



## Review

## Impacts of insect herbivores on rare plant populations

Justin Ancheta, Stephen B. Heard\*

Dept. of Biology, University of New Brunswick, PO Box 4400, Fredericton, NB, Canada E3B 5A3

## ARTICLE INFO

## Article history:

Received 19 April 2011

Received in revised form 12 June 2011

Accepted 21 June 2011

Available online 20 July 2011

## Keywords:

Herbivory

Insects

Population size

Vital rates

Density-dependence

Specialization

## ABSTRACT

Population-level impacts of insect herbivory on rare and endangered plants are poorly understood, being frequently suggested but seldom quantified. We compiled 37 studies from the primary literature encompassing 35 rare plant species and at least 63 insect herbivore species, and assessed patterns in the effects of insect herbivores on rare plant populations and vital rates. Only three studies directly quantified effects of insect herbivory on population size or growth rate, with the vast majority instead extrapolating from vital rates to population size. Few studies (eight) studied herbivory experimentally, and feeding guilds other than seed predators have been relatively neglected. Estimates of population-level impacts vary extremely widely, but for many rare plants insect herbivores cause major reductions in survivorship or fecundity or can even drive local extinctions. Four studies documented positive (plant-) density dependence in insect attack, suggesting that herbivores may have a stabilizing influence on plant populations and thus may play a role in regulating rare plant population size. Most reported herbivores of rare plants are oligophagous or polyphagous, but monophagous herbivores of rare plants do exist, and there was no detectable difference in impact among specialization classes. Attack on rare plants by escaped biocontrol agents can sometimes have significant population-level effects, but such cases appear uncommon. Because insect herbivory can strongly suppress rare plant populations or vital rates, we need to know much more about what ecological and evolutionary factors determine the population-level impacts of insect herbivores. We suggest several ways in which the results of such research could inform conservation practices for rare plant species – for example, the possibility of different management regimes for plants under attack by monophagous, oligophagous, and polyphagous herbivores.

© 2011 Elsevier Ltd. All rights reserved.

## Contents

1. Introduction	2395
2. Materials and methods	2396
3. Results and discussion	2397
3.1. Herbivore impacts on rare plant populations: quantity and quality of data	2397
3.2. Documented impacts of herbivores on rare plant populations	2398
3.3. Density-dependence	2400
3.4. Biocontrol herbivores	2400
3.5. Towards a more sophisticated understanding of insect herbivory on rare plants	2400
4. Conclusions	2401
Acknowledgements	2401
Appendix A. Supplementary material	2401
References	2401

## 1. Introduction

The field of plant conservation biology has been built upon decades of research into plant population dynamics and distributions and the factors that affect them (Harper, 1977; Silvertown and

\* Corresponding author. Tel.: +1 506 452 6047; fax: +1 506 453 3583.

E-mail address: [sheard@unb.ca](mailto:sheard@unb.ca) (S.B. Heard).

Charlesworth, 2001). Historically, heavy emphasis has been placed on abiotic factors influencing populations (e.g., Moloney and Levin, 1996; Pearson and Dawson, 2003), as well as on dispersal (e.g., Schupp and Fuentes, 1995), competition (e.g., Wilson and Tilman, 1993) and vertebrate herbivory (e.g. Crawley, 1988; Mulder, 1999). It is only recently that much attention has been paid to the potential for insect herbivory to affect plant populations. Crawley (1989), among others, argued forcefully that the enormous literature documenting insect herbivore damage to plant individuals supported little in the way of strong conclusions about impacts on populations, and there was (then) little evidence to support the notion that insect herbivory frequently or importantly suppresses plant populations. However, there were dissenting voices, including Louda (2001) who in summarizing her work showing strong effects of insect herbivory on *Hazardia squarrosa* and *Isocoma venata* populations set it in a context of trophic cascade theory (Hairton et al., 1960). Early work by biocontrol specialists, indicating the possibility of plant population suppression by insect attack, also seems to have been underappreciated by the ecological mainstream. More recently, increasing interest in the “enemy escape” hypothesis for success of invasive plants carries a clear implication that insect herbivory must be capable of suppressing plant population growth in some cases (Keane and Crawley, 2002; Halpern and Underwood, 2006). Maron and Crone (2006) reviewed studies of herbivore impact on plant populations, and found that insect herbivory has important effects on the population dynamics of many, but not all, plant species. As a result, a major goal for the study of insect–plant interactions should be to understand when (for what species, at what times or places, or under what ecological conditions) insect herbivory drives plant population dynamics, and when it does not (Halpern and Underwood, 2006; Maron and Crone, 2006).

Population-level effects of insect herbivory are of potentially critical importance in the context of rare plant conservation. Any effect of herbivory on vital rates such as survivorship or fecundity, if transduced into an effect on population size or growth rate, could drive a rare plant to extinction or limit its recovery. Furthermore, rare plants that contend with abiotic stresses or competitive pressure might find those impacts exacerbated, either additively or synergistically, by herbivory. The plant conservation literature has not ignored herbivory, but insect herbivores have received relatively little attention compared to vertebrate herbivores. There is scattered evidence for large impacts of insect herbivory on at least some rare plant populations (e.g. Schöps, 2002), but no systematic assessment of the nature, frequency, and importance of such effects. Such an assessment has the potential to advance conservation practices, for instance by suggesting when intervention to mitigate insect herbivory might be productive, and whether the appropriate intervention might differ for insect herbivores from different feeding guilds or with different degrees of diet specialization.

Unsurprisingly, much of what we know about herbivore impacts on plant populations comes from common species that provide logistically amenable model systems. However, effects of insect herbivory on rare plants do not necessarily follow directly from available data for more common plants. Rare plants, and especially those that have been persistently rare in evolutionary time, may not experience the same degree or kind of herbivory as do their common relatives, and may not respond (ecologically or evolutionarily) the same way. For example, search costs are likely to oppose the evolution of diet specialization on rare hosts. Furthermore, specialists are more likely than generalists to be absent from small populations of their hosts (Zabel and Tschardt, 1998), and so may be unlikely to persist on a host that is rare everywhere even if they do evolve. On the other hand, if rarity makes a plant unapparent, then optimal defense theory suggests allocation to qualitative rather than quantitative defenses (Feeny,

1976), and this could favor attack by specialists. At least some specialist herbivores do exist on rare plants (e.g. Schöps, 2002), and when they have population-level impacts on their hosts they will pose an interesting challenge in balancing the conservation interests of the host plant and the herbivore. Thus, how insect herbivores impact population dynamic of rare plants is an interesting question in its own right and not simply an extrapolation from what we know about more common plants.

