

The effects of invertebrate herbivores on plant population growth: a meta-regression analysis

Daniel S. W. Katz¹

Received: 6 August 2015 / Accepted: 6 March 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract Over the last two decades, an increasing number of studies have quantified the effects of herbivory on plant populations using stage-structured population models and integral projection models, allowing for the calculation of plant population growth rates (λ) with and without herbivory. In this paper, I assembled 29 studies and conducted a meta-regression to determine the importance of invertebrate herbivores to population growth rates (λ) while accounting for missing data. I found that invertebrate herbivory often induced important reductions in plant population growth rates (with herbivory, λ was 1.08 ± 0.36 ; without herbivory, λ was 1.28 ± 0.58). This relationship tended to be weaker for seed predation than for other types of herbivory, except when seed predation rates were very high. Even so, the amount by which studies reduced herbivory

was a poor predictor of differences in population growth rates—which strongly cautions against using measured herbivory rates as a proxy for the impact of herbivores. Herbivory reduced plant population growth rates significantly more when potential growth rates were high, which helps to explain why there was less variation in actual population growth rates than in potential population growth rates. The synthesis of these studies also shows the need for future studies to report variance in estimates of λ and to quantify how λ varies as a function of plant density.

Keywords Insect herbivory · Plant–insect interactions · Integral projection models · Matrix population models · Meta-analysis

Communicated by Julia Koricheva.

An increasing number of experiments are testing the effects of invertebrate herbivores on plant population growth rates, and this study uses a novel meta-regression approach to quantitatively synthesize their results for the first time. Invertebrate herbivores often had substantial effects on plant population growth rates, but their effects were poorly predicted by measured damage rates. Herbivores also had more of an effect on plant populations with higher potential population growth rates; this reduced overall variation in realized plant population growth rates.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-016-3602-9) contains supplementary material, which is available to authorized users.

✉ Daniel S. W. Katz
dwkatz@umich.edu

¹ School of Natural Resources and Environment, University of Michigan-Ann Arbor, 440 Church St., Ann Arbor, MI 48109, USA

Introduction

It has been estimated that herbivores consume roughly 10–20 % of annual net primary production in terrestrial ecosystems (Hartley and Jones 1997) and that foliar herbivory rates average around 5 % of leaf area per year (Turcotte et al. 2014). Although herbivory undeniably has strong effects on individual plant survival, growth, and fecundity (Hawkes and Sullivan 2001; Morris et al. 2007; Zvereva et al. 2010; Stephens and Westoby 2015), assessing its effects on plant population growth rates is less straightforward. Indeed, at one point it was debated whether the effects of herbivory on individuals would even scale up to the population level (e.g., Crawley 1989). Since then, an increasing number of studies have quantified relationships between herbivory and plant population dynamics (Maron and Crone 2006). In most cases, this has been accomplished with stage-structured population models (Caswell 1989) or with integral projection models (IPM; Easterling

et al. 2000). These models respectively divide populations into either discrete categories or continuous variables along the gradients of size, age, or stage in the life cycle. Demographic transition rates (e.g., growth and survival) are then parameterized, generally by repeatedly measuring marked individuals. Reproduction can be measured by observing the number of seeds produced and their germination rates or by recording the number of new seedlings each year. Because plants have varying life histories (e.g., presence of seedbanks, number of distinct stages, backward transitions) and studies use different modeling approaches, particular demographic transitions are often not directly comparable between studies. What is consistent across studies is that demographic transition rates can be used to calculate population growth rates (λ); populations with $\lambda > 1$ are increasing, whereas populations with a $\lambda < 1$ are decreasing. In the case of matrix population models, λ is estimated as the dominant eigenvalue of the demographic transition matrix, whereas IPM models use continuous functions that do not require discrete stage categories. Differences in results between the two methods are minor when sample sizes exceed approximately 300 individuals (Ramula et al. 2009). Separate population models can be constructed using demographic transition rates derived from plants growing under ambient herbivory versus reduced herbivory. Parameter estimates for reduced herbivory can either be determined by experimentally reducing herbivory for a subset of plants (e.g., applying pesticides or constructing herbivore exclosures) or observationally (e.g., measuring seed predation rates by observing the number of damaged seeds and then using seed sowing experiments to see by how much the loss of seeds reduced λ). In both cases, plant population growth rates can be calculated both with and without herbivory; any differences in λ can then be attributed to herbivores.

