

Review

Herbivory: effects on plant abundance, distribution and population growth

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Plants are attacked by many different consumers. A critical question is how often, and under what conditions, common reductions in growth, fecundity or even survival that occur due to herbivory translate to meaningful impacts on abundance, distribution or dynamics of plant populations. Here, we review population-level studies of the effects of consumers on plant dynamics and evaluate: (i) whether particular consumers have predictably more or less influence on plant abundance, (ii) whether particular plant life-history types are predictably more vulnerable to herbivory at the population level, (iii) whether the strength of plant–consumer interactions shifts predictably across environmental gradients and (iv) the role of consumers in influencing plant distributional limits. Existing studies demonstrate numerous examples of consumers limiting local plant abundance and distribution. We found larger effects of consumers on grassland than woodland forbs, stronger effects of herbivory in areas with high versus low disturbance, but no systematic or unambiguous differences in the impact of consumers based on plant life-history or herbivore feeding mode. However, our ability to evaluate these and other patterns is limited by the small (but growing) number of studies in this area. As an impetus for further study, we review strengths and challenges of population-level studies, such as interpreting net impacts of consumers in the presence of density dependence and seed bank dynamics.

Keywords: demography; herbivory; matrix models; plant abundance; plant–consumer interactions; plant population dynamics

1. INTRODUCTION

Plants form the template on which communities and ecosystems are assembled and on which food webs are built. Thus, understanding the factors that determine plant distribution and abundance is central for our understanding of ecology at large. Consumers, as major constituents of most ecosystems and chronic agents of plant damage, have great potential to fundamentally alter plant abundance and distribution. What do we know about how often, and under what circumstances, this potential is realized in terrestrial systems?

At one level, we know from a vast number of individual-level studies that herbivores can have strong deleterious effects on plant growth, reproduction and even survival (reviews by Crawley 1989, 1992, 1997; Louda 1989; Gange 1990; Marquis 1992; Strauss & Zangrel 2002). Yet since these studies have been short term, and have typically examined consumer impacts on only one or a few plant life-history stages, they tell us surprisingly little about how herbivore-driven decrements in plant performance influence long-term patterns of plant abundance, dynamics or distribution. Longer-term community-level studies, on the other hand, have provided ample evidence for the importance of consumers in influencing plant

community composition (reviews by Huntly 1991; Belsky 1992; Milchunas & Lauenroth 1993; Augustine & McNaughton 1998; Olf & Ritchie 1998). Results from these studies, however, often reflect both the direct consumptive effects of herbivores and a variety of indirect effects that are difficult to untangle. As such, they do not always reveal to what degree observed changes in focal species are due to direct effects of consumption, versus other potential mechanisms.

A small, but growing, number of studies have viewed plant–consumer interactions through a population lens. Here, we review these studies to determine the extent to which individual-level effects of consumers translate to changes in plant distribution or abundance. Specifically, we pose four broad questions that provide a test of our understanding of how consumers influence plant abundance and dynamics: (i) do particular guilds of consumers have predictably larger impacts on plant populations than others? (ii) how do consumer effects on plant abundance vary based on plant life-history attributes? (iii) do impacts of consumers on plant dynamics change predictably across environmental gradients? and (iv) do consumers limit the distributional range of plants? In part, our ability to answer these questions is limited by gaps in our knowledge in a few key areas. We explore these issues, particularly as they relate to using population models to explore impacts of consumers on plant abundance and population dynamics.

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2. CONSUMER EFFECTS ON PLANT ABUNDANCE AND DISTRIBUTION: HOW MUCH DO WE KNOW?

Just a few decades ago, even answering the simple question of ‘do herbivores influence plant abundance?’ was difficult. Manipulative experiments of consumer effects on plants were rare, and the prevailing sentiment was that herbivores were unlikely to have meaningful effects on plant abundance and dynamics. Over the past 5–10 years, however, there have been a growing number of studies on effects of herbivores on plant abundance. Many of these have demonstrated that herbivores can directly limit plant abundance. Thus, the relevant question at this juncture is not so much ‘do herbivores influence plant abundance?’ but instead ‘under what conditions do herbivores influence plant abundance?’ We structure the review that follows around several broad questions that ask when and where herbivores have their most meaningful impacts on plant distribution and abundance. As such, these questions evaluate our current state of understanding regarding insect consumer impacts on plant populations.

To obtain answers to our questions, we reviewed studies that documented how consumers influence the number of individuals in future generations. We omitted a large number of ‘within-generation’ studies that quantified how consumers influenced seed, seedling or adult plant survival, because these studies do not allow inference as to whether changes in the abundance of individual plants within one year influences the abundance of plants in future years. We also omitted community-level studies (e.g. Brown & Heske 1990; Carson & Root 2000; Jefferies *et al.* 2004), because these do not usually elucidate the direct consumptive effects of herbivores on plant abundance.

