Disentangling the drivers of context-dependent plant–animal interactions

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Summary

1. A fundamental goal of ecology is to predict how strongly one species affects the abundance of another. However, our ability to do so is hindered by the fact that interaction outcomes are notoriously variable in space and time (i.e. context-dependent) and we lack a predictive understanding of the factors that drive this context-dependence. Determining whether abiotic factors, in particular, predictably shift the outcome of species interactions is of critical importance for many contemporary problems, from forecasting climate change impacts to predicting the efficacy of weed biocontrol.

2. In this essay, we highlight the context-dependent nature of interactions between plants and their pollinators and herbivores. We advocate for approaches that will identify whether particular abiotic factors predictably shift how strongly these interactions influence plant abundance and/or population growth. We review long-standing theory that describes how abiotic context should influence the selective impacts of pollinators and herbivores on plants and articulate why this theory requires modification to predict population-level effects.

3. Finally, we propose several empirical approaches to address gaps in existing knowledge: (i) experiments across broad abiotic gradients to determine whether the outcome of interactions between pollinators or herbivores and plants varies consistently with changing abiotic conditions; (ii) experiments that manipulate the underlying environmental gradient to elucidate whether the abiotic factor that correlates with interaction outcome is causal; and (iii) seed addition studies to explore how strongly seedling recruitment correlates with seed input (as affected by pollen limitation or herbivory) and to quantify how the strength of the seed-to-seedling linkage is influenced by the underlying abiotic gradient.

4. *Synthesis*. Our understanding of the underlying drivers of context-dependent plant–animal interactions is currently not well developed. Progress in this area is essential to better predict when and where species interactions will alter the responses of plant populations to environmental changes as well as to develop more robust theory. Experiments aimed at explicitly exploring the role of abiotic factors in mediating the population-level impact of pollen limitation and herbivory could determine the extent to which variation in the abiotic environment predictably shifts the outcome of these interactions.

Key-words: context-dependence, herbivory, plant population abundance, plant–pollinator interactions, pollen limitation, range limits, seed limitation, species interactions

Introduction

Historically, much ecological research has focused on demonstrating how particular types of species interactions affect the distribution and abundance of plants. For example, exemplary field experiments have shown that plant abundance or population growth can be influenced by competitors (Fonteyn & Mahall 1981; Fowler 1981; Gurevitch 1986), herbivores (Louda 1982; Ehrlén 1995; Louda & Potvin 1995; Ehrlén

2003; Maron & Kauffman 2006; Miller *et al.* 2009), pathogens (Packer & Clay 2000; Mangan *et al.* 2010; Mordecai 2011), and pollinators (Herrera *et al.* 2002; Price *et al.* 2008; Horvitz, Ehrlén & Matlaga 2010). However, the outcome of these interactions (i.e. the magnitude of impact on plant fitness or abundance or population growth) can also be notoriously variable in space and time (MacGarvin, Lawton & Heads 1986; Bronstein 1994; Östergard & Ehrlén 2005; Maron & Crone 2006; Kolb, Ehrlén & Eriksson 2007; Horvitz, Ehrlén & Matlaga 2010; Chamberlain, Bronstein & Rudgers 2014). This spatiotemporal variation in interaction outcome is

often referred to as 'context-dependence,' because there is presumably some underlying factor that varies among sites or years (i.e. an element or attribute of 'context') that is responsible for determining how strongly the interaction affects plant fitness or abundance. Yet the abiotic or biotic factor that drives 'contingency' or 'context-dependence' and the mechanism by which it does so often is a mystery. More frequently than not, spatiotemporal variation in interaction outcome is viewed as noise. Answers to questions about the nature of variability in the outcome of species interactions have been slow to emerge, in-part because experiments are not typically constructed to identify whether a particular environmental attribute predictably produces context-dependence.

In this essay, we advocate for increased emphasis on understanding the underlying drivers of ubiquitous context-dependent effects of mutualist (pollinator) and antagonist (herbivore) partners on plant abundance and population growth. We particularly focus on impacts on plant abundance or population growth, as opposed to individual plant performance, because understanding controls on plant abundance and distribution is fundamental to ecology, yet much less attention has been given to how interactions affect population-level attributes compared with how interactions impose selection on traits and affect the fitness of individuals (Knight *et al.* 2005; Maron & Crone 2006). For example, while theory suggests that variation in environmental factors such as resource availability should influence the selective impacts of various biotic agents on plants (Coley, Bryant & Chapin 1985; Haig & Westoby 1988; Thompson 2005), we lack corresponding theory that considers how environmental variation (either in space or time) might modify how strongly pollinators or herbivores influence plant abundance or population growth. Empirically, understanding this issue is an increasingly pressing priority given current climate change scenarios.

We begin by discussing how determining the underlying drivers of context-dependent plant–animal interactions could lead to fundamental advancements in ecology. We then highlight empirical examples of context-dependent plant–pollinator and plant–herbivore interactions to both illustrate how commonly the outcome of these interactions vary in space or time and to show how poorly we understand the underlying drivers of this variation. We review some long-standing theory that explicitly predicts how underlying gradients in resource availability might influence the fitness impacts of pollinators and herbivores on plants, and suggest that modifications are necessary to predict population-level effects rather than solely fitness effects. Finally, we outline some empirical approaches that will further our understanding of which abiotic conditions drive context-dependent plant–animal interactions.

We focus particular attention on understanding how the abiotic environment might drive predictable variation in interaction outcome because of the increasing need to understand how changing climate might affect biotic interactions (HilleRisLambers *et al.* 2013). Here, we use 'abiotic environment' quite broadly to encompass gradients in light, temperature, precipitation, or other abiotic factors as well as how these abiotic components influence the availability of soil resources

(water and nutrients) to plants. Resource availability, and more broadly, productivity, are important because they play a central role in much of the theory we review.

Abiotic factors such as precipitation or nutrient availability could influence the outcome of plant–animal interactions via several routes (Fig. 1). First, because temperature, precipitation, and soil nutrient availability often play major roles in influencing overall plant community productivity, these factors can influence the number of pollinators and herbivores a system can support, and hence their collective impacts on plants (Fig. 1, arrow 1). These effects should be negative in less productive and more stressful sites (broken thin arrow 1 in Fig. 1a) but positive in more productive environments (i.e. more herbivores and pollinators; unbroken thick arrow 1 in Fig. 1b). Second, the abiotic environment can directly affect individual plant demographic components such as fecundity and survival (Fig. 1, arrow 2), again with these effects decreasing vital rates for most species in resource-poor locales (Fig. 1a, arrow 2) but enhancing vital rates in resource-rich sites (Fig. 1b, arrow 2). Variation in these vital rates can in turn influence the ability of individual plants to tolerate or compensate for herbivore damage. Additionally, by influencing the amount of energy plants have to allocate toward provisioning ovules and seeds, abiotic factors can affect the extent to which variation in pollen receipt alters seed production. Third, abiotic factors can directly influence the magnitude of seedling recruitment, negatively in more stressful locations (Fig. 1a, arrow 3) and positively in less stressful sites (Fig. 1b, arrow 3). However, at very high levels of productivity, safe-sites might limit recruitment (Fig. 2). If recruitment is severely constrained (Fig. 1a, arrow 3), reductions in seed production due to pollen limitation or herbivory may not be reflected in future recruitment (Fig. 1a, arrows 1, 4 & 5), and thus future plant abundance (Fig. 1a, arrow 6, Fig. 2). Finally, abiotic factors can also indirectly affect interaction outcomes by influencing the abundance of enemies of interacting partners, which could in-turn influence partner abundance. Thus, as Fig. 1 shows, the abiotic environment (broadly defined) can influence plant abundance via manifold routes, both through direct effects on plant demography and on interacting partners, and through indirect effects mediated by interactions (Adler, Dalgleish & Ellner 2012).

