Abstract. Resource pulses often involve extraordinary increases in prey availability that "swamp" consumers and reverberate through indirect interactions affecting other community members. We developed a model that predicts predator-mediated indirect effects induced by an epidemic prey on co-occurring prey types differing in relative profitability/preference and validated our model by examining current-season and delayed effects of a bamboo mass seeding event on seed survival of canopy tree species in mixed Patagonian forests.

The model shows that predator foraging behavior, prey profitability, and the scale of prey swamping influence the character and strength of short-term indirect effects on various alternative prey. When in large prey-swamped patches, nonselective predators decrease predation on all prey types. Selective predators, instead, only benefit prey of similar quality to the swamping species, while very low or high preference prey remain unaffected. Negative indirect effects (apparent competition) may override such positive effects (apparent mutualism), especially for highly preferred prey, when prey-swamped patches are small enough to allow predator aggregation and/or predators show a reproductive numerical response to elevated food supply.

Seed predation patterns during bamboo (Chusquea culeou) masting were consistent with predicted short-term indirect effects mediated by a selective predator foraging in large prey-swamped patches. Bamboo seeds and similarly-sized Austrocedrus chilensis (ciprés) and Nothofagus obliqua (roble) seeds suffered lower predation in bamboo flowered than nonflowered patches. Predation rates on the small-seeded Nothofagus dombei (coihue) and the large-seeded Nothofagus alpina (raulí) were independent of bamboo flowering. Indirect positive effects were transient; three months after bamboo seeding, granivores preyed heavily upon all seed types, irrespective of patch flowering condition. Moreover, one year after bamboo seeding, predation rates on the most preferred seed (raulí) was higher in flowered than in nonflowered patches. Despite rapid predator numerical responses, short-term positive effects can still influence community recruitment dynamics because surviving seeds may find refuge beneath the litter produced by bamboo dieback.

Together, our theoretical analysis and experiments indicate that indirect effects experienced by alternative prey during and after prey-swamping episodes need not be universal but can change across a prey quality spectrum, and they critically depend on predator-foraging rules and the spatial scale of swamping.

Key words: apparent competition; apparent mutualism; Chusquea culeou; diet selection; indirect interactions; Nothofagus spp.; Patagonia; predator functional response; prey quality; resource pulse; transient dynamics.

INTRODUCTION

In dynamically pulsed systems, recruitment of sessile organisms is often synchronized with exogenous resource inputs (Stapp and Polis 2003), mass dieback of dominant space holders (Nakashizuka 1988; Taylor 1992, Abe et al. 2001), and/or masting events (Siver-town 1980, Kelly 1994) that swamp the habitat with new propagules. Such episodic events create windows of opportunity for recruitment of dominant species, which can be exploited by resident consumers as well (Witman et al. 2003). During prey-swamping events, functional responses of generalist predators can make an impact on the survival rate of the focal, swamping species. In addition, predator responses to elevated food supply may generate a range of indirect effects on less abundant, alternative prey (Hämback and Ekerholm 1997, Ostfeld and Keesing 2000). While a substantial body of theoretical (e.g., Holt 1977, Abrams 1987, 1993, Holt and Kotler 1987, Brown and Morgan 1995,
Abrams and Matsuda 1996, Brassil and Abrams 2004) and empirical literature (reviews in Holt and Lawton 1994, Chaneton and Bonsall 2000) has been devoted to predator-mediated indirect interactions, little theory has been developed to explicitly address transient indirect effects emerging from resource pulses.

There is a growing interest to understand how extreme resource pulses permeate through food webs via numerical population responses (Polis et al. 1997, McShea 2000, Ostfeld and Keesing 2000, Witman et al. 2003, Kelt et al. 2004). Several studies have focused on the indirect effects transmitted by carnivorous predators (mammals, birds) on their vertebrate prey in response to density fluctuations of one prey population (Dunn 1977, Jaksic et al. 1997, Jedrzejewska and Jedrzejewski 1998, Blomqvist et al. 2002). Models for indirect interactions in two prey–one shared predator systems with cycling populations have been discussed by Abrams et al. (1998) showing that there is ample potential for reciprocally beneficial effects (i.e., apparent mutualism) between the alternative prey. Few studies, however, have examined community-level indirect effects mediated by seed predators during episodic mass-seeding events in plant communities (Schnurr et al. 2002).

The increased food supply associated with extraordinarily large seed crops ("masting") typical of many tropical and temperate forests has traditionally been thought to satiate resident consumers, thus benefiting seed survival of the masting species and of other synchronously seeding species (Janzen 1974, 1976). In spite of its potential importance in promoting patterns of interspecific seed synchrony (or community-wide masting; Curran and Webb 2000), this mechanism has received surprisingly little empirical testing (but see Blundell and Peart 2004, Maycock et al. 2005). In particular, previous works on masting have not considered the differential benefits enjoyed by various seed types of differing profitability. So far, indirect benefits of synchronous seedling have been found in systems of closely related species with seeds of similar size and nutritional quality (Curran and Webb 2000, Kelly et al. 2000, Schauber et al. 2002). Here, we propose that differences in seed size or energetic value among co-occurring species may generate different granivore-mediated indirect effects under prey-swamping/masting scenarios, particularly when masting is not temporally synchronized across sympatric species.

Theoretical models (e.g., Holt and Kotler 1987, Abrams 1993, Brown and Morgan 1995) and a handful of empirical studies (Garb et al. 2000, Veech 2001, Caccia et al. 2006) have focused on understanding how the predator’s diet choice and patch use strategy shape indirect interactions between alternative prey occurring at "normal" densities. However, models have not yet been proposed to account for the consequences of shared predation in systems that become episodically swamped with high quality prey. Moreover, few experiments (if any) have measured the strength of indirect effects on prey species attacked by generalist predators that exploit an infrequent, spatially heterogeneous resource pulse of the kind generated during massing events. Bamboo mass-seeding episodes occur worldwide, being typically separated by long intermast periods (Jaksic and Lima 2003). These natural events constitute ideal, albeit rare, opportunities to examine consumer-mediated indirect effects in resource-pulsed systems. During bamboo blooms, food availability to granivores suddenly becomes several orders of magnitude greater than that produced by typical arboreal seed crops. Little is known about the consequences for seed survival patterns of such extreme resource pulses (Ostfeld and Keesing 2000, Schnurr et al. 2002).