We found 30 studies that fit our criteria (table 1). These studies examined consumer effects on 23 plant genera. The majority of research (15) concerned insect herbivory, although nine considered effects of large mammalian grazers, two studies looked at impacts of voles and/or mice on plant dynamics, two studies documented the effects of snails/slugs on plant abundance and two studies experimentally clipped vegetation to simulate herbivory.

(a) Do particular types of consumers (mammals versus insects, seed predators versus other functional groups) have predictably greater population-level impacts on plants than others?

Whether mammals or insects have greater impacts on plant dynamics has been a topic of considerable debate. This is an interesting question because it touches on a broader issue, which is the relative impact of generalist versus specialist herbivores in affecting plant dynamics (mammals are typically generalists, whereas insects are often specialists). Owing in part to their greater size, Crawley (1988, 1989) first suggested that mammals generally have larger negative effects on plants than do insects. This assertion has subsequently been supported by a majority of studies that have explicitly compared the relative effects of insects and mammals on the performance of a focal species (Hulme 1994a; Palmisano & Fox 1997; Gomez & Zamora 2000; Sessions & Kelly 2001; Warner & Cushman 2002; Maron & Kauffman 2006, but see Strauss 1991; Ehrlén 1995). In contrast, based on a meta-analysis involving 246 comparisons of plant size from consumer exclusion studies, Bigger & Marvier (1998) found that

insects had larger impacts on plant biomass than did mammals. A major problem in interpreting results from these studies, however, is that comparisons have been based on how strongly various herbivores influence single components of plant performance, such as reproduction or biomass. Whether these results extrapolate to the plant population level is uncertain, and clouds generalizations about the relative importance of particular consumers in influencing plant abundance.

To overcome these limitations, we calculated the average reduction in future seedling recruitment or projected plant population growth rate (λ) that has been reported in studies involving native vertebrate and invertebrate consumers, as well as biocontrol insects and domesticated grazers. Our analysis reveals no consistent or overwhelming pattern in terms of whether invertebrate or vertebrate consumers have greater impacts on plant populations. Studies that have experimentally quantified the effects of herbivores on future seedling recruitment (but not λ) have documented substantial effects of both insects (Louda 1982; Maron *et al.* 2002) and mammals (Gómez 2005) on the recruitment of future generations of seedlings. In studies that estimated effects of consumers on plant population growth, on average, native invertebrate consumers decreased λ by 0.12 (\pm s.e.m. 0.06), whereas native mammalian herbivores decreased λ by an average of 0.06 (\pm s.e.m. 0.06). Where quantified, biocontrol insects had even stronger effects on plant abundance, decreasing λ by an average of 0.93 (\pm s.e.m. 0.38). Several studies on effects of non-native grazers (Gillman *et al.* 1993; Bullock *et al.* 1994; Bastrante *et al.* 1995; Lennartsson & Oostermeijer 2001) have shown that these consumers can have positive to mildly or even strongly negative effects on λ depending on whether consumers have mostly indirect or direct effects on vegetation. Where sheep act solely as agents of disturbance and create gaps in vegetation (e.g. Gillman *et al.* 1993; Bullock *et al.* 1994), they can have positive effects on plant population growth. In contrast, where herbivores both create disturbance but also have consumptive effects on the focal plant (such as was the case in Lennartsson & Oostermeijer’s (2001) study on horse herbivory), overall impacts can be mildly negative. Where effects appear to be primarily consumptive (i.e. Bastrante *et al.* 1995), effects can have even greater negative effects on plant population growth (table 1).

Another issue that has garnered considerable discussion in the plant–consumer literature concerns the relative importance of flower and seed predators to plant dynamics (Crawley 1992; Louda & Potvin 1995). Consumers that damage flowers and/or developing or dispersed seeds are common, and seed loss to these consumers can be considerable (reviews by Hendrix 1988; Louda 1989; Hulme 1998). Yet seed loss may have little effect on future plant abundance if: (i) plant populations are more limited by the availability of safe sites rather than seeds (Harper 1977; Crawley 1989) or (ii) compensatory flowering mitigates the negative effects of floral herbivory (McNaughton 1986; Hendrix & Trapp 1989). While there are clear examples of seed predators depressing plant population growth (Rose *et al.* 2005; Kauffman & Maron submitted) and abundance (Louda & Potvin 1995; Maron & Kauffman 2006), there are also counter-examples of

