t}+N_{j,t}} (B_R - C_{R,x}) F_R}{N_{R,t}}. \quad (2.2)$$

In other words, invaders increase when their net seed production, *per capita*, after consumption, exceeds that of the resident. We define the effective competitive ability, α_i , of a species as its realized per-site seed production in the interaction neighbourhood (i.e. the competitive ability of a plant species after consumers remove plant biomass):

$$\alpha_i = \frac{\sum_{x=1}^{N_{i,t}} (B_i - C_{i,x}) F_i}{N_{i,t}}. \quad (2.3)$$

This framework makes competitive interactions a simple function of plant biomass, seed production and consumer pressure.

The inequality in equation (2.2) can be simplified because of our assumption that consumers will only switch to consuming invaders once all resident plant biomass has been consumed. Hence, $C_{I,j} = 0$ for all of parameter space, provided some resident plant biomass remains. Assuming an initially rare invader and a common resident species such that $S_{R,0} \geq D$, the condition for an initial increase in invader frequency, $\alpha_I > \alpha_R$, becomes:

$$B_I F_I > \sum_{x=N_{I,t}+1}^{N_{I,t}+D} \frac{(B_R - C_{R,x}) F_R}{D}. \quad (2.4)$$

Because the number of sites captured in each generation is a function of the relative difference in competitive ability of invaders and residents, the change in the number of sites occupied by species i in each generation, $\Delta S_i = S_{i,t+1} - S_{i,t}$ is also a function of the difference in competitive ability. If both species have populations at least as big as the interaction neighbourhood (i.e. $S_{R,t}$ and $S_{I,t} \geq D$, such that $N_R = N_I = D$), substituting and rearranging the terms from equation (2.3) yields:

$$\Delta S_i = D \left(\frac{\alpha_I - \alpha_R}{\alpha_I + \alpha_R} \right). \quad (2.5)$$

The parenthetical term in equation (2.5) represents the fraction of the interaction neighbourhood captured by the invader, and reiterates the conditions necessary for invasion, as the invader will only gain sites when $\alpha_I > \alpha_R$. Equation (2.5) also shows that the rate of invasion is a function of both the size of the interaction neighbourhood and relative differences in competitive ability.

Below, we explore how the invasion criterion (inequality (2.4)) depends on relative parameter values. To illustrate the dynamical behaviour of the model, we numerically simulate equation (2.1), with invading plants introduced at the left-most portion of the array.

(d) Determinants of consumer impact and conditions for invasion

Because we assume that residents are superior competitors in the absence of herbivory ($B_I F_I < B_R F_R$), invasion will only proceed when differences in competitive ability are offset owing to differences in biomass lost to consumption, such that effective competitive ability (α_i in equation (2.3)) locally favours the invader. Assuming that invaders are not consumed, consumers foraging according to the μ/h rule create changes in the effective competitive ability of resident plants (figure 1) that are a function of the size of the risk shadow (R), the size of the interaction neighbourhood (D) and the amount of resident plant biomass consumed ($\sum_x C_{R,x}$, equivalent to C_T in our model). Changes in α_R owing to the changes in the spatial distribution of consumer pressure can be largely summarized based upon the relative values of R and D , the value of C_T and the pre-consumption amount of native biomass in the risk shadow adjacent to the refuge (RB_R). For succinct notation, we assume that the resident population occupies at least D sites in defining these regions, such that $\sum_{x=N_{I,t}+1}^{N_{I,t}+D} B_R F_R = DB_R F_R$.

If the risk shadow is smaller than the portion of the resident plants in the competitive neighbourhood ($R \leq D$) and the amount of total consumption is greater than the amount of resident biomass in the risk shadow ($C_T > RB_R$), consumers remove all of the biomass in the risk shadow, and then remove biomass from the remaining resident plants (figure 1). As a result, the consumption of the resident in the interaction neighbourhood ($C_{R,x}$ for site x in the interaction neighbourhood), and thus effective α_R , is a function of the size of the entire resident population $S_{R,b}$, the size of R and the size of D . As the resident population becomes larger and R becomes a smaller portion of D , the effect of consumers is effectively diluted because the effect of consumers in D is averaged over the remaining resident population.