Although there is considerable variation in the spatial and temporal scale at which studies assess differences in λ , they provide unique opportunities to answer important questions. First, these studies can show what the range of responses to invertebrate herbivores is at the population level, and whether it varies by type of herbivory. Studies of λ can also be used to assess whether herbivory rates are a good predictor of the effects of herbivores on population growth. Many studies use herbivory to make inferences about population level phenomena (e.g., tests of the enemy release hypothesis) and so would benefit from knowing the strength of the association between measured herbivory and population growth rates. Finally, although these studies are not able to directly answer questions about density dependence and population stabilization (relatively few studies consistently track plant density across time or space), they do offer the chance to check whether invertebrate herbivores are able to prevent plant populations from reaching

high plant population growth rates. Specifically, these data can be used to test whether herbivores decrease plant population growth rates more when they have the potential to be high or if the effects of herbivores are constant across the range of plant population growth rates. This could have important implications for plant population and community dynamics (e.g., competitive exclusion).

Studies that have investigated the impacts of herbivory on λ tend to report disparate results which are frequently discussed, but there has not yet been a meta-analysis of this body of literature (but see an insightful semi-quantitative review by Maron and Crone 2006). This may, in part, be due to the difficulty of the task; formal meta-analysis generally requires the variance of reported estimates and the sample size of each study (Hedges et al. 1999; Gurevitch and Hedges 2001; Koricheva et al. 2013), but these data are frequently not available or are not easily applied to comparisons of plant population growth rates (Crone et al. 2011). One of the key issues is that most plant population growth rates are calculated in a deterministic framework, and as such they produce a single estimate of λ , without an estimate of variance (Crone et al. 2011). For example, in many stage-structured models, an average demographic transition rate might be calculated across an experiment and used in the population model, resulting in a single estimate of λ without variance. In other cases, variance in λ is estimated by simulation; the demographic transition rates recorded in different plots, locations, or years are stochastically sampled, which provides estimates of the mean and 95 % confidence interval of λ . Another issue is that comparing the sample size for different studies is not straightforward; λ is derived from many different parameter estimates that are often derived from methodologically separate experiments (e.g., seed germination trials vs. adult survival), and many of these do not report sample sizes. It would also be problematic to weight different life stages equally (e.g., a comparison of 100 seeds vs. 100 adults) or to make direct comparisons between the number of individual plants and the number or size of plots measured. Finally, some studies use estimates from the literature for a particular demographic transition rate. These issues present serious challenges to the use of traditional meta-analyses on these studies. Fortunately, increasing numbers of studies are providing examples of innovative ways to approach meta-analyses when datasets are incomplete or heterogeneous (e.g., Ibáñez et al. 2014; Ogle et al. 2014).

In the study reported here, I compile the results of experiments that compared plant population growth rates with and without invertebrate herbivory. I include studies that either estimated the effect of herbivory on plant demography by experimentally reducing herbivory or by observing the reductions in demographic rates caused by herbivory. I then use this dataset to conduct a

meta-regression analysis to answer several questions: (1) What is the overall effect of herbivory on plant population growth rates? (2) Is measured herbivory a good indicator for the effects of herbivores on plant population growth rates? (3) Does herbivory have stronger effects on plant populations that have the potential for rapid growth? The answers to these questions provide a better understanding of how invertebrate herbivores affect plant population growth rates.

Methods

In November 2013, I searched for papers that reported the impacts of invertebrate herbivores on plant population growth rates through the Institute for Scientific Information Web of Science using the following terms in the “Topic” category: *plant AND population growth AND insect herbiv* OR mollus* herbiv*; this returned 860 publications. I selected publications that reported plant population growth rates (λ) at naturally occurring amounts of herbivory (λ_{+H}) or with reduced invertebrate herbivory (λ_{-H}). These are respectively referred to as actual population growth and potential population growth rate throughout this paper. I also selected studies that were conducted in natural environments or common gardens, but greenhouse experiments were excluded because they lack ecological complexity that could affect plant and herbivore population dynamics. To ensure that no studies were overlooked, I also systematically searched through the references of the selected publications and through studies that had cited each selected publication. Of the articles retrieved, I only kept those that used field estimates of demographic rates to track the impacts of invertebrate herbivore(s) on host plant λ . If parameter estimates for the importance of herbivory to plant populations were taken from other systems or places and then extrapolated to the study system, then the study was excluded. However, I did include studies that used borrowed parameter estimates for demographic transition rates that were unrelated to the measured type of herbivory. For example, a study that measured seed predation but used seedling growth rates from the literature was included. Applying these criteria, I included a total of 29 studies from 26 publications (study is defined here as an investigation of a particular plant species using a particular methodology; separate experiments assessing seed herbivores and general herbivores reported within the same publication are counted as separate studies). Of these studies, nine reported estimates in multiple years and ten reported estimates in multiple locations, which resulted in a total of 168 data points. One data point was excluded from all analyses as an outlier because the population growth rate reported was approximately an order of magnitude higher than other

observations and the standard deviation (SD) was correspondingly large ($\lambda_{+H} = 20.4 \pm 6.8$, $\lambda_{-H} = 20.3 \pm 6.9$).