Despite the varied ways in which the abiotic environment might influence the outcome of biotic interactions, whether these effects are consistent enough to be predictable remains unclear. Experiments are not typically constructed to explicitly identify the drivers of context-dependence. Instead, experiments are often replicated across space or time to increase scope of inference, a goal that is frustrated frequently by context-dependent outcomes. Broad-scale studies aimed at understanding how the outcome of plant–animal interactions change across abiotic gradients could do much to enhance knowledge of the drivers of context-dependency while also shedding light on important problems in conservation biology. For example, the outcome of weed biocontrol is notoriously context-dependent (Huffaker & Kennett 1959; Syrett, Briese & Hoffmann 2000; Shea *et al.* 2005) and yet the environmen-
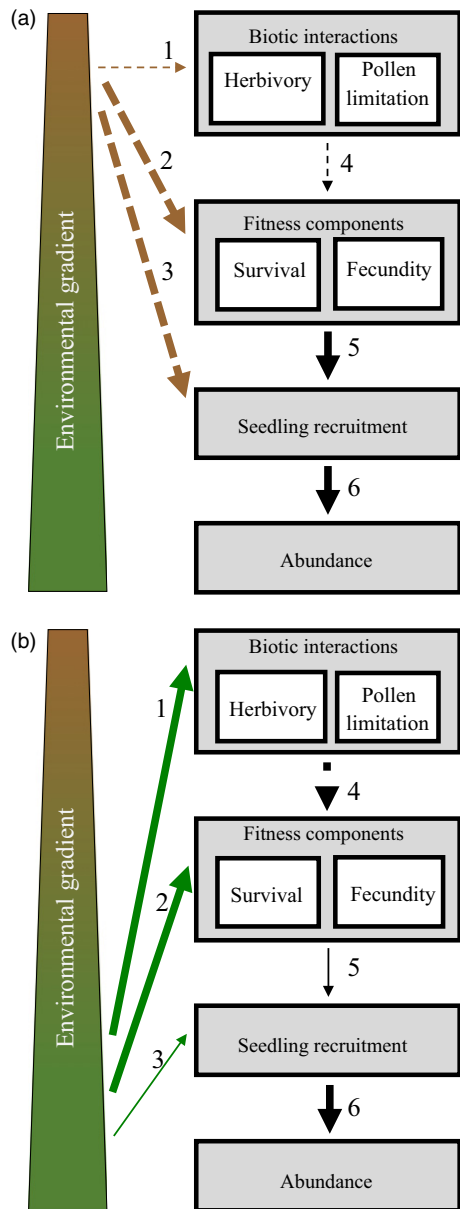
Fig. 1. Flow charts indicating how the environment can indirectly (via its influence on biotic interactions between plants, pollinators, and herbivores) and directly affect plant demography and abundance. Arrows represent causal relationships from one factor to another. Thicker arrows indicate stronger relationships. Solid arrows denote positive relationships, and dashed arrows denote negative relationships. Top panel (a) depicts relationships at the resource-poor end of an environmental gradient (e.g. dry, low nutrient, or cold), while bottom panel (b) depicts relationships at a resource-rich end of an environmental gradient (e.g. wet, high nutrient, or warm). Numbered arrows are referred to throughout the text to explain the rationale for the magnitude and sign of each relationship, as well as additional underlying complexities that are not depicted in these simple flow charts. For simplicity, we have left out how additional factors, such as the presence of a seed bank, or interspecific competition, might change relationships between seed production, recruitment, and plant abundance.

tal factors that might influence this context-dependence are often unclear. Understanding what environmental factors influence this context-dependence could help guide biocontrol
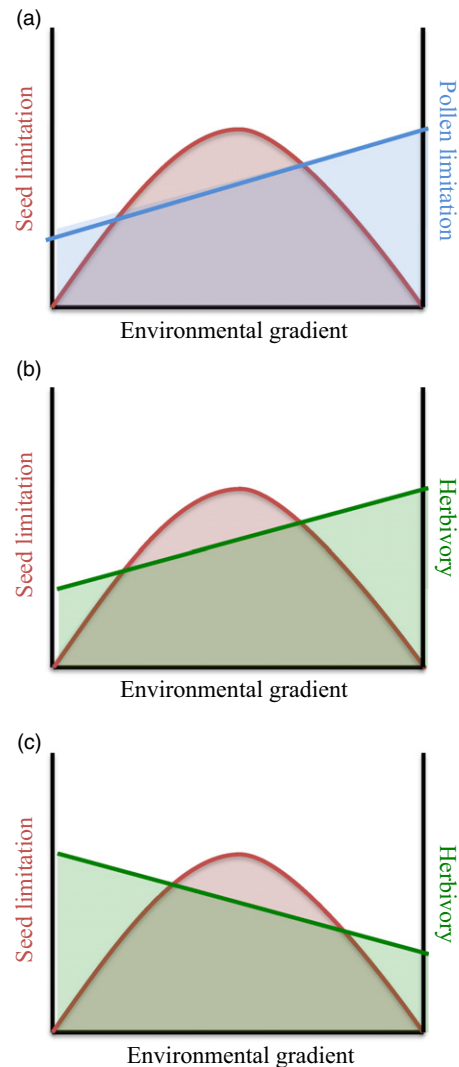

Fig. 2. Schematic diagrams illustrating possible relationships between plant–animal interactions and plant recruitment along an environmental gradient (e.g. a gradient in precipitation, nutrient availability, productivity, etc.). (a) Following predictions from Burd (2008), pollen limitation (blue) might increase with increasing levels of resource availability. Seed limitation (red) might peak at intermediate levels of resource availability. At low levels of resource availability (particularly precipitation), recruitment would be low due to abiotic constraints on recruitment, and even if more seeds were available, recruitment would not increase At high-resource levels, recruitment would be limited more by safe-sites than by seed inputs and similarly, even if more seeds were available, recruitment would not increase. Pollen limitation would constrain population growth where the red curve exceeds the blue curve because this is the zone where increases in seed production could translate to greater recruitment. The impacts of herbivory (green) might be greatest at low (b) or high (c) resource levels depending on how plant defense and tolerance influence the fitness effects of herbivory. Herbivory would constrain population growth where the red curves exceed the green curves. While these panels highlight the interplay between pollen limitation/herbivory and recruitment in determining where the population-level consequences of these interactions might be the greatest, in the strict sense what will determine impacts on population growth is both the magnitude of demographic effects of the interactions and the sensitivity of population growth to recruitment (which itself can be affected by both environmental conditions and other underlying vital rates).

introductions, and also inform management of weed populations so as to increase the probability of biocontrol success. An increased understanding of context-dependence also could help refine predictions about the responses of plant populations and communities to climate change. Currently, much attention has focused on predicting how geographic ranges of organisms might shift to higher latitudes and elevations given warming climate (Hill, Thomas & Huntley 1999; Parmesan 2006; Lenoir *et al.* 2008; Moritz *et al.* 2008; Tingley *et al.* 2009; Crimmins *et al.* 2011). Although climate alone is often viewed as the major determinant of both geographic range limits and range shifts (Woodward 1990; Archibold 2005), at local levels biotic interactions such as herbivory or limited pollen receipt may interact with climate to influence population growth at a range edge. In cases such as these, current niche-modeling efforts are unlikely to accurately forecast range-shift responses (Davis *et al.* 1998a,b; Araújo & Luoto 2007; Brooker *et al.* 2007; Heikkinen *et al.* 2007; Memmott *et al.* 2007; Thuiller *et al.* 2008; Tylianakis *et al.* 2008; Lavergne *et al.* 2010). Thus, enhancing fundamental knowledge of how abiotic conditions underpin the structure of biotic interactions (Martin & Maron 2012) will be of central importance in future efforts to determine species responses to climate change. Particularly needed is information about how climatic data such as precipitation and temperature, which are often incorporated into niche models, might modify the outcome of biotic interactions and so influence how plants respond to altered climate.

One area where substantial progress has been attained in understanding context-dependence is work on plant–plant facilitation. Much of the research on facilitation was motivated by the Stress Gradient hypothesis (Bertness & Callaway 1994), which posits that facilitative interactions should be more common in stressful environments, whereas competitive interactions should be increasingly common in more benign locales. Although there are exceptions to the general idea (Maestre, Valladares & Reynolds 2005; Lortie & Callaway 2006; He, Bertness & Altieri 2013), the hypothesis enjoys wide support (Callaway 2007; He, Bertness & Altieri 2013). In a recent meta-analysis of over 727 tests of the stress gradient hypothesis worldwide, there was broad empirical concordance with the hypothesis (He, Bertness & Altieri 2013). Explicitly incorporating 'context' into both theory and empirical work on facilitation has led to advancements in predicting when and where facilitative versus competitive interactions should be weak or strong. Although plant–pollinator and plant–herbivore interactions are more complex than plant–plant facilitation, the framework of study that we propose below will help elucidate the drivers of context-dependence in the outcome of these interactions.

