

REVIEW

Incorporating the effects of generalist seed predators into plant community theory

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Summary

1. Post-dispersal seed predators contribute substantially to seed loss across many ecosystems. Most research has focused on understanding sources of variation in seed loss, without appreciating the implications of seed predation for plant coexistence, community assembly and broader community theory. Meanwhile, research aimed at understanding coexistence and community assembly processes in plant communities has focused on axes of dispersal and resource competition and the traits influencing these processes, without accounting for the role of generalist seed predators.

2. We review the unique features of post-dispersal seed predation and assess the implications of seed loss on three critical components of plant community organization – coexistence, community structure and plant invasions – pointing to both important gaps in theory and empirical knowledge. We highlight how understanding fundamental controls on plant recruitment is central to determining how seed predation affects plant recruitment and coexistence. We discuss how accounting for seed predator foraging strategies may shift trait-based inferences of community assembly.

3. *Synthesis.* We argue that seed predation by generalist consumers, which is pervasive in temperate communities, should be better incorporated into plant community theory. Experiments that specifically incorporate the presence and attributes of the seed predator community and that follow seed fate would fill important knowledge gaps. Particularly needed are studies focused on strengthening the connections between seed removal and plant establishment and linking selective and density-dependent foraging strategies to plant traits. Advancing our understanding of the processes regulating plant coexistence and community assembly requires that future research not only acknowledge but also incorporate generalist consumers' effects on plant communities.

Key-words: biotic resistance, coexistence, generalist seed predators, plant recruitment, plant-herbivore interactions, post-dispersal seed predation, seed size, trait-based community assembly

Introduction

A long-standing challenge for community ecologists has been to determine the relative strength of key local processes affecting plant community structure. Increasingly, ecologists are approaching this issue by focusing on community assembly, in part because of debates over the importance of neutral processes (Hubbell 2001) to overall community composition (Clark 2012; Rosindell *et al.* 2012). The hallmark of much of this work has been a focus

on traits, particularly those related to resource acquisition. This is because the distribution of traits in a community is thought to provide an inferential basis for assessing the importance of competitive interactions and niche-based processes in determining the outcome of the assembly process (HilleRisLambers *et al.* 2012). Moreover, focusing on traits is often seen as a way to mechanistically link particular plant life-history strategies to coexistence mechanisms (Chesson 2000; Adler *et al.* 2013). Yet, despite studies indicating strong impacts of generalist seed predators on plant communities (Brown & Heske 1990; MacMahon, Mull &

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Crist 2000; Meserve *et al.* 2003), their role in contemporary assessments of community assembly processes has mostly been overlooked (but see, Germain *et al.* 2013). Existing empirical and synthesis efforts have been developed from the perspective that generalist herbivores primarily act to mediate exploitative competitive interactions (Díaz *et al.* 2007; Hillebrand *et al.* 2007; Borer *et al.* 2014), thus only indirectly influencing community assembly processes. Here we argue for the need to further incorporate the direct effects of consumers, specifically generalist post-dispersal seed predators, on plant population and community processes.

In this article, we synthesize evidence demonstrating strong and diverse influences of post-dispersal seed predators on plant populations and communities. We build on contemporary coexistence theory and trait-based ecology by demonstrating how integrating seed predation into these and other conceptual frameworks can advance thinking about community assembly and coexistence. To achieve a more synthetic understanding of the implications of post-dispersal seed predation on plant communities, we: (i) outline the attributes that distinguish post-dispersal seed predation from other forms of herbivory and seed loss, (ii) highlight how a few key processes (i.e. potential seed size trade-offs, foraging strategies and context-dependence) can influence how seed predators affect coexistence and community assembly processes and (iii) discuss how seed predators influence invasions by either limiting or reinforcing exotic abundance, thereby affecting processes at both the population and community level. While some aspects of post-dispersal seed predation have previously been reviewed (Crawley 1992, 2000, 2014; Hulme 1998; Moles, Warton & Westoby 2003; Dalling *et al.* 2011), the many influences of generalist seed predators remain poorly integrated into plant community theory (but see Germain *et al.* 2013). Our overarching goal, therefore, is to present a synthetic argument for the importance of modifying current thinking about community assembly and coexistence in ways that incorporate the diverse and potentially important impacts of seed predators. We end by outlining future research needs.

We develop our framework around research conducted primarily in temperate systems, since lumping all seed predators and systems together is unlikely to reveal clear patterns (Moles, Warton & Westoby 2003). In particular, biases in seed size selection by consumers may not be equivalent across systems. For example in tropical systems seeds are often packaged as fruits and nuts to attract dispersers (Jansen *et al.* 2012), and average seed size is larger than in temperate systems (Moles & Westoby 2003). These features could alter seed size biased foraging. Accordingly, we do not review tropical work here, but the general framework we develop could be applied to those systems.