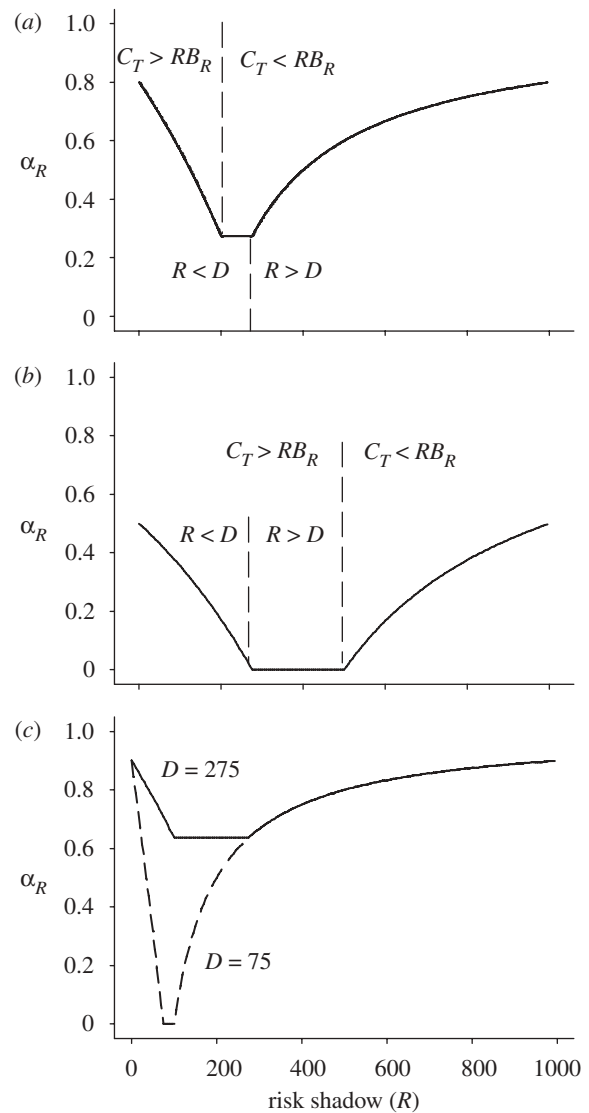


Figure 1. The effective competitive ability of resident plants (α_R ; equation (2.3)) within the interaction neighbourhood is a function of the risk shadow (R), interaction neighbourhood (D) and consumption (C_T). Panels (a,b) differ in the amount of consumption of resident plants: (a) $C_T = 200$; (b) $C_T = 500$. In both panels, $D = 275$. When resident plants cannot become established beyond the interaction neighbourhood, invasion is imminent whenever effective $\alpha_R < \alpha_I$. (c) When consumption is constant ($C_T = 200$ units of resident biomass), changing the size of the interaction neighbourhood (D) alters the effective competitive ability of resident plants. In the absence of consumption, $\alpha_R = 1$ for all panels.

If all consumption occurs within $R(C_T \leq RB_R)$ and $R \leq D$, all consumption also occurs within the interaction neighbourhood. In this portion of parameter space, the size of the risk shadow becomes unimportant for determining invasion (figure 1).

If the risk shadow exceeds the size of the interaction neighbourhood ($R > D$), the size of the interaction neighbourhood (beyond being less than the threshold value of R) no longer affects α_R because the risk shadow, R , determines the average biomass of resident plants surviving within (and beyond) the neighbourhood. Then, if consumers require more resident biomass than is located in the refuge ($C_T \geq RB_R$), they consume all biomass in the risk shadow, which includes all resident biomass in the