Plant–pollinator interactions

For plants requiring pollination by animals, insufficient pollen delivery can result in suboptimal reproductive output (Burd 1994; Ashman *et al.* 2004; Knight *et al.* 2005), a condition known as pollen limitation. Pollen limitation is prevalent, and

because it can strongly influence plant vital rates it has the potential to influence plant abundance. Burd (1994) reviewed work on 285 plant species and found that 62% showed evidence of pollen limitation. In a review of 85 studies, Ashman *et al.* (2004) reported that pollen limitation was present in 73% of cases, and that amelioration of pollen limitation via pollen supplementation resulted in an average 42% increase in seed production. However, the extent to which pollen limitation constrains plant fitness and potentially plant abundance is notoriously variable (Burd 1994; Wilcock & Neiland 2002; Knight *et al.* 2005). For example, Vaughton (1991) showed that in *Banksia spinulosa* (*Proteaceae*), the results of pollen supplementation ranged from no effect in the first year of the study to a 114% gain in fruit set 2 years later. Similarly, Knight (2003) found that increases in seed set resulting from the amelioration of pollen limitation ranged from 0% to 30% for *Trillium grandiflorum*.

Many factors can influence the extent to which individuals suffer from pollen limitation. Biotic factors such as the density and spatial aggregation of plant populations (Kunin 1993; Aizen & Feinsinger 1994; Ågren 1996; Groom 1998; Wilcock & Jennings 1999; Aguilar *et al.* 2006), the identity of coflowering species (Groom 1998; Moeller 2004; Ghazoul 2006; Vamosi *et al.* 2006; Sargent & Ackerly 2008), and pollinator abundance (Baker, Barrett & Thompson 2000; Cunningham 2000; Cosacov, Nattero & Cocucci 2008; Gómez *et al.* 2010) have all been shown to influence the degree of pollen limitation. To the extent that abiotic factors influence plant density or the abundance of pollinators, variation in abiotic factors could drive variation in pollen limitation (Fig. 1, arrow 1; Moeller *et al.* 2012). Limited resources such as light, precipitation, and/or soil nutrients might also play a direct role in affecting pollen limitation. Greater resource availability may render plant reproduction pollen limited if this allows the plant to provision more ovules than those fertilized through pollen receipt (Fig. 1, arrow 2; Haig & Westoby 1988; Burd 2008). Although plant reproduction was traditionally thought to be either resource or pollen limited, it is now considered that the two often act in tandem to determine plant fecundity (Haig & Westoby 1988).

The ubiquity of pollen limitation appears at first glance to contrast with Haig & Westoby's (1988) main prediction that resource limitation plays an equally strong role in controlling seed production. It is important to note, however, that the Haig & Westoby model assumes no variation in either the degree of ovule fertilization (pollen receipt) resulting from the allocation of resources to pollinator attraction or the availability of resources for seed provisioning. Burd's (2008) model shows that when variation is present in pollinator attraction, only those plants at the high end of the distribution of pollen receipt and ovule fertilization will experience resource limitation of seed set; the remainder of the plants will be pollen limited. If there is a variation in both pollinator attraction and resources for seed provisioning, pollen limitation of seed set is expected to be compounded. These predictions help to reconcile the prevalence of pollen limitation observed in empirical studies with the Haig & Westoby model. More

specifically, the above arguments suggest that given similar amounts of variation in a pollinator community, pollen limitation should be greatest in high-resource environments (contrast arrow 4 in Fig. 1a vs. b), where resource constraints on fruit or seed production are greatly reduced (Fig. 2a).

While the Haig & Westoby (1988) and the Burd (2008) models predict how underlying resources influence the extent to which pollen limitation influences individual plant fecundity, theory regarding the conditions under which these individual-level effects might translate to meaningful population-level impacts is still lacking. Empirically, we know that in some cases reductions in plant fitness caused by pollen limitation can limit future plant abundance and/or population growth (Bierzychudek 1982; Parker 1997; Price *et al.* 2008; Horvitz, Ehrlén & Matlaga 2010). However, complexities such as costs of reproduction (Ehrlén & Eriksson 1995), seed bank dynamics and recruitment from dormant seed, compensatory density-dependent seedling recruitment (Kauffman & Maron 2006; Feldman & Morris 2011), and temporal lags in environmental effects (Burkle & Irwin 2009) have great potential to decouple fitness effects from population-level impacts. These complexities have not yet been incorporated into theory that can help predict when and where the population-level consequences of pollen limitation might be weak or strong.

One avenue for progress might be to explore whether variation in the abiotic environment, particularly resource availability, affects the strength of demographic compensation in ways that dampen or magnify the role that resource availability plays in pollen limitation. For example, Jacquemyn, Brys & Jongejans (2010) found that costs of reproduction were negligible in a high-light environment but had significant effects on population growth in a shaded understorey environment for the tuberous perennial orchid *Orchis purpurea*. For heuristic purposes, if we extend this example to the hypothetical case of pollen limitation, we would predict that pollen limitation would be more likely to constrain population growth in the high-light environment, where costs of increased reproduction would be minimal, but not in the low-light environment. On the other hand, resource gradients could counteract the effects of pollen limitation if population growth is less sensitive to seed input when resources are high. In resource-rich environments, overall plant community productivity is typically higher, which can cause plant recruitment to be limited more by safe-sites than by seeds (Harper 1977). This suggests that pollen limitation might suppress population growth most strongly at intermediate resource levels (Fig. 2a).

Where deteriorating abiotic conditions shift the impacts of pollen limitation toward negative population growth rates, this could play a strong role in setting range edges. For example, both Eckhart *et al.* (2011) and Moeller *et al.* (2012) showed that the annual herb, gunsight clarkia (*Clarkia xantiana ssp. xantiana*), experiences significantly higher pollen limitation at its eastern range edge than in range center populations. Reductions in seed set due to pollen limitation cause the population growth of *C. xantiana* to be negative (i.e. λ < 1) in populations at its extreme range edge (Eckhart *et al.* 2011).

Declining rainfall from the range center to the range edge influences the timing of bee emergence and bee population size, which then drives increased pollen limitation at the range edge (Moeller *et al.* 2012). However, in other work examining range-wide patterns of pollen limitation in a narrow endemic, Fernández *et al.* (2012) found that *increased rainfall was correlated with greater pollen limitation*. They speculated that this was likely because plants growing in dry sites were resource limited, and therefore unable to respond to supplementary pollen additions. This latter example squares nicely with the predictions outlined in Haig & Westoby's (1988) optimality model as discussed below.

Plant–herbivore interactions

While debated in the past (Hairston, Smith & Slobodkin 1960; Jermy 1984), it is now appreciated that consumers (i.e. herbivores of all types, including seed predators) can have strong and pervasive negative impacts on plant fitness (Crawley 1989, 1990; Hunter & Price 1992; Marquis 1992; Ehrlén 2003; Maron & Crone 2006; Kolb, Ehrlén & Eriksson 2007). However, as with pollen limitation, these negative fitness effects can be quite variable in magnitude. Biotic factors, such as the presence or absence of predators (Beckerman, Uriarte & Schmitz 1997; Schoener & Spiller 1999; Letourneau, Dyer & Vega 2004), the identity of plant neighbors (Barbosa *et al.* 2009), and the density of conspecifics (Parker & Salzman 1985; Cottam, Whittaker & Malloch 1986; Fagan *et al.* 2005) can all influence the extent to which herbivores affect plant performance. Herbivory can also vary strongly due to variation in abiotic factors such as sunlight (Harrison 1987; Louda & Collinge 1992; Ågren, Ehrlén & Solbreck 2008) and precipitation (Ågren, Ehrlén & Solbreck 2008; Louthan *et al.* 2013; Rodríguez-Castañeda 2013). However, it is not straightforward to make generalizations about how variation in the abiotic environment influences herbivore impacts on plant performance.