Ideally, our synthesis would consider all seed fates, including dispersal, since we know that post-dispersal seed predators such as rodents, ants and birds also disperse seeds (Levey & Byrne 1993; Espadaler & Gómez 1996;

Tewksbury & Nabhan 2001; Vander Wall, Kuhn & Beck 2005; Lichti, Steele & Swihart 2017). While space constraints prevent a broad consideration of the impacts of dispersal, it is clear that a broader understanding of the fate of seeds processed by consumers is needed. Importantly for the discussion that follows, seed predation and seed dispersal may influence community assembly, coexistence and invasion in conceptually similar ways (albeit with opposite effects), since the traits consumers use to select seeds are generally similar whether seeds are immediately consumed or cached for later consumption.

Distinguishing features of post-dispersal seed predation

Post-dispersal seed consumption compounds any seed loss that occurs prior to seed dispersal (Visser *et al.* 2011). However, several features distinguish post-dispersal seed predation from other consumer effects that occur prior to dispersal. First, post-dispersal seed consumption, particularly by rodents, appears on average to be much greater in magnitude than is predispersal seed predation (i.e. predation on seeds while on plants *sensu* Hulme 1998; Traveset 1994; Myser 1997). Short-term seed loss from feeding depots usually exceeds seed destruction over an entire season by pre-dispersal seed feeders (Hulme 2002; Moles, Warton & Westoby 2003). Second, many pre-dispersal insect seed predators are specialists and the percentage of plant species in any community attacked by these consumers is likely lower than the breadth of species whose seeds could be consumed by generalist post-dispersal seed predators (Kolb, Ehlén & Eriksson 2007). Third, plants cannot actively compensate for post-dispersal seed loss whereas plants can often at least partially compensate for the loss of vegetative tissue (Janzen 1971). Finally and perhaps most importantly, through selective foraging, post-dispersal seed predators can act as filters that discriminate on seed traits (Brown & Heske 1990; Reader 1993; Maron *et al.* 2012). Such selective foraging has the potential to alter the trait distributions of propagules that are available for germination or interact with selection driven by plant competition, dispersal or abiotic constraints, thereby influencing the distribution of traits within a community.

Predator attributes influencing seed loss

The specific ways in which post-dispersal seed predation influences plant communities are shaped by attributes of predator foraging. Seed predator size (Vieira, Pizo & Izar 2003; Ness *et al.* 2004; Muñoz & Bonal 2008) and complexity of the seed predator community (Heithaus 1981; Mittlebach & Gross 1984; Pulliam 1985; Reader 1993; Hang-Hau 1997) can influence what seed sizes are selected (Radtke 2011). In temperate grasslands and old fields, rodents often select larger seeds (Mittlebach & Gross 1984; Brown & Heske 1990; Reader 1993; Maron *et al.* 2012), whereas ants favour smaller ones (Crist & MacMahon

1992; Rey *et al.* 2002; Ferreira, Bruna & Vasconcelos 2011; Pearson *et al.* 2014a). Other seed attributes such as coat hardness, nutritional content (Kerley & Erasmus 1991) and/or chemical composition (Rios, Mangione & Marone 2012), and the presence of eliosomes can also influence seed preference (Blate, Peart & Leighton 1998; Kollman, Coomes & White 1998; Moles, Warton & Westoby 2003; Lichti, Steele & Swihart 2017).

Understanding how feeding preferences translate to foraging patterns in complex and highly variable natural systems can be challenging. Preference for different food items may differ substantially from what is actually eaten depending on environmental context (*sensu* Johnson 1980). For example despite specific food preferences seed predators may forage on the most abundant species in the seed pool (Allen 1988; Schnurr *et al.* 2004) to optimize foraging (Inouye, Byers & Brown 1980; Thompson, Brown & Spencer 1991; Howe & Brown 1999). For example, Enders & Vander Wall (2012) found that small mammal seed predators exhibited a preference for large-seeded species but not in years when there was a large seed crop from a local pine tree. Importantly, selective and density-dependent foraging are not mutually exclusive (Inouye, Byers & Brown 1980; Wilby & Shachak 2000; Pirk *et al.* 2009), and in fact both processes are considered important to the maintenance of biodiversity in the tropics (Janzen 1970; Connell 1971). Identifying the underlying mechanisms determining seed selection within a community context is key to understanding how seed predation may interact with local environmental variation across space or time to ultimately affect plant recruitment and coexistence.

Seed removal may vary across space because seed predator foraging can track changes in plant abundance (Mittlebach & Gross 1984; Visser *et al.* 2011), vegetation structure (Díaz, Papic & Armesto 1999; Orrock & Damschen 2005; Yoko-o & Tokeshi 2012; Germain *et al.* 2013) or the presence of interacting species (e.g. predators: Maron & Pearson 2011; neighbouring plant species: Garzon-Lopez *et al.* 2015; invasive ants: Christian 2001). In addition, seed predation may change over time due to changes in the seed pool (Hulme 1994), such as during a masting event (Enders & Vander Wall 2012) or drought (Pirk *et al.* 2009), and with changes in seed predator densities that occur either seasonally (Marone, De Casenave & Victor 2000) or interannually (Ostfeld, Manson & Canham 1997; Kelt *et al.* 2004; Pearson & Callaway 2008; Maron & Pearson 2011). The net strength of this biotic filter will ultimately depend on both rates of seed removal and environmental controls on seedling recruitment.

