Received: 24 May 2022 | Accepted: 26 August 2022

DOI: 10.1111/1365-2745.13996

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

REVIEW

Sprent Review

Long-term impacts of insect herbivores on plant populations and communities

Anurag A. Agrawal[1] | **John L. Maron**[2]

[1]Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York, USA

[2]Division of Biological Sciences, University of Montana, Missoula, Montana, USA

Correspondence
Anurag A. Agrawal
Email: aa337@cornell.edu

Funding information
National Science Foundation, Grant/Award Number: 1901552 and 2209762

Handling Editor: Anne Kempel

Abstract

1. As major consumers of plants, insect herbivores have strong potential to influence long-term patterns of plant abundance and community structure. Nonetheless, remarkably few manipulative experiments exclude insects for three or more years. Thus, how often, and under what conditions insects have enduring impacts remains unclear. Here we summarize the key conceptual issues and evidence from long-term studies on the impact of insects on plant populations and communities.
2. Models that project effects of herbivores on plant population growth, based on demographic study, suggest that insects often limit plant asymptotic population growth. However, empirical estimations of insect impacts on plant abundance based on long-term experimental studies are few. As such, the strength and conditionality of compensatory mechanisms (such as density dependence and seedbanks) that may dampen (or exacerbate) the negative effects of insects on plant populations remains unclear. The influences of insects on plant range size and limits, invasion success and biocontrol are well-established research areas, but are also underexplored in long-term experiments.
3. Insect herbivores can influence plant community structure and diversity, and change successional trajectories, often through modification of plant competitive ability. Nonetheless, effects are mostly known from mesic grasslands, take years to manifest and the extent of insect damage does not always predict their impact. The relative importance of specialist versus generalist herbivores is unclear, as is how feedbacks between plant productivity, herbivory and plant species richness contribute to community dynamics over time.
4. *Synthesis*. The few existing long-term insect suppression experiments, and many short-term studies, suggest that insect herbivores can importantly affect plant populations and communities. Although challenging, experimental studies spanning multiple plant generations could greatly enhance our ability to develop a more predictive framework for how insect herbivores influence plant populations and communities.

KEYWORDS
competition-by-herbivory interaction, determinants of plant community diversity and structure, insect herbivory, long-term manipulative experiments, plant population and community dynamics, plant–herbivore interactions, plant–plant interactions

1 | INTRODUCTION

Long-term ecological experiments have been foundational to understanding the importance of species interactions in population and community ecology (Brown et al., 2001; Power et al., 1996). Such classic studies, to name only a few, include Connell's (1961) removal of barnacles from Scotland's rocky shore, Paine's (1992) experiments involving starfish removal, Lubchenco's (1980) manipulation of algal competition and Carpenter et al.'s (2001) examination of the cascading role of top predators in lakes. These long-term studies were valuable because they assessed the outcome of species interactions as they played out against a background of changes in organismal density, stochasticity in environmental conditions and community change. Indeed, this approach enabled important insights that could not have been predicted from observational studies or shorter-term experiments.

In terms of understanding the enduring effects of herbivores on plants, much of our understanding comes from studies involving vertebrate herbivores. Tansley (1922) was the first to show the power of exclusion experiments in this context. Later, Watt (1981) built on this work, caging out rabbits from British grassland plots for 35 years and demonstrating their strong influences on plant communities. Other long-term experiments have similarly utilized fences or cages to exclude generalist vertebrate herbivores to quantify their manifold impacts (Brown & Heske, 1990; Gómez, 2005; Howe, 2008; Post & Pedersen, 2008; Young et al., 1997). These vertebrate exclusion experiments have occurred across the planet, in tropical, temperate, desert and high-latitude systems (Andriuzzi & Wall, 2017; Chase et al., 2000; Davidson, 1993; Parker et al., 2006). The general message across many of these studies is that vertebrate herbivory reduces the abundance of palatable species, allowing competitively inferior and less palatable species to increase in biomass and abundance (Augustine & McNaughton, 1998; Olff & Ritchie, 1998). These effects, however, can be nuanced, and are often modified depending on underlying ecosystem productivity, with stronger effects occurring in higher versus lower productivity systems (Bakker et al., 2006; Chase et al., 2000; Koerner et al., 2018; Staver et al., 2021).

In contrast to the multitude of exclosure experiments where generalist vertebrate herbivory has been manipulated over long durations, relatively few long-term studies (here conservatively defined as 3 or more years) exist for insect herbivores. Observationally, we know that insect herbivores can occasionally have devastating effects, for example when outbreaking insects kill trees. Yet, chronic low levels of insect herbivory, often inconspicuous, are more the norm, and experiments elucidating the longer-term effects of this type of herbivory on plant populations and communities are relatively scarce (Carson et al., 2004). In an early review of insect suppression on plant productivity, less than 10% of studies were conducted for three or more years (Coupe & Cahill, 2003). Almost 20 years later, the number of longer-term insect herbivore exclusion experiments remains small (Table 1). This is surprising given the ubiquity of plant–insect herbivore interactions, and the voluminous literature documenting negative effects of insect herbivores on plant performance (Hawkes & Sullivan, 2001; Jia et al., 2018; Marquis, 1992).

Although short-term studies have provided the backbone of much of our knowledge about how insects influence plant performance, these studies are often difficult to extrapolate to the population and community levels. The reason for this is that they often do not capture impacts of herbivores across all plant life stages and their transitions, or fail to quantify compensatory effects within or between plant generations. As well, effects of herbivores can be highly variable across years (Cobb et al., 2002; Crawley, 1985; Maron, 1998; Maron et al., 2018; Morrow & LaMarche, 1978; Root, 1996; Shestakov et al., 2020), so single or even two-year studies may not capture true dynamics. As has often been noted for other interactions, longer-term studies are needed to understand how variation in the impacts of insects on plant demographic performance and potential compensatory responses interact to influence plant population abundance. At the community scale, it remains unclear how demographic effects of herbivory within species interact with competitive interactions among species to influence plant community structure. Yet, most models of community change rely on interactions between consumers and competitive ability in predicting outcomes (Mittelbach & McGill, 2019).

In this paper, we outline the key conceptual issues that require longer-term experimental study to predict herbivore impacts on plant populations and communities. We highlight insights that have been gained from the handful of longer-term insect suppression experiments, nearly all of which have been published after Crawley's (1989) seminal review (Table 1). We also discuss some open questions that are central to understanding plant population and community influences of insect herbivores but that require long-term insect suppression studies to answer. Finally, we take inspiration from the larger literature on exclusion of generalist vertebrate herbivores, and where possible, discuss how variation in the level of specialization among insect herbivores may impact predicted outcomes. In addition to differences in specialization and their population biology, vertebrates and invertebrates typically damage plants in distinct ways.

1.1 | The role of insect herbivores in limiting plant populations

The extent to which herbivores impact plant populations bears directly on many core ecological issues (Myers & Sarfraz, 2017), including selection and fitness (Ehrlén, 2003; Metcalf & Pavard, 2007), limits on geographical ranges (Baer & Maron, 2018; Sexton et al., 2009) and the biological control of invasive plants (Havens et al., 2019). Indeed, plant population abundance is a fundamental parameter of both basic and applied ecology. However, short-term measures of effects of insect herbivores on plants do not necessarily translate to changes in future abundances.