Several prominent theories posit how particular abiotic conditions might drive variability in the selective effects of herbivores on plants, but these predictions can be contradictory. For example, Coley, Bryant & Chapin's (1985) Resource Availability hypothesis predicts that low-resource environments should select for plants that have slow growth rates and that this should favor the evolution of high investment in defense because the costs of re-growing tissue lost to herbivores in these environments are high. In high-resource environments where plant growth rates are inherently higher, this hypothesis predicts species should evolve lower (less costly) defenses, since high-resource availability allows plants to tolerate herbivory. This suggests that plants with high growth rates in high-resource environments should suffer higher levels of herbivory than species with lower growth rates (Fig. 1b, arrow 1; Fig. 2b; Fine, Mesones & Coley 2004; Blumenthal 2006). A recent meta-analysis that examined support for this hypothesis found that fast-growing plants invested less in constitutive defenses than did plants adapted to low-resource environments and within the same sites, fast-

growing species generally suffered higher levels of herbivore damage than did slow-growing species (Endara & Coley 2011).

In contrast, Maschinski & Whitham's (1989) Compensatory Continuum model and the Plant Stress hypothesis (White 1969; Rhoades 1983) posit that plants growing in less productive/more stressful habitats should be limited in their ability to compensate for herbivore damage (Compensatory Continuum model) or be more subject to insect outbreaks because of stressful conditions (Plant Stress hypothesis). This implies that the fitness impacts of herbivores should be greater in low-resource versus high-resource environments (in contrast to what is depicted in Fig. 1a, arrow 1; Fig. 2c). Although monocots generally are able to better compensate for herbivore damage in high- versus low-resource environments, the same has not been found for dicots (Hawkes & Sullivan 2001), which has led to modifications of the Compensatory Continuum model (Wise & Abrahamson 2005).

When and where might the negative impacts of consumers on plant fitness/performance translate to reductions in future plant abundance or population growth? Both empirically and theoretically, this question remains open. In a review of 30 studies where population-level consequences of herbivory were assessed, Maron & Crone (2006) found that reductions in seed production due to herbivory appear to have greater consequences for plant abundance in open vs. more vegetated habitats. Maron & Crone (2006) speculated that this outcome was probably due to the fact that the link between seed input and subsequent seedling recruitment is stronger in open habitats compared with heavily vegetated sites, where recruitment can be more influenced by the availability of safe-microsites rather than seeds (Fig. 2b). Yet, whether this and other associations between particular environmental factors and the population impacts of herbivory are casual is not known.

In terms of theory, hypotheses about plant defense or tolerance do not translate easily to making predictions about the impacts of herbivory on plant population abundance across resource gradients. For example, Coley, Bryant & Chapin's (1985) hypothesis is based on how resources shape the evolution of plant growth rates, and by consequence, plant defense. It is meant to make sense of interspecific variation in plant defense, although it might apply intraspecifically in some cases (Fine *et al.* 2013). And while the Compensatory Continuum model predicts how plant tolerance might be influenced by underlying resource gradients, for particular types of herbivory (e.g. pre-dispersal seed predation that occurs later in a growing season), plants may have minimal scope for within-season compensatory growth responses, and thus plant defense may better control herbivore damage than tolerance. Thus, unlike Haig & Westoby's (1988) model for pollination, there is no clear consensus in the plant defense/tolerance literature about how underlying abiotic conditions should influence the strength of consumer impacts within species. Another major difficulty in extending existing hypotheses regarding plant tolerance or defense to population-level responses to herbivory is that even if resource availability pre-dicts the fitness impacts of herbivores on plants, how strongly net decrements in fitness translate to altered plant abundance in the next generation, as influenced by resources, is unclear. As described previously, in resource-rich and therefore productive environments, plant recruitment might be more limited by safe-sites rather than seeds. Alternatively, in extremely resource-poor environments, successful recruitment might be minimal, which could also decouple impacts of herbivores on plant reproduction from future recruitment (Fig. 2b,c). Furthermore, there might be time lags between years when herbivory is intense and when these effects are manifest at the population level. In sum, the influence of abiotic factors, such as resource availability (or climatic variables), on the population-level consequences of herbivory involves the interplay of not only how abiotic conditions influence fitness impacts of herbivores on individual plants but also how those gradients influence plant recruitment and the sensitivities of population growth to altered vital rates (Figs 1, 2b,c). More broadly, making predictions about the net demographic impacts of herbivory is more complicated than for the case of pollen limitation because: (i) there are not consistent predictions about how the fitness impacts of herbivory should vary across abiotic gradients; (ii) herbivory can directly affect multiple vital rates, such as growth and survival as well as fecundity, unlike pollen limitation (because herbivores attack multiple tissue types and plant tissues that vary in age); and (iii) herbivores vary widely in body size (from insects to elephants) which can influence the amount of plant tissue that is damaged and the mode of damage. This makes herbivory an inherently more heterogeneous type of interaction compared with those between plants and their pollinators. Regardless of the underlying complexity of plant–pollinator or plant–herbivore interactions, studies that manipulate the strength of these interactions or the abiotic environment in which they occur will serve as an essential first step toward a greater understanding of the drivers of context-dependency and an enhanced ability to predict the abiotic conditions under which these interactions are expected to have significant population-level impacts.

Future directions

Experiments are often replicated across space and time to obtain a robust estimate of the mean strength of an interaction, and to generalize results across sites and years. But faced with spatial or temporal variability in the outcome of interactions, we often lack strong inference as to what drives this variability. This issue was addressed almost 20 years ago with the Stress Gradient hypothesis (Bertness & Callaway 1994) and advanced by theory related to other context-dependent interactions before that (Menge & Sutherland 1987; Menge & Olson 1990). However, it is as relevant today as it was then. Progress in building a more predictive framework for understanding the abiotic drivers of context-dependence in plant–pollinator or plant–herbivore interactions could be enhanced by two parallel approaches, which we outline below.

EXPERIMENTS TO DETERMINE WHETHER
ENVIRONMENTAL VARIABILITY DRIVES PREDICTABLE
CHANGES IN THE STRENGTH OF PLANT–POLLINATOR
AND PLANT–HERBIVORE INTERACTIONS

Clearly needed are experiments that supplement pollen or
suppress herbivores across gradients in the abiotic environ-
ment. While this may seem obvious, it remains underutilized
(but see Miller *et al.* 2009; Louthan *et al.* 2013; McLaughlin
& Zavaleta 2013; von Euler, Ågren & Ehrlén 2014). Con-
ducting experiments across abiotic gradients is not without
challenges, however. These include the fact that experimental
manipulations must occur across broad spatial scales so that
some underlying gradient in an important abiotic axis is cap-
tured, and transects across an environmental gradient require
replication. Finally, manipulations themselves must be under-
taken with care. Ideally, pollen supplementation should be
conducted across all flowers on a plant (and for perennial
plants across multiple years) so that resource reallocation does
not lead to overestimates of the magnitude of pollen limita-
tion (Knight *et al.* 2005). In situations where this is infeasi-
ble, it is still possible to conduct meaningful partial
supplementations if they are designed to reveal effects of
plant architecture (i.e. flower position within the plant) and
phenology on responses to the supplementation treatment
(Wesselingh 2007). Similar considerations apply to herbivore
suppression experiments on perennial plant species.

While much could be learned from conducting pollen sup-
plementation and herbivore suppression experiments across
environmental gradients, simple monitoring of plant demogra-
phy through time and across abiotic gradients can also be
valuable, for several reasons. First, in many cases, it is
unclear how specific components of environmental variation
influence particular plant vital rates. This has been under-
scored by recent calls for studies of the demography of spe-
cies across large environmental gradients as a way to gain
much needed insight into how species might respond to glo-
bal climate change (Ibáñez *et al.* 2013). Thus, examining vital
rates across strong abiotic gradients can shed light on how
the abiotic factor that varies across space influences particular
plant vital rates (i.e. identifying the thickness of arrows 2 and
3, Fig. 1). Indeed, much of what we know about environmen-
tal drivers of plant demography come from long-term and
large-scale datasets examining correlations between nutrient
and water availability (through space and/or time) and plant
vital rates (Schleuning, Huaman & Matthies 2008; Dahlgren
& Ehrlén 2009; Toräng, Ehrlén & Ågren 2010; Adler, Dalgle-
ish & Ellner 2012; Salguero-Gómez *et al.* 2012; von Euler,
Ågren & Ehrlén 2014). Second, multi-year demographic study
coupled with experiments examining the outcome of plant–
animal interactions across replicated environmental gradients
could enable one to examine how the gradient directly influ-
ences key plant demographic rates (that in themselves could
affect plant abundance or population growth; Fig. 1, arrows 2
and 3) and assess whether the outcome of plant–animal inter-
actions varies predictably across the gradient (Fig. 1, arrows
1, 4, 5, and 6). Finally, this dual approach enables one to

combine demographic information with experimental results
within an analytical framework of stage-based matrix model-
ing to forecast how the population-level consequence of pol-
len limitation or herbivory might vary due to an underlying
abiotic factor (see Maron, Horvitz & Williams 2010 for more
discussion of this approach).

