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Journal

Ecology Letters, 13(1)

ISSN

1461-023X

Authors

Orrock, John L
Holt, Robert D
Baskett, Marissa L

Publication Date

2010

DOI

10.1111/j.1461-0248.2009.01412.x

Peer reviewed

IDEA AND PERSPECTIVE

Refuge-mediated apparent competition in plant–consumer interactions

John L. Orrock,^{1*} Robert D. Holt² and Marissa L. Baskett³

¹*Biology Department, Washington University, Saint Louis, MO 63130, USA*

²*Department of Biology, University of Florida, Gainesville, FL 32611, USA*

³*Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA*

*Correspondence: E-mail:

orrock@wustl.edu

Abstract

At the intersection of consumer behaviour and plant competition is the concept of refuge-mediated apparent competition: an indirect interaction whereby plants provide a refuge for a shared consumer, subsequently increasing consumer pressure on another plant species. Here, we use a simple model and empirical examples to develop and illustrate the concept of refuge-mediated apparent competition. We find that the likelihood that an inferior competitor will succeed via refuge-mediated apparent competition is greater when competitors have similar resource requirements and when consumers exhibit a strong response to the refuge and high attack rates on the superior competitor. Refuge-mediated apparent competition may create an emergent Allee effect, such that a species invades only if it is sufficiently abundant to alter consumer impact on resident species. This indirect interaction may help explain unresolved patterns observed in biological invasion, such as the different physical structure of invasive exotic plants, the lag phase, and the failure of restoration efforts. Given the ubiquity of refuge-seeking behaviour by consumers and the ability of consumers to alter the outcome of direct competition among plants, refuge-mediated apparent competition may be an underappreciated mechanism affecting the composition and diversity of plant communities.

Keywords Allee effects, behaviour, biological invasions, consumers, herbivores, short-term apparent competition.

Ecology Letters (2010) 13: 11–20

INTRODUCTION

Consumers can cause dramatic shifts in the structure of plant communities (e.g., Brown & Heske 1990; Olff & Ritchie 1998), and may alter the course of biological invasions (Levine *et al.* 2004; Mitchell *et al.* 2006; Parker *et al.* 2006). In addition to direct consumer effects, empirical work suggests that apparent competition, where plants compete indirectly by changing the density (Holt 1977) or foraging preferences (Holt & Kotler 1987) of shared consumers, may be important determinants of plant community structure in terrestrial (Chaneton & Bonsall 2000; Palmer *et al.* 2003; Caccia *et al.* 2006; Pearson & Callaway 2008) and aquatic systems (Menge 1995). Previous work on apparent competition has concentrated on trophic links among species. However, as noted by Connell (1990), apparent competition can also arise via a quite different mechanism: a plant may provide a refuge for a consumer, increasing the local abundance or foraging efficiency of the consumer. We use the term ‘refuge’ (Berryman & Hawkins 2006), to indicate that a plant provides a resource for the

consumer other than food (i.e., a non-trophic pathway; Menge 1995; Caccia *et al.* 2006). For example, a plant that is not important as a food source may provide a refuge when its thick cover creates a favourable microclimate for foraging, or when its architecture provides favourable nesting or roosting habitat, or when its structure yields a, safe environment where consumers are protected from their own predators (Berryman & Hawkins 2006). The presence of such refuges could intensify the impact of consumers on nearby plants, thus indirectly benefiting the plant species that provides the refuge (Fig. 1). Evidence suggests that refuge-mediated changes in consumer pressure can generate classic strong ecological patterns, e.g. the ‘bare zone’ around chaparral shrubs (Bartholomew 1970) and ‘halos’ around reefs (Ogden *et al.* 1973). Moreover, in light of the ubiquity of refuge-sensitive foraging and habitat selection (see reviews by Orth *et al.* 1984; Lima & Dill 1990; Brown & Kotler 2004; Caro 2005; Stankowich & Blumstein 2005), and widespread evidence that plant structure influences animal behaviour (Bell *et al.* 1991), opportunities for plants to indirectly interact via ‘refuge-mediated apparent

competition' may be widespread, with significant ecological consequences.

As an example of the potential importance of this refuge-mediated mode of action, field experiments show that consumer pressure on a native grass is increased by the presence of an exotic forb that forms tall, dense stands. Although evidence suggests that the native grass can outcompete many exotic species (Seabloom *et al.* 2003), changes in consumer pressure due to the exotic forb are sufficient to completely eliminate re-establishment of the native competitor (Orrock *et al.* 2008). This increase in consumer pressure is consistent with activity of mammalian consumers (i.e. squirrels, rabbits, mice) that appear to seek refuge near the exotic plant (Orrock *et al.* 2008).