Predicting how strongly insect herbivores influence plant abundance hinges critically on understanding how herbivore damage affects key demographic parameters and the strength of various compensatory mechanisms. Compensatory effects can reduce the

TABLE 1 Long-term (3 years or longer) insect exclusion studies that examine effects on plant populations and communities. All studies employed insecticide except Bach (2001) which used mesh cages

	Duration (years)	Habitat	Treatments/replication	Focal plant species and type of herbivores	Main response variables	Reference
Individual plants treated	2+5 (after treatment)	Mixed grass prairie/dunes (intact)	+/− above-ground insecticide	*Cirsium canescens*; seed predator fly and moth	Fecundity, germination, establishment, maturity	Louda & Potvin, 1995
	3+2.5 (after treatment)	California grassland and dune (semi-intact, planted)	+/− below-ground insecticide	*Lupinus arboreus*; root feeding moth	Maturity, fecundity, seedling recruitment	Maron & Kauffman, 2006
	3	Sage steppe (intact)	+/− above-ground insecticide	*Astragalus utahensis*; seed predator beetle	Fecundity, recruitment from a separate experiment	Baer & Maron, 2018
	3+4 (after treatment)	Primary dune succession along the Great Lakes (intact ecosystem)	+/− cages around shrubs	*Salix cordata* and rest of community; folivorous beetle	Abundance of individual species; functional group analysis	Bach, 2001
	5	Seminatural grassy area	+/− above-ground insecticide	*Vicia angustifolia*; several seed predators	Fecundity, recruitment	Szentesi & Jermy, 2003
	3	Chihuahuan Desert	+/− above-ground insecticide	*Opuntia imbricate*; several specialist herbivores of vegetative and reproductive parts	Seed survival; recruitment, and seedling survival from a separate experiment	Miller et al., 2009
Early successional community studies	5	Florida old field (early succession, herbicide, only *S. carolinense* planted)	+/− above-ground insecticide (only *S. carolinense* treated)	*S. carolinense* and community analyses (leaf feeding beetles and moths)	Plant aggregation, cover of species, composition, richness	Kim et al., 2015, Hakes et al., 2018 (see related studies Coverdale & Agrawal, 2022, Kim et al., 2013)
	10+4 (after treatment)	New York old field (early succession, herbicide, only *O. biennis* planted)	+/− above-ground insecticide	*Oenothera biennis* (seed predator moths), *Taraxacum officinale* (seed and leaf feeders)	Abundance of individual species	Agrawal et al., 2012, 2018, 2021
	3 / 4	European hayfield (early succession, herbicide)	+/− soil/foliar insecticide (factorial)	full community, functional group analysis; all insects	Cover of species, richness	Brown & Gange, 1989, 1992
	3–8	European hayfield (early succession, no herbicide)	+/− soil/foliar insecticide (factorial)	Full community, species analyses; all insects	Cover of species, richness	Schädler et al., 2004, Korell et al., 2019

TABLE 1 (Continued)

	Duration (years)	Habitat	Treatments/replication	Focal plant species and type of herbivores	Main response variables	Reference
Intact communities	3–10	Early succession, with herbicide and intact New York old field	+/− above-ground insecticide	*Solidago altissima* and subordinates; folivorous beetles (and spittlebugs)	Stem density and biomass of species, richness	Carson & Root, 1999, 2000 (see related study McBrien et al., 1983)
	5	European hayfield (managed haying)	+/− soil/foliar insecticide (factorial)	Full community, species and functional group analysis; all insects	Biomass and cover of species, richness	Stein et al., 2010, Kempel et al., 2015
	4–18	English old field (heavily grazed by rabbits)	+/− above-ground insecticide	full community with focal species; all insects	Biomass and cover of species, germination, richness	Edwards & Crawley, 1999, Allan & Crawley, 2011
	3–7	Planted perennial prairie (managed) compared to intact old field (with burning)	+/− above-ground insecticide in 3 richness treatments (1, 4, 16 spp.), also old field control	Full community, species and functional group analysis; all insects	Biomass of species	Borer et al., 2015, Seabloom et al., 2017, 2018
	3	Forest understorey	+/− above-ground insecticide	Herbaceous understorey plants	Abundance and diversity	Jia et al., 2022

direct link between herbivore impacts on one life stage and a proportional impact on the next life stage (Figure 1). One such compensatory mechanism is density dependence. For example, if herbivory reduces seedling recruitment through its effects on fecundity, higher survival of lower density seedlings might compensate for reduced recruitment. While this fact has long been appreciated in theory (Harper, 1977), empirical estimations of these effects, especially in the context of experimental manipulation of herbivores, are lacking (Halpern & Underwood, 2006; Ramula & Buckley, 2009). The key conceptual issue here is not whether density-dependent compensatory effects occur, but how strong they are, and under what conditions they partially or more fully compensate for other measured effects of insect herbivores.

A second compensatory mechanism thought to modify the long-term impacts of herbivores on plant abundance is the presence of a seedbank. Seedbanks can buffer plant populations from the impacts of herbivores when the seedbank is large enough to saturate safe sites for recruitment. In one insect exclusion experiment conducted over several plant generations, strong direct and indirect effects of insect suppression on plant fecundity and population size did not translate to effects on abundance after soil disturbance and resurrection of plants from the seedbank (Agrawal et al., 2021). Alternatively, seed banks can 'store' herbivore-driven reductions in seed input across plant generations, compounding negative effects of herbivores through time (Maron & Gardner, 2000). Thus, here too we are in need of work to understand the conditions under which seedbanks may reverse versus exacerbate the impacts of herbivores on plant demography.

The most common approach to understanding how herbivores influence plant abundance has been to combine demographic study of herbivore impacts with stage-based population models that project how herbivory influences asymptotic plant population growth. The majority of such studies quantify herbivore damage (such as seed loss) observationally, rather than through insect exclusion (Buckley et al., 2010; Katz, 2016; Maron et al., 2010). While these demographic studies have been extremely valuable in adding to our understanding, they make the important assumption that any seeds destroyed by herbivores (either directly or indirectly due to leaf or other tissue damage) would, in the absence of herbivory, add to plant fecundity. However, if there are resource limitations imposed on reproduction, this might not be the case. In other words, seeds lost to herbivores might not otherwise mature due to resource constraints. Furthermore, costs of reproduction might limit seed production across years; these costs might be ameliorated by herbivores causing abortion of damaged reproductive tissue, which suggests that short-term studies may overestimate effects of herbivores. Observational studies that track foliar or root herbivory (as opposed to seed predation) are even more difficult to extrapolate to effects on plant populations because there is an added assumption of the relationship between damage and fecundity. These issues can be circumvented through herbivore suppression experiments, where the demography of individual plants with and without herbivores is followed. To date, however, there are precious few studies conducted for three or more