Here we review available research into the population-level effects of insect herbivory on rare plants. We compare the prevalence of reports – and where possible compare population-level reductions in survivorship and fecundity due to insect attack – among plants showing different forms of rarity, among feeding guilds of herbivores, and among monophagous, oligophagous and polyphagous insects. We also examine the prevalence of reports of impact by biocontrol insects on rare native plants. We use our data to make preliminary tests of a number of hypotheses, among them that seed predators will have stronger impacts than members of other feeding guilds (Crawley, 2000), that monophagous herbivores will have lower impacts than generalists (Gavloski and Lamb, 2000) but that they will be uncommon on rare plants, and that insect herbivory can exert (plant-) density-dependent impact on rare plants, stabilizing plant populations (Heard and Remer, 2008) and thus potentially braking declines toward extinction. We also set out a framework for thinking about management interventions to mitigate insect herbivory, with particular reference to strategies appropriate for monophagous, oligophagous, and polyphagous herbivores. Our review illustrates the potential importance of insect herbivory for plant conservation, but the study of insect–rare plant interactions is clearly still in its infancy.

## 2. Materials and methods

We gathered publications studying effects of insect herbivory on rare plant populations beginning with searches of the Biological Abstracts and Web of Science (Thomson Reuters) databases, using the search string “(rare or threat\* or endang\*) and herbiv\*”. We supplemented our search results with studies cited by, or citing, publications from our original search. We assigned each studied plant to one of Rabinowitz’s (1981) seven forms of rarity (which distinguish combinations of local population sizes, niche breadth, and geographical range; see Fig. 3). Most studies were of globally rare plants, usually endemic to a small geographic range (e.g., Schöps, 2002), but our compilation also includes examples of species that are widespread but uncommon (e.g., Mulvaney et al., 2006), once common plants now reduced to rarity (e.g., Rose et al., 2005), and plants considered threatened in only parts of their range (e.g., Bouchard et al., 2008).

We examined each publication found and retained those that report impacts of insect herbivory on plant population sizes, growth rates or vital rates (here defined as demographic parameters such as survivorship and net fecundity). We use the phrase “net fecundity” to refer to a plant’s production of seed. Reductions in net fecundity due to herbivory may arise because herbivory impairs seed set (e.g., consumption of flowers or ovules, or consumption of vegetative tissue with reproductive consequences) or because herbivores remove seed after it has been set. Impacts on population sizes and growth rates are by definition impacts on population dynamics, while impacts on population-level vital rates are likely (but not certain; see Section 3.1) to have population-dynamic consequences. We were particularly interested in quantitative estimates of population-level impacts, but our compilation includes a number of papers that report the existence of population-level impacts, but do not quantify them. We excluded many papers that simply report the presence of insect herbivores or

herbivory on a rare plant (e.g., Dalrymple, 2007; Messing et al., 2007), or report levels of tissue damage such as defoliation or florivory without connecting this damage to population size or vital rates (e.g., Fletcher et al., 2001; Bouchard et al., 2008). We also excluded studies that use only simulated herbivory or report only laboratory data (e.g., Ancheta et al., 2010) and studies of seed predation that measure removal of artificially presented seed (e.g., Montesinos et al., 2006). We included studies based on observational data (often, longitudinal studies of plants or populations under herbivore attack) or controlled experiments (usually herbivore removals), and a few that use demographic models parameterized with individual-level observational or experimental data to make population-level predictions.

For each study in our compilation, we recorded the documented effect of insect herbivory on plant population size or vital rates. We calculated each effect on vital rates as a percentage decrease in either annualized survivorship or net fecundity. In some cases these were reported directly, but in others we extracted impact estimates from figures or calculated them from other reported quantities. In general, the effects reported were of insects at ambient densities in the field; that is, the herbivore load for which impact was reported was not controlled by the authors and was usually not quantified. This means we report an estimate of the impact actually felt by the real population at ambient herbivore densities, rather than attempting to calculate impact per unit of herbivore load. From a plant population-dynamics point of view, of course, this “ambient” impact estimate is the appropriate one. Where separate estimates of impact were reported for multiple sites or years, we calculated an average impact, weighting by population sizes where possible so that we report the impact on the average plant individual. Many studies surveyed multiple sites (up to 59) but none reported data from more than 2 years.

For studies able to test for (plant) density dependence in herbivore impact, we recorded the sign of density dependence if it was statistically significant – with “positive” density-dependence in impact meaning that herbivory imposes a greater reduction in per-capita reproduction or survival in larger plant populations. Note that positive density-dependence in impact will give rise to negative (stabilizing) density-dependence in plant population dynamics. We use the term “density-dependence” because it is standard in the population-dynamics literature, but there is potential for confusion because many studies report population “density” of local plant patches where patch area is defined by the minimum polygon containing all observed plants. This definition is not useful for population-dynamic purposes; for example, it makes density of a 1-plant patch infinitely large, whereas a population on the brink of extirpation really has a low population density. Thus, the tests we report are generally based on population sizes, with the division by area implicitly assumed.

We recorded two important characteristics of the insect herbivores associated with rare host plants. The first was the herbivore's feeding guild, or type of plant tissue consumed (folivory, florivory, seed predation, etc.). The second was herbivore diet breadth, where we distinguished between monophagous (feeding exclusively on one species), oligophagous (feeding on multiple species within a plant family) and polyphagous (feeding on hosts in more than one plant family) insects. We also checked whether the insect was native or introduced, and if introduced, recorded cases of bio-control agents that expanded their host ranges to include rare native plants. When characteristics of herbivores or plants were not reported, we consulted other literature and online databases as appropriate.