For each study, I collected information on the estimates of plant population growth rates both with and without herbivory and their associated variance. I also collected information on the study system, the plant, the herbivore(s), the type of the study (experimental vs. observational), and the amount of herbivory experienced. When data were reported in figures but not in the text or in tables, the information was extracted using Plot Digitizer (Huwaldt and Steinhorst 2013). In most studies, herbivory was quantified as a percentage of leaf area removed or as the percentage of seeds attacked. However, in one study (Miller et al. 2009), herbivory measurements were reported as the number of damage marks per stem segment; in order to standardize herbivory measurements for this study, I divided all herbivory measurements by the maximum amount of herbivory observed, scaling it to a maximum of 1. I calculated the difference in measured herbivory between the control and the treatment as $\Delta H = H_{\text{control}} - H_{\text{treatment}}$.

Statistical analysis

Plant population growth rate data present several challenges for traditional meta-analysis, including missing data on variation in λ and incomparable or misleading sample sizes. I therefore conducted a Bayesian meta-regression analysis; the statistical approaches and their justifications are described below.

The most common effect size used to compare the means of two continuous outcomes in meta-analysis is a standardized mean difference effect size, such as Hedges’ *D* (Gurevitch and Hedges 2001). However, Hedges’ *D* is calculated in part based on sample variance. This presents a problem because the calculated effect size can be very large for studies that have small differences in means between treatments, but even smaller variances. For example, in one observation included in this analysis, the population growth rates (mean \pm SD) were estimated very precisely ($\lambda_{+H} = 1.0000 \pm 0.0001$, $\lambda_{-H} = 1.1600 \pm 0.0014$), which resulted in a very small variance and an enormous effect size (Hedges’ *D*: 159.76). While this is effective for showing that there was very little chance that the means of the two treatments were the same, the main questions posed in the meta-regression I was conducting focus on the size of the effect rather than on whether the differences in means are significant. I therefore used response ratios, which are a useful alternative (Hedges et al. 1999) and have been widely used for meta-analyses in ecology (Koricheva et al. 2013). I calculated the response ratio for each observation as $R = \frac{\lambda_{-H}}{\lambda_{+H}}$; for example, an *R* of 2 would mean that population growth rates were twofold higher in the herbivory reduction treatment. I then took the natural log of *R*, $\ln R$,

which has several useful statistical properties, including a non-skewed distribution, so differences in $\ln R$ are directly comparable (Koricheva et al. 2013).

Relatively few studies of plant population growth report variation in λ (Halpern and Underwood 2006; Nelson et al. 2010); of the observations included in this study, only 28 of 168 did so. The only other meta-analysis of plant population growth rates that could be found used variability between sites and years to calculate variance in λ (Schmidt et al. 2011). While this approach can answer broader questions, aggregating information based on site or year results in the loss of data from smaller spatial or temporal scales (e.g., averaging across years prevents the analysis of yearly herbivory measurements within a study). I therefore used a simulation method similar to multiple imputation methods (Lajeunesse 2013) to estimate missing values. Specifically, I simulated missing variance values using the observed range of reported variance for the two categories of herbivory: (1) seed predation: $SD \sim \text{Uniform}(0, 0.86)$; (2) other types of herbivory: $SD \sim \text{Uniform}(0, 1.45)$. Next, to calculate the effect size, $\ln R$, I drew 10,000 pairs of random numbers from the distributions of λ_{+H} and λ_{-H} , and divided one by the other and then took the natural log of the quotient. The distribution of λ_{+H} and of λ_{-H} for each observation was assumed to be normally distributed around their measured mean and with a SD that was either extracted from the paper or that was drawn from the uniform distributions described above. Reported means of λ and bootstrapped confidence intervals extracted from the included studies show little skewness in λ , supporting the assumption of normality [see Electronic Supplementary Material (ESM) A: Skewness of λ]. The distribution of $\ln R$ for each observation incorporates both the variance associated with λ_{+H} and λ_{-H} , and, when data were missing, the range of uncertainty associated with missing data. This simulation approach adds considerable variation to estimates of $\ln R$ in cases where the SD of λ was unreported because observed SD are positively skewed (ESM B: Observed standard deviations). By adding large amounts of variation to each observation with missing data, this approach leads to highly conservative estimates of the effect size and, therefore, systematically underestimates the strength of observed patterns. To assess whether the simulation of λ 's SD affected model results, I also conducted a version of the analysis where I only included observations or studies that reported variance in λ or for which the variance in λ could be calculated across years or locations. Although this approach reduces sample sizes and the temporal and spatial resolution of analysis, its results (ESM C: Non-simulation model results) can be used to assess the validity of the simulation approach. Neither of these models weights $\ln R$ by the sample size of the observation because of the incomparability of sample sizes across studies; variation is calculated as

described above, not according to the standard equation of variance for $\ln R$.