Seed predators may strongly influence plant recruitment in years when consumer populations are high and growing conditions are favourable to recruitment (Meserve *et al.* 2003). However, environmental conditions such as drought could limit recruitment, thereby overriding impacts of seed loss due to predation. The extent to which the strength of seed predation effects vary with the environment could have important selective implications for the evolution of

seed traits (Dalling *et al.* 2011). Moreover, at the population level, both the absolute magnitude of seed predation and abiotic influences on plant demographic components together can affect how strongly seed loss translates to reductions in future plant abundance. Although the impacts of consumers on plant abundance is very context dependent, our understanding of environmental factors that drive spatial variation in the population-level impacts of seed predation remains poor (Maron & Crone 2006; Maron, Baer & Angert 2014). Many seed offering experiments have demonstrated that environmental conditions like moon phase, precipitation and temperature can influence small mammal foraging behaviour (Brown & Kotler 2004; Orrock & Danielson 2009; Orrock *et al.* 2015a), but fewer studies have demonstrated how abiotic factors mediate the effects of seed predation on plant recruitment and abundance (Allington *et al.* 2013; von Euler, Ågren & Ehrlén 2014; Maron, Baer & Angert 2014; Pearson *et al.* 2014b).

Post-dispersal seed predation, community structure and coexistence

At the population level, seed loss can have substantial impacts on native plant recruitment in coastal dunes and deserts (Inouye, Byers & Brown 1980; Brown & Heske 1990; Samson, Philippi & Davidson 1992; Maron & Kauffman 2006; Longland 2007), annual (Borchert & Jain 1978; Orrock, Witter & Reichman 2008), perennial semi-arid (Peters *et al.* 2005; Pearson & Callaway 2008; Bricker, Pearson & Maron 2010; Maron *et al.* 2012) and mesic grasslands (Edwards & Crawley 1999; Howe & Brown 2000), old fields (Mittlebach & Gross 1984; Reader 1993; Orrock *et al.* 2006) and woodlands (Andersen 1987; Albert, Escudero & Irionodo 2005; Ferreira, Bruna & Vasconcelos 2011).

The classic test case for long-term rodent and ant effects on plant community dynamics comes from the famous work of Jim Brown and his colleagues. Using large exclosures in both the Chihuahuan and Sonoran desert, these authors showed that long-term rodent exclusion leads to large changes in the relative abundance of plants in these desert communities. Over time, large-seeded species became more dominant inside rodent exclosures compared to control plots (Inouye, Byers & Brown 1980; Brown & Heske 1990; Valone & Schutzenhofer 2007; Chen & Valone *In Press*). Similar community-level impacts of small mammal granivory have been found in shorter term studies conducted at forest-old field margins (Manson, Ostfeld & Canham 2001), planted prairie (Howe & Brown 2000) and perennial semi-arid grasslands (Maron *et al.* 2012). Yet compared to the multitude of longer term experiments that have excluded consumers such as ungulates from systems (Kay & Bartos 2000; Gómez 2005; Manier & Hobbs 2006; Pringle *et al.* 2007), our understanding of how generalist seed predators influence long-term patterns of community structure are limited. In the following section, we

outline how post-dispersal seed predators can be integrated into emerging theories of coexistence, community assembly and invasion biology by understanding a few key processes: (i) potential seed size trade-offs, (ii) selective vs. density driven foraging strategies and (iii) context dependence.

Seed traits have long been considered central to coexistence. The impressive variation in seed size among coexisting species (Leishman, Westoby & Jurado 1995; Jakobsson & Eriksson 2000) is thought emblematic of competition-colonization trade-offs that ensure coexistence among strongly interacting species (Shmida & Ellner 1984; Tilman 1994; Chesson 2000; Rees *et al.* 2001). Large-seeded species can have inherent advantages over smaller seeded ones through a greater ability to tolerate local hazards such as shade, litter and adult competitors (Leishman & Westoby 1994; Leishman *et al.* 2000; Moles & Westoby 2004). In contrast, higher fecundity small-seeded species are presumed to be superior colonizers. This enables them to reach microsites that large-seeded species cannot reach and provides small-seeded species advantages in rare microsites that reflect niche differences (Levine & Rees 2002). Empirical support for competition-colonization trade-offs driving variation in abundance among species that vary in seed size is conflicting (Rees 1995; Turnbull, Rees & Crawley 1999; Turnbull, Manley & Rees 2005), and other trade-offs involving seed size remain poorly explored.

Recent theory posits that seed size reflects a trade-off between fecundity and stress tolerance. Large- and small-seeded species co-exist because seedlings of less fecund large-seeded species are more tolerant of local stressors, and small-seeded species have advantages at benign sites where they have numerical superiority as seeds (Muller-Landau 2010). This assumption is reasonable for species whose recruitment is limited by the availability of microsites, but for those species limited by absolute seed number, seed predation may exacerbate recruitment and alter coexistence dynamics (Crawley 1992; Fig. 1). The ramifications of ignoring seed predation was illustrated by Reader (1993) who demonstrated that while large-seeded species gained a clear advantage over small-seeded species in the presence of heavy litter, rodent seed predation that selected against large-seeded species completely negated this advantage. Seed predators like ants, who additionally act as dispersers, may alternatively augment recruitment for small-seeded species by moving seeds to more favourable microsites via secondary dispersal (Hughes & Westoby 1992). Accounting for these seed predator driven changes in the diversity of species within a system is key to ensure that local diversity patterns are not incorrectly attributed to either other deterministic drivers such as environment or stochastic processes of community assembly such as ecological drift (Germain *et al.* 2013 but see Pinto, Pearson & Maron 2014; Table 1).