Our compilation included relatively few studies, and many did not support the kind of standardized effect-size calculation needed for most formal statistical meta-analyses (Cooper et al., 2009). However, we did use our compiled quantitative estimates of herbi-

vore impact to make statistical tests of a number of hypotheses. Because of the recently shifting literature view of the importance of insect herbivory for plant population dynamics (compare Crawley, 1989; Maron and Crone, 2006), we used regression to test for changes over time in the rate of publication. We divided the period from 1985 to 2009 into 5-year intervals and tabulated the number of publications appearing in our compilation per interval. To specifically detect changes in interest in insect herbivory, we normalized these raw publication rates to the overall publication rate of papers in conservation biology for the same intervals (searching the same database on “conservation” but using Web of Science's “refine results” tool to exclude papers from other fields). We compared effects reported on survivorship vs. net fecundity, effects on plants showing different forms of rarity (Rabinowitz, 1981), and effects on vital rates due to monophagous, oligophagous, and polyphagous herbivores using analyses of variance, testing significance by randomization because of concern about distributional assumptions. Because these analyses have limited statistical power, they are best seen as illustrative rather than rigorous tests of hypotheses. Regression was conducted with R (R Development Core Team, 2010), randomization ANOVAs with software written in Microsoft QuickBASIC (Microsoft Inc., Redmond, WA) by one of us (SBH), and power analysis using SAS version 8.0 PROC POWER (SAS Institute, Cary, NC).

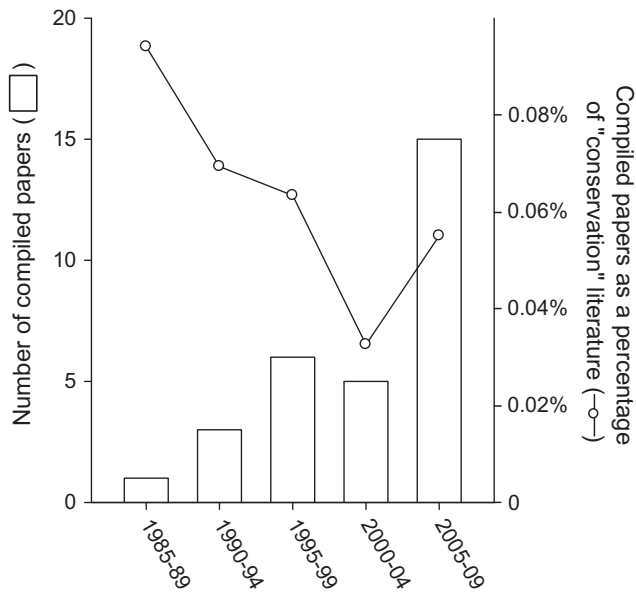
### 3. Results and discussion

#### 3.1. Herbivore impacts on rare plant populations: quantity and quality of data

We know very little about the population-level impacts of insect herbivory on rare plants. We could locate just 37 publications reporting such impacts on 35 rare plant species (involving at least 63 herbivores). Of these, 29 studies (of 27 plant species) included quantitative estimates of impact (Appendix S1), with a further eight studies (of eight plant species) implying but not quantifying population-level impacts (Appendix S2). While the rate of publication of papers qualifying for inclusion in our compilation has increased over the last 25 years, this is entirely accounted for by an increasing publication rate for conservation biology in general (Fig. 1; publication rate vs. 5-year interval,  $F_{1,4} = 0.75$ ,  $p = 0.45$ ). Most studies (27) report only observational data, with just eight using controlled experiments and two combining observational data with demographic modeling.

The most obvious limitation of our data is that just three studies provide direct estimates of herbivore impacts on population size or growth rate, and none of those used controlled experiments: one study observed local extinctions of an endemic New Zealand speargrass under attack by a monophagous weevil (Schöps, 2002), and two used demographic models parameterized with observational data to predict major population declines of thistles under attack by seed predators and other herbivores (for Pitcher's thistle, attack accelerates 50% population decline from 67 to 5 years; Louda et al., 2005; and for Platte thistle, attack has the potential to cause extinction; Rose et al., 2005). The remaining 34 studies focused instead on how herbivory affected vital rates (net fecundity or survivorship), in most cases discussing but not testing extrapolations to population size.

Extrapolations from vital rates to population sizes are problematic (Halpern and Underwood, 2006) in part because, when vital rates are non-independent, changes in vital rates need not lead to population-size change. For instance, insect-induced and resource-controlled fruit abortion may be compensatory (Casper and Niesenbaum, 1993; Shapiro and Addicott, 2004; Kaiser et al., 2008). Even when herbivore attack directly reduces net fecundity,



**Fig. 1.** Publication rate for studies reporting population-level impacts of insect herbivory on rare plants. Bars show raw number of publications (counts of those papers included in Table 1). Open circles show publication rate, normalized to a Web of Science search for “conservation” (using Web of Science’s ‘refine results’ tool to include conservation biology and exclude other disciplines).

effects on seedling recruitment and thus population growth are not guaranteed. For example, if recruitment is site-limited (Louda, 1983; Eriksson and Ehrlén, 1992), then even large changes in seed survivorship may not lead to population-level change (Crawley, 1989). Discussions of seed-predator impact rarely consider the likelihood of seed- vs. site-limitation, at least for rare plants (but see Beville et al., 1999).

The observational nature of most studies allows another important kind of non-independence: in some cases insects may prefer (Price, 1991), or their effects may be amplified on, plants weakened due to pathogens or stress. Such plants could have shown reduced reproduction or survivorship regardless of insect attack, and attack may be a symptom as much as a cause of observed differences in vital rates. Experimental manipulation of insect attack allows stronger tests of causal hypotheses, but such approaches are uncommon (8/37 studies). Feasible experimental approaches include contrasts of control plants with herbivore exclusions by pesticides or enclosures (e.g., Beville et al., 1999; Watts et al., 2010). Experimental increases in herbivore pressure would be extremely informative but may not be ethically or legally acceptable with endangered host plants. In fact, ethical and legal issues may often weigh against the use of experimental methods in the study of herbivory on rare plants, as will the logistical challenges often associated with field experiments. Fortunately, both shortages of available plants and reluctance to experimentally inflict damage can be overcome by using plants grown *ex situ* and either exposed to captive herbivores or transplanted into the field for exposure to natural herbivory (e.g., Wiles et al., 1996; Stiling et al., 2004; Ancheta et al., 2010). This approach does, however, carry the issue of differences in plant condition from greenhouse to field, and depends on the availability of efficient propagation methods for plants and perhaps herbivores.