Beyond understanding how environmental drivers might
influence particular plant demographic transitions, there is a
clear need to determine how these abiotic effects mediate the
impacts of interacting species on plant performance (but see
Pascarella & Horvitz 1998; Dahlgren & Ehrlén 2011; von
Euler, Ågren & Ehrlén 2014). If the outcome of an interaction
varies consistently across a strong environmental gradient, it
provides clues that underlying abiotic factors that varies spa-
tially may play an important role in mediating interaction out-
come (Anderson, Ritchie & McNaughton 2007). Another
advantage of studying an interaction across a predictable envi-
ronmental gradient is that it also enables one to determine
whether there are non-linearities or threshold effects in how
underlying abiotic factors determine interaction outcomes.
Such non-linearities are being revealed in how plant facilita-
tive interactions change across elevational gradients (Callaway
et al. 2002; Kawai & Tokeshi 2007; Levenbach 2009; le
Roux & McGeoch 2010). A final advantage of explicitly
examining the strength of pollen limitation or the impact of
herbivory on plants across environmental gradients is that it
would shed light on how strongly resource abundance pre-
dicts fitness effects of these interactions. Both plant–pollinator
and plant–herbivore theories suggest that underlying resource
availability should mediate the strength of plant-animal inter-
actions (Haig & Westoby 1988; Maschinski & Whitham
1989). Yet, direct tests of these predictions using the same
focal plant species are not common.

As a complement to experimental manipulation of species
interactions along environmental gradients, we also advocate
experiments manipulating abiotic factors to determine the
effects on the outcome of an interaction. Thus, rather than
correlating interaction outcomes with variables such as pro-
ductivity, this methodology would test whether the underlying
environmental variation (perhaps precipitation, as it influences
productivity) was causative. This approach addresses a major
statistical difficulty with observational studies along gradients,
namely determining which of several correlated environmental
variables are causal to affecting interaction outcomes. How-
ever, a major challenge here is manipulating the environment
on the appropriate spatial scale. For example, adding water to
focal plants could help assess how resource availability influ-
ences fitness effects of herbivory or pollination. However, in
nature, resource availability might also determine herbivore or
pollinator abundance at a much larger spatial scale, which
would contribute to the overall interaction outcome. Further-
more, changes in productivity could also influence levels of
competition among plants as well as competition for safe-sites
for recruitment. Although it may not be logistically feasible to
manipulate environmental conditions in ways that influence
the abundance of interacting partners, resource addition exper-

iments could be conducted at scales large enough to mimic natural variation in resource availability as it influences focal plant neighborhoods.

LINKING IMPACTS OF POLLEN LIMITATION OR HERBIVORY ON PLANT PERFORMANCE TO LONGER-TERM EFFECTS ON POPULATION ABUNDANCE OR POPULATION GROWTH

As this review suggests, considerable research has centered on understanding when and where the selective effects of pollinators and/or herbivores should be weak or strong. Yet, we lack theory and empirical work aimed at enhancing understanding of the drivers of variation in the population-level impacts of plant–animal interactions (Gripenberg & Roslin 2007). To make progress in this area, it is essential to determine whether environmental gradients that influence plant–animal interactions have amplifying or dampening effects on other aspects of plant demography. In particular, it is critical to determine how environmental gradients that affect the strength of plant–animal interactions on plant fecundity also influence plant recruitment. If recruitment varies across environmental gradients differently than impacts of interactions on plant fecundity do, then the overall effects of an interaction on plant abundance and population dynamics cannot be predicted based solely on the fitness impacts of the interaction (Fig. 2). This is because the population-level impacts of an interaction depend on both the magnitude with which it influences key demographic components (such as fecundity) and the relative importance of those demographic components to future population growth (i.e. elasticities). As variation in the magnitude of recruitment can greatly influence the elasticity of the seed-to-seedling demographic transition, it is important to understand both how environmental variation influences the fitness impacts of plant–animal interactions and how this translates to recruitment into populations. For example, Ashman *et al.* (2004) found that variation among studies in how strongly pollen limitation influenced plant population growth was a function of both the magnitude of pollen limitation and the elasticity values for fecundity and seed–seedling transitions. More recently, von Euler, Ågren & Ehrlén (2014) found that seed predation, as well as the sensitivity of plant population growth to seed predation, strongly co-varied across environmental gradients in soil depth and soil moisture.

These considerations suggest that fully understanding how environmental context influences the population-level impacts of an interaction requires experiments that explore how changes in abiotic conditions shift (i) the magnitude with which a particular interaction influences plant demography and (ii) the sensitivities of population growth to demographic transitions. Understanding environmental controls on seedling recruitment, in particular, is a key to determining how variation in seed production, as influenced by pollen limitation or herbivory, translates to numbers of individuals in the next generation. Toward this end, seed addition experiments can be extremely valuable in helping determine the magnitude of seed versus safe-site limitation in plant populations (Turnbull,

Crawley & Rees 2000; Clark *et al.* 2007), and they have a long history in plant ecology (Harper 1977). These experiments can help shed light on how variation in seed production, and the quality of seed produced, as influenced by mutualists or antagonists, may or may not translate to variation in recruitment and future plant abundance (i.e. quantifying the thickness of arrows 5 and 6, Fig. 1; see e.g. Louda 1995; Bricker & Maron 2012 of this approach). An ideal design would involve seed additions at locations across an environmental gradient. At each location, seeds would be added to plots in a manner that would span the range of seed rain densities produced by individual plants in the presence and absence of an interacting partner. Control plots with no seeds added would assess whether there is any recruitment out of an existing seed bank. If, for example, protecting plants from herbivores results in a doubling of plant seed set, seed addition experiments can test how this increase in seed production might influence recruitment and adult plant establishment. An added benefit of adding a graded series of seed densities to plots is that it enables a full characterization of the recruitment function, and also provides insight into the degree to which density-dependent seedling survival might be compensatory (Maron & Gardner 2000; Poulsen *et al.* 2007).

Seed addition experiments need to be designed carefully, however, to avoid several potential pitfalls, as discussed by Louda (1995). Specifically, seed addition plots should: (i) be located within the seed shadow of focal plants to adequately sample sites where seeds would naturally land, (ii) sample the range of background vegetation conditions to adequately sample local variation in how competition might influence recruitment, (iii) receive appropriate densities of seeds so as not to provide an unnaturally dense food resource for granivores, and (iv) receive seeds in a temporal manner that approximates the natural timing of seed rain so that seeds are not added all at once as one large bolus to plots. Additionally, if low seed densities are meant to mimic seed input for plants attacked by consumers, whereas high seed input is meant to mimic herbivore-free plants (or plants that do not suffer from pollen limitation), then seeds added to low- versus high-density plots should come from plants exposed and protected from herbivores, respectively. This enables one to manipulate consumer impacts on both seed quality and quantity and examine how these two components simultaneously might influence the magnitude of seedling recruitment.

We know from long-term seed sowing experiments that there can be substantial variability in seedling establishment among sites and years (Ehrlén *et al.* 2006). As such, performing seed sowing experiments across environmental gradients can help provide insight into whether there are strong correlations between particular environmental components and seedling recruitment. More importantly, such experiments would allow for a determination of how environmental variation in the impacts of an interaction on plant fecundity or survival might differentially act on recruitment.