Frequency-dependent foraging by generalist seed predators may create negative feedbacks thereby establishing a stabilizing mechanism that promotes coexistence over time,

as has been hypothesized for specialists (e.g. storage effect, Chesson & Kuang 2010; Table 1). The potential strength of this stabilizing mechanism may depend on (i) the extent to which traits that promote seed defence coincide with other traits such as seed dormancy that can additionally promote coexistence and (ii) the physical environment (Dalling *et al.* 2011). Environmental conditions may influence the strength of other biotic hazards such as pathogen loads and the length of seed persistence in a seedbank, further influencing where on the continuum of physical to chemical seed defence a species will lie (Dalling *et al.* 2011). Importantly, if a seed predator inhibited the recruitment of a subset of species within a community through predation of large-seeded species, they could still function as a stabilizing mechanism that promotes coexistence if other density-dependent mechanisms (e.g. pathogen load, resource competition) are at play for other species (Chesson 2000) or if recruitment were enhanced through directed dispersal (e.g. via scatterhoarding), thereby promoting coexistence via a spatial storage effect (Snyder & Chesson 2003). Conversely, predation on large-seeded species may be a key 'equalizing mechanism' (Chesson 2000) that promotes diversity particularly if these species are competitive dominants as adults.

Trait-based community assembly and seed predation

Increasingly, patterns of community trait composition have been used to infer the strength of both environmental filters and interspecific competitive interactions in structuring plant communities (Fig. 2; Cornwell & Ackerly 2009; Spasojevic & Suding 2012; Germain *et al.* 2013). To date, most research has focused on plant traits from the 'leaf economic spectrum' such as specific leaf area (SLA) because these traits relate to resource acquisition and are thought important for inferring the role of competition or facilitation in affecting community structure. Traditionally, seed mass has been considered an orthogonal trait axis to leaf traits and used to help explain the response to disturbances (Grime 1977; Westoby *et al.* 2002; Myers & Harms 2009) or the ability of seedlings to deal with seedling-seedling competition, shade and litter (Leishman & Westoby 1994; Leishman *et al.* 2000; Moles & Westoby 2004). Yet, seed mass can also influence seed selection by granivores that both consume seeds (Brown & Heske 1990; Reader 1993; Maron *et al.* 2012) as well as disperse them (Howe & Smallwood 1982).

Although there have been significant advances in trait-based approaches, much of the trait-based community assembly work does not recognize or integrate the role of generalist seed predators in driving functional trait patterns or plant community structure (Lavorel *et al.* 2013). In one of the few papers to examine the effects of rodent seed predators on community assembly, Germain *et al.* (2013) found that rodents shifted trait composition and reduced diversity via selective foraging. Interestingly,