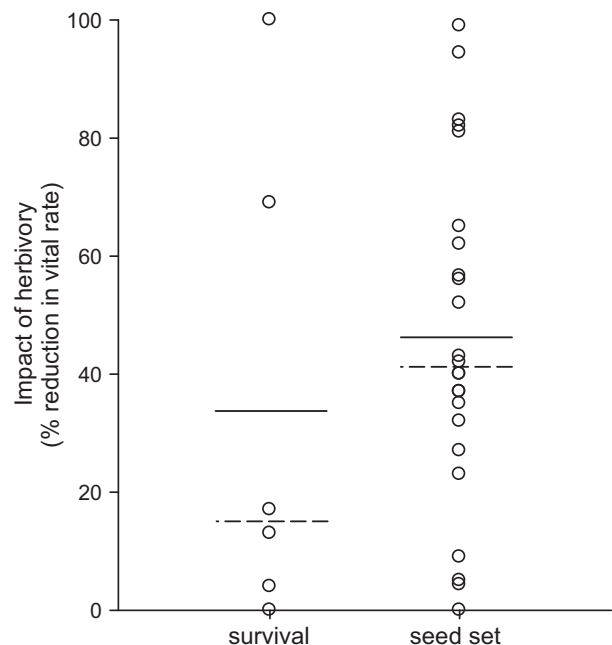
### 3.2. Documented impacts of herbivores on rare plant populations

Most studies of insect herbivory on rare plant populations have emphasized impacts on vital rates, usually net fecundity (28 cases) or survivorship (10 cases; some studies examined more than one vital rate). A few studies reported effects on other vital rates,

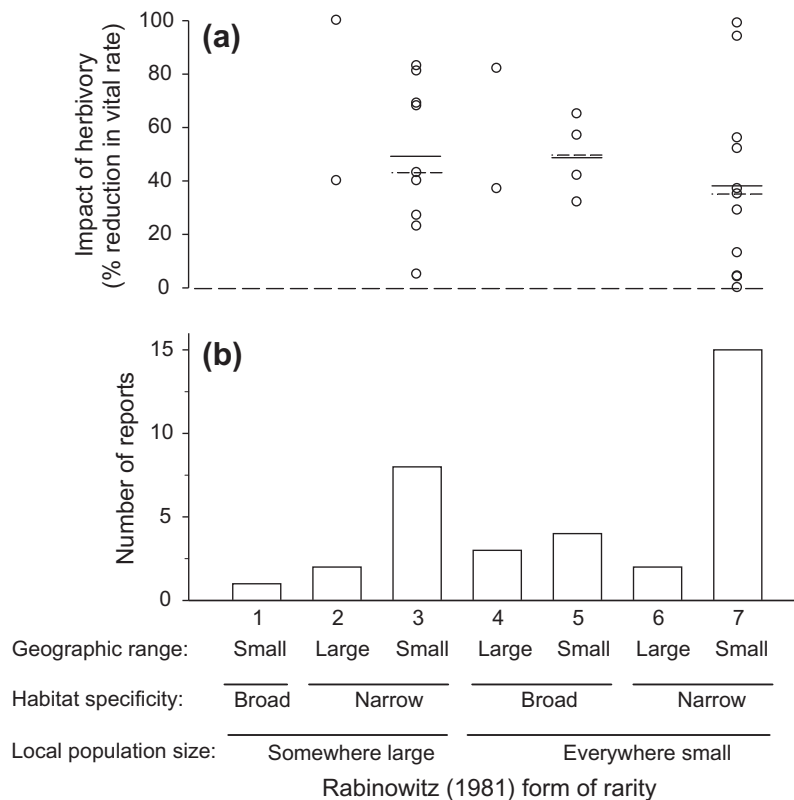
including fruit set (four studies), floral production (three), and seedling recruitment (one). Average reported impacts of herbivory on survivorship and net fecundity do not differ significantly ( $F_{1,28} = 0.75$ ,  $p = 0.39$ ), and span virtually the entire possible range (survivorship, 0–100% reduction; net fecundity, 0–99% reduction; Fig. 2). Mean impacts are substantial (~35–45%). The few studies directly examining population size or growth rate report similarly substantial effects (see previous section). Broad ranges in impact estimates are unsurprising, as herbivore impact will depend on variation within and among species in many traits of both insect and plant (for instance, seed size for seed predators; Carillo-Gavilán et al., 2010; or secondary chemistry for folivores and phloem-feeders; Mooney and Agrawal, 2008).

It is striking that a large fraction of compiled studies show strong herbivore impacts. This establishes that insect herbivory can be an important threat for rare plants, but it need not mean that most rare plants experience such impacts. Researchers may target their investigations on plants that appear to be impacted, or may study plants regardless of expected impact but not publish (or not be able to publish) studies in which no significant impact is found (the “file-drawer problem”; Rosenthal, 1979). Indeed, the only two studies in our compilation reporting negligible effects of insect herbivory (Menges et al., 1986; Kettenring et al., 2009) did so in comparison with other herbivores with substantial impacts. Methods for quantifying file-drawer effects require better effect-size data than are available in the compiled studies.

Fortunately, file-drawer problems should not prevent meaningful comparisons within our compiled data – for instance, across herbivore feeding guilds or forms of plant rarity. We begin with feeding guilds, because of considerable literature interest in relative impacts of herbivores feeding in different ways (e.g. Crawley, 2000; Maron and Crone, 2006). Over half the studies in our compilation involve seed predators (34/63); folivores are the next most common guild (12 cases), followed by florivores (9), phloem-suckers (8) and stem-borers (4). There is considerable overlap in definition of feeding guilds, as many insects feed on multiple parts of their hosts. Although frugivory was rarely reported (one study), many seed predators presumably also damage fruits. There were



**Fig. 2.** Distribution of reported impacts of herbivore attack on annualized survivorship and net fecundity. Impact is quantified as percent reduction in the vital rate, compared with the expected value in the absence of herbivore attack. Solid horizontal lines are means; dashed lines are medians.



**Fig. 3.** (a) Reported impacts of herbivore attack, for each of Rabinowitz's (1981) seven forms of rarity. Impacts are on annualized survivorship or net fecundity (or in one case, impact on product of survivorship and net fecundity). Solid horizontal lines are means; dashed lines are medians. (b) Reported cases of rare plants with herbivore impact on population sizes or vital rates. Studies reporting but not quantifying impacts occur in the bottom panel but not the top.

only three studies of root herbivores, which likely reflects the difficulty of studying below-ground herbivory as much as the true prevalence of such interactions.