I then performed a hierarchical Bayesian meta-regression to analyze how reduced herbivory treatments and other covariates affected population growth rates. Several different models were explored (e.g., quadratic effects for herbivory), and I selected the model with the lowest deviance information criterion (DIC; Spiegelhalter et al. 2002) that allowed the questions to be addressed. I performed separate analyses for observations that focused on seed predation and for observations that measured other types of herbivory (synonymously referred to as general herbivory).

The final models included two covariates: (1) the difference in measured herbivory between the control and the herbivory reduction treatment, ΔH , (continuous, ranging from -0.007 to 0.92) and (2) the potential population growth rate without herbivory, λ_{-H} , (continuous, ranging from 0.06 to 5.20). For observations where ΔH was not reported ($n = 80$), I drew it from a non-informative distribution, $\Delta H \sim \text{Uniform}(-0.007, 0.92)$. I also explored drawing missing values of ΔH from a distribution that better matched the observed data, $\Delta H \sim \text{Beta}(1.1, 2.0)$, but this resulted in only minimal differences in parameter estimates (ESM D: Herbivory beta distribution). The models also included random effects for each study, j , which were drawn from a normal distribution with a mean of μ : $\gamma_{\text{study}j} \sim N(\mu, \sigma_{\text{study}}^2)$; μ was in turn drawn from a non-informative normal distribution, $\mu \sim N(0, 1000)$. The effect size for each observation i , $\ln R_i$, was centered around a normal distribution with a mean of θ_i and the reported or simulated SD σ_i associated with the effect size:

$$\ln R_i \sim N(\theta_i, \sigma_i^2)$$

$$\theta_i = \beta_1 \times \Delta H_i + \kappa \times \lambda_{-H_i} + \gamma_{\text{study}j(i)}$$

The model for studies that focused on seed predation was the same, except an exponential term for the effect of ΔH resulted in a lower DIC value:

$$\ln R_i \sim N(\theta_i, \sigma_i^2)$$

$$\theta_i = e^{\beta_2 \times \Delta H_i} + \kappa \times \lambda_{-H_i} + \gamma_{\text{study}j(i)}$$

I then simulated θ across the range of ΔH , while holding λ_{-H} at its mean value (1.28) to visualize the model results. Similarly, I simulated θ across the range of λ_{-H} , while holding ΔH at its mean value (34 %).

For these analyses, posterior densities of the parameters were obtained by Gibbs sampling (Geman and Geman 1984) using JAGS 3.4 (Plummer 2003) via the rjags package (Plummer 2014) in R (R Core Team 2013). Convergence occurred after 1000–5000 iterations, and chains were

inspected visually. Each model was run for 50,000 iterations, and posterior parameter values were based on post-convergence results. Fixed effects coefficients were considered to be statistically significant when their 95 % credible intervals (CI) did not overlap with zero.

To show the overall effects of herbivores on plant population growth rates, I also conducted a traditional random effects meta-analysis that weighted each study by the reported variance associated with $\Delta\lambda$. Relatively few observations reported variance in λ ($n = 27$), so I used inter-annual and inter-site differences to calculate variances for other studies. Combined, this resulted in a total of 54 observations from 14 studies. Although the variance in these extra observations reflects both inter-annual variability and uncertainty in parameter estimates, many of the studies that did report variation were themselves parameterized over multiple years and also used year-to-year differences to estimate variability (e.g., Ehrlén 1995). I also used $\ln R$ for this analysis, but the variance was calculated in the traditional manner (Hedges et al. 1999). I then used the metafor package to conduct a random effects meta-analysis with study random effects (Viechtbauer 2010).

The distribution of effect sizes was not depressed around zero, suggesting a lack of publication bias against publishing non-significant results (Greenland 1987). In order to further assess the possibility of publication bias, I calculated a failsafe number (Orwin 1983) and created funnel plots (both are available in ESM E: Funnel plots and publication bias). All analyses were conducted using R (R Core Team 2013). Visualization was conducted using the ggplot2 package (Wickham 2009).