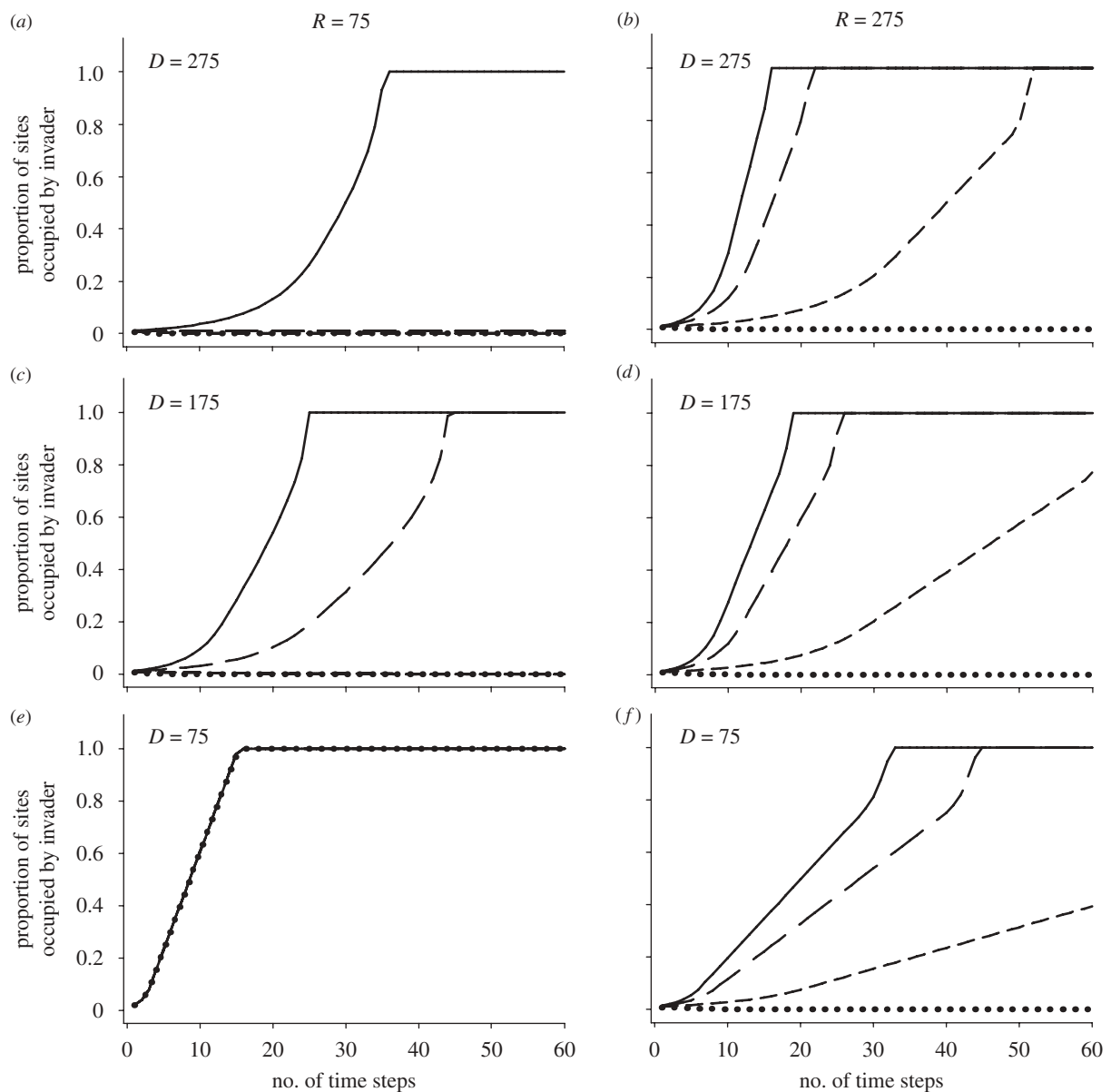


Figure 2. Whether an invasion occurs, and the rate at which it happens, is a function of the interaction neighbourhood and the competitive ability of invading plants. For all panels, the landscape begins with $S_T = 1000$ total sites, $S_{R,0} = 990$ sites occupied by residents and $S_{I,0} = 10$ sites occupied by invaders. In the absence of consumption, $\alpha_R = B_R F_R = 1$. Consumers remove 175 units of resident biomass (i.e. $C_T = 175$), and the risk shadow (R) extends either 75 or 275 sites (*a,c,e* and *b,d,f* columns, respectively) beyond the edge of the boundary between residents and invaders. Solid line, $\alpha_I = 0.85$, big dashed line, $\alpha_I = 0.65$, small dashed line, $\alpha_I = 0.45$, dotted line, $\alpha_I = 0.25$.

interaction neighbourhood, before foraging in the remaining native sites. As a result, the resident does not produce seeds in the interaction neighbourhood ($\alpha_R = 0$), and an invasion occurs for all biologically relevant invader parameters ($B_I F_I > 1$).