Table 1. Studies that have quantified population-level impacts of consumers on plants. (Multiple citations in a given row indicate cases where multiple studies were performed on the same study system. In 'type of herbivore and damage' column, 'sd', shoot damage; 'cb', caudex boring; 'prdsp', pre-dispersal seed predation; and 'podsp', post-dispersal seed predation'. In 'outcome' column, ' Δ in λ ' refers to λ (the density-independent population growth) without consumers minus λ in the presence of consumers. ' Δ in recruitment' refers to the percentage of increase (or decrease) in seedling establishment in plots without herbivores compared to plots with herbivores. In some cases where numerical values for λ were difficult to extract from the literature, we report the percentage change in λ due to herbivory.)

authors	plant studied	type of herbivore and damage	plant life history	outcome
Louda (1982)	<i>Haplopappus squarrosus</i>	insects: prdsp	perennial shrub	Δ in recruitment: increased 2670%
Louda (1983)	<i>Haplopappus venetus</i>	insects: prdsp	perennial shrub	reduced recruitment but compensatory mortality
Gillman <i>et al.</i> (1993), Bullock <i>et al.</i> (1994)	<i>Cirsium vulgare</i>	sheep: grazing	monocarpic herb	Δ in λ : -1.1 density independent, Δ in λ : -1.59 to -2.1 ^a
Louda & Potvin (1995), Rose <i>et al.</i> (2005)	<i>Cirsium canescens</i>	insects: prdsp	monocarpic herb	reduced recruitment and subsequent adult density; Δ in λ : 0.33
Baistrate <i>et al.</i> (1995)	<i>Anthyllis vulneraria</i>	sheep: grazing	perennial herb	Δ in λ : 1.5
Augustine <i>et al.</i> (1998)	<i>Laportea canadensis</i>	deer: grazing	perennial herb	Δ in λ : -0.16 ^b
McEvoy <i>et al.</i> (1993), McEvoy & Combs (1999) ^c	<i>Senecio jacobaea</i>	biocontrol insects	monocarpic herb	reduced recruitment; Δ in λ : ~1.6 ^b
Fagan & Bishop (2000), Bishop (2002), Fagan <i>et al.</i> (2005)	<i>Lupinus lepidus</i>	insects: cb/folivory/prdsp	perennial shrub	reduced recruitment and spatial spread
Parker (2000)	<i>Cytisus scoparius</i>	biocontrol insect: prdsp	shrub	Δ in λ : ~0.1-0.5 ^d
Lennartsson & Oostermeijer (2001)	<i>Gentianaella campestris</i>	horse: grazing	biennial herb	Δ in λ : 0.001 or 0.038 ^e
García & Ehrlén (2002)	<i>Primula veris</i>	simulated herbivory	perennial herb	Δ in λ : 0.06 (early season)
Herrera <i>et al.</i> (2002)	<i>Helleborus foetidus</i>	mice/insects: flower and fruit predators	perennial herb	Δ in recruitment: increased ~100% ^f
Kelly & Dyer (2002)	<i>Liatris cylindracea</i>	insects: prdsp	perennial herb	Δ in λ : 0.04
Maron <i>et al.</i> (2002)	<i>Cirsium occidentale</i>	insects: prdsp	monocarpic herb	Δ in recruitment: increased 116%
Ehrlén (2003)	<i>Lathyrus vernus</i>	slugs: defoliation	perennial herb	Δ in λ : 0.14
Rooney & Gross (2003)	<i>Trillium grandiflorum</i>	deer: grazing	perennial herb	altered spatial distribution; Δ in λ : 0.001
Frøborg & Eriksson (2003)	<i>Actaea spicata</i>	insects: prdsp	perennial herb	Δ in λ : 0.007-0.049 or 0.001-0.046 depending on site
Knight (2004)	<i>Trillium grandiflorum</i>	deer: grazing	perennial herb	Δ in λ : 0.005
Ehrlén <i>et al.</i> (2005)	<i>Primula veris</i>	simulated grazing	perennial herb	Δ in λ , vegetation removal only: 0; vegetation + litter removal: 0.35
Gómez (2005)	<i>Erysimum mediohispanicum</i> and <i>E. baeticum</i>	sheep and ibex: flower and fruit predation	perennial herb	Δ in recruitment: for <i>E. baeticum</i> , increased ~600% ^g for <i>E. mediohispanicum</i> , decreased ~500% ^g
McGraw & Furedi (2005)	<i>Panax quinquefolius</i>	deer grazing	perennial herb	Δ in λ : 0.05
Horvitz <i>et al.</i> (2005)	<i>Ardisia escallonioides</i>	insect: flower gall	perennial shrub	Δ in λ : 6% reduction in λ under historic hurricane frequency
Shea <i>et al.</i> (2005)	<i>Cirsium nutans</i>	biocontrol insects: prdsp and meristem damage	monocarpic herb	Δ in λ : 0.662 and 1.1 ^h
Maron & Kauffman (2006), Kauffman & Maron (submitted)	<i>Lupinus arboreus</i>	voles/mice/insects: seedling defoliation, root boring and podsp	perennial shrub	reduced recruitment and subsequent adult abundance; Δ in λ : 0.19 (voles) ^b , 0.66 (granivorous mice) ⁱ

^a Average change in λ across two blocks. Lower value from λ represents 9 cm sward height, larger value, 3 cm sward height.