In this paper, we analyze both theoretically and experimentally the nature and strength of indirect effects induced by a massive seeding event on seed survival of various species via the functional and numerical responses of generalist granivores. We asked (1) How does predation affect seed survival on the focal (masting) species and co-occurring seed types during and following a mass-seeding event? and (2) How does prey profitability affect the sign and strength of indirect effects mediated by consumers exploiting a high-quality resource pulse? We begin by proposing a model that allows for asymmetrical, positive (+, 0) and negative (−, 0) indirect effects induced by an eruptive prey species on other prey types sharing a common predator. Our model predicts the changes in mortality rate experienced by different prey types that co-occur with the focal, swamping species, under contrasting foraging scenarios. We then present data from seed removal trials in which seeds of the native bamboo Chusquea culeou (the swamping prey) and of various canopy trees were offered to resident granivores during and after an extensive bamboo flowering/seeding event in temperate mixed forests of northern Patagonia, Argentina. These experiments allowed us to test model predictions under natural field conditions.

The Model

Conceptual background

Indirect interactions between prey species sharing a common predator may range from positive to negative and may affect both prey or just one of them (Holt 1977, Abrams 1987, 1993, Holt and Kotler 1987, Abrams and Matsuda 1996, Chaneton and Bonsall 2000). In the absence of predator numerical responses, shared predation may induce short-term “apparent mutualism” between alternative prey, when an increase in the density of one prey leads to predator satiation thus reducing its functional response to the other prey (Holt 1977, Abrams 1987, Abrams and Matsuda 1996). This may occur because of space or time constraints on the predator’s foraging and food processing activities (Murdoch and Oaten 1975), and is particularly true for nutritionally substitutable prey (Abrams 1993). In
other cases, the predator may stop feeding upon one prey when the density of the more preferred prey increases above a certain threshold (Hughes 1979, Holt and Kotler 1987). A shared predator may alternatively induce short-term “apparent competition” whenever the increased abundance of one prey enhances the attack rate on a second prey, negatively affecting its survival and local abundance (Holt and Kotler 1987). This indirect effect may arise because predators numerically aggregate or spend more time feeding in patches that contain both prey or when the two prey are nutritionally complementary (Abrams 1993). As a result, predation on both prey species should be higher when they occur together than when in separate patches (Holt and Kotler 1987, Chaneton and Bonsall 2000). Ultimately, the net short-term indirect effect induced by shared predation on alternative prey types will be determined by the balance of opposing satiation/diet selectivity vs. aggregation/patch use effects. While apparent competition may lead to spatial segregation and local extinction of certain prey (Holt 1977, Holt and Kotler 1987), apparent mutualism could favor aggregative phenomena such as community-wide masting (Curran and Webb 2000, Kelly et al. 2000) and associational defense guilds (Atsatt and O’Dowd 1976) in plants and mixed-species herds, flocks, and schools in animals (Estes et al. 2001).

We developed a simple model to predict the relative strength of asymmetrical, short-term indirect effects mediated by a generalist predator in the context of habitat swamping by one prey species. By subtracting per capita prey mortality rates at baseline vs. elevated food situations, we analyze how different quality prey benefit from sharing predators with the swamping prey. We begin by analyzing the role of predator satiation and diet selectivity on the magnitude of apparent mutualism induced by the swamping species on other prey types differing in relative profitability to the shared predator. We then examine effects of predator aggregation in prey-swamped patches on the severity of apparent competition across a prey profitability gradient. Lastly, we consider the longer-term consequences of the predator’s numerical response to prey swamping.

**Apparent mutualism induced by predator satiation**

We start by assuming a polyphagous, food-limited predator foraging at a fixed abundance (i.e., no numerical response within the timeframe of analysis; “short” time-scale; sensu Holt and Lawton [1994]) within a closed, homogeneous habitat. Note that the latter condition prevents the type of predator aggregation often leading to apparent competition between prey under shared predation (Holt and Kotler 1987). We also assume that the predator feeds upon two non-self-regulated prey species with densities $N_i$ and $N_j$ and has a saturating functional response that can be adequately described by the two-species case of Holling’s disc equation (Murdoch and Oaten 1975). If the two prey are treated as nutritionally substitutable resources (Abrams 1993), an increase in density of either prey reduces the instantaneous consumption rate on the other prey, having a positive indirect effect on its survival rate. The instantaneous consumption rates ($C$) of prey species $i$ and $j$ are, respectively,

$$C_i = a_i N_i / [1 + (a_i t_i N_i) + (a_j t_j N_j)]$$

$$C_j = a_j N_j / [1 + (a_i t_i N_i) + (a_j t_j N_j)]$$

where $t_i$ and $t_j$ and $a_i$ and $a_j$ are the respective handling times and instantaneous attack rates for prey species $i$ and $j$. The ratio of prey types being consumed by the shared predator is described by the following equation:

$$C_i / C_j = a_i N_i / a_j N_j.$$  

Hence, $a_i / a_j$ is a measure of the predator’s relative preference for prey $i$ over prey $j$.

Let us now suppose that species $i$ “swamps” the system, reaching density $S$. An index of apparent mutualism on species $j$ ($AM_j$) will then equal the percentage difference in the per capita mortality rate experienced by species $j$ in the normal and the swamped system:

$$AM_j = 100a_j [1/(1 + a_j t_i N_i + a_j t_j N_j)] - [1/(1 + a_i t_i S + a_j t_j N_j)].$$

Now assume that both prey have equal handling times, $t_i = t_j = 1$; setting species $i$ attack rate to $a_i = 1$ and the density of prey $j$ to $N_j = 1$ yields

$$AM_j = 100a_j [1/(1 + N_i + a_j) - 1/(1 + S + a_j)].$$

(1)

If we vary the preference of prey $j$ relative to prey $i$, a family of bell-shaped curves of $AM_j$ for increasing swamping densities emerges (Fig. 1). The indirect effect on the alternative prey is positive over the entire range of $a_j$ values; however, as prey $j$ becomes relatively less preferred ($a_j < 1$), the magnitude of the mutualistic effect declines. Under very large swamping densities ($S = 2–3$ orders of magnitude over $N_i$), the largest positive effects are predicted for prey types that are more preferred than the swamping prey ($a_i > 1$).