In general, there are two approaches that can be used to scale up from the kinds of manipulations described above to determine the strength with which pollen limitation or herbiv-

ory influences long-term plant abundance. The first way is to conduct long-term experiments that manipulate herbivory and pollen receipt and empirically examine how this influences recruitment and future plant abundance. An advantage of this approach is that one can quantify the strength of compensatory mechanisms, such as density-dependence, in ameliorating any initial effects of pollen limitation or herbivory on plant recruitment (see Louda & Potvin 1995 for an excellent example of this methodology). The difficulty with this approach is that for long-lived plants (or those that have a long-lived seed bank), it is not usually logistically possible to conduct an experiment long enough to document how suppression of herbivores or supplemental pollen affects plant abundance across multiple plant generations. Thus, the second approach is to combine experimental results and demographic data in stage-based population models to forecast how herbivory or pollen limitation might influence transient or long-term plant population growth. It is important to recognize that while this approach has traditionally ignored density-dependence, this need not be the case (Halpern & Underwood 2006). One advantage of this methodology is that one can determine how particular demographic components influence population growth. Combining experiments, demography and population models, as advocated by Maron, Horvitz & Williams (2010), remains underutilized but is potentially powerful. If experimental manipulations of abiotic drivers are conducted across large-scale climatic gradients, it should be possible to parameterize variation in vital rates as functions of key abiotic drivers such as temperature and precipitation (Gornish 2014) and then project changes in population growth under future climate change scenarios (see e.g. Doak & Morris 2010 for climate-driven population projections using observational data). When crossed with experimental manipulations of pollen limitation or herbivory across the same climatic gradient, these projections could quantify how species interactions have the potential to modify the impacts of climate change on abundance across environmental gradients.

Conclusions

Several challenges remain in advancing understanding of what drives context-dependent plant–pollinator and plant–herbivore interactions. First, our knowledge of context-dependency would be strengthened by an increased number of experiments across strong environmental gradients, regardless of whether these gradients occurred at the local or regional scale. One benefit of this approach, particularly in studies across regional scales, is that it would enhance our ability to predict how biotic interactions might change given changing climate. Second, while there is ample theory that suggests that the selective effects of pollinators and herbivores should vary strongly across environmental gradients, it is unclear how this theory translates to predicting population-level impacts. Thus, development of theoretical models that predict how environmental conditions either couple or decouple fitness impacts of interactions to population-level effects would be quite useful. Finally, by empirically examining the congruence or incongruence in

the impacts of environment on interactions and seedling recruitment, we can begin to understand when and where plant abundance should be most limited by herbivory or pollen limitation. The basic approach we have advocated should be applicable to understanding the drivers of context-dependence in other interactions as well, whether these be antagonistic ones such as interspecific plant–plant competition, or beneficial ones such as those that involve plants and mycorrhizal fungi.

References

Adler, P.B., Dalgleish, H.J. & Ellner, S.P. (2012) Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *Journal of Ecology*, **100**, 478–487.
Ågren, J. (1996) Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology*, **77**, 1779–1790.
Ågren, J., Ehrlén, J. & Solbreck, C. (2008) Spatio-temporal variation in fruit production and seed predation in a perennial herb influenced by habitat quality and population size. *Journal of Ecology*, **96**, 334–345.
Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M.A. (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters*, **9**, 968–980.
Aizen, M.A. & Feinsinger, P. (1994) Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology*, **75**, 330–351.
Anderson, T.M., Ritchie, M.E. & McNaughton, S.J. (2007) Rainfall and soils modify plant community response to grazing in Serengeti National Park. *Ecology*, **88**, 1191–1201.
Araújo, M.B. & Luoto, M. (2007) The importance of biotic interactions for modeling species distributions under climate change. *Global Ecology and Biogeography*, **16**, 743–753.
Archibold, O.W. (2005) *Ecology of World Vegetation*. Chapman & Hall, London.
Ashman, T.L., Knight, T.M., Steets, J.A., Amarasekare, P., Burd, M., Campbell, D.R. *et al.* (2004) Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology*, **85**, 2408–2421.
Baker, A.M., Barrett, S.C.H. & Thompson, J.D. (2000) Variation of pollen limitation in the early flowering Mediterranean geophyte *Narcissus assoanus* (Amaryllidaceae). *Oecologia*, **124**, 529–535.
Barbosa, P., Hines, J., Kaplan, I., Martinson, H., Szczepaniec, A. & Szendrei, Z. (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. *Annual Review of Ecology, Evolution, & Systematics*, **40**, 1–20.
Beckerman, A.P., Uriarte, M. & Schmitz, O.J. (1997) Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences USA*, **94**, 10735–10738.
Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.
Bierzychudek, P. (1982) The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecological Monographs*, **52**, 335–351.
Blumenthal, D.M. (2006) Interactions between resource availability and enemy release in plant invasion. *Ecology Letters*, **9**, 887–895.
Bricker, M. & Maron, J.L. (2012) Seed predation lowers population growth rate in a long-lived perennial forb (*Lithospermum ruderale*). *Ecology*, **93**, 532–543.
Bronstein, J.L. (1994) Conditional outcomes in mutualistic interactions. *Trends in Ecology & Evolution*, **9**, 214–217.
Brooker, R.W., Travis, J.M.J., Clark, E.J. & Dytham, C. (2007) Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of Theoretical Biology*, **245**, 59–65.
Burd, M. (1994) Bateman principle and plant reproduction – the role of pollen limitation in fruit and seed set. *Botanical Review*, **60**, 83–139.
Burd, M. (2008) The Haig-Westoby model revisited. *American Naturalist*, **171**, 400–404.

Burkle, L.A. & Irwin, R.E. (2009) The effects of nutrient addition on floral characters and pollination in two subalpine plants, *Ipomopsis aggregata* and *Linum lewisii*. *Plant Ecology*, **203**, 83–98.

Callaway, R.M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Springer, Dordrecht.

Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R. *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.

Chamberlain, S.A., Bronstein, J.L. & Rudgers, J.A. (2014) How context dependent are species interactions? *Ecology Letters*, **17**, 881–890.

Clark, C.J., Poulsen, J.R., Levey, D.J. & Osenberg, C.W. (2007) Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist*, **170**, 128–142.

Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985) Resource availability and plant antiherbivore defense. *Science*, **230**, 895–899.

Cosacov, A., Nattero, J. & Cocucci, A.A. (2008) Variation of pollinator assemblages and pollen limitation in a locally specialized system: the oil-producing *Nierembergia linariifolia* (Solanaceae). *Annals of Botany*, **102**, 723–734.

Cottam, D.A., Whittaker, J.B. & Malloch, J.C. (1986) The effects of chrysomelid beetle grazing and plant competition on the growth of *Rumex obtusifolius*. *Oecolgia*, **70**, 452–456.

Crawley, M.J. (1989) Insect herbivores and plant population dynamics. *Annual Review of Entomology*, **34**, 531–564.

Crawley, M.J. (1990) The population dynamics of plants. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **330**, 125–140.

Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzaglou, J.T. & Mynsberge, A.R. (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, **331**, 324–327.

Cunningham, S.A. (2000) Depressed pollination in habitat fragments causes low fruit set. *Proceedings of the Royal Society of London B*, **267**, 1149–1152.

Dahlgren, J.P. & Ehrlén, J. (2009) Linking environmental variation to population dynamics of a forest herb. *Journal of Ecology*, **97**, 666–674.

Dahlgren, J.P. & Ehrlén, J. (2011) Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. *Oikos*, **120**, 1183–1190.

Davis, A.J., Lawton, J.H., Shorrocks, B. & Jenkinson, L.S. (1998a) Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology*, **67**, 600–612.

Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998b) Making mistakes when predicting shifts in species range in responses to global warming. *Nature*, **391**, 783–786.

Doak, D.F. & Morris, W.F. (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature*, **487**, 959–962.

Eckhart, V.M., Geber, M.A., Morris, W.F., Fabio, E.S., Tiffin, P. & Moeller, D.A. (2011) The geography of demography: long-term demographic studies and species distribution models reveal a species boarder limited by adaptation. *American Naturalist*, **178**, S26–S43.

Ehrlén, J. (1995) Demography of the perennial herb *Lathyrus vernus*. II. Herbivory and population dynamics. *Journal of Ecology*, **83**, 297–308.

Ehrlén, J. (2003) Fitness components versus total demographic effects: evaluating herbivore impacts on a perennial herb. *American Naturalist*, **162**, 798–810.

Ehrlén, J. & Eriksson, O. (1995) Pollen limitation and population growth in a herbaceous perennial legume. *Ecology*, **76**, 652–656.

Ehrlén, J., Münzbergova, Z., Kiekmann, M. & Eriksson, O. (2006) Long-term assessment of seed limitation in plants: results from a 11-year experiment. *Journal of Ecology*, **94**, 1224–1232.