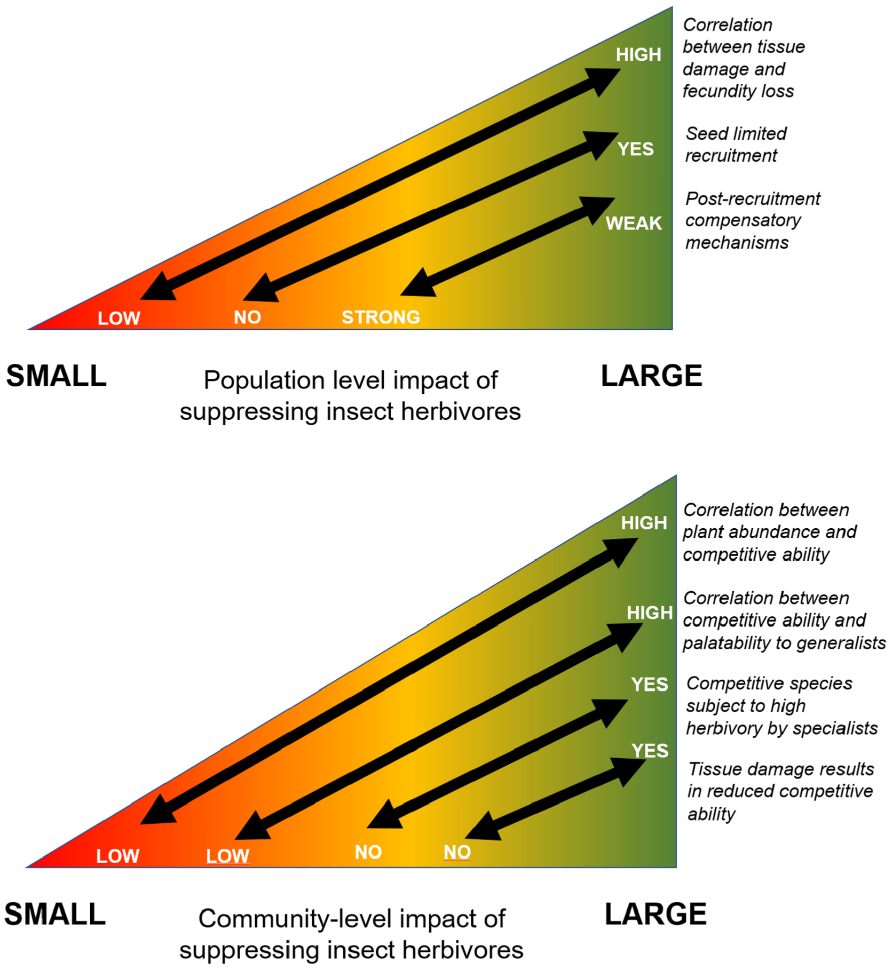

FIGURE 1 Schematic diagram predicting conditions under which we predict there to be smaller versus larger effects of insect suppression on plant abundance (top panel) and community diversity (bottom panel). Note that the factors on the right could exhibit additive or multiplicative effects on the outcome of insect suppression, which we ignore here. These empirically motivated predictions are primarily based on more competitive grassland habitats for community-level effects.

years, and even fewer that track multiple plant generations (Table 1). Note that we have excluded several excellent long-term experiments that simultaneously manipulated both insects and other taxonomic groups (e.g. Heckman et al., 2022; Ritchie et al., 1998), or that primarily focus on biomass and other ecosystem measures (e.g. Blue et al., 2011; Wright et al., 2014), simply because it is more difficult to interpret the direct effects of insects on plant populations and communities in these studies.

Louda and Potvin (1995) conducted one of the classic studies to examine how insect herbivores influence multiple generations of plants. They treated individual thistles with either insecticide or water (as a control for the water in the insecticide) and quantified individual plant growth, survival and fecundity. Importantly, they followed natural recruitment around individual focal plants that had enhanced seed production due to herbivore suppression (versus controls), and followed the fate of these offspring across years. This enabled the authors to determine whether higher seed production, which translated to gains in recruitment around herbivore-suppressed plants, resulted in higher adult density in future generations. By following plants and recruitment across generations, studies can begin to assess compensatory ecological effects that may limit gains at the population level (i.e., increased plant abundance) when herbivores are suppressed and components of plant fitness increase. Clearly, the strength of inference about population-level impacts of herbivores increases with the number of years and plant generations that are studied.

In aggregate, existing shorter-term experimental studies or longer-term observational ones have yielded several generalizations. First, insect herbivores commonly reduce plant population growth, particularly for plant species that have inherently high population growth rates (Katz, 2016). Second, the amount of herbivore damage (i.e., leaf area loss or reduction in seed production) is often not a strong predictor (at least alone) for how strongly insects affect plants at the population level (Katz, 2016). Nonetheless, these conclusions are based mostly on observational studies that determine effects of herbivory on components of plant demography and use these data to make forecasts based on population models. Continued work is needed that employs long-term insect suppression experiments in populations, particularly those that occur across meaningful environmental gradients. This would enable greater insight into how gradients in environmental factors may shift the strength with which herbivores suppress plant abundance. For example, in highly competitive mesic grasslands, germination and establishment of plants are likely to be primarily site limited, implying that reductions in fecundity due to insect herbivory are likely to have more limited effects on recruitment and thus future plant abundance. In contrast, in more arid ecosystems with more open space between plants, populations

BOX 1 Effects of herbivores on forest structure via Janzen–Connell effects

A somewhat different conceptual issue than that discussed through most of the paper relates to the hypothesis that progeny density and distance from parent plants influence plant establishment in the face of specialist enemies, thereby maintaining plant diversity (i.e., the Janzen–Connell Hypothesis; Bagchi et al., 2014). Mostly examined in tropical forest communities, the consensus is that microbial pathogens have stronger negative effects (at high density and short distances from parents) compared to insect herbivores, although most work in this area does not experimentally manipulate herbivores (Song & Corlett, 2021). In a remarkable 45-month study conducted in Amazonia, Swamy and Terborgh (2010) experimentally showed that enemies disproportionally reduce tree seedling survival (across 11 species) near parent trees compared to far away; nonetheless, although insect herbivores reduced seedling survival these effects were similar near and far from parents. A key point, however, is that effects tended to accumulate gradually, and less than 4 years may not have been sufficient to capture many of the enemy-mediated effects. The importance of temporal effects was echoed by Bagchi et al. (2014) who reported that insect herbivores mediated negative density dependence on tropical seedling abundance and composition.

may be more likely to be seed limited. While these general differences across systems have long been postulated, comparative experimental studies would add to our ability to more accurately predict when and where herbivores have their greatest impacts.

1.2 | Insect herbivores and plant communities

At the community scale, influences of insect herbivores on metrics of plant community structure often occur indirectly, by modifying competitive relationships between species (Figure 1). Competition may also in turn reduce a plant's ability to compensate for (or tolerate) herbivore damage, exacerbating the direct effects of herbivory. Thus, when insects are suppressed at the plot level (on all coexisting plants), the resultant changes in plant community attributes may be driven by both direct and indirect effects, mediated by changes in plant abundance or cover that alter plant–plant interactions (Hulme, 1996; Kim et al., 2013, 2015).