The above model predicts the indirect effects of prey swamping mediated by a “naive” predator (Oksanen et al. 2001), which feeds upon both its primary and secondary prey species over the entire range of primary prey densities (i.e., the predator has a suboptimal diet choice; Holt and Kotler 1987). Clearly, the swamping magnitude does not substantially modify the strength of indirect mutualism on the less preferred prey types ($a_i / a_j < 1$) because predators concentrate on the more preferred, swamping species. Upper bounds for mutualistic effects are given by prey mortality rates in the normal (non-swamped) situation, which decline with the prey’s relative preference (the less attractive the prey, the less eaten it would be, even without swamping). Likewise, as the preference for the alternative prey increases, a larger swamping event is necessary to induce
critical density of prey

increasing orders of magnitude with respect to the density of
cause mortality in the normal vs. swamped systems) expected to be
(apparent mutualism on species $j$) expected to be
caused by a satiating predator having prey $i$ in densities ($S$) of
increasing orders of magnitude with respect to the density of
alternative prey $j$ for a range of relative preference values (log scale) of prey $j$ from $a_j/a_i = 0.01$ (prey $i$ 100-times more preferred than prey $j$) to $a_j/a_i = 100$ (prey $j$ 100-times more preferred than prey $i$; solid lines). The abundance of prey $i$ in the normal situation was set to $N_i = 1$. The dotted line indicates $AM_j$ for a predator that remains as a generalist at normal prey densities but switches to be a specialist for $i$ in the swamped situation.

an increase in the intensity of apparent mutualism (Fig. 1).

**Apparent mutualism induced by predator selectivity**

Let us assume now that the predator switches its foraging behavior from being an opportunistic generalist to a selective specialist according with the relative availability and profitability of different prey types. This is a predator with an optimal dietary behavior that will consume both prey (and behave as a satiating opportunist) as long as its energetic yield exceeds the expected yield of foraging only upon the focal prey $i$ (Hughes 1979). The less profitable prey $j$ is dropped from the diet and the predator becomes a specialist for prey $i$ when

$$k_j/t_j < k_i/[t_i + (1/a_i N_i)]$$

where $k_i$ and $k_j$ are the per capita energetic values of the more and less profitable prey, respectively. Again, assuming equal handling times $t_i = t_j = 1$, then the critical density of prey $i$ ($N_{i-crit}$) above which the predator becomes a specialist on that prey is

$$N_{i-crit} = 1/[a_i(k_i/k_j - 1)].$$

Note that $k_j/k_i$ asymptotically approaches 1 with increasing $N_i$ (Appendix A), which implies that the predator quickly becomes a specialist when the density of the higher quality prey increases. We now proceed to analyze the range of indirect (positive) effects on different prey types arising when the system is swamped by either a high- or low-profitability prey.

**Swamping by a highly profitable prey.**—Suppose that the energetically rich prey $i$ swamps the system, while the alternative prey $j$ is of low quality (coded as swamping [S] and non-swamping [NS] prey, respectively, left half of Fig. 2). Setting $k_i$ and $a_j$ to a reference value $= 1$ in Eq. 2, the critical profitability below which a prey is ignored by a selective predator is $k_{j-crit} < 1/[1 + (1/N_j)]$. Any prey $j$ of such a low quality will be dropped from the diet in both the normal and swamped situations and no indirect interaction will be detected ($AM_j = 0$, Eq. 1; Fig. 2a, region A).

This critical profitability value, and therefore the shape of $AM_j$ is a function of the density of the energetically richer prey in the normal situation ($N_j$). When $N_j$ decreases (i.e., a sharper contrast between the swamping and normal densities), $k_{j-crit}$ tends to 0.5. All prey types ranging in relative profitability ($k_j$) between 0.5 and 1 will be benefited by the swamping prey (Fig. 2a). As the density of the energetically richer species in the normal situation reaches $S$ (a smaller difference between the swamping and normal densities), even if $S$ is high, $k_{j-crit}$ tends to 1 and no alternative prey benefits from swamping (region A in Fig. 2a becomes larger and the AM bell shape narrower). As the alternative prey profitability ($k_j$) increases approaching $k_i$, $N_{j-crit}$ becomes increasingly larger, and the predator acts as a generalist in the normal situation but switches to become a specialist for prey $i$ in the swamped situation (Fig. 2a, region B). According to Eq. 2, this will occur when

$$1/[1 + (1/N_j)] < k_{j-crit} < 1/[1 + (1/S)].$$

Given this selective predator behavior, prey $j$ has no mortality in the swamped situation, and the strength of apparent mutualism on prey $j$ becomes

$$AM_j = a_j 100/[1/(1 + a_i N_i + a_j N_j) - 0]$$

(see Eq. 1). Setting again $a_i = 1$ and the abundance of prey $j$ to a density of $N_j = 1$,

$$AM_j = a_j 100/(1 + N_i + a_j).$$

Clearly the strength of apparent mutualism within this range of prey profitability values depends on the density of prey $i$ relative to the alternative prey in the normal situation. A higher abundance of the more profitable prey will decrease prey $j$ mortality in the normal situation and thus decrease the strength of apparent mutualism. A lower capture rate on prey $j$ (i.e., lesser preference) will also decrease apparent mutualism.

When profitability of $j$ becomes similar to that of $i$, the predator behaves as an opportunistic generalist (Appendix A). When

$$1/[1 + (1/a_i S)] < k_{j-crit} < k_i$$

FIG. 1. Magnitude of the mutualistic effect ($AM_j$, index of apparent mutualism on species $j$, the percentage differential mortality in the normal vs. swamped systems) expected to be caused by a satiating predator having prey $i$ in densities ($S$) of increasing orders of magnitude with respect to the density of alternative prey $j$ for a range of relative preference values (log scale) of prey $j$ from $a_j/a_i = 0.01$ (prey $i$ 100-times more preferred than prey $j$) to $a_j/a_i = 100$ (prey $j$ 100-times more preferred than prey $i$; solid lines). The abundance of prey $i$ in the normal situation was set to $N_i = 1$. The dotted line indicates $AM_j$ for a predator that remains as a generalist at normal prey densities but switches to be a specialist for $i$ in the swamped situation.
and for the case in which \( a_i = 1 \) and \( k_i = 1 \),
\[
1/[1 + (1/S)] < k_{crit} < 1
\]
(Fig. 2a, region C), the predator behaves as a generalist and AM\(_i\) follows Eq. 1 (dotted line in Fig. 1). Note that this region can be narrow because \( S \) is generally large (\( k_{crit} \) tends to 1).