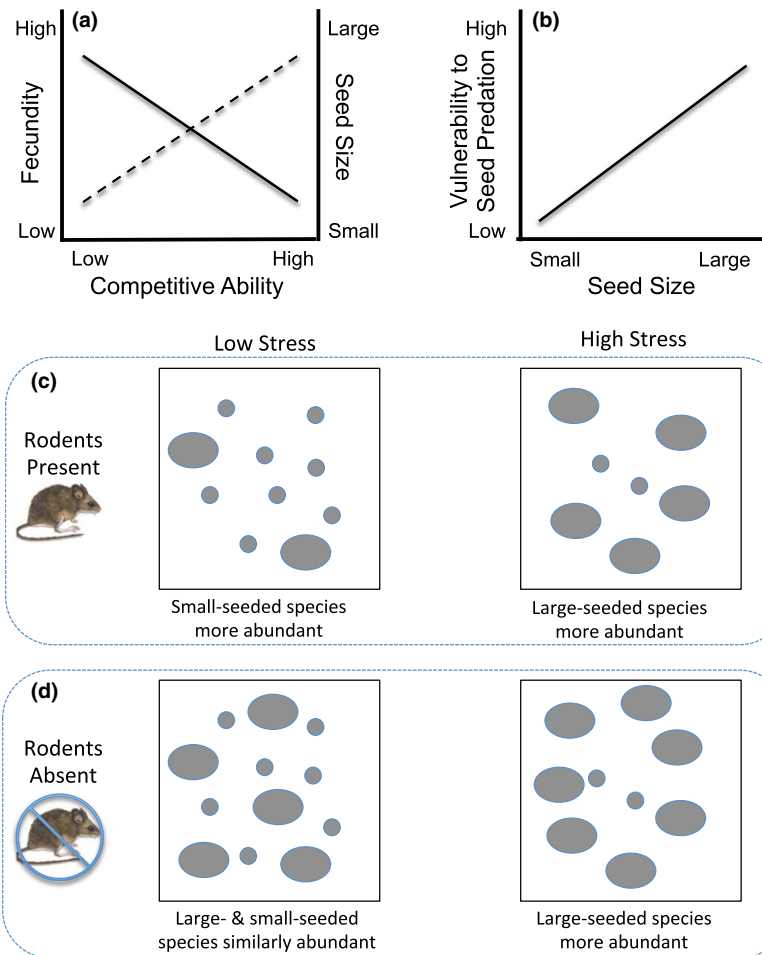


Fig. 1. The classic competition-colonization trade-off (a, solid line) highlights how seed size is a trait central to coexistence theory as it can mediate a trade-off between fecundity and competitive ability (a, dashed line). This trade-off often neglects the trade-off between seed size and rodent seed predation, particularly in temperate herbaceous communities (b). More recently, the fecundity-tolerance trade-off predicts small-seeded species (small circles) to be more abundant in lower stress environments and large-seeded species (large circles) to be more abundant in high stress environments (after Muller-Landau 2010) (c). However, this prediction, similar to the classic competition-colonization trade-off, assumes the presence of seed predators (e.g. rodents) but neglects their effects. If seed predators preferentially consume large-seeded species, removing seed predators would result in increased recruitment of these species in all environments (d).

however, current trait-based studies would likely have interpreted this convergence pattern as indicating a strong role of environmental filtering rather than considering the importance of granivory in driving this pattern. Importantly, Germain *et al.* 2013 demonstrated that these seed predation effects varied spatially as seed predation decreased with decreasing vegetation cover resulting in areas where diversity patterns were driven by more stochastic assembly processes. Germain *et al.* (2013) clearly demonstrates that stochastic processes like dispersal interact with deterministic, selective seed predation (and seedling herbivory) to influence alpha and functional diversity of these small-scale communities.

Building on Germain *et al.* (2013)'s findings, we outline a framework that highlights the scenarios under which seed predators may influence both trait composition and diversity of plant communities (Table 1). We focus on seed size, but these dynamics could be applied to other traits influencing foraging (e.g. palatability as in Germain *et al.* 2013). If seed predators preferentially consume either large- or small-seeded species within a local seed pool with high functional diversity and a large mean seed size or small-seeded species from a seed pool with high functional diversity and a small mean seed size, seed predation could reduce the functional diversity of recruited individuals (Fig. 2,

community i, Germain *et al.* 2013). Conversely, if seed predators were not selective for seed size, the density of propagules could either be reduced evenly (Matthies *et al.* 2004) or the most abundant species in the seed pool might be reduced (i.e. frequency-dependent predation; Allen 1988). In the first scenario, seed predation would not impact functional diversity (Fig. 2, community ii) and would not influence the assessment of other assembly processes. However, frequency-dependent predation could shift and increase functional diversity by increasing the colonization of rare species in the community (Fig. 2, community iii). This latter scenario indicates that by not considering seed predation, we may incorrectly infer that competition via limiting similarity alone plays a dominant role in the divergence of trait composition. While we highlight these dynamics for a single community, these dynamics can occur at fine spatial scales and result in heterogeneous patterns of trait composition within a community (Germain *et al.* 2013); therefore, fully assessing seed predator effects on community attributes and trait distributions additionally requires information on any attribute of the habitat such as cover, predation risk, etc. that can influence small mammal numbers or behaviour (Germain *et al.* 2013).

Studies that quantify the relative strength of all local filters that can influence local community composition, and

Table 1. Summary table of three key areas in plant community theory where incorporating seed predation can improve our understanding of the ecological processes regulating plant populations and communities. Context dependence refers to factors that can shift the strength with which seed predation influences predicted patterns

Ecological theory/topic	Hypothesized ecological mechanism	Seed predator foraging	Incorrect conclusions	Context-dependence
Coexistence theory	Seed-size: fecundity-stress tolerance tradeoff	Seed-size dependent	Recruitment limited by ecological drift instead of predation	Effects dependent on seed vs. microsite limitation
	Storage effect	Frequency dependent	Coexistence via resource use trade-offs instead of via predation	
Trait-based community assembly	Environmental filtering vs. plant competition	(i) Selective (e.g. seed-size)	(i) Convergence in traits due to environmental filtering instead of predation	Foraging behaviour may be influenced by local-scale vegetation patterns or predator risk
		(ii) No preference	(ii) No error in inference	
		(iii) Frequency dependent	(iii) Divergence in traits due to competition instead of predation	
Plant invasions	Biotic resistance	Selective (e.g. seed-size)	Invader establishment/spread is limited by plant-plant interactions	Foraging behaviour affected by range of seed sizes available or additional seed traits
	Apparent Competition	Selective for natives	Competitive interactions reinforce invader	Seasonal changes in consumer abundance and behaviour influenced by invader cover

examine how the strength of these filters change over relevant ecological or environmental gradients could advance our understanding of drivers of community structure and trait distributions in plant communities. However, evolutionary and ecological interactions among filters can influence seed traits and filtering processes in complex ways. For example soil microbial communities can function as important post-dispersal ‘seed predators’ that drive selection for specific physical and chemical seed traits (Dalling *et al.* 2011) that can influence bird and mammal seed predators. In perhaps the best example of this, capsaicin, the secondary compound, which makes wild chili peppers (*Capsicum* spp.) hot, evolved as a defence against *Fusarium* pathogens that destroy fruits and seeds, but it also inhibits destructive rodent seed predation and facilitates bird dispersal of these seeds (Tewksbury & Nabhan 2001; Tewksbury *et al.* 2008).