Fundamental to much of the work in this area has been the hypothesis that highly competitive species (especially above-ground for light) are also highly palatable to herbivores, as has been reported from classic studies of vertebrate grazing (Augustine & McNaughton, 1998; Olff & Ritchie, 1998). This notion has been adopted in studies of insect herbivores on plants, where insects may serve as keystone species promoting species diversity (Carson & Root, 2000; Kempel et al., 2015; Seabloom et al., 2017). In communities dominated by generalist insect herbivores like grasshoppers, the response of plants to herbivore exclusion may thus be driven by the preference hierarchy of the herbivore, with the most palatable species enjoying the biggest release from herbivory. If resistance to generalists trades off with plant competitive ability, then highly palatable competitive species should dominate communities in which herbivores are excluded, and plant palatability may be predictive of plant species responses to insect suppression in community-level experiments (e.g., Kempel et al., 2015). As discussed below, persistence in a plant community is determined by not only by resistance to herbivory and competitive ability, but also by tolerance to plant damage, which may or may not be a correlated trait.

In contrast to communities dominated by generalist herbivores, in some plant communities specialist insect herbivores may play a strong role. In such instances, plant palatability may be less relevant in predicting herbivore impacts (see also Box 1). For example, in eastern US old fields, goldenrod *Solidago altissima* is a community dominant. Studies have shown that goldenrod's competitive dominance is reduced through herbivory by specialist herbivores (Box 2; Carson & Root, 2000; McBrien et al., 1983; Root, 1996). In this example, factors such as the history of coevolution between goldenrod and its specialist herbivores, rather than palatability per se, likely affect both the extent of herbivore damage and plant tolerance to herbivores (Uriarte et al., 2002). Measures of palatability may thus be uncorrelated with competitive ability. A key point is that where there is not a common axis of palatability across species, trade-offs between resistance and competitive ability may be less predictive of how plant communities respond to release from herbivory. One interesting hypothesis that remains untested is that competitively dominant plant species will either be highly palatable to generalists *or* have specialist herbivores that occasionally outbreak, thus typically controlling their abundance and plant community structure (Carson et al., 2004).

Depending on the preferences, level of specialization and intensities of attack, insect suppression can have non-intuitive effects at the community level. For example, in our long-term (10 year) studies of herbivory on *Oenothera biennis* (a monocarpic annual or biennial) in an early successional community, we found that insect suppression increased per capita fecundity by 20%, yet caused a *reduction* in the abundance of experimentally planted populations (Agrawal et al., 2012; Maron et al., 2018). Here the major herbivores were seed-feeding specialist insects which affected plant fecundity. However, the decrease in abundance was mediated by competition with naturally occurring *Taraxacum officinale*. Critically, *T. officinale* enjoyed a substantially greater benefit than *O. biennis* when released from its own herbivory, thereby tipping the balance of competition in its favour, resulting in smaller *O. biennis* populations over multiple generations (Agrawal et al., 2012, 2021). Even in a simple scenario of a few competing plant species, the impacts of insect suppression in the short term will depend on (1) the tolerance of each plant species

BOX 2 The goldenrod case study

A long-term set of studies on the impact of insect herbivores on old fields dominated by tall goldenrod, *Solidago altissima*, has provided notable insight into the effects of herbivores on plant individuals, populations and communities. In the native range of eastern North America, overall, herbivore pressure on goldenrod reduced the size and biomass of individual stems, and lowered the probability of flowering (Root, 1996). After 7 years of above-ground insect suppression in 20 m^2 plots in central New York (USA), height of goldenrod stems and the length, biomass and number of underground rhizomes were substantially enhanced (19%–64%) compared to treatments with ambient insects (Cain et al., 1991). These strong impacts on individual performance open the door to population effects, although because goldenrod is highly clonal and prioritizes maintaining established individuals over sexual reproduction (flowering and seed production), such effects were challenging to measure.

Over a 10-year experiment in similar old fields, goldenrod stem density was not impacted by herbivore suppression in the first 7 years of the experiment (Carson & Root, 2000). However, after an outbreak of a specialist leaf beetle *Microrhopala vittata* in year 7, goldenrods were >80% more abundant in insect-suppression plots compared to controls, and this effect persisted for at least 2 years after the outbreak ended (Carson & Root, 2000). Stem mortality and rhizome production were both implicated in the population effects of insects on goldenrod. Consequently, understorey plant species richness was enhanced 30% where herbivores suppressed goldenrod, and this effect was attributed to light reaching the understorey. Critically, these effects would have been missed in a shorter-term study. In a parallel study conducted much earlier (1975–1980), McBrien et al. (1983) showed that 5 years of insecticide application in similar goldenrod fields in southern Ontario suppressed an outbreak of another specialist leaf beetle (*Trirhabda* sp.). Here too there were community impacts of suppressing herbivores, including enhanced cover of understorey plants and substantial enhancement of grasses.

An additional study of goldenrod early in succession (beginning with bare soil) found that *S. altissima* became nearly threefold more abundant (measured in terms of biomass per plot) after 3 years of above-ground insect suppression compared to control plots with ambient insects (Carson & Root, 1999). Allowing for *S. altissima*'s dominance by suppressing insects reduced plant species richness, suggesting that population-level effects on one species can impact other species. In this experiment, the xylem-feeding and extreme generalist meadow spittlebug, *Philaenus spumarius*, was implicated as the most impactful herbivore driving the community effects. Here, the preference of spittlebugs (presumably favouring *S. altissima*) as well as the relative plant tolerance to spittlebug feeding (see Meyer, 1993) both likely contributed to the effects of insect suppression on plant populations individually and the plant community as a whole.

Finally, a close relative of *S. altissima* (*S. canadensis*) is invasive in Europe and Asia, and a long-term insect exclusion study in Germany found that native herbivory promoted the invasive success (stems and biomass over 8 years) of *S. canadensis* (Korell et al., 2019). In other words, as an invader, where its specialist herbivores were absent, insects suppressing other vegetation enhanced the competitive dominance of *S. canadensis*. Remarkably, the effects of herbivores in this experiment were to decrease community pant diversity, and this was associated with dominance by *S. canadensis*. We interpret the results of this experiment as an exception that proves the rule: although the population and community effects of insect suppression on *S. canadensis* in Europe were opposite to those in North America, the difference appears to be driven by the non-native status of *S. canadensis* and its lack of specialist herbivores in the Europe.

BOX FIGURE 1. Two major defoliating leaf beetles of tall goldenrod that occasionally outbreak: Adult *Trirhabda virgata* (left, photo by A.A. Agrawal) and *Microrhopala vittata* (right, photo by A. Kessler) observed in central New York (USA).

to the typical amount of herbivory received and (2) the difference in competitive ability of each plant species with versus without the typical amount of herbivory. Long-term impacts on plant populations will follow from these effects, depending on the relationship between fecundity and population size.

Studies like the one above have used insect suppression to examine early successional dynamics. In two experiments by Brown and Gange (1989, 1992), suppression of below-ground insects in tilled English hayfields benefitted perennial forbs over annual forbs or grasses, resulting in higher plant species richness. In contrast, suppressing above-ground insects favoured competitive grasses, which reduced plant species richness. A similar experimental design in a third study conducted in Germany also revealed stronger below- versus above-ground effects of herbivory, although the community consequences were via divergent effects on plant functional groups (Schädler et al., 2004). Overall, these three studies found divergent successional dynamics driven by suppressing above- versus below-ground insects, with the effects of the latter being stronger.