Swamping by a low-profitability prey.—Suppose now that the energetically poor prey \( j \) is the species that swamps the system, and prey \( i (k_j < k_i) \) occurs at normal densities (coded as swamping [S] and non-swamping [NS] prey, respectively; right half of Fig. 2). The predator will consume both prey and behave as a satiating opportunist (Fig. 2a, region C) as long as its energetic yield exceeds the expected yield of feeding only on prey \( i \) (Eq. 2)
\[
k_i/t_i < k_i/[t_i + (1/a_iN_i)]
\]
assuming equal handling times \( t_i = t_j = 1 \) and setting profitability of the swamping species \( k_j = 1 \) and \( N_j = 1 \):
\[
k_{crit} < 1 + (1/a_i).
\]
As \( k_j \) remains below \( k_{crit} \), the predator maintains an opportunistic foraging behavior and the effect of swamping by prey \( j \) on prey \( i \) becomes (see Eq. 1)
\[
AM_i = [a_i100/(1 + a_i t_i N_i + a_j t_j N_j)] - [a_i100/(1 + a_i t_i N_i + a_j t_j S)].
\]
Setting species \( j \) to a reference value \( a_j = 1 \) and setting the abundance of prey \( i \) to \( N_i = 1 \),
\[
AM_i = a_i100/(1 + a_i) - a_i100/(1 + a_i + S)
\]
\[
AM_i = a_i100[1/(1 + N_j + a_i) - 1/(1 + S + a_i)]
\]
which is equivalent to Eq. 1 (but exchanging species \( i \) and \( j \)). Therefore, functions depicted in Fig. 1 are valid when \( a_i < a_j \) as long as \( k_{crit} < 1 + (1/a_i) \). Note that when \( a_i > a_j = 1 \), \( k_{crit} \) remains within the range 1–2 (Appendix B). The high density but less profitable prey \( j \) is dropped and the predator becomes a specialist for prey \( i \) when
\[
k_{crit} > 1 + (1/a_i).
\]
When the prey is highly preferred (high \( a_i \) relative to \( a_j \)), \( k_{crit} \) tends to 1 (Appendix B), and the predator quickly becomes a specialist for the non-swamping prey in both the swamped and non-swamped situations (Fig. 2a, region D). Prey species that are as preferred as the swamping species \( (a_i/a_j = 1) \) need to be at least twice as
profitable \(k_{\text{crit}} > 2\) in order to become the only item in the optimal predator’s diet. Finally, species more than twice as profitable as the swamping species are always preferred, irrespective of swamping magnitude. Given these conditions, species \(j\) will have no indirect effect on the survival of prey \(i\):

\[
\text{AM}_i = a_i 100 [1/(1 + a_i N_j)] - a_i 100 [1/(1 + a_i N_j)] = 0.
\]

To summarize, assuming that prey profitability and preference are linearly related (for seed predators’ see Reichmann 1977, Henderson 1990), we can generalize a model of apparent mutualism for the case of a predator that uses a simple optimality criterion (maximizing energy gain) for prey selectivity (Fig. 2a). Four major regions defined within a prey profitability parameter space can be identified in Fig. 2a: (A) the predator is a specialist for the swamping prey at both the swamped and normal situations; (B) the predator is a specialist for the swamping prey at the swamped situation but becomes a generalist at the normal density situation; (C) the predator is a generalist in both the swamped and normal situations; and (D) the predator drops the swamping prey and becomes a specialist for the non-swamping prey at both the swamped and normal situations (Fig. 2a). Note that the boundaries for regions A and C are only determined by the relative preference and density of the higher quality prey in the normal situation, whereas only the boundary between B and C shifts with the magnitude of swamping. Thus, the swamping magnitude determines the strength of the positive effect (height of the curve in Fig. 2a), but has no influence on setting quality thresholds for prey species benefiting from the indirect interaction (width of the curve in Fig. 2a).

**Apparent competition induced by predator aggregation**

So far, we have assumed that the spatial extent of swamping largely exceeded the predator’s foraging range, precluding its potential numerical aggregation in swamped habitats. We now relax this assumption to allow for the aggregative behavior of shared predators in response to spatial patchiness in food supply (Holt and Kotler 1987) as created by the prey swamping event. This may happen when swamped patches are small compared to predator mobility. In this case, the amount of predation suffered by different prey types in swamped vs. non-swamped patches will not only be influenced by their relative profitability, but also by the time predators spend foraging in a patch and the number of predators attracted to the patch (Holt and Kotler 1987). Optimally foraging predators should aggregate and remain feeding in swamped patches as long as the payoff for staying is larger than the mean yield of foraging over the entire habitat composed of swamped and non-swamped patches, including the costs of traveling among patches (Charnov 1976). Alternative prey types should then experience apparent competition (\(-, 0\)) from being spatially associated with the swamping species, whenever predators numerically aggregate and/or remain over longer time periods in the prey-swamped patches.

The magnitude of short-term, behaviorally mediated apparent competition will be, among other things, a function of (1) the difference in prey density between the swamped and non-swamped patches, (2) the relative profitability of the swamping prey, and (3) the predator’s mobility and capacity to distinguish high quality/quantity patches (Hughes 1979). Spatially extensive swamping events (e.g., Koenig and Knops 1998, Schauber et al. 2002) should not commonly lead to short-term apparent competition, even between nutritionally substitutable prey, because of mobility constraints to shared predators (Kelly et al. 2001, Koenig et al. 2003). In contrast, small, prey-swamped patches may attract predators moving from non-swamped habitat patches.

Predators will leave a patch if the yield of foraging in the patch declines below the mean yield over the entire habitat in which the predator is foraging (Charnov 1976, Holt and Kotler 1987). Because of the extremely high prey densities associated with masting events, we assume that, in the short-term, predators are unable to depress prey densities below a “patch-leaving” threshold. Thus, within the timeframe of our model, once a predator enters a swamped patch it will not leave the patch. Our model considers that rather static differences in absolute number of predators foraging in swamped and non-swamped patches will induce short-term apparent competition on alternative prey types. Furthermore, as relative prey proportions should be nearly unaltered (since there is a much greater abundance of the swamping prey), we expect the intensity of apparent competition to be uniform among other resident prey types differing in relative preference/profitabilty from the swamping prey.

Assuming that per capita mortality rates are linearly related to predator density, the net indirect effect (i.e., balance of apparent mutualism and apparent competition) of species \(i\) on species \(j\) (NE\(_j\)) in swamped patches will be

\[
\text{NE}_j = a_j 100 \left[ P_{NS}/(1 + a_j t_i N_i + a_j t_j N_j) \right] - \left[ P_S/(1 + a_j t_S + a_j t_j N_j) \right]
\]

\[
\text{NE}_j = a_j 100 \left( P_{NS} - P_S \right) [1/(1 + N_i + a_j) - 1/(1 + S + a_j)]
\]

where \(P_S\) and \(P_{NS}\) are densities (or residence times) of predators in the swamped and non-swamped patches, respectively. If predators aggregate (or remain foraging for longer periods) in swamped patches \(P_S > P_{NS}\), the strength of apparent mutualism is reduced by a constant rate determined by the difference in predator densities, until eventually the net outcome for the alternative prey switches to apparent competition. In the graphical model for an optimal selective predator (Fig. 2a), net effects incorporating apparent competition can be
represented by a constant decrease \((P_{NS} - P_S)\) across the prey profitability parameter space (Fig. 2b). The model (Fig. 2c) thus predicts a net negative effect on poor-quality prey. As predators increase their foraging time in swamped patches, some usually ignored prey items may eventually be harvested. On the opposite end of the spectrum, net negative effects may arise as more frequent encounters with the highly preferred prey items are possible. Only prey types similar in preference to the swamping prey can still experience net apparent mutualism, as long as the apparent competition component associated with predator aggregative behavior is not intense enough to overshadow this effect (Fig. 2c). The latter may occur when swamping patches are very small or the predator is highly mobile.