Our aim is to articulate the concept of refuge-mediated apparent competition and argue that this indirect interaction may play an important role in determining the structure and invasibility of plant communities. A substantial literature attests to how neighbouring plants can exert strong positive and negative effects on target plants (e.g., Atsatt & O'Dowd 1976; McNaughton 1978; Brown & Ewel 1987; Menge 1995; White & Whitham 2000; Hambäck *et al.* 2003; Palmer *et al.* 2003; Baraza *et al.* 2006). Refuge-mediated apparent competition describes how asymmetrical associational susceptibility (Brown & Ewel 1987; White & Whitham 2000) generated by consumer behaviour can create opportunities for local competitive exclusion. In essence, refuge-mediated competition involves a form of ecological engineering (Jones *et al.* 1994) via habitat modification (Bell *et al.* 1991; Menge 1995; Didham *et al.* 2007), whereby the refuge-providing species

modifies the activities of a natural enemy so as to negatively affect a competing species. Below, we first use a simple model to formalize the notion of refuge-mediated apparent competition and sketch ways that this model might be made more general. Then, we discuss the potential for refuge-mediated apparent competition to play a key role in generating heterogeneity in community dynamics, for instance by the creation of emergent thresholds and alternative stable states. We close by suggesting avenues for future research to document the presence of refuge-mediated apparent competition and to quantify its consequences for plant communities.

A MODEL OF REFUGE-MEDIATED APPARENT COMPETITION

As a first step towards a formal theory of refuge-mediated apparent competition, we consider a simple limiting case. We imagine that a generalist consumer is globally regulated in its own numbers by its consumption of a wide range of food types at a landscape scale, but that its intensity of use of a particular patch of habitat with two plant species is governed specifically by the availability of local refuges (e.g. from own natural enemies, harsh microclimatic conditions, inclement weather, etc.). The overall dynamics of generalist consumers are often effectively decoupled from changes in the abundance of any particular victim species (Crawley 1997). As a tractable limiting case, we assume that one of the plant species (the 'invader', species *I*) provides the refuge (but no food), and competes with other plant species (the 'resident', species *R*), which provides food for the consumer. This assumption is consistent with the general observation that consumer attack rates often differ greatly among plant species, and this limiting case may also occur when exotic plants escape consumers in their introduced range (i.e., the phenomenon of 'enemy release'). The model we develop thus assumes that the local abundance of the consumer is determined by its (non-consumptive) response to the refuge-providing species *I*, rather than by the abundance of the resident plant species *R* (but see below).

The plants themselves compete for a single limiting resource of quantity *S*. We make the usual assumptions of resource competition theory (MacArthur 1972; Tilman 1982), such as continuous overlapping generations, no age/stage structure, and no direct density dependence. Changes in the density of each species, N_i ($i = I, R$) in the absence of the consumer are given by:

$$\frac{dN_i}{dt} = N_i F_i(S). \quad (1)$$

The per-capita growth rate of each species, $F_i(S)$, is assumed to increase with resource density. Alone, each species reaches an equilibrium at a particular level of

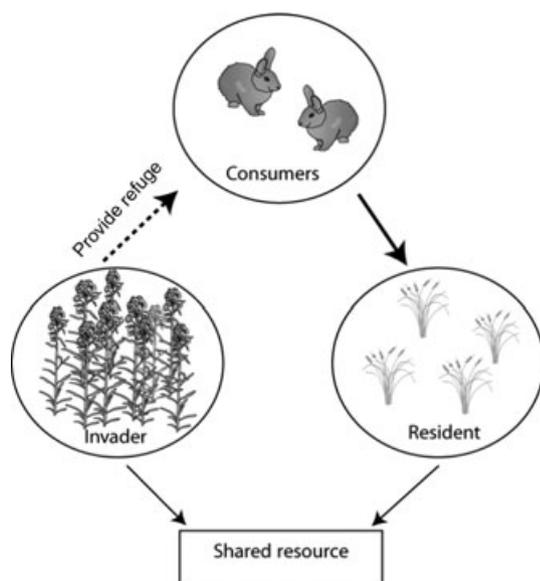


Figure 1 A conceptual diagram of the trophic linkages in refuge-mediated apparent competition. Solid lines indicate consumption or resource usage, while broken lines indicate indirect interactions.

resource, S_i^* (i.e., the value of S where $F_i(S^*)=0$). Given that resource levels decline with consumption, the species with the lower S_i^* will be competitively superior, when both species occur together (Tilman 1982). We assume that the resident species (R) is the superior competitor, so $S_I^* > S_R^*$.