Surprisingly, relatively few long-term experiments have manipulated insect herbivores within non-disturbed plant communities and examined the consequences (Table 1, Box 2). Work by Crawley and coworkers factorially manipulated insects, rabbits, molluscs, nutrients, competition and soil pH over 18 years (Allan & Crawley, 2011; Edwards & Crawley, 1999; Leverkus & Crawley, 2020). Focusing on their results from insect suppression alone, they found no impact of herbivory on the vegetation community, germinable seeds in the soil or the total number of seedlings emerging in vegetation gaps after 4 years. A single species (*Rumex acetos*) showed eight-fold greater abundance in sprayed compared to control gaps (Edwards & Crawley, 1999). Nonetheless, impacts of insects on vegetation emerged after 8 years and depended on the presence of molluscs and rabbits (Allan & Crawley, 2011). Overall, insects served to maintain diversity and when taken out of the community, plant diversity declined by 25%. Some of these effects occurred through a competitively dominant grass *Holcus mollis* that was suppressed by sucking insects (Heteroptera). A key insight of this study was that the impacts of insect herbivores in intact temperate grasslands can take years to emerge, and can occur through modifying competitive interactions between plants (and through interactions with other invertebrate and vertebrate herbivores; see also Box 2).

Insect suppression experiments that are of longer duration have mostly been conducted in productive and highly competitive grasslands in eastern North America and Europe. In general, these communities are dominated by herbaceous perennials (including many clonal species) with relatively little recruitment from seed. In these systems, recruitment into plant populations is often mostly site limited, implying that herbivory has its impacts primarily through competitive displacement occurring among adult plants. The general message across these studies is that insect suppression typically impacts plant community composition through direct negative effects on different species and indirect positive effects, with strong herbivory-by-competition interactions shaping overall community responses. How suppression of plant fecundity by insect herbivores translates (or not) into effects on seedling recruitment across species, and ultimately metrics of community diversity, remains unclear. In particular, in seed-limited ecosystems, or those where positive plant–plant interactions are common, the impacts of herbivores at the community level may differ substantially.

Ultimately, a connection between plant species' competitive ability (or competitive tolerance), palatability (or probability of attack), tolerance to herbivory and changes in fitness (through survival, competition or recruitment) will need to be made to predict impacts of herbivores on plant communities. The relationship between plant resistance to herbivory, tolerance to damage and competitive ability has not been well explored, yet is critical to understand the impacts of insect herbivores on plant populations and communities (Fornoni, 2011; Uriarte et al., 2002). Here we have primarily considered above-ground competition for light, although underground competition is clearly an important axis as well.

When herbivores are suppressed at the community scale, the extent to which herbivores impact the abundance of dominant versus subordinate species should influence the net effect on diversity. In the classic case of goldenrod meadows (Box 2), herbivores suppress a competitive dominant and increase plant species richness (Carson & Root, 2000). More recent work has also specifically addressed the relative impact of herbivory on intraspecific and interspecific competitive dynamics between goldenrod and a subordinate competitor, providing insight into the mechanisms of herbivores as keystone species (Kim et al., 2013). Under other conditions, herbivores may ultimately reduce plant diversity by reducing the abundance of rare plant species (Myers & Sarfraz, 2017; Schmidt et al., 2020). Indeed, insect herbivores can reduce the spatial distribution of plants, reducing their abundance in some communities (e.g. cases where specialist herbivores restrict plants to shadier habitats, Louda & Rodman, 1996). Although effects on plant diversity have not been studied in this context, in such cases the impact of herbivores overall could be to reduce diversity and increase competitive dominance (as reported for an invaded grassland in Europe; Korell et al., 2019). Across a broad swath of vertebrate exclosure studies, when grazers had the effect of suppressing competitive dominants, the result was to increase species richness; however, in a substantial fraction of the reviewed studies, grazers increased competitive dominants, and here community richness declined (Koerner et al., 2018). Whether insect herbivores have comparable effects on plant communities is an open question.

1.3 | Effects of insects on plant communities of varying diversity

Given that plant diversity itself shapes the intensity of herbivory, insect diversity and higher trophic interactions (Agrawal et al., 2006; Wan et al., 2020), over longer temporal scales there may be feedbacks between plant diversity and the regulation of those plant communities by insects. There may also be an interplay between productivity, herbivory and plant species richness. In vertebrate herbivore exclusion studies, the impacts of herbivores on plant species richness are typically stronger at higher productivities (Koerner et al., 2018; Staver et al., 2021). The answer to the analogous question with insect herbivores has been less well established (Schädler et al., 2003). There may be additional consequences of such interactions for plant community dynamics as well. For example, biotic resistance to invasion is influenced by factors such as productivity and plant diversity; it follows then that native herbivores which impact diversity may have consequences for plant invasions (Levine et al., 2004; Parker et al., 2006). Although such effects have been hypothesized, few longer-term studies on the topic have been conducted (Korell et al., 2019; Schmidt et al., 2020).

Planted and managed communities have been used to examine the relative importance of, and interaction between, plant diversity and insect herbivores in grassland ecosystems (Schmidt et al., 2020; Seabloom et al., 2017; Siemann et al., 1998). Such field experiments, although highly controlled, equilibrate over years and have revealed important insight to the roles of plant community interactions and consumption. For example, in European hayfields of varying diversities (i.e. 15–35 plant species), 5 years of insect suppression had stronger effects on overall plant productivity as plant diversity increased (Stein et al., 2010). In other words, herbivores seem to exert greater consumption in more diverse plant communities. This effect is likely due to many direct and indirect effects. Nonetheless, by examining individual plant species responses that were differentially impacted by insect suppression, predictive insight can be gained. Among several leaf trait predictors tested, an independent measure of plant palatability (to two generalist herbivores) predicted the outcome of insect suppression across years (Kempel et al., 2015). In particular, the most preferred plant species (i.e. least defended) showed the greatest increase following insect suppression. This follows from palatable species having the most to gain from insect suppression; in addition, however, the least palatable species decreased in abundance after insect suppression, underscoring a likely competitive effect suppressing unpalatable species after removal of herbivory.

In a similar long-term plant diversity experiment conducted in Minnesota grasslands (Borer et al., 2015; Seabloom et al., 2017, 2018), a key result was that changes in a plant species' biomass over time due to insect suppression were not concordant in monocultures compared to polycultures. In other words, differential outcomes were likely caused by interactions between herbivory and plant competition, which varied among diversity treatments. Here species with the weakest competitive ability (gauged by nitrogen utilization) were the most responsive to insecticide, supporting a species-level trade-off between plant defence and competitive ability.

2 | WHAT SHORT-TERM STUDIES MISS

Although shorter-term studies have served as much of the basis for what we know about the impacts of insects on plants, these studies can miss key events (e.g. insect outbreaks) and are unlikely to address the relative importance of critical factors (e.g. compensatory demographic mechanisms, community change) that might modify the strength and direction of herbivore effects over time. In habitats where seedling recruitment is common, short-term studies may often miss how variation in recruitment, driven my insect exclusion, influences individual species' abundance and ultimately community diversity. Nonetheless, in systems where recruitment is minimal and clonal growth is more important, effects of insect exclusion on plant communities could manifest more quickly (although this does not seem to be the case, Table 1).