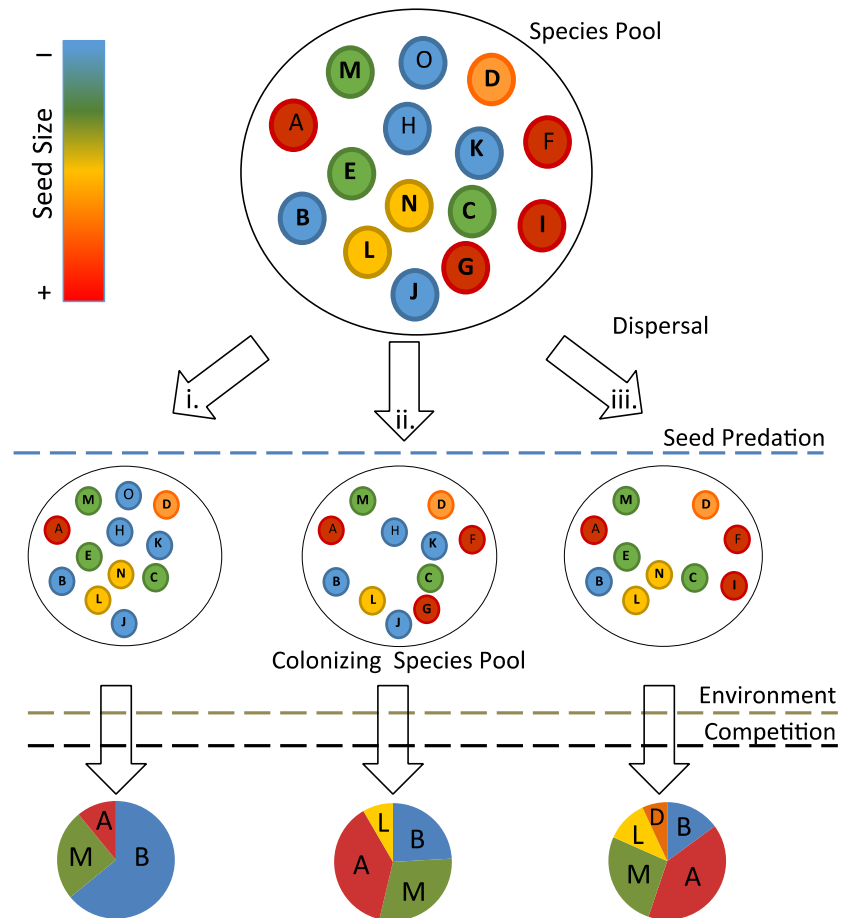
The diversity of the consumer community also has the potential to influence the selection for seed sizes, as has been recently observed with grasshoppers and plant leaf traits (Deraison *et al.* 2015). Prey selection tends to correlate positively with consumer body size across animals (Rosenzweig 1966; Wheelwright 1985; Scharf, Juanes & Rountree 2000; Sinclair, Mduma & Brashares 2003), with the important caveat that larger consumers often accommodate a wider range of food sizes (Sinclair, Mduma & Brashares 2003; Muñoz & Bonal 2008). Small mammal body size also correlates positively with seed size selection across systems (Brown & Lieberman 1973; Vieira, Pizo & Izar 2003; Muñoz & Bonal 2008), and this correlation has been similarly observed for birds (Pulliam 1985). Together, these factors can result in the following patterns: In a relatively simple seed predator community there may be strong

selection for a particular seed size (e.g. for larger seeds: Mittlebach & Gross 1984; Reader 1993; Howe & Brown 2000; Pearson & Callaway 2008; Maron *et al.* 2012; small seeds: Pirk & De Casenave 2011) or there may be no selection for seed size if this community consists of only a few large consumers that exploit a broader range of seed sizes within a larger-seeded community (Hang-Hau 1997). Similarly, a species-rich seed predator community, either within a single guild (e.g. multiple rodent species) or across guilds (e.g. ants, birds and rodents present), may result in no pattern of seed size selection if the seed predators fill a range of consumer niches (Pearson *et al.* 2014b) or during periods of seed scarcity (Pulliam 1985; Pirk *et al.* 2009). A more nuanced framework could be applied to understand how seed removal might differ across systems supporting varied compositions of seed predators inhabiting diverse plant communities with different seed size ranges and could be additionally expanded to understand how seed removal might differ across post-dispersal seed predation guilds or in the presence of multiple seed predator guilds.