If the risk shadow exceeds the size of the interaction neighborhood ($R > D$), but all resident biomass in the risk shadow is not consumed ($C_T < RB_R$), the amount of consumption that occurs for each location x in the interaction neighbourhood is $C_{R,x} = C_T/R$, and invasion occurs if: $B_I F_I > (B_R - C_T/R) F_R$. For a fixed total amount of consumption, an increase in the size of the risk shadow weakens the impact of consumption upon plant biomass, making it harder for an inferior but refuge-providing species to increase when rare.

Which of the relative values of R , D , C_T and B_R applies to a given situation depends on the characteristics of

the particular plant–consumer system. For example, if $D > C_T/B_R$, it is not possible for both $R < D$ and $C_T > RB_R$; conversely, if $D < C_T/B_R$, it is not possible for both $R > D$ and $C_T < RB_R$ (figure 1). In all cases, decreasing the competitive disadvantage of invaders significantly increases the parameter space where invasion is possible (figure 2).

Regardless of the intrinsic competitive ability of the invader, there is often a combination of D , R and C_T that allows inferior invaders to succeed. For example, success is guaranteed when $R > D$ and $C_T \geq RB_R$ as long as $B_I F_I > 1$; under this condition, the competitive ability of the invader has essentially no bearing on the outcome of invasion because the consumers consume all of the resident biomass in the interaction neighbourhood (figures 1 and 2), freeing up space for the invader to increase when rare. This can occur even in systems that

experience very little total consumer effect averaged over the landscape (figure 1c), or when consumers target plant life stages with little biomass (e.g. seedlings).

(e) Components determining invasion rate

Once underway, the invasion ratchets forward with each time step. This ‘invasion ratchet’ occurs because consumers track the edge of the invasion front, such that as invading plants expand into resident habitat, the frame of consumption continues to move forward. The rate at which the invasion proceeds depends upon the relationship between α_R and α_I (equation (2.5)), which itself depends upon the values of R , D and C_T . For any starting values of α_R and α_I , combinations of R , D and C_T that maximally reduce α_R will increase invasion rates by increasing the proportion of the interaction neighbourhood won by the invading plant each time step (figure 2). The rate of invasion increases as it proceeds because the landscape is finite, such that consumers necessarily consume more biomass within the refuge as total resident biomass is reduced across the landscape (figure 2).

(f) When plants compete via long-distance dispersal

The basic model does not allow the resident species, assumed to be the superior competitor in the absence of consumption, to re-take invaded habitats beyond the interaction neighbourhood and risk shadow via long-distance dispersal (or via germination of dormant seeds). We explored this possibility in a modified version of the model, by allowing superior resident competitors to re-establish within a proportion of invaded sites beyond the interaction neighbourhood at each model time step (see electronic supplementary material for details). If resident plants are capable of re-invading anywhere in the landscape where invading plants are not protected by consumers, the outcome of invasion depends upon the relative rate at which resident plants replace invading plants and vice versa (figure 3). When resident plants replace invading plants more rapidly than invaders replace residents, the invasion may stop, but it does not retreat. Coexistence at the landscape scale occurs as long as consumer pressure within the interaction neighbourhood is great enough that invaders cannot be replaced there (figure 3); coexistence can arise because of a tradeoff between colonizing ability and refuge-mediated apparent competition.

3. DISCUSSION

Our work shows that the spatial extent of plant competition and consumer behaviour can interact to determine the outcome of plant competition. Once a threshold number of invaders has established (e.g. owing to local disturbance), the refuge they provide can catalyse the formation of a feeding front of mobile consumers (e.g. van de Koppel *et al.* 2002; Silliman *et al.* 2005), and refuge-providing invaders may advance into the space cleared by consumers, creating positive feedback yielding an advancing invasion wave (figures 2 and 3). This invasion ratchet leads to a displacement of the resident plant species not predicted based on competitive ability alone. By explicitly considering the spatial nature of these