Results

Summary of selected studies

The selected publications (ESM F: Selected publications) included studies where fieldwork was carried out between 1982 and 2010 and which were conducted in temperate forests ($n = 7$) and tropical forests ($n = 3$), grasslands ($n = 14$), mountains ($n = 4$), and a desert ($n = 1$). Of the observations, the parameterization time period ranged from 1 to 11 (average 1.4) years, although if data were reported separately for each year, they are reported as such here. While λ was somewhat more variable for observations that were parameterized in ≥ 2 years (ESM G Effect of the number of study locations and years), this is due to study random effects.

The plants studied included woody or herbaceous perennials (158 observations from 26 species), perennial grasses (7 observations from 1 species), and herbaceous annuals (3 observations from 2 species). Some plants were classified

by the authors as exotic (9 observations from 6 species), but most plants were classified as native or not explicitly classified (159 observations from 24 species; a species was planted in both its native and exotic range). Similarly, a few herbivores were classified as exotic (3 observations), but most of the herbivores were classified as native or not classified at all (165 observations). Of the data points, 121 were collected using observational techniques, whereas 47 were derived from experimentally manipulating herbivory using pesticides ($n = 46$) or in one case insect exclusion cages ($n = 1$). Herbivory was reported on flowers ($n = 12$), seeds ($n = 120$), juveniles ($n = 41$), and adults ($n = 45$); in some cases, herbivory was quantified on a specific subset of life stages or plant tissues. Of those studies that reported host specificity of the herbivores, most observations were of specialists (49 observations from 9 studies), but several were of generalists (4 observations from 3 studies); in several cases it was not reported at all (7 observations from 3 studies). Many studies reported damage caused by invertebrate herbivore communities (108 observations from 13 studies). Differences between studies that used IPM and matrix population models were small, as were differences between studies that used only internally collected data to parameterize demographic transition rates and those studies that used one or more demographic transition rates from the literature (ESM H: Model type and data source).

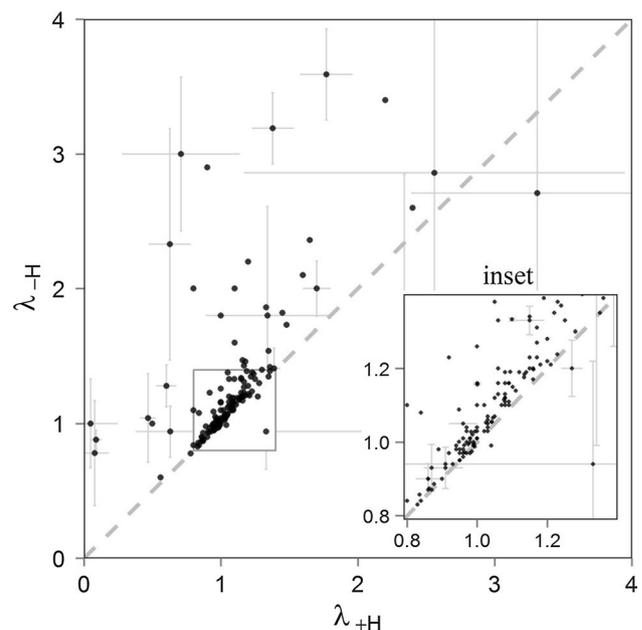


Fig. 1 The effects of herbivory on plant population growth rates with ambient herbivory (λ_{+H}) and with reduced herbivory (λ_{-H}) for all observations from native plants. Values above the one:one line indicate that reducing herbivory had a positive effect on the plant population growth rates; standard deviations (SD) are included when available. Inset Enlarged view of the box to the left

Of the 167 analyzed data points, $\ln R$ was positive in most cases ($n = 145$), although in some cases it was exactly zero ($n = 14$) or negative ($n = 8$) (Fig. 1). The average value of λ including herbivory was $\lambda_{+H} = 1.08$ (SD 0.36), and the average value of λ without herbivory was $\lambda_{-H} = 1.28$ (SD 0.58). There were 67 observations of plant populations that had decreasing population growth rates ($\lambda_{+H} < 1$) in control conditions; in 20 of these observations, the population growth rate was >1 in the reduced herbivory treatment (λ_{-H}).

Measured herbivory was extracted for approximately half of all observations ($n = 87$), from a total of 22 studies (some studies either did not measure herbivory or did not report it in a form that could be linked to particular observations). The amount of herbivory in controls ranged from 0 to 98 %, with a mean of 41 %, whereas in reduced herbivory treatments, herbivory ranged from 0 to 56 %, with a mean of 3 %. The effectiveness of the herbivory reduction treatments also varied widely; the difference in measured herbivory (ΔH) between controls and the reduced herbivory treatment ranged from -1 to 92 %, with a mean of 34 %.