Our goal here is to highlight the value of longer-term experiments to fully elucidating the extent to which insect herbivores drive population or community change. This is not to undervalue shorter-term studies; in fact, many of the ideas examined in this essay were derived from shorter-term work. An important link extrapolating from short-term studies to long-term impacts is the shape of ecological relationships, for example, between the extent of herbivory and impacts on plant fecundity. In a simplified world, effects would be linear and additive over time. Nonetheless, given that this often is not the case, some progress could be made by evaluating the shapes of such relationships and simulating their impacts.

In many classic long-term experiments examining interactions other than herbivory, the impact of the interaction was often not fully captured for many years. This was certainly the case for how herbivores affected goldenrod fitness (Root, 1996), which formed the basis for the community effects in that system (Box 2). The accumulation of weaker effects (e.g. low levels of persistent herbivory), whether at the population or community level, often take time to manifest ecologically and may not be linear. Annual variability in insect herbivore abundance, as well as key plant parameters such as seedling recruitment, plant cover and flowering can together create variability in population and community responses. Detecting a coherent signal through this 'noise' can only be accomplished by longer-term work. Additionally, we make a plea for characterizing the insect community (in terms of species identity, level specialization, feeding guild and abundance) in the control plots of exclusion experiments; variability in the insect community undoubtedly shapes their ecological effects over space and time. Of course, factorially excluding generalists versus specialists, or insects with unique feeding modes, to tease apart their individual effects is extremely challenging (Siemann et al., 2004).

3 | CONCLUSION

Although we hesitate to add yet another voice to the many cries over the years that ecologists do larger, longer and more multi-factor experiments, it is clear that these approaches are irreplaceable for filling substantial gaps in our knowledge of how insects influence plant populations and communities. While there is much to be gained, we want to acknowledge that there are difficult logistical issues involved in attempting long-term insect exclusion. Clearly, excluding insect herbivores is not as straightforward as using fences to exclude larger herbivores. Fences require maintenance, but are typically long lasting. In contrast, using insecticide typically requires weekly (or bimonthly) application. Furthermore, in some cases, particular insecticides can be difficult to obtain due to environmental regulations (Siemann et al., 2004), and some can have phytotoxic or even plant stimulatory effects. As well, without judicious and well-timed application, insecticides may negatively influence pollinator abundance or behaviour. Yet, despite these limitations, insecticides (or other approaches that suppress insect herbivores) are valuable tools that can be vital to addressing fundamental and applied issues related to controls on plant abundance and distribution. These questions remain mostly unresolved in part because of the lack of longer-term experiments.

At the community scale, although we know that insect herbivores can act as keystone species that enhance plant species richness, this work has been highly restricted to north temperate mesic grasslands. Work on the relative roles or interactions between specialist versus generalist herbivores in the maintenance of plant communities deserves attention. In addition to classic long-term insect exclusion studies, one future approach might be to conduct comparative studies of the impacts of insect exclusion in neighbouring ecosystems, on closely related plants with differing life histories, or other contrasts predicted to show differences. And finally, studies that explore the differential impacts of suppressing insects on individual plants versus plot-level suppression in the same communities may reveal important insights into the importance of herbivory-by-competition interactions in determining community outcomes.

AUTHOR CONTRIBUTIONS

Anurag A. Agrawal and John L. Maron jointly researched and wrote the manuscript.

ACKNOWLEDGEMENTS

We thank Yvonne Buckley and Jason Fridley for the opportunity to contribute this article and Tyler Coverdale, Kailen Mooney, Anne Kempel and two anonymous reviewers for comments on the manuscript. Max Goldman helped with the literature review and compiling Table 1. Our work on the impact of insect herbivores on plant populations and communities has been funded by the US National Science Foundation (most recently NSF IOS-2209762 to A.A.A. and NSF DEB-1901552 to J.L.M.).

CONFLICT OF INTEREST

The authors have no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13996.

DATA AVAILABILITY STATEMENT

This study does not contain any original data.

ORCID

Anurag A. Agrawal https://orcid.org/0000-0003-0095-1220
John L. Maron https://orcid.org/0000-0002-4066-3322

REFERENCES

Agrawal, A. A., Hastings, A. P., Fines, D. M., Bogdanowicz, S., & Huber, M. (2018). Insect herbivory and plant adaptation in an early successional community. *Evolution*, *72*, 1020–1033.

Agrawal, A. A., Hastings, A. P., Johnson, M. T. J., Maron, J. L., & Salminen, J. P. (2012). Insect herbivores drive real-time ecological and evolutionary change in plant populations. *Science*, *338*, 113–116.

Agrawal, A. A., Hastings, A. P., & Maron, J. L. (2021). Evolution and seed dormancy shape plant genotypic structure through a successional cycle. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, 118.

Agrawal, A. A., Lau, J. A., & Hambäck, P. A. (2006). Community heterogeneity and the evolution of interactions between plants and insect herbivores. *Quarterly Review of Biology*, *81*, 349–376.

Allan, E., & Crawley, M. J. (2011). Contrasting effects of insect and molluscan herbivores on plant diversity in a long-term field experiment. *Ecology Letters*, *14*, 1246–1253.

Andriuzzi, W. S., & Wall, D. H. (2017). Responses of belowground communities to large aboveground herbivores: Meta-analysis reveals biome-dependent patterns and critical research gaps. *Global Change Biology*, *23*, 3857–3868.

Augustine, D. J., & McNaughton, S. J. (1998). Ungulate effects on the functional species composition of plant communities: Herbivore selectivity and plant tolerance. *Journal of Wildlife Management*, *62*, 1165–1183.

Bach, C. E. (2001). Long-term effects of insect herbivory and sand accretion on plant succession on sand dunes. *Ecology*, *82*, 1401–1416.

Baer, K. C., & Maron, J. L. (2018). Pre-dispersal seed predation and pollen limitation constrain population growth across the geographic distribution of *Astragalus utahensis*. *Journal of Ecology*, *106*, 1646–1659.

Bagchi, R., Gallery, R. E., Gripenberg, S., Gurr, S. J., Narayan, L., Addis, C. E., Freckleton, R. P., & Lewis, O. T. (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*, *506*, 85–88.

Bakker, E. S., Ritchie, M. E., Olff, H., Milchunas, D. G., & Knops, J. M. (2006). Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters*, *9*, 780–788.

Blue, J. D., Souza, L., Classen, A. T., Schweitzer, J. A., & Sanders, N. J. (2011). The variable effects of soil nitrogen availability and insect herbivory on aboveground and belowground plant biomass in an old-field ecosystem. *Oecologia*, *167*, 771–780.

Borer, E. T., Lind, E. M., Ogdahl, E. J., Seabloom, E. W., Tilman, D., Montgomery, R. A., & Kinkel, L. L. (2015). Food-web composition and plant diversity control foliar nutrient content and stoichiometry. *Journal of Ecology*, *103*, 1432–1441.

Brown, J. H., & Heske, E. J. (1990). Control of a desert-grassland transition by a keystone rodent guild. *Science*, *250*, 1705–1707.

Brown, J. H., Whitham, T. G., Ernest, S. M., & Gehring, C. A. (2001). Complex species interactions and the dynamics of ecological systems: Long-term experiments. *Science*, *293*, 643–650.

Brown, V. K., & Gange, A. C. (1989). Differential-effects of above-ground and below-ground insect herbivory during early plant succession. *Oikos*, *54*, 67–76.