Invasions – a special case of community assembly

Biological invasions provide a unique opportunity to identify and assess the strength of relevant community assembly processes (Sax *et al.* 2007), and in particular, the dual roles that seed predators may have in either suppressing the initial establishment of exotic species or conversely, in reinforcing their higher abundance. In the context of inhibiting invasions, post-dispersal seed predators can provide biotic resistance (*sensu* Elton 1958) by: (i) reducing an invader's population growth rate when it is rare or

Fig. 2. Local plant community assembly is influenced by a suite of ecological filters (dispersal, environment, competition) that select for species (letters) with a particular suite of plant traits (colours). The trait distributions of the local communities (pie charts) are often used to infer the processes that regulated the ecological filters structuring that community. Seed predation is often neglected in this framework, yet it can shift the composition of the colonizing species pool in three distinct ways: seed predators can forage (i) for a specific trait (i.e. large seeds), (ii) evenly across the seed pool or (iii) in a frequency-dependent manner. These shifts in the colonizing pool can result in an incorrect interpretation of convergence (i) or divergence (iii) or have no effect on the interpretation of the strength of environmental or competitive filtering (ii).



inhibiting establishment altogether or (ii) differentially reducing an invader's population growth rate when it is abundant, thereby potentially limiting opportunities for spread within the community (Levine, Adler & Yelenik 2004). Most research on biotic resistance has focused on plant-plant competition and the role of resident community diversity and native generalist herbivores (Levine & D'Antonio 1999; Callaway *et al.* 2004; Levine, Adler & Yelenik 2004; Parker, Burkepile & Hay 2006). Despite the fact that most terrestrial plants initially invade new environments as seeds, our understanding of seed predation as a filter that inhibits invader establishment is more limited.

We know from seed offering studies that rodents or ants remove exotic seeds, sometimes differentially compared to native seed (e.g. Pemberton & Irving 1990; Crist & MacMahon 1992; Blaney & Kotanen 2001; Vilà & Gimeno 2003; Jensen & Six 2006; Shahid, Garneau & Mccay 2009; Alba-Lynn & Henk 2010; Carrillo-Gavilán, Lalague & Vilà 2010; Ostojia, Schupp & Klinger 2012; Pearson *et al.* 2014a). However, fewer studies have demonstrated that granivory results in reduced exotic recruitment (Borchert & Jain 1978; Nuñez, Simberloff & Relva 2008; Pearson, Callaway & Maron 2011; Maron *et al.* 2012; Pearson, Potter & Maron 2012; Connolly, Pearson & Mack 2014; Pearson *et al.* 2014a,b) or adult plant abundance (Pearson, Potter & Maron 2012; Allington *et al.* 2013; Pearson *et al.*

2014b), or alternatively, that consumers disperse exotic seed, thereby facilitating invasion (Smith 1989).

Although seed predation on exotics can be inhibitory, it can sometimes have stronger effects on native than exotic recruitment (Maron *et al.* 2012). In perennial grasslands, Pearson, Callaway & Maron (2011) found that recruitment of larger seeded aster species was more strongly inhibited by rodent seed predation than that of smaller seeded asters (regardless of whether these species were native or exotic). However, the strongly invasive *Centaurea stoebe* did not fit this trend (Pearson, Callaway & Maron 2011). Although *C. stoebe*'s seeds were large enough to be targeted for predation, mice strongly avoided its seeds, resulting in this large-seeded invader escaping the seed size trade-off and gaining a strong recruitment advantage. In contrast, other large-seeded exotics were strongly suppressed in this system as predicted based on their seed size, and this effect resulted in long-term suppression of the population density of one large-seeded exotic (Pearson, Potter & Maron 2012). In a desert system, Allington *et al.* (2013) showed that the annual exotic, *Erodium cicutarium*, was kept in check for decades until a decline in granivore abundance and change in climate allowed it to become dominant. In central Argentina grasslands, ant seed predation was strongly biased against exotics relative to natives as predicted by size-dependent seed selection, a factor

contributing to the low invasibility of this system (Pearson *et al.* 2014a). These studies suggest that: (i) native seed predators can impose biotic resistance on a range of plant invaders, (ii) their effects can at least in-part be predicted by plant traits such as seed size and (iii) some invaders may increase their success by circumventing *in situ* filters (Table 1).

Seed predators can also reinforce patterns of invasion by differentially reducing recruitment of co-occurring native species (Table 1). For example, invading plants can provide cover that elevate rodent populations and correspondingly increase seed predation on native plants (Orrock, Witter & Reichman 2008; Dangremond, Pardini & Knight 2010), a process referred to as refuge-mediated apparent competition (Orrock, Holt & Baskett 2010). Seeds, fruit and insects associated with exotic species may also serve as food subsidies that boost native rodent populations and their corresponding impacts on native plant recruitment (Noonberg & Byers 2005; Pearson & Callaway 2008; Orrock *et al.* 2015b). In some cases, however, rodent populations do not respond to the increased cover of exotic species and as a result, their impacts remain unchanged (Bartowitz & Orrock 2016). Understanding how post-dispersal seed predators influence invasions ultimately relies on determining the relative magnitude with which seed predation suppresses recruitment and establishment of exotic vs. co-occurring native species (either through direct or indirect pathways), and also determining how the fate of native vs. exotic seeds that are cached rather than eaten influence plant establishment.