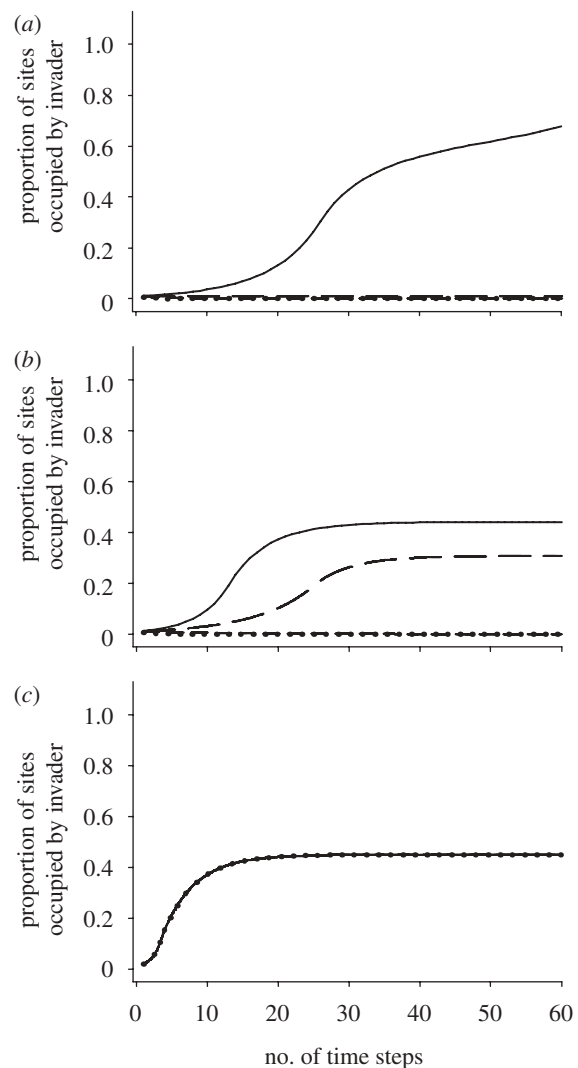


Figure 3. Invasion dynamics when resident plants are capable of colonizing areas of exotic plants outside the interaction neighbourhood, with probability $E = 0.2$. All other model parameters are identical to those in figure 2 for panels (a,c,e). When residents are capable of recolonization, a stable equilibrium may arise, whereby invaders and residents indefinitely coexist. Solid line, $\alpha_I = 0.85$; big dashed line, $\alpha_I = 0.65$; small dashed line, $\alpha_I = 0.45$; dotted line, $\alpha_I = 0.25$. (a) $D = 275$. (b) $D = 175$. (c) $D = 75$.

interactions, our model illustrates novel opportunities for invasion and coexistence and quantifies the spatial scale of refuge provision, consumer pressure and plant competition that interact to determine which of these outcomes will occur. Our model illustrates how invasion may occur in systems where total consumer pressure is not sufficient to generate invasion in the absence of the refuge effect, i.e. by focusing consumer impact onto a subset of resident plants, refuge-mediated apparent competition makes it possible for an invasion to occur at much lower levels of average consumer pressure.

Our spatially explicit model provides three novel insights that extend our earlier model using implicit space (Orrock *et al.* 2010). The primacy of refuge-seeking behaviour in consumers (Caro 2005) and the importance of refuge-based consumer effects on terrestrial and aquatic plants, and indeed for any space-occupying organism (Connell 1990; Bell *et al.* 1991; Menge 1995) suggests that these results may be applicable in a wide array of

ecological situations. We have shown that: (i) changes in consumer risk caused by plants themselves may interact with the spatial scale of plant dispersal and competition to alter the strength of refuge-mediated apparent competition and determine whether or not the invasion ratchet begins; (ii) the size of the risk shadow also determines the opportunity for spatial spread of the invader and thresholds for invasion; and (iii) the degree to which resident plants are capable of establishing via long-distance dispersal may determine whether or not an invader can replace the resident or if coexistence occurs.

(a) *The interplay of the risk shadow and the competitive neighbourhood*

Because the risk shadow alters the spatial dynamics of consumer foraging, the spatial coincidence of the risk shadow and plant competition change the relative strength of refuge-mediated apparent competition by determining the degree to which consumption is focused on individual plants that are also directly engaged in competition (figure 1). As the size of the risk shadow changes, thresholds arise depending upon the extent of the competitive neighbourhood, the total amount of biomass eaten by consumers and the amount of resident biomass available for consumption (i.e. values of D , C_T and B_R , respectively) leading to qualitatively different patterns for how consumers alter the effective competitive ability of residents (figure 1).