^b Maximum (density-independent) rate of increase from density-dependent model.

^c Difference in arithmetic means inferred from graphical presentation of geometric mean.

^d Depending on population studied and assuming biocontrol insects remove 90% of viable seeds.

^e First value, horse grazing versus mowing only; second value, horse grazing plus mowing versus mowing only.

^f Results from plots where pollinators were not excluded. Pollinator exclusion reduces consumer effects.

^g Data from open microhabitat only. Results at edge or under shrubs different.

^h Depending on region and identity of most damaging biocontrol herbivore.

ⁱ Maximum (density-independent) rate of increase from density-dependent model. Values for voles taken from grassland habitat, value for mice taken in dune habitat.

seed predators having minimal impacts (Andersen 1989; Myers & Bazely 2003).

We compared the average reduction in plant population growth reported in studies on floral, pre- and post-dispersal seed predators compared to those reported for all other herbivore types identified in our review. On average, seed predators reduced λ by 0.43 (\pm s.e.m. 0.19), whereas other herbivores reduced λ by 0.33 (\pm s.e.m. 0.26). If we exclude studies of biocontrol insects and domestic grazers which might artificially inflate the effects of herbivory, on average seed predators reduce λ by 0.16 (\pm s.e.m. 0.05), whereas other herbivores decrease λ by 0.11 (\pm s.e.m. 0.14). While these results should be viewed cautiously, they are surprising because they suggest that seed predators may be as important as other types of consumers in affecting plant population growth. Moreover, they demonstrate that demographic sensitivities alone may not provide accurate predictions about whether consumers that attack specific life stages will or will not have population-level consequences. Equally important is the relative magnitude of response of particular life stages to the experimental exclusion of consumers (Ehrlén *et al.* 2005).

(b) Are particular plant life-histories more vulnerable to population-level impacts of consumers than others?

We know from the large literature on the effects of herbivores on plant performance that plant life history can often influence how much herbivore damage plants incur. For example, plants that produce large seeds are clearly more vulnerable to post-dispersal seed predation than plants that produce small seeds (Mittelbach & Gross 1984; Schupp *et al.* 1989; Hulme 1993, 1994b; Reader 1993). Often less-defended fast-growing plants receive more herbivore damage than slow-growing better-defended species (Coley *et al.* 1985). Can similar predictions be generated regarding how plant life history influences the vulnerability of plants at the population level?

One recurrent suggestion is that short-lived fugitive plants with a strong reliance on current seed rain for regeneration should be more negatively affected by herbivores that reduce seed production than long-lived perennials or short-lived annuals with long-lived seed banks (Louda & Potvin 1995). Species with long lifespans, either as adults or as dormant seeds, should be more buffered from heavy herbivory, because they can compensate across years for times when herbivore pressure is particularly intense. For example, regeneration out of a long-lived seed bank can compensate for years of low seed production. Additionally, species with long adult lifespans often have sufficient energy reserves to enable substantial compensatory regrowth after defoliation compared to shorter-lived species lacking reserves in energy.

How well are these predictions borne out by empirical studies? Of the studies we reviewed where population-level effects of herbivores are quantified (table 1), most (19/24 or 79%) have been conducted on herbaceous species with either limited adult longevity or transient seed banks. Thus, the only comparisons we can make with this dataset are differences between herbs of open versus forest habitats, and taxa with and without seed banks. Through direct consumptive effects,

herbivores decreased λ by an average of 0.46 (\pm s.e.m. 0.27) for herbs found in open grassland habitats, whereas herbivores reduced λ by an average of only 0.09 (\pm s.e.m. 0.03) for species that inhabit forest understory. It is tempting to speculate that this reflects the fact that forest herbs are relatively insensitive to changes in growth and fecundity, but the limited sample size and wide standard errors caution against reading too much into this result. Only 10 studies examined the effects of consumers on plants with persistent seed banks; two of these studies ignored seed banks in their population model (McEvoy & Coombs 1999; Parker 2000), and only one of the remaining studies was on a species with a seed bank that persisted for longer than 5 years (Kauffman & Maron submitted). Nevertheless, excluding studies of biocontrol and studies where grazers created gaps in vegetation and increased plant population abundance, herbivores decreased λ by an average of 0.3 (\pm s.e.m. 0.19) for species lacking a seed bank, whereas herbivores decreased λ by an average of only 0.08 (\pm s.e.m. 0.03) for species with persistent seed banks.