**Apparent competition induced by reproductive numerical responses**

The above models assumed that predators could not respond in a population-dynamic fashion to unusually large pulses in prey availability. The occurrence of a reproductive numerical response to prey swamping will depend crucially on the predator’s generation time and reproductive rate, relative to the duration of the resource pulse and the time scale of observation. Indeed, an increase in prey supply at time \(t\) may well lead to an increase in predator abundance at time \(t + 1\) as a result of in situ reproduction, so by time \(t + 1\), predator densities in swamped patches may have increased to a level \(P_{S(t+1)}\). Elevated predator densities may remain higher in previously swamped than in non-swamped patches because large patch sizes and low predator mobility would prevent major “spillover” effects. On the other hand, by time \(t + 1\), prey densities will tend to be similar in previously swamped and non-swamped patches due to higher overall consumption in swamped patches \((S = N)\).

Replacing \(S\) with \(N_i\) in Eq. 3, the net effect of swamping by prey \(i\) on prey \(j\) at time \(t + 1\) becomes

\[
NE_j = a_i 100(P_{NS} - P_S).
\]

As noted by others before (Holt 1977, Holt and Lawton 1994, Abrams and Matsuda 1996), such numerical responses will generally override the details in the predator’s functional response, promoting apparent competition between alternative prey types. In the present case, the strength of the apparent competition effect will be a linear function of the difference in density generated by the numerical response of the predator in previously swamped patches, as well as its relative preference for different non-swamping prey.

**FIELD EXPERIMENTS**

Seeds can be regarded as short-lived prey items relative to the generation time of most vertebrate granivores. Seeds may quickly germinate or become unavailable to consumers due to burial by litter. Therefore, from a seed survival perspective, short-term behavioral responses of granivores to extreme resource pulses may be far more important than their numerical response. Whereas direct competition between seeds is unlikely, apparent mutualism or competition are plausible mechanisms whereby different seed species may affect each other’s survival through altered predation risk (Brown and Morgan 1995, Veech 2000, 2001, Caccia et al. 2006).

In 2000–2001, patchy flowering and subsequent mass seeding by the monocarpic bamboo *C. culeou* occurred in northern Patagonian forests. This event allowed us to compare predation rates for different gravity/wind-dispersed canopy tree seeds against highly contrasting background densities of bamboo seeds.

**Study system**

Experiments were conducted in southern Láin National Park, Argentina (−40° S, 71°30’ W) during bamboo seedfall in April 2001 (fall, year 0), June 2001 (winter, year 0), and April 2002, one year after bamboo seedfall (fall, year +1). In this system, the 3–6 m tall dominant understory bamboo *C. culeou* synchronously flowered over 80000 ha in the spring (November) of 2000, shedding seeds in the fall (March and April) of 2001, after a nonflowering period of >60 years. Within the area of massive flowering, numerous *C. culeou* patches remained nonflowered. Before dispersal, in February 2001, the estimated amount of sound bamboo seeds reached ~500 000 seeds/m² in a 4 m tall, densely (~20 culms/m²) flowered *C. culeou* thicket. These estimates are within the same order of magnitude as seed densities on the forest floor (~200 000 seeds/m²; Sage 2003) during the same masting event. By spring of year 0 (September 2001), before seedling emergence, no sound bamboo seeds were found on the ground, whereas ~11 000 seeds/m² sound seeds were buried under a 7–10 cm thick litter layer (T. Kitzberger, unpublished data).

Seed removal experiments were established within three study areas differing in dominant forest community (Table 1). Study sites at Pichi Traful and Lago Hermoso represented forests dominated by *Nothofagus dombeyi* (coihue) with codominance of the conifer *Austrocedrus chilensis* (ciprés). The Lago Currhé site had forests codominated by *N. dombeyi* and the deciduous trees *Nothofagus obliqua* (roble) and *Nothofagus alpina* (rauí) (Table 1; hereafter, species are referred to by common name). None of the four tree species showed signs of masting during the fall of 2001. Although not assessed in this study, ranges in normal mean seedfall densities within dense canopies were 86–2200 seeds/m² for coihue, 17–86 seeds/m² for rauí, 127–310 seeds/m² for roble (Donoso 1995), and 25–350 seeds/m² for ciprés (Kitzberger 1994). Potential post-dispersal seed predators in these forests include the granivorous rodent *Oligoryzomys longicaudatus*, omnivorous rodents such as *Abrothrix olivaceus* and *A. longipilis* (Murúa et al. 1996, Gallardo and Mercado 1999, Caccia et al. 2006), granivorous birds such as the
Table 1. Study site locations, characteristics, and descriptions of experimental design testing for granivore-mediated indirect effects during and after a bamboo masting event in northern Patagonian forests, Argentina.

<table>
<thead>
<tr>
<th>Location</th>
<th>Coordinates</th>
<th>No. sites</th>
<th>Forest type</th>
<th>Patch size (ha)</th>
<th>Seed species offered</th>
<th>Year 0, fall</th>
<th>Year 0, winter</th>
<th>Year +1, fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pichi Traful</td>
<td>40°28' S, 71°37' W</td>
<td>1</td>
<td>coihue–ciprés</td>
<td>5</td>
<td>coihue, ciprés, bamboo</td>
<td>30</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lago Hermoso</td>
<td>40°21' S, 71°32' W</td>
<td>1</td>
<td>coihue–ciprés</td>
<td>50</td>
<td>coihue, ciprés, bamboo</td>
<td>30</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lago Curruhé</td>
<td>39°50' S, 71°32' W</td>
<td>3</td>
<td>coihue–roble–rauli</td>
<td>10–15</td>
<td>coihue, roble, rauli, bamboo</td>
<td>40</td>
<td>40</td>
<td>40</td>
</tr>
</tbody>
</table>

Notes: Each study site comprised a pair of flowered and nonflowered understory bamboo patches. Seeds of designated tree species and bamboo were offered in separate dishes and in equal numbers within both patch types. During winter, year 0, seed predation trials were conducted in only one forest site at Lago Curruhé.

columbid *Zenaida auriculata*, and rhyncryptid ground-feeding birds *Scelorchilus rubecula* and *Pteroptochos tarnii* (Rozzi et al. 1996).