Despite this complexity, several key points emerge. In general, invasion is less likely to proceed if the risk shadow is spread over a sufficiently large area, such that consumer impact is diluted over a large portion of resident plants (figure 1). However, when levels of consumption are similar to the amount of resident biomass in the risk shadow (i.e. $C_T \approx RB_R$) and the interaction neighbourhood is comparable in size to the risk shadow (i.e. $D \approx R$), the realized competitive ability of the resident can be greatly reduced because consumer pressure is focused precisely on the region over which plants compete (figures 1 and 2). Depending upon the degree of concordance between consumption and competition, systems characterized by very small levels of consumer impact can nonetheless be invaded by plants that cause dramatic changes in consumer foraging (e.g. figure 1c). As a result, even communities with small amounts of total consumption can be invaded via refuge-mediated apparent competition if the risk shadow is in the appropriate range relative to the interaction neighborhood (figures 1 and 2). Once the invasion ratchet is underway, the invader will persist (and spread) as long as the resident cannot establish beyond the invasion front, owing to limited dispersal, microsite limitation, allelopathy or other factors. This tendency towards displacement could be further exacerbated if the refuge also acts to increase total consumer pressure by attracting consumers from adjacent resident habitats, thus increasing total consumer density (i.e. short-term apparent competition; Holt & Kotler 1987).

In our model, the invasion ratchet occurs because annual plants modulate the local intensity of consumer foraging on resident plants. We believe that our model mimics terrestrial annual plant communities where both residents and invaders recruit from seed each year.

However, comparable phenomena could arise in other terrestrial and aquatic systems dominated by clonal, space-occupying organisms, if clonal growth at the resident/invader boundary is determined by the interplay of competition and consumption. The model assumption of discrete generations may limit the literal application of our model to some such systems (as it requires the production of clonal biomass to occur on annual time scales for interacting species). We expect that if residents are long-lived, refuge-mediated apparent competition may allow invaders to replace residents only when other factors (e.g. episodic disturbance, fire) reduce the abundance of perennial residents. Once residents were sufficiently reduced, invaders could move into and persist in the open habitat via refuge-mediated apparent competition. For example, the 'bare zone' along the border of grassland and chaparral communities is a classic example of a pattern generated by refuge-mediated foraging (Bartholomew 1970); when annual precipitation and fire regimes are favourable, chaparral may be able to expand into native grassland.

Refuge-mediated apparent competition may also be important in cases where the refuge-providing species is a superior competitor. For example, woody shrubs that are likely to be strong competitors for light may also provide a refuge for small-mammal consumers (Mattos & Orrock 2010); refuge-mediated apparent competition may serve to increase the rate of invasion by facilitating invader recruitment near the invasion front. Even in cases where competitive superiority of the invader is due to consumers (e.g. if consumer attack rates on residents are sufficient for invasion in the absence of refuge-mediated apparent competition), the provision of a refuge would be expected to accelerate the invasion if replacement rates near the invader–resident boundary are a function of remaining resident biomass.

(b) *Consumer behaviour mediates the rate of invasive spread and thresholds of invasion*

Our model shows that the spatial extent of consumer foraging and spatial constraints on consumption owing to risk-averse behaviour may play a key role in determining the rate at which spread occurs (figure 2). Propagule dispersal distance, a component of the interaction neighborhood in our model, is often considered a key component of invasive spread (e.g. Skellam 1951). However, in systems where invasion is via refuge-mediated apparent competition, the distance of propagule dispersal may not be a key determinant of invasion rate (figure 2), because seeds of invasive plants may only gain a foothold when close to the invasion front, where consumers tip the balance in their favour. This observation suggests that long-distance dispersal by the inferior invader will only be successful if invader propagules happen to establish in environments with suitable consumer pressure. As such, although inferior invaders may be superior colonizers and may persist via the competition–colonization tradeoff, refuge-mediated apparent competition would limit their establishment to areas of sufficient consumer pressure. Moreover, any factor that changes consumer abundance (e.g. habitat fragmentation, the presence of top predators) may change total consumer pressure and thus mediate spread via refuge-mediated apparent competition.