Brown, V. K., & Gange, A. C. (1992). Secondary succession: How is it modified by insect herbivory? *Vegetatio*, *101*, 3–13.

Buckley, Y. M., Ramula, S., Blomberg, S. P., Burns, J. H., Crone, E. E., Ehrlén, J., Knight, T. M., Pichancourt, J. B., Quested, H., & Wardle, G. M. (2010). Causes and consequences of variation in plant population growth rate: A synthesis of matrix population models in a phylogenetic context. *Ecology Letters*, *13*, 1182–1197.

Cain, M. L., Carson, W. P., & Root, R. B. (1991). Long-term suppression of insect herbivores increases the production and growth of Solidago altissima rhizomes. *Oecologia*, *88*, 251–257.

Carpenter, S. R., Cole, J. J., Hodgson, J. R., Kitchell, J. F., Pace, M. L., Bade, D., Cottingham, K. L., Essington, T. E., Houser, J. N., & Schindler, D. E. (2001). Trophic cascades, nutrients, and lake productivity: Whole-lake experiments. *Ecological Monographs*, *71*, 163–186.

Carson, W. P., Patrick, J., & Long, Z. T. (2004). A general rule for predicting when insects will have strong top-down effects on plant communities: On the relationship between insect outbreaks and host concentration. In W. W. Weisser & E. Siemann (Eds.), *Insects and ecosystem function* (pp. 193–211). Springer-Verlag.

Carson, W. P., & Root, R. B. (1999). Top-down effects of insect herbivores during early succession: Influence on biomass and plant dominance. *Oecologia*, *121*, 260–272.

Carson, W. P., & Root, R. B. (2000). Herbivory and plant species coexistence: Community regulation by an outbreaking phytophagous insect. *Ecological Monographs*, *70*, 73–99.

Chase, J. M., Leibold, M. A., Downing, A. L., & Shurin, J. B. (2000). The effects of productivity, herbivory, and plant species turnover in grassland food webs. *Ecology*, *81*, 2485–2497.

Cobb, N. S., Trotter, R. T., & Whitham, T. G. (2002). Long-term sexual allocation in herbivore resistant and susceptible pinyon pine (Pinus edulis). *Oecologia*, *130*, 78–87.

Connell, J. H. (1961). Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of barnacle *Balanus balanoides*. *Ecological Monographs*, *31*, 61–104.

Coupe, M. D., & Cahill, J. F. (2003). Effects of insects on primary production in temperate herbaceous communities: A meta-analysis. *Ecological Entomology*, *28*, 511–521.

Coverdale, T. C., & Agrawal, A. A. (2022). Experimental insect suppression causes loss of induced, but not constitutive, resistance in *Solanum carolinense*. *Ecology*, in press. https://doi.org/10.1002/ecy.3786

Crawley, M. J. (1985). Reduction of oak fecundity by low-density herbivore populations. *Nature*, *314*, 163–164.

Crawley, M. J. (1989). Insect herbivores and plant population dynamics. *Annual Review of Entomology*, *34*, 531–562.

Davidson, D. W. (1993). The effects of herbivory and granivory on terrestrial plant succession. *Oikos*, *68*, 23–35.

Edwards, G., & Crawley, M. (1999). Herbivores, seed banks and seedling recruitment in Mesic grassland. *Journal of Ecology*, *87*, 423–435.

Ehrlén, J. (2003). Fitness components versus total demographic effects: Evaluating herbivore impacts on a perennial herb. *The American Naturalist*, *162*, 796–810.

Fornoni, J. (2011). Ecological and evolutionary implications of plant tolerance to herbivory. *Functional Ecology*, *25*(2), 399–407.

Gómez, J. M. (2005). Long-term effects of ungulates on performance, abundance, and spatial distribution of two montane herbs. *Ecological Monographs*, *75*, 231–258.

Hakes, A. S., Halpern, S., & Underwood, N. (2018). Insect herbivores increase the spatial aggregation of a clonal plant. *International Journal of Plant Sciences*, *179*, 209–216.

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

Harper, J. L. (1977). *Population biology of plants*. Academic Press.

Havens, K., Jolls, C. L., Knight, T. M., & Vitt, P. (2019). Risks and rewards: Assessing the effectiveness and safety of classical invasive plant biocontrol by arthropods. *Bioscience*, *69*, 247–258.

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

Heckman, R. W., Halliday, F. W., & Wilfahrt, P. A. (2022). Nutrients and consumers impact tree colonization differently from performance in a successional old field. *Oecologia (Berlin)*, *198*, 1–9.

Howe, H. F. (2008). Reversal of fortune: Plant suppression and recovery after vole herbivory. *Oecologia*, *157*, 279–286.

Hulme, P. E. (1996). Herbivory, plant regeneration, and species coexistence. *Journal of Ecology*, *84*, 609–615.

Jia, S., Wang, X., Hao, Z., & Bagchi, R. (2022). The effects of natural enemies on herb diversity in a temperate forest depend on species traits and neighbouring tree composition. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.13973

Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Hao, Z., & Luskin, M. S. (2018). Global signal of top-down control of terrestrial plant communities by herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 6237–6242.

Katz, D. S. (2016). The effects of invertebrate herbivores on plant population growth: A meta-regression analysis. *Oecologia*, *182*, 43–53.

Kempel, A., Razanajatovo, M., Stein, C., Unsicker, S. B., Auge, H., Weisser, W. W., Fischer, M., & Prati, D. (2015). Herbivore preference drives plant community composition. *Ecology*, *96*, 2923–2934.

Kim, T. N., Spiesman, B. J., Buchanan, A. L., Hakes, A. S., Halpern, S. L., Inouye, B. D., Kilanowski, A. L., Kortessis, N., McNutt, D. W., Merwin, A. C., & Underwood, N. (2015). Selective manipulation of a non-dominant plant and its herbivores affects an old-field plant community. *Plant Ecology*, *216*, 1029–1045.

Kim, T. N., Underwood, N., & Inouye, B. D. (2013). Insect herbivores change the outcome of plant competition through both inter-and intraspecific processes. *Ecology*, *94*, 1753–1763.

Koerner, S. E., Smith, M. D., Burkepile, D. E., Hanan, N. P., Avolio, M. L., Collins, S. L., Knapp, A. K., Lemoine, N. P., Forrestel, E. J., & Eby, S. (2018). Change in dominance determines herbivore effects on plant biodiversity. *Nature Ecology & Evolution*, *2*, 1925–1932.

Korell, L., Schädler, M., Brandl, R., Schreiter, S., & Auge, H. (2019). Release from above-and belowground insect herbivory mediates invasion dynamics and impact of an exotic plant. *Plants*, *8*, 544.

Leverkus, A. B., & Crawley, M. (2020). Temporal variation in effect sizes in a long-term, split-plot field experiment. *Ecology*, *101*, e03009.

Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, *7*, 975–989.

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

Louda, S. M., & Rodman, J. E. (1996). Insect herbivory as a major factor in the shade distribution of a native crucifer (*Cardamine cordifolia* a. gray, bittercress). *Journal of Ecology*, *84*, 229–237.

Lubchenco, J. (1980). Algal zonation in the New England rocky intertidal community: An experimental analysis. *Ecology*, *61*, 333–344.