As Louda & Potvin (1995) originally asserted, it is likely that plant vulnerability to consumers lies along a continuum of life-history variation. Our review suggests that fugitive forbs with no or a very limited seed bank may sit at one end of this spectrum. Effects of consumers on populations of annual species with abundant seed banks have seldom been studied, but species with this life-history type may lie at the other end of the continuum. Recruitment for many annual plants with abundant seed banks may be more safe-site than seed limited, making these taxa insensitive to seed predation, whereas this is not the case for fugitives. What is less clear is how vulnerable may be plants with intermediate life histories. For example, how buffered from population impacts of herbivores are plants that produce dormant seeds, but with dormancy of moderate duration (say, 10 years)? Based on simulations, Maron & Gardner (2000) found that a hypothetical seed predator could significantly influence plant abundance even when seed dormancy (and hence seed bank persistence) was prolonged. Their results suggested that while seed banks can clearly 'buffer' populations, they also provide a 'memory' of the cumulative effects of consumers on past seed production.

Another area in need of research is how consumers impact populations of plants that reproduce clonally in addition to or instead of sexually. One might assume that these species would be buffered from population impacts of consumers, both because some of these species have multiple means of reproduction, but also because they often have substantial stored resources that can be used to compensate for herbivory. Of the population-level papers we reviewed, we could find no study on a clonal forb. However, we note that research on rhizomatous cordgrass, *Spartina alterniflora*, suggests that grazers can play a key role in affecting its distribution in tidal marshes on the east coast of the US (Silliman & Bertness 2002; Silliman *et al.* 2005). Strong long-term effects of insect herbivores on populations of rhizomatous goldenrod (*Solidago altissima*) have also been demonstrated (Carson & Root 2000).

(c) Does the impact of consumers on plant population abundance change predictably across environmental gradients or habitat types?

Individual-level studies have commonly demonstrated strong spatial variation in the magnitude of herbivory across gradients in elevation (Galen 1990; Bruelheide & Scheidel 1999), tidal height (Olf *et al.* 1997; Rand 2002), disturbance (Knight & Holt 2005) and sunlight (Holloway 1957; Lincoln & Mooney 1984; Louda & Rodman 1996). Levels of plant defence can also vary across elevation gradients (Ganders 1990), and arthropod species richness can also vary based on gradients in plant species richness (Siemann *et al.* 1998) and intraspecific genetic diversity (Johnson *et al.* 2006). How might this variation in arthropod abundance or the damage imposed by herbivores translate to spatial variation in plant abundance?

Our review reveals that spatial variation in the population-level impacts of consumers is ubiquitous. Of the 15 studies where herbivore impacts were compared among sites, microhabitat, or habitats, strong context-dependent effects were found in every case except the study by Herrera *et al.* (2002). For example, Fagan & Bishop (2000) and Fagan *et al.* (2005) found striking spatial variation in herbivory within patches of *Lupinus lepidus* growing on recently erupted Mount St Helens. Variation in herbivory was based on lupine density. Herbivory was more intense, and had greater effects on population growth at the edges of lupine patches where plants grow at lower density than it did in the middle or 'core' of dense patches where plants occur at high density (Fagan *et al.* 2005). Finally, on a larger spatial scale, Louda (1982, 1983) found differential effects of herbivory on plant abundance across a distributional gradient from coast to inland sites.

Given that spatial variation in both the performance and population-level effects of herbivory is extremely common, can these context-dependent effects be placed in a broader predictive framework? That is, can we predict the strength of plant–consumer interactions based on particular attributes of the abiotic or biotic environment or do herbivore impacts vary idiosyncratically across a plant's distribution?

One environmental factor that can clearly affect how greatly herbivores influence plant abundance is the extent to which there is open space or bare ground for recruitment. In open habitats, there is often a close correspondence between seed input and recruitment (Harper 1977; Fenner 1985; Maron *et al.* 2002). Recruitment is more likely to be seed limited in more open or disturbed habitats with less interspecific competition than in closed habitats with greater litter or plant cover, where populations may be microsite limited (Crawley 1997). This suggests that herbivory that reduces seed production should have greater impacts on plant abundance in open versus closed microhabitat. This prediction appears to be borne out in studies conducted to date. For example, Maron & Kauffman (2006) found that post-dispersal seed predation by mice had large effects on the abundance of bush lupine in open dune habitat but not in adjacent grasslands where there was greater cover. Louda & Potvin (1995) and Maron *et al.* (2002) similarly found differences in consumer impacts on two related native thistles based on their microhabitat. Pre-dispersal insect herbivores had greater effects on plant recruitment

in more sparsely vegetated areas than in microhabitats with greater plant cover. McEvoy & Coombs (1999) found that biocontrol insects had their greatest effect on the population growth of ragwort (*Senecio jacobaea*) when habitat was disturbed and competition reduced compared to situations where habitat was undisturbed and plants faced stiff competition for safe sites during recruitment. Yet, even though biocontrol agents had their greater effect on reducing *Senecio* population growth in disturbed habitats, the combination of low disturbance and biocontrol was the most successful strategy for eliminating *Senecio* populations, simply because of the powerful effects of competition exerted on suppressing *Senecio* recruitment.