Consumer behaviour may also generate Allee effects because consumers may only respond to stands of plants as a potential refuge when those plants reach a threshold size or density. Small, isolated patches of invading plants may not be large enough to create a refuge from the consumer's perspective. If a large disturbance removes resident plants, the size of the invader patch may then become large enough to constitute a refuge, triggering refuge-mediated apparent competition and the invasion ratchet. Importantly, this Allee effect may occur in addition to other types of Allee effects that arise when consumption becomes sufficient to overwhelm differences in direct competitive ability (Orrock *et al.* 2010).

The size of the risk shadow may vary depending upon the consumer species considered, consumer characteristics such as escape speed and morphological defences (Stankowich & Blumstein 2005), the seasonal abundance of food and mates, and the abundance of predators and predator cues (Caccia *et al.* 2006). The risk shadow will also interact with the size and shape of patches of resident plants to determine the area affected by refuge-mediated apparent competition, because patch geometry determines the degree to which the risk shadow penetrates resident habitat (Fagan *et al.* 1999; Cantrell *et al.* 2001). As a result, consumer behaviour and the risk shadow interact with patch size and shape to set geometric thresholds for an invasion to occur and for residents to persist.

(c) *Refuge-mediated competition as a mechanism of coexistence*

Our results suggest that spatial variation in refuge-mediated apparent competition may be a general mechanism affecting coexistence in plant communities (Connell 1990). Coexistence becomes more likely when resident plants can re-establish in invader-dominated habitats beyond the influence of consumers (figure 3), as an equilibrium can be achieved where rates of competitive replacement equal the rates of replacement owing to consumption-mediated competition. Because invaders continue to provide a refuge, plant coexistence is guaranteed as long as levels of consumption are unchanged. Because consumption rises sharply in the refuge, it may be possible that refuge-mediated apparent competition is a relatively widespread mechanism facilitating coexistence by generating spatial heterogeneity in the strength of consumption and competition. Patterns of consumer effect are often highly heterogeneous (e.g. Crawley 1997) and associated with small-scale vegetation heterogeneity (Connell 1990). Just as mortality and disturbance create sites available for inferior competitors that increase the potential for coexistence (Tilman 1994), heterogeneity produced by refuge-mediated apparent competition may promote coexistence in plant communities.

4. FUTURE DIRECTIONS

Several extensions of the spatial model presented here would provide fruitful avenues for future research. Extending the model to include non-uniform species-specific dispersal kernels within and outside the interaction neighbourhood, incorporating differences in palatability among plant species, and including other components of plant dynamics (e.g. abiotic stress) could

identify mechanisms that oppose or complement competitive effects owing to refuge-mediated apparent competition. For example, the effect of consumers on native plants may depend jointly on refuge-providing species and the composition of the neighbourhood directly adjacent to native species (Orrock & Witter 2010), abiotic stress beyond the refuge may reduce plant survival (Caccia *et al.* 2009), and there may be low densities of resident plants that are ignored by consumers. It would be instructive to incorporate greater complexity of consumer foraging; in our model consumers do not assess how patch depletion might change patch quality. Although incorporating depletion would not change the order in which consumers begin foraging in a habitat (i.e. they still forage first in habitats with the lowest value of μ/h), depletion would promote switching among patches because patches are treated identically once foraged such that all μ/h are equal (Gilliam & Fraser 1987), even if consumers have not fully depleted the current patch. When depletion affects consumer foraging, initial differences in μ/h are expected to determine heterogeneity in consumption.

Several field studies have demonstrated changes in consumer impact consistent with refuge-mediated apparent competition (e.g. Connell 1990; Menge 1995; Chaneton & Bonsall 2000; Caccia *et al.* 2006, 2009; Orrock *et al.* 2008; Chaneton *et al.* 2010; Orrock & Witter 2010), but comprehensive empirical tests are still scant. Given the importance of spatial patterning in rates of attack illustrated by our model, strong experimental tests of this effect will require manipulation of consumer pressure and competitive interactions at varying distances from presumed refuges (e.g. Bartholomew 1970; Orrock *et al.* 2008; Chaneton *et al.* 2010; Orrock & Witter 2010), or will require experimental manipulation of the refuge itself. Although field studies may simplify dynamics by examining species in the absence of direct competition (e.g. Orrock & Witter 2010), future studies capable of quantifying the balance of direct and indirect interactions, including positive interactions such as facilitation (Chaneton *et al.* 2010) will be important for determining the relative importance of refuge-mediated apparent competition in comparison with other, better-documented modes of interspecific interactions.

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