To this familiar model, we now add the refuge effect upon consumption. We assume that consumers are attracted to the patch by the availability of refuges (Fig. 2a), and that more such refuges are provided by species I (Fig. 2b), the more consumers will be present (Fig. 2c). Formally, we express the local density of consumers C as a function of the number of invaders present, so $C = \phi(N_I)$. It is well-known that selective predation upon a dominant competitor can reverse competitive dominance. If an inferior competitor, by providing a refuge for a consumer, enhances attacks upon the dominant competitor, this in effect raises the minimal level of resources needed for the stronger competitor to persist, say from S_R^* to $S_R'^*$. If each consumer imposes a constant per-capita rate of mortality δ upon the resident plant species, the growth rate of the species R becomes:

$$\frac{dN_R}{dt} = N_R F_R(S) - N_R \delta \phi(N_I). \quad (2)$$

The second term of eqn 2 expresses refuge-mediated apparent competition as a form of indirect interference

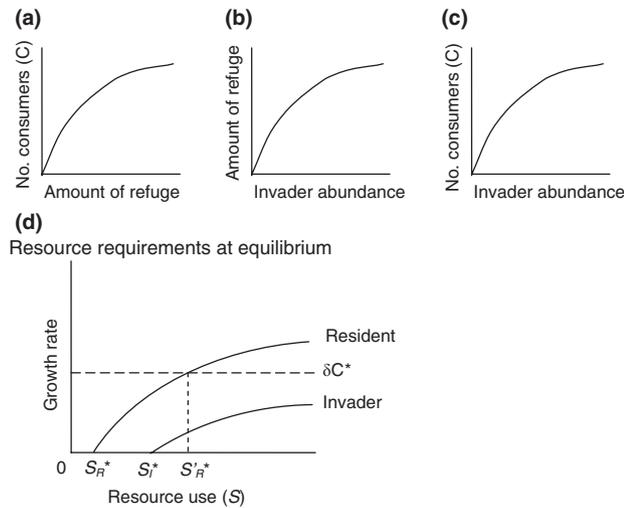


Figure 2 Graphical depiction of the components of the non-spatial model. (a) The relationship between consumers and the density of refuge habitat; (b) the density of refuge habitat is a function of the density of invaders; (c) as a result, the local density of consumers is a function of the density of invading plants. (d) Equilibrium solutions for the case where residents are superior competitors in the absence of consumers ($S_R^* < S_I^*$), but invaders are superior competitors when consumers are present ($S_R^* < S_I^* < S_R'^*$). Note that the scale of the x-axis in (c) is rescaled compared to (b).

competition. This in turn makes it possible for the patch to exist in alternative states. If we start with very few of species I , then the number of consumers will be negligible and species R will exclude species I . If instead, we assume that species I is present alone at an equilibrium density of N_I^* , resources will be at S_I^* (from eqn 1). At higher N_I , many consumers are attracted, and the dominant competitor will then be suppressed in numbers, freeing resources that can be used by the invader. Numbers of the invader can then increase even more, thus permitting it to grow and potentially supplant the resident species. For any fixed N_I , we can set eqn 2 to zero and solve for the level of resources $S_R'(N_I)$ needed for the resident to increase when rare, given ambient resources and the rate of mortality it experiences from the refuge-seeking consumer. If $F_R(S_I^*) - \delta \phi(N_I^*) < 0$, then resident species R will be excluded. Figure 2d shows a graphical example of such exclusion.

To characterize in more detail which of these alternative states is likely to occur, and to analyse the possibility of stable coexistence, one must specify explicit functions for resource recruitment and exploitation. As a simple but tractable example, assume the resource is abiotic, and that both the functional and numerical responses of the competitors are linear with resource density:

$$\frac{dS}{dt} = Q(S) - \sum_{i=I,R} (a_i S) N_i, \quad (3)$$

$$\frac{dN_i}{dt} = (a_i b_i S - m_i) N_i.$$

Here, $Q(S)$ is resource recruitment, and a_i , b_i and m_i are, respectively: exploitation rates, a factor converting resource consumption into new individuals (i.e. births), and intrinsic death rates. A standard recruitment function is the chemostat expression for an abiotic nutrient, $Q(S) = G - \mu S$, where G is the rate of input from external sources (e.g. nitrogen mineralization rates in the soil, or nutrient input loading in aquatic systems), and μ a washout rate. Assuming that the number of consumers attracted to refuges increases in a linear fashion with invader abundance, with a proportionality constant p , the per-capita consumption rate inflicted on the resident is $\delta p N_I$, and the dynamics of species R become:

$$\frac{dN_R}{dt} = (a_R b_R S - m_R) N_R - N_R \delta p N_I \quad (4)$$

The resource level at equilibrium for species R when alone is $S_R^* = m_R / a_R b_R$. For species I alone, the resource level at equilibrium is $S_I^* = m_I / a_I b_I$. If species I is present and at equilibrium, using eqn. 4, the level of resource required for the resident to persist increases to:

$$S_R^* = \frac{m_R + \delta p N_I^*}{a_R b_R} \quad (5)$$

If species *I* reduces the resource to a lower level than this, i.e. $S_I^* < S_R^*$, we can substitute $S_R^* = m_R/a_R b_R$ and rearrange to give the following necessary condition for an alternative state (i.e. species *I* excludes species *R*) generated by refuge-mediated apparent competition in this system:

$$N_{I,\text{threshold}}^* > \left(\frac{a_R b_R}{\delta p} \right) (S_I^* - S_R^*) \quad (6)$$