Beyond predicting how seed loss might influence recruitment in different microhabitat types, there are insufficient data to generate more robust predictions about how limits to plant abundance imposed by consumers should change across larger spatial scales. Menge & Olson's (1990) work on stress response gradients offers an interesting conceptual framework in which to start to make these predictions. Menge & Olson (1990) assert that when and where consumers have their greatest effects on plants depend on whether any given environment is more stressful to plants or consumers. Critically evaluating these ideas will require a more mechanistic understanding of how context mediates the per capita effects of herbivores on plant abundance. Especially, future studies would be helpful that simultaneously: (i) quantified population effects of consumers across environmental gradients, (ii) measured environmental variation across this gradient and (iii) experimentally manipulated aspects of the abiotic environment to determine whether the strength of consumer effects on plants could be experimentally switched to reproduce observed patterns in herbivore impacts across environment gradients.

(d) To what extent do consumers control local patterns of plant distribution or range limits?

At least in some cases, herbivores control the local distribution of plants among habitat types. Louda's (1982, 1983) research was one of the first exclusion studies to determine whether local patterns of plant distribution might be controlled by insect herbivory. In this classic work, Louda (1982) documented that the shrub *Haplopappus squarrosus* (current name: *Hazardia squarrosa*) was more abundant at inland sites than at sites close to the coast. By excluding pre-dispersal seed-feeders on plants across this gradient, Louda (1982) found that herbivory on *H. squarrosus* was intense at all sites, but that insect exclusion led to greater gains in recruitment at coastal versus inland sites. Thus, herbivory appeared to drive the pattern in plant abundance across this geographical gradient.

More recent work has similarly implicated herbivores in affecting local plant distribution. For example, Gómez (2005) demonstrated that herbivores influence the spatial distribution of two species of *Erysimum* that typically gain refuge from ungulate herbivory by growing under shrubs. Ungulate exclusion enabled these species to colonize the interstitial spaces between shrubs, thereby altering their habitat distribution. As well, recent work by Fine *et al.* (2004) demonstrated that heavy insect herbivory on tropical tree seedlings may be responsible for limiting the local distribution of particular tree species to sites with

specific soil conditions. Thus, researchers have found effects of consumers on local distributions where they have looked for them, but too few studies exist to generalize the importance of consumers, relative to abiotic conditions.

The importance of consumers for local patterns of distribution suggests that herbivores could also affect the broader distributional limits of plants. Might herbivores influence plant range boundaries? Although range boundaries of plants are often assumed to be 'fixed', it is likely that range boundaries are very dynamic, expanding or contracting depending on how variation in the abiotic or biotic environment constrains or facilitates population growth. Historically, thinking on the factors that limit plant distributional ranges has been dominated by a focus on abiotic factors, such as climate and edaphic conditions (Salisbury 1926; Arris & Eagleson 1989; Demers *et al.* 1998). Theory suggests that homogenizing gene flow coming from the range centre makes it difficult for species to adapt to conditions at or beyond their current range edge (Kirkpatrick & Barton 1997). Yet, areas immediately beyond the range of many plants are often abiotically similar to sites within the range of these species, and it appears that many plants could physiologically tolerate areas outside their current distribution. For example, Stokes *et al.* (2004) found that population growth rates for two species of *Ulex* were not lower at their range boundaries compared to more interior sites. A few other studies have failed to detect a decline in plant performance from interior to range edge (Prince & Carter 1985; Carey *et al.* 1995). In cases such as these, it is not clear what limits distribution, which begs the question of whether biotic rather than abiotic factors may be important. Though the idea that species interactions can set range boundaries has been floated for some decades (Rochow 1970; MacArthur 1972; Galen 1990), few studies of range limits explicitly consider how biotic factors influence range edges. In fact, no study, to our knowledge, has examined how consumers may influence either the location of plant range boundaries, or the dynamics of plant populations at their range boundary compared to the centre of their range (Strauss & Zangrel 2002). Future work that combined transplant experiments (*sensu* Prince & Carter 1985; Stokes *et al.* 2003) with consumer exclusion to estimate how consumers combined with spatial variation in abiotic conditions influenced plant population growth both at a range edge and beyond would be informative and extremely valuable.