Endara, M.-J. & Coley, P.D. (2011) The resource availability hypothesis revisited: a meta-analysis. *Functional Ecology*, **25**, 389–398.

von Euler, T., Ågren, J. & Ehrlén, J. (2014) Environmental context influences both the intensity of seed predation and plant demographic sensitivity to attack. *Ecology*, **95**, 495–504.

Fagan, W.F., Lewis, M., Neubert, M.G., Aumann, C., Apple, J.L. & Bishop, J.G. (2005) When can herbivores slow or reverse the spread of an invading plant? A test case from Mount St. Helens. *American Naturalist*, **166**, 669–685.

Feldman, T.S. & Morris, W.F. (2011) Higher survival at low density counteracts lower fecundity to obviate Allee effects in a perennial plant. *Journal of Ecology*, **99**, 1162–1170.

Fernández, J.D., Bosch, J., Nieto-Ariza, B. & Gómez, J.M. (2012) Pollen limitation in a narrow endemic plant: geographical variation and driving factors. *Oecologia*, **170**, 421–431.

Fine, P.V.A., Mesones, I. & Coley, P.D. (2004) Herbivores promote habitat specialization by trees in Amazonian forests. *Science*, **305**, 663–665.

Fine, P.V.A., Metz, M.R., Lokvam, J., Mesones, I., Zuñiga, J.M.A., Lamarre, G.P.A., Pilco, M.V. & Baraloto, C. (2013) Insect herbivores, chemical innovation, and the evolution of habitat specialization in Amazonian tress. *Ecology*, **94**, 1764–1775.

Fonteyn, P.J. & Mahall, B.E. (1981) An experimental analysis of structure in a desert plant community. *Journal of Ecology*, **69**, 883–896.

Fowler, N. (1981) Competition and coexistence in a North Carolina grassland. II. The effects of the experimental removal of species. *Journal of Ecology*, **69**, 843–854.

Ghazoul, J. (2006) Floral diversity and the facilitation of pollination. *Journal of Ecology*, **94**, 295–304.

Gómez, J.M., Abdelaziz, M., Lorite, J., Muñoz-Pajares, A.J. & Perfectti, F. (2010) Changes in pollinator fauna cause spatial variation in pollen limitation. *Journal of Ecology*, **98**, 1243–1252.

Gornish, E.S. (2014) Demographic effects of warming, elevated soil nitrogen and thinning on the colonization of a perennial plant. *Population Ecology*, doi: 10.1007/s10144-014-0442-5.

Gripenberg, S. & Roslin, T. (2007) Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. *Oikos*, **116**, 181–188.

Groom, M.J. (1998) Allee effects limit population viability of an annual plant. *American Naturalist*, **151**, 487–496.

Gurevitch, J. (1986) Competition and the local distribution of the grass *Stipa neomexicana*. *Ecology*, **67**, 46–57.

Haig, D. & Westoby, M. (1988) On limits to seed production. *American Naturalist*, **131**, 757–759.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960) Community structure, population control, and competition. *American Naturalist*, **94**, 421–425.

Halpern, S.L. & Underwood, N. (2006) Approaches for testing herbivore effects on plant population dynamics. *Journal of Applied Ecology*, **43**, 922–929.

Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.

Harrison, E. (1987) Treefall gaps versus forest understory as environments for a defoliating moth on a tropical forest shrub. *Oecologia*, **72**, 65–68.

Hawkes, C.V. & Sullivan, J.J. (2001) The impact of herbivory on plants in different resource conditions: a meta-analysis. *Ecology*, **82**, 2045–2058.

He, Q., Bertness, M.D. & Altieri, A.H. (2013) Global shifts towards positive species interactions increasing environmental stress. *Ecology Letters*, **16**, 695–706.

Heikkinen, R.K., Luoto, M., Virkkala, R., Pearson, R.G. & Körber, J.-H. (2007) Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Global Ecology & Biogeography*, **16**, 754–763.

Herrera, C.M., Medrano, M., Rey, P.J., Sanchez-Lafuente, M., Garcia, M.B., Guitian, J. & Manzaneda, A.J. (2002) Interaction of pollinators and herbivores on plant fitness suggests a pathway for correlated evolution of mutualism and antagonism-related traits. *Proceedings of the National Academy of Sciences USA*, **99**, 16823–16828.

Hill, J.K., Thomas, C.D. & Huntley, B. (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society B*, **266**, 1197–1206.

HilleRisLambers, J., Harsch, M.A., Ettinger, A.K., Ford, K.R. & Theobald, E.J. (2013) How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences*, **1297**, 112–125.

Horvitz, C.C., Ehrlén, J. & Matlaga, D. (2010) Context-dependent pollinator limitation in stochastic environments: can increased seed set overpower the cost of reproduction in an understorey herb? *Journal of Ecology*, **98**, 268–278.

Huffaker, C.B. & Kennett, C.E. (1959) A ten-year study of vegetational change associated with biological control of Klamath Weed. *Journal of Range Management*, **12**, 69–82.

Hunter, M.D. & Price, P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, **73**, 724–732.

Ibáñez, I., Gornish, E.S., Buckley, L., Debinski, D.D., Hellmann, J., Helmuth, B., HilleRisLambers, J., Latimer, A.M., Miller-Rushing, A.J. & Uriate, M. (2013) Moving forward in global-change ecology: capitalizing on natural variability. *Ecology & Evolution*, **3**, 170–181.

Jacquemyn, H., Brys, R. & Jongejans, E. (2010) Size-dependent flowering and costs of reproduction affect population dynamics in a tuberous perennial woodland orchid. *Journal of Ecology*, **98**, 1204–1215.

Jermy, T. (1984) Evolution of Insect/host plant relationships. *American Naturalist*, **124**, 609–630.

Kauffman, M. & Maron, J.L. (2006) Influence of density-dependence and seed bank dynamics in habitat-specific population dynamics of bush lupine, *Lupinus arboreus*. *American Naturalist*, **168**, 454–470.

Kawai, T. & Tokeshi, M. (2007) Testing the facilitation–competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proceedings of the Royal Society B*, **274**, 2503–2508.

Knight, T.M. (2003) Floral density, pollen limitation, and reproductive success in *Trillium grandiflorum*. *Oecologia*, **137**, 557–563.

Knight, T.M., Steets, J.A., Vamosi, J.C., Mazer, S.J., Burd, M., Campbell, D.R., Dudash, M.R., Johnston, M., Mitchell, R.J. & Ashman, T.L. (2005) Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology, Evolution & Systematics*, **36**, 467–497.

Kolb, A., Ehrlén, J. & Eriksson, O. (2007) Ecological and evolutionary consequences of spatial and temporal variation in pre-dispersal seed predation. *Perspectives in Plant Ecology, Evolution & Systematics*, **9**, 79–100.

Kunin, W.E. (1993) Sex and the single mustard-population-density and pollinator behavior effects on seed-set. *Ecology*, **74**, 2145–2160.

Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010) Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, & Systematics*, **41**, 321–350.

Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**, 1768–1771.

Letourneau, D.K., Dyer, L.A. & Vega, G. (2004) Indirect effects of a top predator on a rain forest understory plant community. *Ecology*, **85**, 2144–2152.

Levenbach, S. (2009) Grazing intensity influences the strength of an associational refuge on temperate reefs. *Oecologia*, **159**, 181–190.

Lortie, C.J. & Callaway, R.M. (2006) Re-analysis of meta-analysis: support for the stress-gradient hypothesis. *Journal of Ecology*, **94**, 7–16.

Louda, S.M. (1982) Distribution ecology: variation in plant recruitment over a gradient in relation to insect seed predation. *Ecological Monographs*, **52**, 25–41.

Louda, S.A. (1995) Effect of seed predation on plant regeneration: evidence from Pacific basin Mediterranean scrub communities. *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California, and Australia* (eds M.T.K. Arroyo, P.H. Zedler & M.D. Fox), pp. 311–344. Springer-Verlag, New York.

Louda, S. & Collinge, S.K. (1992) Plant resistance to insect herbivores: a field test of the environmental stress hypothesis. *Ecology*, **73**, 153–169.

Louda, S.M. & Potvin, M.A. (1995) Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology*, **76**, 229–245.

Louthan, A.M., Doak, D.F., Goheen, J.R., Palmer, T.M. & Pringle, R.M. (2013) Climatic stress mediates the impacts of herbivory on plant population structure and components of individual fitness. *Journal of Ecology*, **101**, 1074–1083.