Model results

Herbivores tended to reduce plant population growth rates, as shown by the mean value and 95 % CI for θ (Fig. 2). The estimated values of θ were generally higher for studies of general herbivores than for seed predators, except at very high levels of seed predation (Fig. 2). For studies of general herbivores, ΔH did not have a significant effect, as can be

seen by the almost flat line in Fig. 2a, although studies with very small differences in herbivory had very small effect sizes (β_1 : mean 0.01, 95 % CI $-0.01, 0.03$). In studies of seed predation, the effect size was often relatively higher when ΔH was higher, but this trend was not statistically significant after study random effects were included (β_2 : mean 0.14, 95 % CI $-0.10, 0.35$; Fig. 2).

Herbivore reduction treatments allowed some plant populations to reach much higher growth rates. This means that herbivores tend to prevent plant populations with the potential for high growth rates from realizing them or, alternately worded, that herbivores had larger effects on plant populations that had the potential for high growth rates. This results in higher variation in growth rates in the herbivory reduction treatments than in the control treatments (λ_{+H} SD = 0.36 vs. λ_{-H} SD = 0.58). The pattern of herbivores having the largest effect on populations with high potential growth rates held both for studies of general herbivory (κ : mean 0.25, 95 % CI 0.17, 0.30) and for seed predation studies (κ : mean 0.25, 95 % CI 0.07, 0.45; Fig. 3). For seed predation studies this was in part because the largest proportions of seeds were eaten in cases where there was high λ_{-H} (Fig. 3; ESM I: Seed predation and λ_{-H}). However, there was high variability, and despite a general trend, there were some cases in which herbivores had large effects even at low potential population growth rates. The R^2 for the model of general types of herbivory and for seed predation was 0.10 and 0.83, respectively (ESM J: Parameter estimates). Results from the model where λ 's SD was calculated across years or locations instead of simulated were qualitatively similar

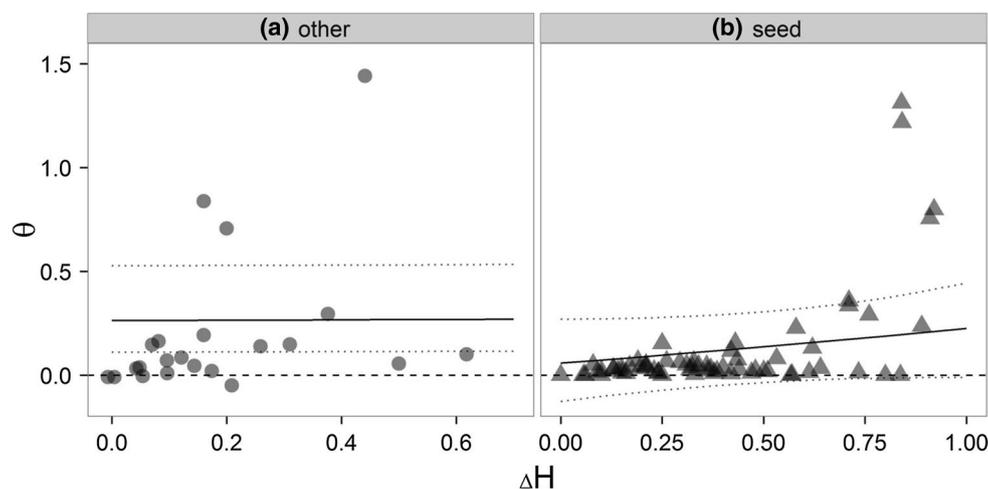


Fig. 2 The estimated effect of herbivory reduction treatments on population growth rate (θ) across the observed range of measured herbivory values (ΔH), simulated at the average levels of λ_{-H} for observations of other types of herbivory (1.57) and seed predation (1.18). Mean modeled values are shown (solid lines) as are 95 % confidence

intervals (CIs; dotted lines). Raw data (circles and triangles) from observations that measured herbivory are plotted for comparison. The fit of the model for other types of herbivory was $R^2 = 0.09$ and for seed predation it was $R^2 = 0.83$

Fig. 3 The estimated effect of herbivory reduction treatments on population growth rate (θ) across the observed range of potential population growth rates (λ_{-H}), simulated at the average levels of ΔH for other types of herbivory (19 %) and seed predation (40 %). Mean modeled values are shown (solid lines) as are 95 % CIs (dotted lines). Raw data (circles and triangles) are plotted for comparison and if herbivory was measured, ΔH is depicted by shading