3. CAVEATS

We have combined results from disparate studies to gain insight into population-level effects of consumers on plants. Such comparisons across a relatively small number of studies, however, unavoidably are potentially confounded by 'uncontrolled' factors that might skew results. For example, in comparing population-level impacts of herbivores among plant life-history types it is not possible to 'control' for herbivore identity. Similarly, in comparing effects of different herbivores it is impossible to 'control' for plant identity or life history. These potentially confounding effects suggest that our results should be treated cautiously at this stage, as refined hypotheses that require additional testing.

4. EXPERIMENTS AND POPULATION MODELS

Increasingly, studies of consumer impacts on plant populations involve a combination of experimental manipulation, demographic monitoring of individual performance, and population models to extrapolate long-term effects from observations made over shorter time spans. For example, 17 of the studies shown in table 1 used population models to infer effects of herbivores on the long-term population growth rates of plants. Although population models coupled with demographic data offer a powerful and attractive vehicle for projecting consumer effects on plant dynamics, there are several key challenges in parameterizing these models.

(a) *Estimating the strength of density dependence*

Most simply, herbivores can reduce plant abundance if they directly kill plants or their seeds *and* this mortality reduces the number of individuals in subsequent generations. The challenge in determining whether consumers limit plant abundance is that there are many cases where the first condition applies but not the second. For example, if consumer-induced mortality of either seedlings or adults ultimately reduces the density of adult plants, the survival or fecundity of plants that escape herbivory may be enhanced due to reduced intraspecific competition. This can counterbalance losses due to herbivory.

Although density dependence is common in plant populations (Watkinson 1997; Willis *et al.* 1997), the extent to which it is fully or partially compensatory for losses due to herbivory is poorly understood. The tendency in the plant–consumer literature has been to treat density dependence as binary (i.e. density dependence 100% compensatory or not). The same is true with thinking about safe-site limitation (i.e. plants are either safe-site limited or not). However, plant populations can be: (i) both seed *and* safe-site limited (Eriksson & Ehrlén 1992) or (ii) seed limited in some years and safe-site limited in others. Seed limitation need not occur across all years of a plant's lifetime in order for seed predation to have meaningful effects on plant abundance (Maron & Gardner 2000).

Despite widespread recognition that compensatory density dependence can profoundly mediate the impacts of consumers on plant populations, only two studies that we know of have estimated the magnitude of spatial and temporal variation in the strength of density dependence in the context of examining consumer effects on plants (Augustine *et al.* 1998; Kauffman & Maron *submitted*). More typically, models of consumer effects on plant populations have assumed density-independent plant population growth. In some of these cases, this may be appropriate, in that it accurately reflects the biology of the plants involved (e.g. for forest understory herbs). In many cases, however, the lack of density dependence in plant–consumer models may simply reflect the broader reality that few plant population models of any type have incorporated empirical estimates of density dependence (Menges 2000; some notable exceptions are presented in the electronic supplementary material).

This paucity of density-dependent matrix population models likely reflects two factors. First, empirically estimating both the life stage where density dependence occurs, and its relative strength at each life stage, can be

challenging. The strength and direction of density dependence can change markedly depending on plant life stage (Howard & Goldberg 2001). Furthermore, density-dependent changes in a particular demographic rate can result from effects of either adult or juvenile density (electronic supplementary material). As such, experimentally manipulating density to measure the strength of density dependence involves making difficult decisions about where in a plant's life stage to impose these manipulations, and where to measure the effects. Second, much of the emphasis on using population models has been to estimate elasticities, to determine what demographic rate most constrains population growth (λ). With density dependence, population growth is no longer exponential, and this makes calculating sensitivities problematic (Caswell 2001).

Since it is clear that the impacts of consumers hinge tightly on the strength of compensatory (density-dependent) growth, fecundity and mortality, estimating density dependence is a fundamental area for plant–consumer research. How might this be accomplished? At the seed and seedling levels, the strength of density dependence can be estimated by sowing seeds at different densities, and observing survival as a function of sowing density. For adult plants, manipulations are less straightforward; it is not necessarily feasible to transplant mature plants, nor is it likely that transplantation would not affect plant performance in most species. However, vital rates of surrounding plants could be measured as a function of damage to target plants, as a preliminary assessment of density-dependent growth, survival and fecundity of adult plants. Neighbourhood models (Pacala & Silander 1985; Garrett & Dixon 1998) allow density-dependent vital rates to be inferred from spatial plant distributions, rather than full experiments.