MacGarvin, M., Lawton, J.H. & Heads, P.A. (1986) The herbivorous insect communities of open and woodland bracken: observations, experiments and habitat manipulations. *Oikos*, **47**, 135–148.

Maestre, F.T., Valladares, F. & Reynolds, J.F. (2005) Is the change of plant-plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. *Journal of Ecology*, **93**, 748–757.

Mangan, S.A., Schnitzer, S.A., Herre, E.A., Mack, K.M.L., Valencia, M.C., Sanchez, E.I. & Bever, J.D. (2010) Negative plant-soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, **466**, 752–756.

Maron, J.L. & Crone, E. (2006) Herbivory: effects on plant abundance, distribution, and population growth. *Proceedings of the Royal Society B*, **273**, 2575–2584.

Maron, J.L. & Gardner, S.N. (2000) Consumer pressure, seed versus safe-site limitation, and plant population dynamics. *Oecologia*, **124**, 260–269.

Maron, J.L., Horvitz, C.C. & Williams, J.L. (2010) Using experiments, demography and population models to estimate interaction strength based on transient and asymptotic dynamics. *Journal of Ecology*, **98**, 290–301.

Maron, J.L. & Kauffman, M. (2006) Habitat-specific consumer impacts on plant population dynamics. *Ecology*, **87**, 113–124.

Marquis, R.J. (1992) The selective impact of herbivores. *Plant Resistance to Herbivores and Pathogens* (eds R.S. Fritz & E.L. Simms), pp. 301–325. University of Chicago Press, Chicago.

Martin, T.E. & Maron, J.L. (2012) Climate impacts on bird and plant communities from an altered plant-animal interaction. *Nature Climate Change*, **2**, 195–200.

Maschinski, J. & Whitham, T.G. (1989) The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist*, **134**, 1–19.

McLaughlin, B.C. & Zavaleta, E.S. (2013) Shifting bottom-up and top-down regulation of oak recruitment across a regional resource gradient. *Global Ecology & Biogeography*, **22**, 718–727.

Memmott, J., Craze, P.G., Waser, N.M. & Price, M.V. (2007) Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, **10**, 710–717.

Menge, B.A. & Olson, A.M. (1990) Role of scale and environmental factors in regulation of community structure. *Trends in Ecology & Evolution*, **5**, 53–57.

Menge, B.A. & Sutherland, J.P. (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist*, **130**, 730–757.

Miller, T.E.X., Louda, S.M., Rose, K.A. & Eckberg, J.O. (2009) Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient. *Ecological Monographs*, **79**, 155–172.

Moeller, D.A. (2004) Facilitative interactions among plants via shared pollinators. *Ecology*, **85**, 3289–3301.

Moeller, D.A., Geber, M.A., Eckhart, V.M. & Tiffin, P. (2012) Reduced pollinator service and elevated pollen limitation at the geographic range limit of an annual plant. *Ecology*, **93**, 1036–1048.

Mordecai, E.A. (2011) Pathogen impacts on plant communities: unifying theory, concepts, and empirical work. *Ecological Monographs*, **81**, 429–441.

Moritz, C., Patton, J.L., Conroy, C.J., Parra, J.L., White, G.C. & Beissinger, S.R. (2008) Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, **322**, 261–264.

Packer, A. & Clay, K. (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, **404**, 278–281.

Parker, I.M. (1997) Pollinator limitation of *Cytisus scoparius* (Scotch broom), an invasive exotic shrub. *Ecology*, **78**, 1457–1470.

Parker, M.A. & Salzman, A.G. (1985) Herbivore exclosure and competitor removal: effects on juvenile survivorship and growth in the shrub *Gutierrezia microcephala*. *Journal of Ecology*, **73**, 903–913.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology & Systematics*, **37**, 637–669.

Pascarella, J.B. & Horvitz, C.C. (1998) Hurricane disturbance and the population dynamics of a tropical understory shrub: megamatrix elasticity analysis. *Ecology*, **79**, 547–563.

Poulsen, J.R., Osenberg, P.W., Clark, C.J., Levey, D.L. & Bolker, B.M. (2007) Plants as reef fish: fitting the functional form of seedling recruitment. *American Naturalist*, **170**, 167–183.

Price, M.V., Campbell, D.R., Waser, N.M. & Brody, A.K. (2008) Bridging the generation gap in plants: Pollination, parental fecundity, and offspring demography. *Ecology*, **89**, 1596–1604.

Rhoades, D.F. (1983) Herbivore population dynamics and plant chemistry. *Variable Plants and Herbivores in Natural and Managed Systems* (eds R.F. Denno & M.S. McClure), pp. 3–53. Academic Press, New York.

Rodríguez-Castañeda, G. (2013) The world and its shades of green: a meta-analysis on trophic cascades across temperature and precipitation gradients. *Global Ecology & Biogeography*, **22**, 118–130.

le Roux, P.C. & McGeoch, M.A. (2010) Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia*, **162**, 733–745.

Salguero-Gómez, R., Siewert, W., Capser, B.B. & Tielbörger, K. (2012) A demographic approach to study effects of climate change in desert plants. *Philosophical Transactions of the Royal Society B Biological Sciences*, **367**, 3100–3114.

Sargent, R.D. & Ackerly, D.D. (2008) Plant-pollinator interactions and the assembly of plant communities. *Trends in Ecology & Evolution*, **23**, 123–130.

Schleuning, M., Huaman, V. & Matthies, D. (2008) Flooding and canopy dynamics shape the demography of a clonal Amazon understorey herb. *Journal of Ecology*, **96**, 1045–1055.

Schoener, T.W. & Spiller, D.A. (1999) Indirect effects in an experimentally staged invasion by a major predator. *American Naturalist*, **153**, 347–358.

Shea, K., Kelly, D., Sheppard, A.W. & Woodburn, T.L. (2005) Context-dependent biological control of an invasive thistle. *Ecology*, **86**, 3174–3181.

Syrett, P., Briese, D.T. & Hoffmann, J. (2000) Success in biological control of terrestrial weeds by arthropods. *Biological Control: Measures of Success* (eds S.D. Wratten & G. Gurr), pp. 189–230. Kluwer, Amsterdam.

Thompson, J.N. (2005) *The Geographic Mosaic of Coevolution*. University of Chicago Press, Chicago, USA.

Thuiller, W., Albert, C., Araújo, M., Berry, P.M., Cabeza, M., Guisan, A. *et al.* (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution & Systematics*, **9**, 137–152.

Tingley, M.W., Monahan, W.B., Beissinger, S.R. & Mortiz, C. (2009) Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Sciences USA*, **106**, 19637–19643.

Toräng, P., Ehrlén, J. & Ågren, J. (2010) Linking environmental and demographic data to predict future population viability of a perennial herb. *Oecologia*, **163**, 99–109.

Turnbull, L.A., Crawley, M.J. & Rees, M. (2000) Are plant populations seed-limited? A review of seed sowing experiments. *Oikos*, **88**, 225–238.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.

Vamosi, J.C., Knight, T.M., Steets, J.A., Mazer, S.A., Burd, M.A. & Ashman, T.L. (2006) Pollination decays in biodiversity hotspots. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 956–961.

Vaughton, G. (1991) Variation between years in pollen and nutrient limitation of fruit-set in *Banksia spinulosa*. *Journal of Ecology*, **79**, 389–400.

Wesselingh, R.A. (2007) Pollen limitation meets resource allocation: towards a comprehensive methodology. *New Phytologist*, **174**, 26–37.

White, T.C.R. (1969) An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology*, **50**, 905–909.

Wilcock, C.C. & Jennings, S.B. (1999) Partner limitation and restoration of sexual reproduction in the clonal dwarf shrub *Linnaea borealis* L. (Caprifoliaceae). *Protoplasma*, **208**, 76–86.

Wilcock, C. & Neiland, R. (2002) Pollination failure in plants: why it happens and when it matters. *Trends in Plant Science*, **7**, 270–277.

Wise, M.J. & Abrahamson, W.G. (2005) Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory. *Oikos*, **109**, 417–428.

Woodward, F.I. (1990) The impact of low temperatures in controlling the geographical distribution of plants. *Philosophical Transactions of the Royal Society of London B*, **326**, 585–593.