If we assume, for simplicity, that washout is negligible relative to both the invader and resident attack rates ($\mu \ll a_i$), then the equilibrium density of species *I* alone is:

$$N_I^* \approx \frac{b_I G}{m_I}. \quad (7)$$

Stability analysis, detailed in the online supporting information (Appendix S1), confirms that this simple model has just two stable equilibria (either the resident or invading species present alone) and an unstable internal equilibrium (corresponding to the threshold that defines the conditions necessary for invasion given in inequality 6).

By inspection of inequality 6, the threshold density of the species *I* that suffices to exclude species *R* via refuge-mediated apparent competition is lower if: a) the competing species do not differ greatly in their resource requirements (small $S_I^* - S_R^*$), and b) there is a strong numerical response of predators attracted by the refuge (high p), and/or c) each predator so attracted has a high attack rate upon the resident species (high δ). The potential abundance of the invader (species *I*) should be greater when resource input rates (G) or birth rates are high (eqn. 7), serving to attract more consumers and making it more likely that inequality 6 will be satisfied. Thus, this simple model suggests that refuge-mediated apparent competition is more likely to be stronger in environments with high potential biomass than in environments with lower biomass.

There are many ways this simple model can be made more elaborate and realistic. One would be to recognize that, in some circumstances, the number of consumers attracted to a patch could depend jointly upon refuges and food availability in a patch. If the number of generalist consumers attracted to the patch is responsive not just to refuge availability, but also to food availability in the patch (e.g., Orrock & Witter, in press), one would substitute a term such as $C = \phi^*(N_b, N_R)$ into eqn. (2). This in effect generalizes an assumption commonly made in models of insect generalist predator-prey interactions, where the number of generalist predators attacking a focal prey

species in a patch is expressed as an increasing function of that prey species density (e.g., Hassell 2000). Although the basic dynamics of refuge-mediated apparent competition would be expected to hold as long as the preference for attacking the resident species was sufficiently high, the model could also be extended to the case where the consumer will attack both plant species. There could also be saturating functional and numerical responses by the consumer to food availability in the patch, and interference among consumers could cap the influence of the refuge upon consumer abundance. Finally, the consumer itself could be a specialist, dependent entirely upon the food plant, so might need its own dynamical equation.

INSIGHTS FROM REFUGE-MEDIATED APPARENT COMPETITION

Our model suggests that plants that are inferior competitors may nonetheless invade a community via refuge-mediated apparent competition (Fig. 2) as long as their initial abundance is sufficient to attract a critical density of consumers. Below we discuss how this mechanism can foster changes in plant community composition by altering conditions for coexistence, create alternative stable states and cryptic consumer effects, and inform applied management issues regarding biological invasions, conservation, and restoration.

When is refuge-mediated apparent competition likely to be important?

The potential exists for refuge-mediated apparent competition to be common in plant communities because the components that generate it are widespread. First, consumer foraging is assumed to be altered by the presence of a refuge; changes in consumer activity, abundance, and foraging in association with a refuge have been repeatedly documented across a diverse array of terrestrial and aquatic systems (Covich 1976; Orth *et al.* 1984; Bell *et al.* 1991; Menge 1995; Caro 2005; Cooper 2005; Stankowich & Blumstein 2005). Second, consumers often have differential effects on plants sufficiently large to outweigh direct competitive asymmetries between residents and invaders. Studies document how mobile consumers can transform plant communities (e.g., van de Koppel *et al.* 2002; Palmer *et al.* 2003); such consumer impacts on plant communities are substantial and found in a wide range of systems (e.g., Menge 1995; Olff & Ritchie 1998; Levine *et al.* 2004; Parker *et al.* 2006). Finally, field studies clearly demonstrate that consumer refuges can lead to strong, differential effects on plants (Reader 1992; Wada 1993; Burger & Louda 1994; Menge 1995; Sessions & Kelly 2002; Caccia *et al.* 2006; Lambrinos 2006; Orrock *et al.* 2008; Caccia *et al.* 2009) and

create emergent changes in plant communities (Bartholomew 1970; Chase 1998; Schmitz *et al.* 2004).