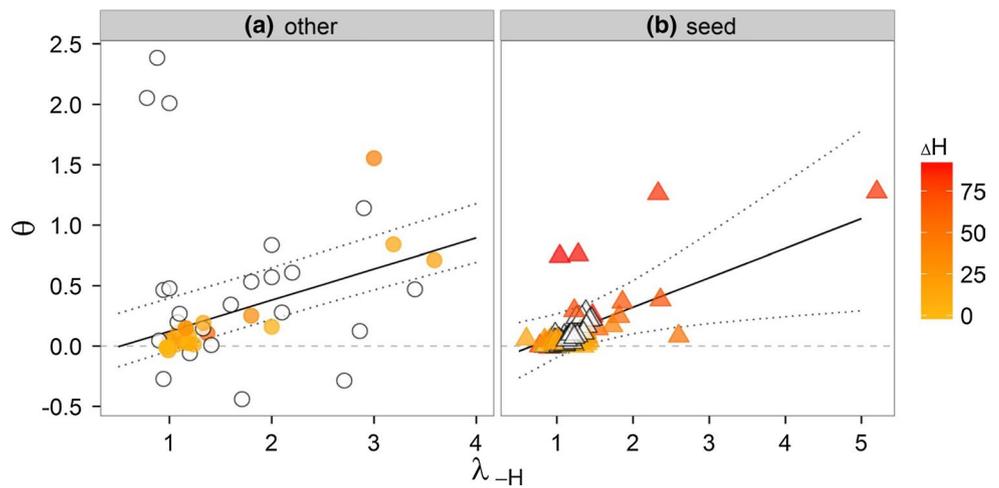
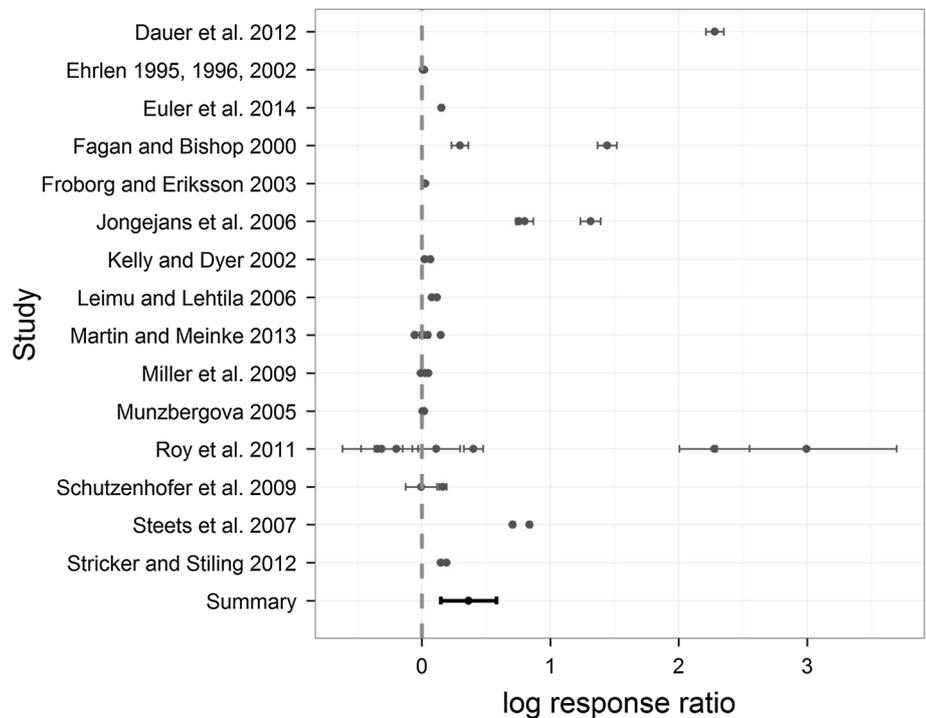


Fig. 4 Traditional random effects meta-analysis, including study random effects. A forest plot of the effects of herbivores on plant population growth is shown below. Mean effect size and 95 % CI are shown for each observation for which variance was provided or could be calculated. This analysis used inverse variance weighting



(ESM C: Non-simulation model results). The one noteworthy difference is that κ , the coefficient for λ_{-H} for seed predation studies, had a broader 95 % credible interval that overlapped zero [averaged model had κ mean = 0.27 (95 % CI -0.10, 0.60) vs. the simulation model with κ mean = 0.25 (95 % CI 0.07, 0.45)]. The general conclusions from the model were robust to the inclusion of the outlier; with it there was still a significant effect of λ_{-H} on LnR (κ : mean 0.14, 95 % CI 0.10, 0.18; β was not strongly affected and other parameter estimates from this version of the model are not shown). Versions of Figs. 2 and 3 that display the study number are presented in ESM K (Contributions of individual studies).

Traditional meta-analysis results

The traditional random effects meta-analysis with study level effects showed wide variability in the effect of herbivores on plant populations across and within studies (Fig. 4). Even so, the overall effect was significant (mean 0.37, 95 % CI 0.07, 0.67; $p = 0.017$).