Maron, J. L. (1998). Insect herbivory above- and belowground: Individual and joint effects on plant fitness. *Ecology (Washington, DC)*, *79*, 1281–1293.

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

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

Maron, J. L., Johnson, M. T., Hastings, A. P., & Agrawal, A. A. (2018). Fitness consequences of occasional outcrossing in a functionally asexual plant (*Oenothera biennis*). *Ecology*, *99*, 464–473.

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

Marquis, R. J. (1992). Selective impact of herbivores. In R. S. Fritz & E. L. Simms (Eds.), *Plant resistance to herbivores and pathogens* (pp. 301–325). University of Chicago Press.

McBrien, H., Harmsen, R., & Crowder, A. (1983). A case of insect grazing affecting plant succession. *Ecology*, *64*, 1035–1039.

Metcalf, C. J., & Pavard, S. (2007). Why evolutionary biologists should become demographers. *Trends in Ecology & Evolution*, *22*, 205–212.

Meyer, G. A. (1993). A comparison of the impacts of leaf-and sap-feeding insects on growth and allocation of goldenrod. *Ecology*, *74*, 1101–1116.

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

Mittelbach, G. G., & McGill, B. J. (2019). *Community ecology*. Oxford University Press.

Morrow, P., & LaMarche, V. C. (1978). Tree ring evidence for chronic insect suppression of productivity in subalpine eucalyptus. *Science*, *201*, 1244–1246.

Myers, J. H., & Sarfraz, R. M. (2017). Impacts of insect herbivores on plant populations. *Annual Review of Entomology*, *62*, 207–230.

Olff, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution*, *13*, 261–265.

Paine, R. T. (1992). Food-web analysis through field measurement of per capita interaction strength. *Nature*, *355*, 73–75.

Parker, J. D., Burkepile, D. E., & Hay, M. E. (2006). Opposing effects of native and exotic herbivores on plant invasions. *Science*, *311*, 1459–1461.

Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 12353–12358.

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., Daily, G., Castilla, J. C., Lubchenco, J., & Paine, R. T. (1996). Challenges in the quest for keystones. *Bioscience*, *46*, 609–620.

Ramula, S., & Buckley, Y. M. (2009). Multiple life stages with multiple replicated density levels are required to estimate density dependence for plants. *Oikos*, *118*, 1164–1173.

Ritchie, M. E., Tilman, D., & Knops, J. M. H. (1998). Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology*, *79*, 165–177.

Root, R. B. (1996). Herbivore pressure on goldenrods (*Solidago altissima*): Its variation and cumulative effects. *Ecology*, *77*, 1074–1087.

Schädler, M., Jung, G., Auge, H., & Brandl, R. (2003). Does the Fretwell-Oksanen model apply to invertebrates? *Oikos*, *100*, 203–207.

Schädler, M., Jung, G., Brandl, R., & Auge, H. (2004). Secondary succession is influenced by belowground insect herbivory on a productive site. *Oecologia*, *138*, 242–252.

Schmidt, R., Deising, H. B., Hensen, I., Schädler, M., & Auge, H. (2020). Natural enemies do not contribute to negative frequency-dependence in native and exotic grassland plants. *Perspectives in Plant Ecology, Evolution and Systematics*, *46*, 125565.

Seabloom, E. W., Borer, E. T., & Kinkel, L. L. (2018). No evidence for trade-offs in plant responses to consumer food web manipulations. *Ecology*, *99*, 1953–1963.

Seabloom, E. W., Kinkel, L., Borer, E. T., Hautier, Y., Montgomery, R. A., & Tilman, D. (2017). Food webs obscure the strength of plant diversity effects on primary productivity. *Ecology Letters*, *20*, 505–512.

Sexton, J. P., McIntyre, P. J., Angert, A. L., & Rice, K. J. (2009). Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 415–436.

Shestakov, A. L., Filippov, B. Y., Zubrii, N. A., Klemola, T., Zezin, I., Zverev, V., Zvereva, E. L., & Kozlov, M. V. (2020). Doubling of biomass production in European boreal forest trees by a four-year suppression of background insect herbivory. *Forest Ecology and Management*, *462*, 117992.

Siemann, E., Carson, W. P., Rogers, W. E., & Weisser, W. W. (2004). Reducing herbivory using insecticides. In W. W. Weisser & E. Siemann (Eds.), *Insects and ecosystem function. Ecological studies* (Vol. *173*, pp. 303–327). Springer.

Siemann, E., Tilman, D., Haarstad, J., & Ritchie, M. (1998). Experimental tests of the dependence of arthropod diversity on plant diversity. *The American Naturalist*, *152*(5), 738–750.

Song, X., & Corlett, R. T. (2021). Do natural enemies mediate conspecific negative distance-and density-dependence of trees? A meta-analysis of exclusion experiments. *Oikos*, *2022*, e08509. https://doi.org/10.1111/oik.08509

Staver, A. C., Abraham, J. O., Hempson, G. P., Karp, A. T., & Faith, J. T. (2021). The past, present, and future of herbivore impacts on savanna vegetation. *Journal of Ecology*, *109*, 2804–2822.

Stein, C., Unsicker, S. B., Kahmen, A., Wagner, M., Audorff, V., Auge, H., Prati, D., & Weisser, W. W. (2010). Impact of invertebrate herbivory in grasslands depends on plant species diversity. *Ecology*, *91*(6), 1639–1650.

Swamy, V., & Terborgh, J. W. (2010). Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. *Journal of Ecology*, *98*, 1096–1107.

Szentesi, Á., & Jermy, T. (2003). Pre-dispersal seed predation and seed limitation in an annual legume. *Basic & Applied Ecology*, *4*, 207–218.

Tansley, A. (1922). Studies of the vegetation of the English chalk: II. Early stages of redevelopment of woody vegetation on chalk grassland. *Journal of Ecology*, *10*, 168–177.

Uriarte, M., Canham, C. D., & Root, R. B. (2002). A model of simultaneous evolution of competitive ability and herbivore resistance in a perennial plant. *Ecology*, *83*(10), 2649–2663.

Wan, N.-F., Zheng, X.-R., Fu, L.-W., Kiær, L. P., Zhang, Z., Chaplin-Kramer, R., Dainese, M., Tan, J., Qiu, S.-Y., & Hu, Y.-Q. (2020). Global synthesis of effects of plant species diversity on trophic groups and interactions. *Nature Plants*, *6*, 503–510.

Watt, A. (1981). A comparison of grazed and ungrazed grassland a in east Anglian Breckland. *Journal of Ecology*, *69*, 499–508.

Wright, P., Cregger, M. A., Souza, L., Sanders, N. J., & Classen, A. T. (2014). The effects of insects, nutrients, and plant invasion on community structure and function above-and belowground. *Ecology and Evolution*, *4*, 732–742.

Young, T. P., Okello, B., Kinyua, D., & Palmer, T. M. (1997). KLEE: A long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range & Forage Science*, *14*, 94–102.

How to cite this article: Agrawal, A. A., & Maron, J. L. (2022). Long-term impacts of insect herbivores on plant populations and communities. *Journal of Ecology*, *110*, 2800–2811. https://doi.org/10.1111/1365-2745.13996