Key areas for future research

ASSESSING SEED FATE

Death due to predation is but one potential fate of seeds. Fully integrating the effects of generalist seed predators into plant community theory requires understanding how the magnitude of predation stacks up against other processes that influence the demography of seeds (Lichti, Steele & Swihart 2017). For example, seeds removed by bird or rodent predators can be cached, or ants can discard viable seeds at their nests. If these dispersed or cached seeds have a higher probability of germinating than seeds that are not removed by consumers, it could influence population and community dynamics and potentially negate the effects of seed predation. Some species clearly benefit from ant (Kjellsson 1991), rodent (Longland *et al.* 2001) or bird (Tella *et al.* 2016) dispersal. Yet, the process of caching creates additional filters to seed survival (Lichti, Steele & Swihart 2017), and discerning what fraction of dispersed or cached seeds germinate and how this compares to the fraction of non-dispersed seeds that germinate remains a poorly explored area of seed dynamics (but see Horvitz & Schemske 1994; Vander Wall 1994; Longland *et al.* 2001; Forget *et al.* 2005; Nicolai & Boeken 2012). Our understanding of seed fate is better for larger seeded

tree species, but in herbaceous systems where seeds tend to be smaller, following the movements and fates of dispersed seeds continues to be a major challenge (Levey & Sargent 2000; Forget & Wenny 2005). More studies assessing the relative impacts that both predation and dispersal of cached seeds have on plant dynamics are needed to fully account for the role that generalist seed predators play in plant community dynamics.

SEED PREDATION AS A MECHANISM OF COEXISTENCE

Despite the importance of seed size trade-offs to coexistence in the theoretical literature (Shmida & Ellner 1984; Tilman & Pacala 1993; Chesson 2000), empirical tests remain rare. The few existing studies have been restricted to annual grasslands (where controls on recruitment are likely different than in perennial systems) and have focused on seed size and number, to the exclusion of other traits (Rees 1995; Turnbull, Rees & Crawley 1999; Leishman 2001; Turnbull, Manley & Rees 2005; Chen & Valone *In Press*). Elucidating the factors that drive interspecific variation in the magnitude of recruitment requires: (i) evaluating how seed-limited recruitment varies with seed size and (ii) determining how seed predation and other interactions such as competition influence these recruitment functions. Finally, exploring how these factors change over natural gradients in the abiotic environment can shed light on how environmental factors influence recruitment of incoming species that vary in seed size and correlated traits. Although a subset of these elements are represented in a few studies (Mouquet *et al.* 2004; Turnbull *et al.* 2004; Turnbull, Manley & Rees 2005; Aicher, Larios & Suding 2011), no study to our knowledge has combined these approaches.

IMPROVING TRAIT-BASED PREDICTIONS OF COMMUNITY ASSEMBLY

Future research aimed at disentangling the relative contribution of seed predation vs. competition in affecting trait distributions will require moving beyond phenomenological approaches. Factorial experiments are needed to assess the relative importance of particular interactions to community assembly. Comparing the seed size distribution of a local plant assemblage in the presence and absence of seed predators to a null model is an important first step to assessing whether size biased seed predation and/or dispersal has a significant effect on the trait distribution of the community (de Bello 2012). Seed size may also be part of a broader syndrome of functional traits (such as SLA, plant height, water use efficiency, leaf nitrogen and carbon) spread across the life-history of a plant that represents an individual's ability to acquire resources vs. its ability to tolerate abiotic conditions, consumer pressure and competition (Grime 1977; Dalling *et al.* 2011; Seifan *et al.* 2013; Reich 2014). Other seed traits (e.g. seed coat thickness, secondary chemicals) in addition to seed size may similarly

influence seed predation, but their relative importance may be contingent on environmental context (Dalling *et al.* 2011; Paulsen *et al.* 2014). Therefore to ultimately determine the relative importance of the seed predation filter compared to other filters or to assess whether the seed predation filter may influence the inference of other assembly processes, future studies should additionally evaluate any potential trade-offs between seed size and resource use traits (Laughlin 2014).

Conclusion

This review, along with others (Crawley 1992, 2000, 2014; Hulme 1998; Moles & Westoby 2003), suggests that post-dispersal seed predation can have important consequences for plant populations and communities. Yet, generalist seed predator effects are poorly integrated into broader population and community theory. In part, this reflects a limited number of empirical studies that have directly linked the spatial and temporal sources of variation in seed predation to the longer term consequences of seed predation for plant abundance and community structure. Thus, future work needs to move beyond only quantifying seed removal and evaluate how abiotic conditions, plant community type and seed predator composition may interact with relative and absolute seed predator food preferences (e.g. via seed traits or seed density) to affect seedling recruitment and community composition. Integrating seed predators into predictions of species coexistence and community assembly requires more work discerning how density-dependent foraging vs. selective foraging strategies may act as or disrupt stabilizing mechanisms and shift trait distributions of plant communities. Advancing our understanding of the processes that regulate plant population and community structure requires that future research not only acknowledge but incorporate generalist consumer effects on plant communities.

Authors' contributions

L.L., D.E.P. and J.L.M. all contributed to the intellectual development of the manuscript, and all authors were involved in writing it.

Acknowledgements

We thank Phil Hahn, John Orrock, Marko Spasojevic, Lauren Waller and anonymous reviewers for constructive comments on the manuscript. L.L. was supported by the NSF Postdoctoral Research Fellowship in Biology Award #1309014.

Data accessibility

This manuscript does not use data.

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Received 26 January 2016; accepted 9 May 2017

Handling Editor: Alison Brody