Experimental design

In each of five study sites, one pair of flowered and nonflowered bamboo patches was randomly selected (Table 1). These paired patches were chosen so that massively flowered bamboo patches (>90% of clumps flowered) were nearby to nonflowered (<10% of clumps flowered) bamboo patches within forest stands of similar overstory composition. Bamboo patches ranged from 5 to 50 ha in size. Areas where flowering was too extensive (>100 ha), not allowing to find a comparable forest composition with nonflowering bamboo understories, or where flowered and nonflowered patches were too small (individual clumps < 1 ha), were avoided.

Seed removal of the locally dominant canopy trees and of bamboo was monitored during fall, year 0 in all five sites (Table 1). Mean seed mass was used as a measure of prey quality and energetic value for granivores (Hubbard et al. 1982). In addition, in one coihue–roble–rauli forest site, seed removal was monitored during winter, year 0. In addition, seed predation was again tested in all three coihue–roble–rauli forest sites (Lago Curruhé) during fall, year +1 (see Table 1). In each patch, arboreal and bamboo seeds were offered separately, by randomly placing 10 Petri dishes with 25 seeds/dish for each species. A total of 360 dishes and 9000 seeds were offered during the fall of year 0 ([2 sites × 2 flowering conditions × 3 species × 10 dishes × 25 seeds] + [3 sites × 2 flowering conditions × 4 species × 10 dishes × 25 seeds]). In the winter of year 0 we offered 80 dishes and 2000 seeds (1 site × 2 flowering conditions × 4 species × 10 dishes × 25 seeds); in the fall of year +1, we offered 240 dishes and 6000 seeds (3 sites × 2 flowering conditions × 4 species × 10 dishes × 25 seeds; Table 1). Dishes were placed on the forest floor along a randomly located transect at distances of ~5 m. The species location was randomized along each individual transect. To prevent the rain from washing the seeds away, each dish was protected with a 15 × 20 cm plastic roof supported by wooden pegs. The dishes were collected after four nights of exposure to natural predators. The remaining seeds were counted to estimate seed predation (i.e., removal) rates.

Seed removal rates of the falls of year 0 and year +1 were arcsine square-root transformed and analyzed using a split-plot ANOVA with replicated blocks (Snedecor and Cochran 1967). The bamboo flowering status was used as the main plot, while the different species represented the subplot level of the analysis. Based on our models, we expected a significant bamboo flowering × species interaction on seed predation rates. We conducted a priori contrasts to test for the effect of bamboo flowering on each individual seed species. This allowed us to evaluate the predictions of our model in terms of differential indirect effects on species differing in seed quality (mass). The amount of differential predation caused by bamboo flowering (%DP) was calculated for each species in each site as the difference in mean percentage removal of seeds between nonflowered and flowered patches. A positive %DP value for bamboo itself would be indicative of inverse density-dependent predation (Janzen’s satiation effect), whereas a positive %DP on arboreal seeds would be interpreted as net apparent mutualism (+) from prey swamping. Conversely, a negative %DP for bamboo or any arboreal seeds would suggest density-dependent predation and net apparent competition (0, –), respectively. The overall relationship between %DP and log-transformed seed mass was examined through nonlinear least-squares regression.

Effects of bamboo flowering

Immediate effects during seedfall.—Seed species experienced significantly different predation rates during fall, year 0 (coihue–roble–rauli forest, *F*<sub>3,228</sub> = 25.62, *P* < 0.0001; coihue–ciprés forest, *F*<sub>3,108</sub> = 47.39, *P* < 0.0001; Fig. 3a, d) indicating that they represented very different food items to granivores. The preference ranking based on overall mean predation rates was coihue < ciprés < roble < bamboo < rauli, which is similar to the ranking based on seed mass: coihue < roble < ciprés < bamboo < rauli.

During fall, year 0, bamboo flowering alone did not have a significant effect on seed predation rates (coihue–roble–rauli, *F*<sub>1,2</sub> = 6.73, *P* = 0.12; coihue–ciprés, *F*<sub>1,1</sub> = 1.39, *P* = 0.45). However, we found a strongly significant
flowering × species interaction in both forest communities (coihue–roble–rauí, $F_{3, 228} = 10.37, P < 0.0001$; coihue–ciprés, $F_{2, 108} = 27.59, P < 0.0001$; Fig. 3a, d). Bamboo itself was the most highly benefited seed type in flowered patches. Bamboo seed removal decreased by 2–5 times (Fig. 3a, d) when seeds were offered in flowered patches relative to nonflowered ones ($F_{1, 216} = 48.98, P < 0.0001$ and $F_{1, 216} = 126.2, P < 0.0001$, in coihue–roble–rauí and coihue–ciprés forests, respectively). Seeds of two tree species, roble and ciprés, showed moderate (~20%) reductions in predation associated with bamboo flowering (roble, $F_{1, 216} = 7.75, P = 0.006$; ciprés, $F_{1, 104} = 3.43, P = 0.067$; Fig. 3a, d). The remaining tree seed types, coihue and rauí, did not show significant changes in predation associated with bamboo flowering (both species $P > 0.45$; Fig. 3a, d).

The magnitude of differential predation (%DP) varied significantly among species ($P = 0.005$). Species %DP decreased in the order bamboo > roble > ciprés > coihue > rauí. Differential predation varied with the species’ seed mass in an asymmetric, bell-shaped fashion (Fig. 4a). Differential predation was positive and maximal for bamboo (55.1% ± 9.1%; mean ± SE), consistent with Janzen’s (1976) satiation hypothesis. Net indirect effects were nearly 0 (neutral) for the small-seeded and least preferred coihue (1.7% ± 4.1%), as well as for the large-seeded and most preferred rauí (1.6% ± 3.6%). Seed types slightly smaller than bamboo (roble and ciprés), showed positive %DP (16.8% ± 6.2% and 11.0% ± 3.5%, respectively, Fig. 4a), reflecting net apparent mutualism.

Lagged effects.—Only three months after seedfall (winter, year 0), seed predation rates increased markedly in both flowered and nonflowered bamboo patches. During this period, species-specific differences in predation rates disappeared, since all four seed types including the least preferred coihue seeds were equally and heavily removed by granivores (Fig. 3b).