Beyond incorporating these ubiquitous components of plant–consumer interactions, our model helps to reveal conditions when refuge-mediated apparent competition is more likely to play a significant role in structuring plant communities. For example, refuge-mediated apparent competition is more likely to play a role in competitive outcomes among plant species when competitors are closely matched. Although ecologists may debate the strength of competitive interactions in nature, i.e. niche vs. neutral structuring of communities (see Adler *et al.* 2007), many cases may exist where competitors have comparable resource dependencies and impacts (i.e. competitors are nearly equivalent). When this is the case, only slight changes in consumer behaviour may be necessary for refuge-mediated apparent competition to create competitive asymmetry. Thus, refuge-mediated apparent competition may be most important in systems where competitors are thought to exhibit neutral, or nearly neutral, dynamics, e.g. as has been suggested for tropical forest trees (Hubbell 2001). For this conclusion to hold, the plants must still differ in some ways that matter to the shared consumer, so that it focuses its attacks on plant species that do not provide refuge.

Refuge-mediated apparent competition is also more likely to be important when consumers exhibit strong responses to the refuge. Because consumer body size, mobility, morphology, and a suite of other factors affect the degree to which consumers respond to refuges (Caro 2005; Cooper 2005; Stankowich & Blumstein 2005), the characteristics of dominant consumers in a system will affect the potential for refuge-mediated apparent competition. The link between consumer identity and refuge-mediated apparent competition suggests that contemporary, often anthropogenic, changes in consumer communities, such as increased deer densities (Cote *et al.* 2004) and fragmentation effects (Bolger *et al.* 1997), might alter the strength of ongoing refuge-mediated apparent competition by altering the number of consumers available to respond to the refuge.

Plant characteristics are also likely to be important, as plants with thick, dense growth forms may be more likely to benefit from refuge-mediated apparent competition because they provide a better refuge from the consumer's perspective (Bell *et al.* 1991; Orrock *et al.* 2008). For example, bamboos provide a refuge for small-mammal consumers, reducing tree seed and seedling survival within bamboo-dominated habitats (Wada 1993; Caccia *et al.* 2006, 2009). Dense patches of an introduced grass caused an increase in consumer pressure on a native fern by providing a refuge for an introduced slug (Sessions & Kelly 2002). Rodent consumers that sought refuge within dense stands of the introduced beachgrass, *Ammophila arenaria*, restricted the distribution of the beach plant *Cakile maritima* to areas

beyond the patch of *A. arenaria* (Boyd 1988). The importance of plant architecture suggests that refuge-mediated apparent competition may play a role in transitions between plant communities with different physical structures (Bell *et al.* 1991), such as in the case of oldfield succession to forest, the conversion of grasslands to plants dominated by woody shrubs, and situations where exotic plants experience increased growth in the introduced range (see below).

A non-intuitive implication of our model is that refuge-mediated apparent competition may be more likely in environments where high productivity or low loss rates translate into higher plant abundance. There could thus be systemic shifts in the importance of this indirect interaction along environmental gradients, or changes in local communities because of anthropogenic nutrient deposition (Vitousek *et al.* 1997), and large-scale increases in productivity and eutrophication (Tilman *et al.* 2001). Moreover, because resource enrichment can be associated with biological invasions (Blumenthal 2006), refuge-mediated apparent competition may play a role in the establishment of exotic plant species (see below).

Although consumers may create opportunities for inferior competitors to invade a resident plant community once the threshold refuge density is achieved, invading plants must be capable of capitalizing upon this opportunity. For example, consumers that seek refuge in chaparral have strong effects on grassland vegetation in adjacent habitats, producing conspicuous 'bare zones' at the chaparral/grassland boundary (Bartholomew 1970). However, chaparral does not always invade grasslands, because chaparral plants are likely limited by factors other than (or in addition to) competition with resident grassland plants. Similarly, if resident plants are strongly seed-limited, but resident perennials can live for decades once established, consumers may only work to reduce resident recruitment and not affect overall adult resident survival. Thus, an established patch of long-lived adult resident plants may not readily yield to consumer-mediated invasion until a disturbance (e.g. fire) reduces the abundance of adult residents. Another example where refuge-mediated apparent competition may not facilitate spread comes from coral reef systems: although grazing urchins that seek shelter in the reef produce distinct 'halos' nearly devoid of marine grasses near the reef (Ogden *et al.* 1973), reef expansion is likely to operate on much longer timescales and be subject to additional ecological constraints.