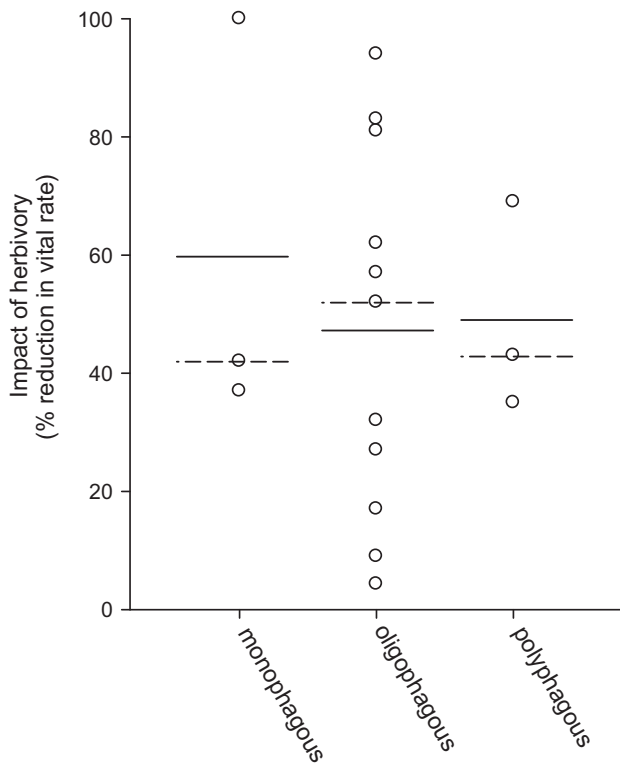
Many ecologists have argued that among feeding guilds, seed predators have particularly strong effects on plant population biology (Crawley, 2000), with plants likely to tolerate (in contrast) considerable damage by herbivores attacking non-reproductive tissue. However, meta-analysis by Maron and Crone (2006) found no significant difference in the population-level impact of seed predators and insects from other feeding guilds. For rare plants, we found seed predators to have severe population-level impacts (average reduction in vital rates of 46%), but strong impacts of insects from other feeding guilds are certainly possible (for example, Helenurm (1998) documented a 69% decrease in survivorship for lupines under attack by a folivorous caterpillar). Unfortunately, there are too few quantitative estimates to compare impacts among feeding guilds: only seed predators had more than three estimates.

Rarity is not a simple thing. The expected impact of herbivory could be quite different on a host plant that has recently declined to rarity vs. one that has been rare through evolutionary time, but unfortunately the former class is represented in our compilation by just a single study (Rose et al., 2005, Platte thistle). Similarly, impacts could differ among host plants showing different forms of rarity with respect to niche breadth, geographic range, and local population sizes (Rabinowitz, 1981). Among three Rabinowitz forms of rarity with enough impact estimates for analysis (classes 3, 5, and 7; Fig. 3b), there was no difference in impacts ( $F_{2,21} = 0.36$ ,  $p = 0.69$ ). However, these classes are all of endemics, so we cannot make any comparison with widespread but uncommon plants.

We assessed feeding specialization for the insects in our compilation for two reasons: first, generalists and specialists might have different impacts on their hosts, and second, mitigating their im-

pacts might require different conservation strategies. Gavloski and Lamb (2000) argued that specialists might have lower impacts because they can evolve high feeding efficiencies, but found no such pattern for seven insect herbivores of canola. Similarly, we found no difference in impact among specialization classes ( $F_{2,14} = 0.17$ ,  $p = 0.84$ ; Fig. 4). Unfortunately, our power to make this comparison is low because we had quantitative impact estimates for only three studies each of polyphagous and monophagous herbivores. (For a large effect size,  $f = 1.0$  (Cohen, 1988), this test with 11, 3, and 3 cases has power = 0.15; power would increase to 0.25 for the same number of cases spread evenly across specialization classes, or to 0.50 for 11 cases in each class.) The paucity of studied monophagous herbivores on rare plants is not surprising, since arguments based on foraging efficiency suggest they should be unusual. However, such specialization does occur, and monophagous herbivores may even be underreported since they are less likely than generalists to be abundant or to be discovered away from the focal host.

The existence of monophagous herbivores of rare plants raises interesting conservation issues, because they may exert strong impacts on threatened hosts while themselves being targets of conservation concern (Hopkins et al., 2002). The specialist weevil *Hadramphus spinipennis* attacking Dieffenbach's speargrass in New Zealand (Schöps, 2002) provides a good example. Weevils extirpate local speargrass populations, but a program to protect the host plant from damage would only exacerbate the threat to the weevils, which have no other host. Similar pairs of threatened monophagous herbivores and hosts include the non-pollinating yucca moth *Teguticula corruptrix* and its host *Yucca glauca* in western Canada (COSEWIC, 2006) and two Australian *Acizzia* plant-lice and their host trees *Acadia veronica* and *Pultenaea glabra* (Taylor and Moir, 2009).



**Fig. 4.** Reported impacts of herbivore attack as a function of degree of host specialization. Impact is quantified as percent reduction in annualized survivorship or net fecundity, compared with the expected value in the absence of herbivore attack. Solid horizontal lines are means; dashed lines are medians.

Oligophagous and polyphagous herbivores of rare plants should be much more common, and conservation efforts might usefully treat them differently. (While polyphagous herbivores are poorly represented in our compilation, we suspect they may be under-sampled as researchers focus on tightly interacting species pairs rather than “incidental” attack by broad generalists.) When oligophagous herbivores have significant impacts, the presence of related plants providing alternative hosts can increase damage on the focal, rare, host by spill-over herbivory (e.g., Pemberton et al., 1985; White and Whitham, 2000). Impacts of such herbivores might be controlled by local removal of alternative hosts, although to our knowledge this approach has not been attempted in the field. A related strategy has been suggested (Stiling et al., 2004) for reducing *Cactoblastis* moth attack on the endangered Florida cactus *Opuntia corallicola*, involving outplanting of *O. corallicola* far from the alternative host (*O. stricta*). Reducing the impact of polyphagous herbivores will require different management strategies, because removal of all potential hosts will usually be infeasible (but see Norden and Kirkman, 2004). Instead, broad-spectrum measures such as pesticide spraying might be the only way to deal with damaging polyphagous herbivores. For example, Watts et al. (2010) recommended use of bacterial insecticide to control seed predation on an endangered broomrape by tortricid caterpillars in the genus *Clepsis*, of which most are polyphagous (Alford, 1976; Harris et al., 1985).