One year after bamboo seedfall (fall, year +1), overall predation rates in the coihue–roble–rauí forest sites tended to decrease relative to fall year 0 and were unrelated to bamboo flowering ($F_{1, 216} = 1.15, P = 0.39$; Fig. 3c). Interspecific differences in predation rates were, however, still evident during fall year +1 ($F_{3, 228} = 203.60, P < 0.0001$; Fig. 3c). More importantly, bamboo flowering effects on seed predation remained strongly species-dependent (flowering × species, $F_{3, 228} = 5.24, P = 0.0016$). Yet, by this time, the largest seeded species (bamboo and rauí) suffered higher predation rates in previously flowered than in nonflowered bamboo patches (bamboo, $F_{1, 216} = 5.49, P = 0.02$; rauí, $F_{1, 216} = 45.9, P < 0.0001$). Predation on the other two tree seeds was not affected by bamboo flowering (Fig. 3c). In fall, year +1, %DP showed an overall tendency toward negative values indicative of apparent competition, particularly for larger seeds. However, there was no overall consistent relationship between %DP and seed mass ($R^2 = 0.11, P > 0.05$; Fig. 4b).
DISCUSSION

Field experiments showed that bamboo flowering influenced seed survival patterns through a suite of granivore-mediated indirect effects. As predicted by our model, the relative magnitude of short-term apparent mutualism varied markedly across a prey-quality gradient, being larger for the masting species itself and for tree seeds of similar quality to that of bamboo. Moreover, the nature of the intra- and interspecific indirect effects, as detected in one forest community, shifted from positive to negative with the time elapsed since the masting event. Together, our modeling and empirical results indicate that predator foraging behavior during infrequent prey-swamping events, coupled with post-swamping predator numerical responses, can create a complex spatiotemporal array of indirect effects altering propagule survival probabilities for various dominant space holders in the community. These results highlight the importance of relative prey quality to understand and predict both the short- and long-term heterospecific indirect effects that may result from extraordinary resource pulses.

Short-term indirect effects associated with masting

In the short term, bamboo flowering indirectly reduced predation on bamboo seeds and co-occurring tree seeds of slightly lower quality (cipre's and roble), a pattern predicted by our model for prey-swamping scenarios with selective predators showing a saturating functional response (Fig. 2, regions B and C). In contrast, masting had no impact on seed species of either higher (raulié) or much lower quality (coihue) than the masting species (Fig. 2, regions A and D). Thus, against a background of large seed densities produced by a masting species, only certain seed species may temporarily benefit through apparent mutualism associated with predator selective foraging behavior. Low quality prey types are normally ignored, even in the presence of low densities of a more profitable prey and, therefore, may not be expected to benefit by sudden increases in higher quality prey densities. Likewise, highly preferred prey types should not benefit from occurring together with a lower quality swamping prey because predators will actively search for them regardless of elevated background prey densities. The relative advantage of being “similar but slightly less preferred” than the masting species represents an interspecific extension of the intraspecific satiation effect proposed by Janzen (1976; see also Maycock et al. 2005). These results agree with those of Sullivan (1979), who reported that addition of large quantities of low quality oats did not reduce rodent predation on target Douglas-fir seeds. However, addition of sunflower, a seed of similar caloric content to Douglas-fir seeds, produced a 10-fold increase in survival of Douglas fir seeds. A further reduction in Douglas-fir predation was observed when sunflower seeds were added at even higher densities (Sullivan 1979).

We did not directly manipulate bamboo seed densities, and flowering bamboo patches might have differed from the surrounding matrix in other aspects, such as understory cover. Yet during masting, plant cover was likely as high in flowered as in nonflowered patches because bamboo dieback is a slow process involving several months to years (Raffaele et al. 2007). Most bamboo foliage was lost during the first year after seed shed and could have potentially influenced predator behavior during year +1. Reduced bamboo cover in flowered patches would have reduced microhabitat quality to granivores (Wada 1993, Caccia et al. 2006) leading to lower predation during fall, year +1. Instead, by that time, we found increased seed predation on the most preferred species in flowered patches (Fig. 3c). Thus, it seems unlikely that bamboo cover had confounded our interpretation of differences in seed predation.
removal patterns as resulting from bamboo mass seeding.

Our theoretical analyses are simplistic in that handling times were set to be equal for all prey types, and prey size was used as shorthand for profitability, while ignoring variation in other components of prey quality (e.g., presence of toxic compounds) that can affect predator selectivity. Similar patterns of indirect effects might hold for prey types of similar sizes but different handling times. Yet more experimental work is needed to address the effects of various prey traits influencing predator diet selection during prey-swamping episodes such as masting events. In our experiment, we found that the prey type that most benefited from masting were bamboo seeds themselves. It is possible that factors associated with seed species identity other than size or energetic content (e.g., degree of nutritional complementarity; Abrams 1993) had influenced granivores dietary behavior determining the reduced consumption of bamboo seeds observed in experimental dishes in the context of seed-swamped bamboo patches.

Intriguingly, although ecological conditions leading to apparent mutualism appear to be common, direct experimental demonstration of predator-mediated positive effects has been elusive (Abrams 1993, Abrams and Matsuda 1996, Brassil and Abrams 2004). It may well be that positive indirect effects through shared predation are only transient (Holt and Lawton 1994) or smaller in magnitude (Brassil and Abrams 2004) than negative, apparent competition effects (see Chaneton and Bonsall 2000). In natural masting situations, positive intra- or interspecific interactions mediated by post-dispersal consumers has rarely been documented (Jensen 1982, Nilsson and Wåstljung 1987, Maycock et al. 2005). In most reported cases, seed survival was either not affected by masting (Shaw 1968, Ballardie and Whelan 1987, Schupp 1990) or was negatively associated with masting (Gardner 1977). In our system, large amounts of bamboo seeds (hundreds of thousands per square meter) produced over large forest areas apparently created a sufficiently large food pulse to saturate resident granivores in the short term, prevent predator aggregation, and reduce predation rates on bamboo and other nutritionally similar arboreal seeds.