Transitions among stable states: emergent Allee effects and the ghost of consumption past

Our simple model illustrates how there is likely to be some threshold density at which the refuge-providing invader

sufficiently changes local consumer abundance (Fig. 2c) for refuge-mediated apparent competition to outweigh direct exploitative competition. As a result, refuge-mediated Apparent competition can effectively produce an indirect Allee effect (Stephens *et al.* 1999), where increasing invaders draw more consumers, which leads to decreasing competition from natives and a further increase in the realized invader per-capita growth rate. This realized invader growth rate is positive only if the invader density is above a critical threshold for a sufficient period of time to increase consumer pressure on the resident species such that it requires more resources than the invader to persist. Arrival at this threshold could occur via a disturbance that locally eliminates the resident species; the precise value of the threshold likely depends upon consumer behaviour, refuge quality, and the difference in competitive ability between the resident and the invader (Fig. 2).

If consumers have no other food supply than the resident plant species, a more complicated dynamic may ensue that is not captured by our model, whereby refuge-mediated apparent competition may not always lead to complete competitive exclusion. For example, if an invader becomes abundant via refuge-mediated apparent competition, consumer pressure will eventually drop as consumers start to forage away from the refuge to obtain food. The reduction in consumer pressure could allow residents to increase in abundance, until consumers again started using the refuge in sufficient numbers to provide the invader with an advantage. As a result of this dynamic, we hypothesize that resident and invader may coexist, possibly in stable cycles or in more chaotic dynamics. More detailed models that explicitly incorporate the spatial dynamics of consumer foraging and plant competition (e.g. extending the model to explicitly consider consumer dynamics and plant dispersal) will be required to determine if this form of coexistence is a stable equilibrium, whether more complex dynamics are possible, and whether refuge-mediated apparent competition is most important mainly during transient phases of plant community re-organization.

The possibility of consumer departure after invasion suggests that refuge-mediated apparent competition may be most important in facilitating the initial establishment of the invader within the resident community. Then, once established, the invader may retain control of the community via quite different mechanisms (e.g. via changes in soil characteristics; Levine *et al.* 2006). In this case, communities structured by refuge-mediated apparent competition can essentially be created by the ghost of consumption past (Howe & Brown 2001). That is, the evidence of consumer-mediated entry into the resident community may no longer be evident once consumers have moved to other areas. Thus, short-term field studies might not capture the full

significance of historical consumer impacts on contemporary plant communities.

Refuge-mediated apparent competition and biological invasions

Empirical and theoretical evidence suggests that apparent competition via changes in consumer density may be important in biological invasions by exotic species (e.g., Noonburg & Byers 2005; Borer *et al.* 2007). Refuge-mediated apparent competition may also be a mechanism by which exotic plants gain entry into native communities, and may explain several frequently observed features of biological invasion by exotic species such as lag phases and Allee effects.

Biological invasions often have a lag phase (Sakai *et al.* 2001), during which an invasive exotic plant species exists in resident communities, but does not aggressively spread through resident populations. The lag phase is often explained as arising due to stochastic losses of exotic invaders while populations are small, or due to the time required for exotic plants to undergo evolution in order to become invasive (Mack *et al.* 2000; Sakai *et al.* 2001; Holt *et al.* 2005). Our model suggests a novel mechanism for the lag phase by demonstrating how refuge-mediated apparent competition generates Allee effects (Stephens *et al.* 1999). As our model illustrates, a biological invasion shifts from being impossible to being imminent when the abundance of the exotic plant reaches the threshold needed to drive refuge-mediated apparent competition. Near the unstable equilibrium with both resident and invader present, numbers of each would be expected to change slowly, such that an imminent invasion may be well underway before it is detected (although not examined as part of our model, the time required for consumer density to change in response to the refuge could also contribute to a lag). This Allee effect may interact with habitat alteration (Didham *et al.* 2007), such that disturbance or degradation allows exotic plants to achieve populations large enough to exceed the threshold size (Fig. 2).

Refuge-mediated apparent competition could interact with other mechanisms of biological invasion. For example, changes in exotic plant growth and architecture due to enemy release (Callaway & Maron 2006; Mitchell *et al.* 2006; Parker *et al.* 2006) or evolved increase in competitive ability (EICA, Bossdorf *et al.* 2005; Callaway & Maron 2006) could subsequently increase exotic plant performance by fostering refuge-mediated apparent competition, because taller plants may be more likely to provide a refuge for consumers (Caro 2005). As a result, refuge-mediated apparent competition could increase the rate of biological invasion compared to that expected from enemy release, resource-enemy release, or EICA alone. In a corollary to the idea of enemy release, one untested possibility is that invasion may occur as a result

of release from refuge-mediated apparent competition, i.e., a species that is a good competitor but is typically maintained at low abundance in its native range by refuge-mediated apparent competition may become invasive in an introduced range where it escapes the refuge-providing plant species.