### 3.3. Density-dependence

A critically important question for plant population dynamics and conservation is whether the per-capita impact of herbivory changes with plant population density. When insect attack is positively density-dependent – so that damage increases and plant

reproduction or survival declines as plant populations grow – herbivory has the potential to regulate plant population size, perhaps maintaining rarity but also opposing declines towards extinction. In contrast, negatively density-dependent attack would be destabilizing and could drive extirpation of populations below a critical size. The achievement of stable biocontrol of invasive plants in some systems (e.g. McConnachie et al., 2003; Moran et al., 2005) strongly implies that density-dependent attack can regulate plant populations, but does not establish whether it can do so for rare, native plants. Ouborg et al. (2006) argued that small plant populations might be less vulnerable to herbivory, but were unable to cite data for rare plant species.

Our compilation includes just six studies that allow tests for density dependence, but strikingly, positive (stabilizing) density-dependence was detected in four of them (Bigger, 1999; Kéry et al., 2001; Colling and Matthies, 2004; Camper, 2007). Density-dependence was strong in each case; for instance, across the ambient range of plant densities seed damage per plant doubled for a rare aster (Bigger, 1999) and the fraction of flower heads damaged increased from 0% to 90% for a rare *Scorzonera* (Colling and Matthies, 2004). A fifth study (Stanforth et al., 1997) trended non-significantly in the same direction, and no study showed any trend towards negative density-dependence. While we considered only the possibility of linear density-dependence, nonlinearity in the response of attack to density is possible (for instance, with a type III functional response by the herbivore) although much more data would be required for powerful tests of nonlinearity.

Advancing our understanding of density dependence in insect attack on rare plants will, unfortunately, be a substantial challenge. Tests for density dependence are rare because they require measurement of herbivore impact in multiple populations or at multiple time points (with or without density manipulation by the researcher) – something that is logistically challenging for any system but particularly difficult for rare plants.

### 3.4. Biocontrol herbivores

The possibility that exotic herbivores introduced for biocontrol might expand their host ranges to impact rare native plants is frequently discussed (e.g., Louda et al., 2003; Sheppard et al., 2005; Chalak et al., 2010). However, we could locate just two well-studied examples: attack by the weevil *Rhinocyllus conicus* on the threatened thistles *Cirsium canescens* and *C. pitcheri* (Louda et al., 2005; Rose et al., 2005), and attack by the moth *Cactoblastis cactorum* on the endangered cactus *O. corallicola* (Stiling et al., 2004). In the latter case, considerable range expansion by the herbivore preceded its non-target impact. While the danger biocontrol agents represent to rare native plants is important, currently this threat is either seldom realized (perhaps because of extensive pre-release screening in modern biocontrol programs) or else seldom documented.

### 3.5. Towards a more sophisticated understanding of insect herbivory on rare plants

While the small size of our compilation (Appendix S1) is troubling enough, simply adding more quantitative estimates will not close what we have identified as a major knowledge gap. Nearly all compiled studies take a phenomenological approach. A few studies (e.g., Bevill et al., 1999) have explored plant–herbivore interactions in detail to yield mechanistic insight and predictive power, but in most cases we struggled just to extract point estimates of herbivore impact on a single vital rate. We should aim to do better than point estimates, because insect herbivory often shows extremely high spatial and temporal variance (e.g., Royama et al., 2005; Halverson et al., 2008), which can lead to complex

ecological and evolutionary interactions in time and space (Thompson, 2005). Glossing over spatial variation could lead us to underestimate potential herbivore impacts at local scales, which may determine microdistribution of a plant and thus limit its regional population size. For example, White and Robertson (2009) documented nearly complete seed predation by harvester ants on an endangered peppergrass, but only for plants located within 10 m of harvester ant colonies.

A final complication is that our review, like most of the literature on which it is based, considers insect herbivory in isolation from other stresses on plant populations. If herbivory interacts non-additively with other stresses such as competition, then studies manipulating herbivory alone will have little predictive power. From a more applied perspective, when stresses interact conservation strategies will need to consider how interventions aimed at mitigating one stress will affect the impact of another. This is illustrated well by Norden and Kirkman (2004), who showed that exclusion of competing vegetation from *Schwalbea americana* populations increased attack by a nymphalid caterpillar as plants became more apparent. Our knowledge is far too limited to support generalizations about the frequency of such interactions, which appear to exist for a few rare plants (e.g., Norden and Kirkman, 2004), to be absent for a few others (e.g., Ancheta et al., 2010), but are simply unstudied for most.

#### 4. Conclusions

We have demonstrated that major gaps exist in our understanding of how insect herbivory affects rare plant populations. Because many documented impacts on vital rates are severe, these gaps are important. The potential for insect herbivory to have significant population-level impacts on rare plant species is best documented for seed predators, but we found no evidence that impacts are any lower for herbivores in other feeding guilds. Herbivore impacts are similarly high across all sufficiently studied forms of plant rarity, and survivorship (while less frequently studied) is impacted as strongly as net fecundity. Monophagous herbivores of rare plants do exist, can have very strong impacts, and will present important conservation challenges. Importantly, our compilation suggests that insect herbivory could provide a stabilizing influence on population dynamics of rare plants, as positive density dependence in attack appears to be common. We echo Beville et al. (1999) in arguing that insect herbivory needs to be considered in the conservation of rare plant species. However, moving from general concern to detailed understanding and predictive power will require a considerable increase in research on insect–rare plant interactions. This represents a substantial challenge, but the severity of at least some herbivore impacts and the extent of the modern biodiversity crisis (Stork, 2010) should make a compelling case for the importance of rising to that challenge.

#### Acknowledgements

We are grateful to D. Giberson, S. Hendrix, L. Jesson, R. Larmer, D. Quiring and four anonymous reviewers for comments on the manuscript. R. Johns ran power analyses in SAS for us. Financial support for our work was provided by the (Canadian) Natural Sciences and Engineering Research Council (Discovery Grant to S.B.H.).

#### Appendix A. Supplementary material

Our compilations of studies reporting quantitative estimates of insect herbivore impacts on rare plant populations (Appendix S1) or reporting but not quantifying such impacts (Appendix S2)

are available online. Citations for the tabulated materials are in online Appendix S3. Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2011.06.019.