(b) *Estimating seed bank dynamics*

A second major challenge in building demographic models to assess consumer effects is to incorporate realistic estimates of seed bank dynamics (*sensu* Kalisz & McPeck 1992) into these models. Accurate estimates of seed persistence in plant–consumer studies are critical, because seed banks are common (Baskin & Baskin 1998) and seed bank dynamics can influence the degree to which populations are seed limited, or at least the degree to which reductions in current seed rain due to consumers influences the magnitude of subsequent recruitment.

Obtaining realistic estimates of seed bank dynamics requires estimation of three important demographic parameters: seed production, seed germination rate and the survival rate of seeds that do not germinate but remain dormant and viable in the seed bank. Each of these demographic rates may be age-specific, although estimates of age-specific germination and seed mortality are rare (Doak *et al.* 2002) and difficult to obtain.

Estimating seed production is relatively straightforward, so we will not discuss it further here. Estimating seed germination and seed mortality, however, is more problematic. In many plant demography studies, rather than measuring seed mortality directly, seed survivorship is instead estimated based on experiments that quantify seedling emergence. The problem with this approach, however, is that it fails to quantify how many viable seeds may be left in the soil after some fraction of seeds have emerged (Rees & Long 1993; Doak *et al.* 2002).

Furthermore, as Doak *et al.* (2002) point out, estimates of seedling emergence from field-collected soil samples that are arrayed in a greenhouse may greatly overestimate germination rate. An alternative is to add seeds to plots in the field, preferably in areas that do not contain dormant seeds. This approach is commonly used to obtain field estimates of the seed-to-seedling transition (Fröberg & Eriksson 2003), and to estimate the extent to which a population may be seed limited (Turnbull *et al.* 2000). One caveat to this approach, however, is that seed addition experiments may poorly mimic the timing, density and spatial array of naturally dispersed seed. To the extent that these factors influence rates of seed germination or persistence, they may provide imprecise estimates of the quantitative relationship between seed rain and seedling recruitment (Louda & Potvin 1995; Nathan & Muller-Landau 2000; Maron *et al.* 2002; Van Mourik *et al.* 2005). An alternative approach is to estimate seed rain and seedling emergence in demography plots, in which consumers have or have not been excluded. If one has some knowledge about levels of seed dormancy and viability, maximum-likelihood techniques can be used to estimate levels of germination, given the relationship between seed input and seed output and how this varies spatially and between years (Wright *et al.* 2005; Kauffman & Maron submitted).

In addition to measuring germination rates, accurately estimating seed bank dynamics requires knowledge about how many seeds germinate but fail to emerge, and how many dormant seeds die, either through declining viability or predation of seeds in the seed bank. A common approach to modelling seed survival is to assume that survival of dormant seeds decays exponentially through time. Often, the slope of this decay function is set by some estimate of the maximum seed dormancy. Yet as Rees & Long (1993) have found, seed banks may not always decay according to a negative exponential pattern. As with estimating rates of seedling emergence, maximum-likelihood techniques based on observations of seed input and emergence in plots protected and exposed to consumers can be used to infer how seed viability may change through time, although these observations need to be made over long enough time spans to obtain reasonable estimates.

5. FUTURE DIRECTIONS

The past decade has seen a slow but steady rise in the number of studies that have examined how consumers influence plant abundance and distribution. Certainly considerable progress has been made since Crawley's (1989) now classic review. At this juncture we are beyond the point of asking 'do herbivores influence plant dynamics?' The more relevant and interesting questions concern 'under what abiotic and biotic conditions do consumers have meaningful effects on plant dynamics?'

Our review suggests that population-level effects of consumers differ among taxa and habitats in ways that are at least partly systematic. However, they do not always follow general expectations based on individual and community-level studies of consumers, or demographic studies of plants in isolation of consumers. For example, in contrast to individual-level studies, vertebrates and invertebrate consumers equally affected plant population

growth rates. As well, after removing studies on biocontrol and domestic grazers, floral and seed predators had roughly equivalent effects on plant population growth than other herbivores, in opposition to expectations based on plant life-history theory. Merging demographic information on the effects of herbivores on plants with population models offers a simple and powerful way to integrate net effects of consumers on plants. Important methodological issues include adequately addressing the role of density dependence and seed banks in plant population dynamics.

Many of the issues raised in this review apply equally to understanding how other common processes, such as pollen limitation or plant-plant competition, influence plant abundance. We know surprisingly little about how these interactions influence plants at the population level (Howard & Goldberg 2001; Ashman *et al.* 2004), nor their importance relative to other abiotic or biotic factors. The challenge for the future is to refine experiments and models so that impacts of consumers on plant dynamics can be placed in a more holistic framework where complexities of plant life history can be integrated with experimental demography to understand the important drivers of plant abundance.

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