Refuge-mediated apparent competition may also form the basis of biotic resistance: if resident plants provide a refuge, they may successfully prevent invasion by otherwise competitively superior invaders. An excellent example comes from Lambrinos' (2006) work: mammalian consumers seeking refuge away from the edge of chaparral create strong biotic resistance against the invasive grass *Cortaderia jubata*. As meta-analyses demonstrate that herbivores can play an important role in biological resistance (Levine *et al.* 2004; Parker *et al.* 2006), an important question is whether these consumer effects are in part due to refuge-mediated apparent competition.

Restoration of invaded plant communities may also be affected by refuge-mediated apparent competition. For instance, consumers seeking refuge near a tall, dense exotic forb species thwarted the re-establishment of a native grass (Orrock *et al.* 2008). Although many approaches to plant conservation and restoration focus on seed addition and direct removal of competing species, if refuge-mediated apparent competition is important, it may not be necessary to remove the entire exotic population. Rather, removing the refuge provided by the exotic (e.g. via mowing or tilling) may be effective for reducing consumer pressure, thus facilitating establishment of restored populations or the expansion of remnant stands of plant species that would otherwise be eliminated via refuge-mediated apparent competition. Similarly, measures aimed at reducing overall consumer pressure (e.g. construction of consumer enclosures) may also be promising, and need not entail widespread consumer manipulation if timing of activities or restoration approach is used to minimize consumer impacts during critical times. For example, although refuge-mediated apparent competition reduces the establishment of a native grass (Orrock *et al.* 2008; Orrock & Witter, in press), these effects may be reduced by adding large enough numbers of native seeds to offset consumer impacts (Orrock *et al.* 2009).

FUTURE DIRECTIONS: HOW COMMON IS REFUGE-MEDIATED APPARENT COMPETITION?

Given the potential importance of refuge-mediated apparent competition, especially in light of empirical evidence (Connell 1990; Reader 1992; Burger & Louda 1994; Menge 1995; Chaneton & Bonsall 2000; Caccia *et al.* 2006; Orrock *et al.* 2008; Caccia *et al.* 2009), an important next step is to empirically determine how frequently it affects coexistence

and invasion in plant communities. In marine intertidal food webs, Menge (1995) identified several potential examples of refuge-mediated apparent competition, suggesting that other studies are needed in aquatic systems to characterize the degree to which it is widespread. As Connell (1990) and Chaneton and Bonsall (2000) have observed, robust experimental studies of apparent competition in terrestrial plant communities, including refuge-mediated apparent competition, are relatively rare. In their review, Chaneton and Bonsall (2000) provide experimental protocols for evaluating apparent competition. Below, we outline additional approaches that can be used to specifically evaluate refuge-mediated apparent competition.

Manipulation of the refuge provides a primary experimental approach for examining the existence and importance of refuge-mediated apparent competition. In some ecological systems, it may be possible to manipulate the refuge with minimal impact on other components of competitive interactions among plants (e.g. living plant biomass, seed production), especially in studies where other plant interactions (e.g. direct competition) are thought to be of negligible importance or are eliminated as part of the experimental design (e.g. by weeding plots so plants cannot directly compete). For example, *Brassica nigra* is a late-growing exotic annual forb that leaves dense thickets of standing stems after plants have senesced and seeds are dispersed (Bell & Muller 1973). These stems may provide a consumer refuge that influences consumer impact on native grasses that emerge early in the growing season. In this system, if refuge-mediated apparent competition is important, removal of the refuge-providing senescent stems should reduce the successful establishment of the next generation of *B. nigra* plants and increase establishment of native grasses (assuming that these species are not dispersal limited). If refuge-mediated apparent competition is not important, removal of stems should have little impact on *B. nigra* or native plants, and suggests that other mechanisms (e.g. direct competition or an alternative form of apparent competition) are responsible.

On the other hand, when manipulation of the refuge requires removal of living plant biomass, creation of the refuge may have additional effects (e.g. changing plant competitive ability or palatability) that are important for studies where other potential plant interactions may also be of interest. In these studies, artificial refuges constructed using materials that mimic the biotic refuge (e.g., Hambäck *et al.* 2003) may be used to evaluate refuge-mediated apparent competition. If artificial refuges cannot be constructed, it will be prudent to have suitable experimental controls. For example, a treatment where the refuge is manipulated but consumers do not have access will allow the effect of refuge manipulation on direct competition to be estimated, and consumer preference trials can be used to

assess whether refuge creation changes palatability of the refuge-providing plant.