#### References

- Alford, D.V., 1976. The host range of *Clepsis spectrana* (Treits.) (Lepidoptera: Tortricidae). *Plant Pathology* 25, 166.
- Ancheta, J., Heard, S.B., Lyons, J.W., 2010. Impacts of salinity and simulated herbivory on survival and reproduction of the threatened Gulf of St. Lawrence Aster, *Symphyotrichum laurentianum*. *Botany* 88, 737–744.
- Beville, R.L., Louda, S.M., Stanforth, L.M., 1999. Protection from natural enemies in managing rare plant species. *Conservation Biology* 13, 1323–1331.
- Bigger, D.S., 1999. Consequences of patch size and isolation for a rare plant: pollen limitation and seed predation. *Natural Areas Journal* 19, 239–244.
- Bouchard, A.M., McNeil, J.N., Brodeur, J., 2008. Invasion of American native lily populations by an alien beetle. *Biological Invasions* 10, 1365–1372.
- Camper, T.G., 2007. Factors affecting pollination and seed set of a rare plant (*Sidalcea malachroides*). Humboldt State University.
- Carillo-Gavilán, M.A., Lalagüe, H., Vilà, M., 2010. Comparing seed removal of 16 pine species differing in invasiveness. *Biological Invasions* 12, 2233–2242.
- Casper, B.B., Niesenbaum, R.A., 1993. Pollen versus resource limitation of seed production – a reconsideration. *Current Science* 65, 210–214.
- Chalak, M., Hemerik, L., van der Werf, W., Ruijs, A., van Ierland, E.C., 2010. On the risk of extinction of a wild plant species through spillover of a biological control agent: analysis of an ecosystem compartment model. *Ecological Modelling* 221, 1934–1943.
- Cohen, J., 1988. *Statistical Power Analysis for the Behavioral Sciences*. Lawrence Erlbaum Associates, Hillsdale, NJ.
- Colling, G., Matthies, D., 2004. The effects of plant population size on the interactions between the endangered plant *Scorzonera humilis*, a specialised herbivore, and a phytopathogenic fungus. *Oikos* 105, 71–78.
- Cooper, S., Hedges, L.V., Valentine, J.C., 2009. *The Handbook of Research Synthesis and Meta-analysis*, 2nd ed. Russell Sage Foundation Publications, New York, NY.
- COSEWIC, 2006. COSEWIC assessment and status report on the non-pollinating Yucca Moth *Tegeticula corruptrix* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON.
- Crawley, M.J., 1988. The relative importance of vertebrate and invertebrate herbivores in plant population dynamics. In: Bernays, E.A. (Ed.), *Insect–Plant Interactions*. CRC Press, Boca Raton, FL, pp. 45–71.
- Crawley, M.J., 1989. Insect herbivores and plant population dynamics. *Annual Review of Entomology* 34, 531–564.
- Crawley, M.J., 2000. Seed predators and plant population dynamics. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*, 2nd ed. CAB International, Wallingford, UK, pp. 167–182.
- Dalrymple, S.E., 2007. Biological flora of the British Isles: *Melampyrum sylvaticum* L. *Journal of Ecology* 95, 583–597.
- Eriksson, O., Ehrlén, J., 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91, 360–364.
- Feeny, P.P., 1976. Plant apparency and chemical defence. *Recent Advances in Phytochemistry* 10, 1–40.
- Fletcher, J.D., Shipley, L.A., McShea, W.J., Shumway, D.L., 2001. Wildlife herbivory and rare plants: the effects of white-tailed deer, rodents, and insects on growth and survival of Turk's cap lily. *Biological Conservation* 101, 229–238.
- Gavloski, J.E., Lamb, R.J., 2000. Specific impacts of herbivores: comparing diverse insect species on young plants. *Environmental Entomology* 29, 1–7.
- 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.
- Halverson, K.L., Heard, S.B., Nason, J.D., Stireman III, J.O., 2008. Differential attack on diploid, tetraploid, and hexaploid *Solidago altissima* L. by five insect gallmakers. *Oecologia* 154, 755–761.
- Harper, J.L., 1977. *Population biology of plants*. Academic Press, NY.
- Harris, P., Dunn, P.H., Schroeder, D., Vonmoos, R., 1985. Biological control of leafy spurge in North America. In: Watson, A.K. (Ed.), *Leafy Spurge*, #3. Weed Science Society of America Monograph, pp. 78–92.
- Heard, S.B., Remer, L.C., 2008. Travel costs, oviposition behaviour and the dynamics of insect–plant systems. *Theoretical Ecology* 1, 179–188.
- Helenurm, K., 1998. Outplanting and differential source population success in *Lupinus guadalupensis*. *Conservation Biology* 12, 118–127.
- Hopkins, G.W., Thacker, J.L., Dixon, A.F.G., Waring, P., Telfer, M.G., 2002. Identifying rarity in insects: the importance of host plant range. *Biological Conservation* 105, 293–307.
- Kaiser, C.N., Hansen, D.M., Muller, C.B., 2008. Habitat structure affects reproductive success of the rare endemic tree *Syzygium mamillatum* (Myrtaceae) in restored and unrestored sites in Mauritius. *Biotropica* 40, 86–94.
- Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy-release hypothesis. *Trends in Ecology and Evolution* 17, 164–170.
- Kéry, M., Matthies, D., Fischer, M., 2001. The effect of plant population size on the interactions between the rare plant *Gentiana cruciata* and its specialized herbivore *Maculinea rebeli*. *Journal of Ecology* 89, 418–427.