Alternatively, the failure to detect apparent mutualism in natural settings could be a matter of scale (Ostman and Ives 2003). Experimental studies generally have not detected indirect mutualistic effects among seed species, possibly because they typically involve manipulating relative low seed numbers at the scale of Petri dishes or trays (Brown and Morgan 1995, Veech 2000, 2001, Caccia et al. 2006). Such experiments would be biased toward detecting apparent competition between seed species because offered seed densities are unlikely to cause predator saturation, a necessary condition for positive, behaviorally mediated indirect effects under shared predation (Abrams and Matsuda 1996). Small seed patches would further reinforce the importance of predator aggregation and patch selection based on optimal-like strategies, two processes often leading to apparent competition between alternative prey (Holt and Kotler 1987, Veech 2001). In addition, under masting scenarios, potential net positive effects on non-swamping prey may be obscured by indirect effects via predator numerical responses to elevated food supply (cf. Holt and Lawton 1994, Abrams and Matsuda 1996). Realistic field experiments on masting are difficult to perform since satiating predators over a meaningful area would require experimentally increasing seed densities on very large field plots (Crawley 1989, 1992, Ostfeld et al. 1996). Exceptions to this rule come from studies in which large amounts of artificial food or alternative prey were manually added in order to alter predation rates on a target prey by changing the predator’s foraging behavior (Sullivan 1979, Hämbäck and Ekerholm 1997, Harmon and Andow 2004).

Positive effects of masting on co-occurring seed types can be obscured by indirect effects via short-term aggregative responses of mobile predators. The increased abundance of one prey species can depress another prey’s survival when predators concentrate on or spend more time in patches with higher combined prey densities (Abrams 1987, 1993, Holt and Kotler 1987). We did not find field evidence that bamboo flowering induced substantial short-term apparent competition on arboreal seeds. The spatial extent of flowering was presumably large enough to prevent predator aggregation, at least away from the flowered patch boundaries, where our predation trials were conducted. Hence, the spatial extent and intensity of masting, the contrast between high and low prey density patches, and predator mobility will all contribute to determine the sign and strength of short-term indirect effects via shared predation.

**Lagged indirect effects induced by bamboo masting**

Holt and Lawton (1994) suggested that the sign of the indirect effect may be reversed when the reproductive numerical response of the shared predator is allowed for. In our system, only three months after bamboo seedfall, high seed predation rates strongly decreased survival of all seed types, irrespective of patch flowering condition. Independent trapping assessments of rodent abundance showed that late winter of year 0 was the time of peak rodent density after bamboo flowering (Sage 2003), suggesting that the large quantities of available bamboo seeds induced a rapid numerical response of resident granivores. This numerical response, however, was brief. By August of year 0, bamboo seeds were becoming unavailable to granivores. Measurements of sound seed at different depths in the litter layer indicated that 100% of seeds exposed on the soil surface were removed; these predation figures declined to 85% when seeds were located between 0.1–1 cm, and were only 20% for bamboo seeds at 1–3 cm beneath the litter. By this time, rodents appeared to drastically change their feeding
behavior due to starvation, feeding on green foliage of nonflowered bamboo and tree saplings and producing extensive forest litter turnover in search of seeds (T. Kitzberger, personal observation). This period was followed by massive drowning of rodents in all major lakes within the region, as recorded in October of year 0 (Sage 2003). As a result, one year after masting seed, predation dropped dramatically across all patches. However, higher predation rates in previously flowered patches, particularly of highly preferred seeds (Fig. 3c), suggest that a legacy of the numerical response related to bamboo flowering was still evident.

Integration of current season patterns and protracted patterns of seed survival induced by masting should consider the timing of predator functional and numerical responses and prey depletion trajectories in seed-swamped patches, as well as relative prey preference/profitability (see Holt and Kotler 1987). In our system, positive short-term effects occurred shortly after seed-fall and were relatively strong on the masting species and similarly preferred food types. These prey items may further benefit in the long-term from masting and gain dominance in the community because a large portion of seeds quickly became buried during post-flowering bamboo dieback and therefore presumably escaped predator numerical responses in winter, year 0. By the following spring these seeds may readily germinate after granivore densities have already crashed. Such a fast cycle of population boom and crash may further ensure that seedlings emerging from the litter may not encounter high predation rates by granivore/seedling-gnawing rodents (Caccia and Ballaré 1998, Sato 2000).

Implications for resource-pulsed systems

Predator swamping by conspecific or heterospecific prey has been invoked as a general mechanism explaining the selective advantages of reproductive synchrony (Silvertown 1980, Kelly 1994), community-wide masting (Curran and Leighton 2000, Curran and Webb 2000, Kelly et al. 2000, Liebhold et al. 2004), and other aggregative phenomena in plants and animals (Estes et al. 2001). If short-term mutualistic effects were to translate into community composition and plant fitness, an aspect beyond the scope of this paper, higher recruitment should be expected for species with seeds nutritionally similar to that of the masting species. Species with highly contrasting seed nutritional values may even be at a disadvantage during masting, a selective pressure that might conceivably favor asynchronal flowering patterns across sympatric species (see Sork et al. 1993, Koenig et al. 1994, Schnurr et al. 2002). Rather, this mechanism may favor “masting guilds” composed by species with similar seed qualities, as opposed to “community-wide” masting patterns involving species with very different seed types. Indeed, most examples of heterospecific masting synchrony come from systems dominated by closely related species with seeds that are similar in size and nutritional quality (Kelly et al. 2000, Schauber et al. 2002). While the benefits of cross-species reproductive synchrony in the latter systems may be established through phylogenetic inertia and shared predation on similar seed types, we suggest that more diversified prey assemblages may constitute masting guilds based on their propagules’ nutritional quality and/or size.

Resource pulses occurring in temperate forest ecosystems in the form of interannual variability in seed production can produce a wide variety of direct and indirect interactions through generalist consumers (Liebhold et al. 2000, McShea 2000, Ostfeld and Keesing 2000, Schmidt and Ostfeld 2003). We have shown that short-term net positive interactions induced by prey swamping should operate when (1) single or combined prey densities rise several orders of magnitude above normal densities, (2) the swamping and alternative prey are similarly profitable to selective predators, and (3) short-term apparent competition is unlikely to occur (e.g., due to large-scale synchronously masting patches, low predator mobility, and low preference/profitability of the swamping prey).

The longer term consequences of such positive indirect effects on prey recruitment patterns remain to be investigated. We suggest that short-term positive indirect effects would most likely translate into enhanced recruitment opportunities if the favored prey manages to evade predator numerical responses, by finding either a physical refuge (e.g., litter burial) or a life-stage refuge (e.g., through seedling emergence). Although, by definition, windows of opportunity for recruitment generated by prey-swamping events should be rare and can be highly transient, they have the potential to influence community dynamics in the long term (see Witman et al. 2003). Therefore, indirect effects via shared consumers should be studied in other resource-pulsed systems to determine the generality of our findings.

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Literature Cited


APPENDIX A

A figure showing minimum relative energetic profitability as a function of relative preference (Ecological Archives E088-153-A1).

APPENDIX B

A figure showing critical densities at which a selective predator drops alternate prey as a function of prey quality (Ecological Archives E088-153-A2).