Because refuge-mediated apparent competition could work in concert with density-mediated apparent competition (Holt 1977), experiments that disentangle the two will require systems where food resources and the refuge attributes can be separately manipulated. For example, many invasive plants provide food resources (e.g. fruits, seeds) that can be manipulated in addition to the shelter the plants provide (i.e., the refuge). Factorial manipulation of food, refuge, and consumer access potentially provide a strong foundation for understanding the role that different mechanisms of apparent competition may play in plant communities. This is illustrated by an ongoing experiment with the invasive honeysuckle, *Lonicera maackii*, where shelter (i.e., woody plant stems) and consumer food resources (i.e. honeysuckle fruits) are being manipulated in a factorial design and coupled with consumer exclosures to determine the degree to which consumer-mediated effects are important (H. Dutra, personal communication). Because plants are typically senescent for portions of the growing season, grassland systems may also be amenable to manipulation of consumer access, food resources for granivorous consumers (i.e., seeds), and shelter in the form of standing plant biomass. These treatments could be further crossed with monoculture treatments (Chaneton & Bonsall 2000) to gain insight into the interplay of direct competition and density-, and refuge-mediated apparent competition. Because grassland communities may be experimentally assembled and may change over observable timescales, they may also be promising for evaluating two of our model's predictions: increasing refuge-mediated apparent competition with increasing system productivity and the existence of Allee effects at threshold densities of the refuge-providing species.

Observational studies may also be informative for evaluating the presence the refuge-mediated apparent competition, especially when observations on rates of consumer impact are coupled with assays that examine the effect of the refuge on consumer behaviour, such as giving-up densities (Brown 1988) and assessment of flight-initiation distance (Stankowich & Blumstein 2005). If refuge-mediated apparent competition is underway, reduced perceived risk by consumers should coincide with the presence of the refuge-providing plant species and also coincide with consumer impacts on the plant species that does not provide a refuge. Specialist consumers introduced for biological control may provide a similar opportunity for examining components of refuge-mediated apparent competition. If specialist biological control consumers target the refuge-providing invader and reduce the quality of the refuge that it provides, use of the refuge by resident consumers (and thus the strength of subsequent apparent competition) should be reduced.

A pragmatic implication of our model is that studies must be explicitly designed to measure consumer impact and changes in plant communities with the temporal components of competitive replacement in mind: in cases where refuge-mediated apparent competition takes place among long-lived plants, short-term studies of plant–consumer interactions may fail to find refuge-mediated apparent competition even if it exists. Long-term studies are also essential because the strength of refuge-mediated apparent competition may also vary in time and interact with changes in resource availability and consumer density, as illustrated by significant annual variation in refuge-mediated effects observed by Caccia *et al.* (2006). Moreover, because refuge-mediated apparent competition may be important for the initial establishment of invaders, but invaders may resist replacement via other mechanisms once established (i.e., the ghost of consumption past), short-term experiments may also provide misleading insights into the actual historical importance of consumers in affecting contemporary community structure. Although not modelled here, field evidence suggests that refuge-mediated apparent competition may generate local clines in consumer pressure (e.g., Bartholomew 1970; Orrock *et al.* 2008); empirical studies that do not consider the possibility of this spatial variation may fail to uncover the mechanism creating heterogeneity in consumer impact.

By demonstrating that inferior competitors can invade and persist via refuge-mediated competition, our work suggests that the role of indirect effects in generating emergent patterns in plant communities may be underestimated. Although our model stresses competitive refuge-mediated effects, future work should also examine the potential for refuge-mediated effects to cascade through the food web (see Menge 1995), and the implications of positive refuge-mediated interactions. For example, thicket-forming plants that provide preferred microhabitat for foraging lizards lead to increased pollination of a nearby endemic plant (Hansen *et al.* 2007). Experiments testing model predictions, as well as additional theoretical examination (e.g., spatially explicit models that incorporate individual consumer behaviour and plant dispersal dynamics) are needed if we are to begin to understand the degree to which refuge-mediated apparent competition affects plant community composition.

ACKNOWLEDGEMENTS

Discussions with Jim Reichman were critical for honing the ideas presented here. Thanks to J. Levine, J. Chase, T. Steury, C. Christopher, J. Vonesh, E. Damschen and L. Patchepsky for helpful discussions and suggestions. Comments from J. Bascompte, C. Christopher, E. Damschen, J. Levine, M. Barfield and three anonymous referees improved the final

manuscript. We appreciate the support of the National Science Foundation (Grants DEB-0444217 and DEB-0502069), the University of Florida Foundation, and the National Centre for Ecological Analysis and Synthesis, a Centre funded by NSF (Grant DEB-0072909), the Univ. California, and the Santa Barbara Campus.

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Editor, Ross Crozier

Manuscript received 14 September 2009

First decision made 3 October 2009

Manuscript accepted 10 October 2009