- Kettenring, K.M., Weekley, C.W., Menges, E.S., 2009. Herbivory delays flowering and reduces fecundity of *Liatris ohlingerae* (Asteraceae), an endangered, endemic plant of the Florida scrub. *Journal of the Torrey Botanical Society* 136, 350–362.
- Louda, S.M., 1983. Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae), along a climatic gradient. *Ecology* 64, 511–521.
- Louda, S.M., 2001. Discovering an effect of insect floral herbivory on plant population density and distribution in a “green world”. *Bulletin of the Ecological Society of America* 82, 229–231.
- Louda, S.M., Arnett, A.E., Rand, T.A., Russell, F.L., 2003. Invasiveness of some biological control insects and adequacy of their ecological risk assessment and regulation. *Conservation Biology* 17, 73–82.
- Louda, S.M., Rand, T.A., Arnett, A.E., Mcclay, A.S., Shea, K., McEachern, A.K., 2005. Evaluation of ecological risk to populations of a threatened plant from an invasive biocontrol insect. *Ecological Applications* 15, 234–249.
- Maron, J.L., Crone, E.E., 2006. Herbivory: effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society (London) B* 273, 2575–2584.
- McConnachie, A.J., Hill, M.P., Bryne, M.J., de Wit, M.P., 2003. Economic evaluation of the successful biological control of *Azolla filiculoides* in South Africa. *Biological control* 28, 25–32.
- Menges, E.S., Waller, D.M., Gawler, S.C., 1986. Seed set and seed predation in *Pedicularis furbishiae*, a rare endemic of the St. John River, Maine. *American Journal of Botany* 73, 1168–1177.
- Messing, R.H., Tremblay, M.N., Mondor, E.B., Foottit, R.G., Pike, K.S., 2007. Invasive aphids attack native Hawaiian plants. *Biological Invasions* 9, 601–607.
- Moloney, K.A., Levin, S.A., 1996. The effects of disturbance architecture on landscape-level population dynamics. *Ecology* 77, 375–394.
- Montesinos, D., Garcia-Fayos, P., Mateu, I., 2006. Conflicting selective forces underlying seed dispersal in the endangered plant *Silene diclinis*. *International Journal of Plant Sciences* 167, 103–110.
- Mooney, K.A., Agrawal, A.A., 2008. Plant genotype shapes ant-aphid interactions: implications for community structure and indirect plant defense. *American Naturalist* 171, E195–E205.
- Moran, V.C., Hoffmann, J.H., Zimmermann, H.G., 2005. Biological control of invasive alien plants in South Africa: necessity, circumspection, and success. *Frontiers in Ecology and the Environment* 3, 77–83.
- Mulder, C.P.H., 1999. Vertebrate herbivores and plants in the Arctic and subarctic: effects on individuals, populations, communities and ecosystems. *Perspectives in Plant Ecology Evolution and Systematics* 2, 29–55.
- Mulvaney, C.R., Molano-Flores, B., Whitman, D.W., 2006. Is insect herbivory contributing to the threatened status of *Agalinis auriculata* (Orobanchaceae) in Illinois? *Journal of the Torrey Botanical Society* 133, 560–565.
- Norden, A.H., Kirkman, L.K., 2004. Herbivory of the federally endangered *Schwalbea americana*. *Castanea* 69, 67–68.
- Ouborg, N.J., Vergeer, P., Mix, C., 2006. The rough edges of the conservation genetics paradigm for plants. *Journal of Ecology* 94, 1233–1248.
- Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12, 361–371.
- Pemberton, R.W., Turner, C.E., Rosenthal, S.S., 1985. New host records for tephritid flies (Diptera) from *Cirsium* and *Saussurea* thistles (Asteraceae) in California. *Proceedings of the Entomological Society of Washington* 87, 790–794.
- Price, P.W., 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62, 244–251.
- R Development Core Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rabinowitz, D., 1981. Seven forms of rarity. In: Synge, H. (Ed.), *The Biological Aspects of Rare Plant Conservation*. John Wiley and Sons, New York, NY, pp. 205–217.
- Rose, K.E., Louda, S.M., Rees, M., 2005. Demographic and evolutionary impacts of native and invasive insect herbivores on *Cirsium canescens*. *Ecology* 86, 453–465.
- Rosenthal, R., 1979. The file drawer problem and tolerance for null results. *Psychological Bulletin* 86, 638–641.
- Royama, T., MacKinnon, W.E., Kettela, E.G., Carter, N.E., Hartling, L.K., 2005. Analysis of spruce budworm outbreak cycles in New Brunswick, Canada, since 1952. *Ecology* 86, 1212–1224.
- Schöps, K., 2002. Local and regional dynamics of a specialist herbivore: overexploitation of a patchily distributed host plant. *Oecologia* 132, 256–263.
- Schupp, E.W., Fuentes, M., 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2, 267–275.
- Shapiro, J., Addicott, J.F., 2004. Re-evaluating the role of selective abscission in moth/yucca mutualisms. *Oikos* 105, 449–460.
- Sheppard, A.W., van Klinken, R.D., Heard, T.A., 2005. Scientific advances in the analysis of direct risks of weed biological control agents to nontarget plants. *biological control* 35, 215–226.
- Silvertown, J.W., Charlesworth, D., 2001. *Introduction to Plant Population Biology*. Blackwell Scientific Publications, Oxford, UK.
- Stanforth, L.M., Louda, S.M., Beville, R.L., 1997. Insect herbivory on juveniles of a threatened plant, *Cirsium pitcheri*, in relation to plant size, density and distribution. *Ecoscience* 4, 57–66.
- Stiling, P., Moon, D., Gordon, D., 2004. Endangered cactus restoration: mitigating the non-target effects of a biological control agent (*Cactoblastis cactorum*) in Florida. *Restoration Ecology* 12, 605–610.
- Stork, N.E., 2010. Re-assessing current extinction rates. *Biodiversity and Conservation* 19, 357–371.
- Taylor, G.S., Moir, M.L., 2009. In threat of co-extinction: two new species of *Acizzia* Heslop-Harrison (Hemiptera: Psyllidae) from vulnerable species of *Acacia* and *Pultenaea*. *Zootaxa* 2249, 20–32.
- Thompson, J.N., 2005. *The Geographic Mosaic of Coevolution*. University of Chicago Press, Chicago, IL.
- Watts, S.M., Uhl, M.M., Maurano, S.P., Nuccio, E.E., 2010. Using small-scale studies to prioritize threats and guide recovery of a rare hemiparasitic plant: *Cordylanthus rigidus* ssp. *littoralis*. *Plos One* 5, e8892. doi:10.1371/journal.pone.0008892.
- White, J.A., Whitham, T.G., 2000. Associational susceptibility of cottonwood to a box elder herbivore. *Ecology* 81, 1795–1803.
- White, J.P., Robertson, I.C., 2009. Intense seed predation by harvester ants on a rare mustard. *Ecoscience* 16, 508–513.
- Wiles, G.J., Schreiner, I.H., Nafus, D., Jurgensen, L.K., Manglona, J.C., 1996. The status, biology, and conservation of *Serianthes nelsonii* (Fabaceae), an endangered Micronesian tree. *Biological Conservation* 76, 229–239.
- Wilson, S.D., Tilman, D., 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology* 74, 599–611.
- Zabel, J., Tschardtke, T., 1998. Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially? *Oecologia* 116, 419–425.