Discussion

This quantitative synthesis demonstrates that invertebrate herbivores often cause substantial reductions in plant

population growth rates (Fig. 1). While there is extensive variability in the population effects of herbivores across and within study systems, these results contradict the once tenable perspective that invertebrate herbivores do not have strong effects on plant populations (Crawley 1989). However, even within systems, reducing herbivory by larger amounts does not necessarily lead to greater increases in population growth rates. The weak relationship between these variables suggests that measured herbivory rates are a poor proxy for the importance of herbivory in that population. The compiled evidence from these studies also emphasizes that herbivores are effective at preventing plants from attaining high population growth rates. These findings are broadly corroborated by the analysis that used only studies for which SD were reported or could be calculated across time or space (ESM C: Non-simulation model results).

A weak relationship between the amount of herbivory and population level effects

The amount by which studies reduced herbivory (ΔH) was a poor predictor of increases in plant population growth rates, although for studies that focused on seed predation there was a general trend towards higher effect sizes at higher ΔH . Thus, when comparing across study systems, years, or sites, it was not uncommon for the population with lower ΔH (synonymous with herbivory in the control population for seed predation studies) to be more affected by herbivores (e.g., Ehrlén 1995, 1996, 2002). This synthesis therefore confirms that damage rates do not always reflect the true importance of herbivory to plant population growth rates (Crawley 1989; Ehrlén 2003; Maron and Crone 2006) and goes one step further by showing the weakness of this relationship. One reason why herbivory rates are a poor proxy for population growth is that sensitivity to the impacted demographic rate(s) can vary considerably over ontogeny, space, and time (Ehrlén 1996, 2002; Dauer et al. 2012; von Euler et al. 2014), not to mention across plant species. It is also possible that above-ground pesticide application could have affected herbivory types that were not measured (e.g., below ground or on stems). These results reiterate the problematic nature of using damage rates to test questions like whether escape from natural enemies is responsible for a species expansion in a new area (Chun et al. 2010). While the main modeling approach (simulation of the SD of λ) produces conservative results, the model that used only points that reported variance of λ shows similar patterns (ESM C: Non-simulation model results), suggesting that while a pattern between these variables may very well exist, it is at best weak.

Herbivory is often most important when potential population growth is high

Invertebrate herbivores tended to reduce population growth rates more when there was more potential for higher growth rates, although this relationship had poor predictive power for the general herbivory type; the three cases where herbivory had the largest effect had low potential population growth rates (Fig. 3). The stronger effects of herbivory when potential population growth rates are high can occur in cases where herbivores have the strongest effects on early life stages, such as seeds and seedlings, as is common in some systems (Green et al. 2014; Zhu et al. 2015). This is because these life stages are often most important in years with high population growth rates (e.g., Silvertown et al. 1993; Ehrlén 2002; von Euler et al. 2014); consequently, in years with high potential growth rates, herbivory would have a larger effect. However, of the studies that reported elasticity analyses, the elasticity of the seed and seedling stages was only strong (>0.25) in four of 17 studies (Elder and Doak 2006; Jongejans et al. 2006; Schutzenhofer et al. 2009; Dauer et al. 2012). Although these studies were characterized by high effect sizes, in only one of them (Jongejans et al. 2006) did high effect size contribute strongly to the observed pattern (ESM K: contributions of individual studies), which suggests other mechanisms are creating this pattern.

For seed predation, this correlation could also be caused by a scenario in which λ_{-H} is correlated with per capita seed production, which could result in higher rates of seed predation, in turn leading to a correlation between λ_{-H} and the effects of herbivory. This is supported by the observation that seed predation rates were the highest for observations with high λ_{-H} (Fig. 3), and very high rates of seed predation had strong effects at the population level (Fig. 2). Moreover, several authors observed higher seed predation rates for individual plants or plants in plots that produce more seeds (e.g., Ehrlén 1996, 2002; Egan and Irwin 2008; von Euler et al. 2014). Regardless of mechanism, the results of these studies show that herbivory often prevents plant populations from attaining high population growth rates, and this helps to explain why there is less variation in actual population growth rates (SD 0.36) than in potential population growth rates (SD 0.58; see Fig. 1). When the analysis was restricted to studies that reported variance in λ (ESM C: Non-simulation model results), the mean parameter estimates remained very similar, although the 95 % CI broadened enough to overlap zero for seed predation studies, suggesting that the correlation discussed in this section is unlikely to be an artifact of the statistical approach.

General herbivory versus seed predation

Studies that focused exclusively on seed predation generally reported smaller effects of herbivores on population growth rates. These results are also corroborated by the literature; seed predation reduces fecundity, which is generally one of the less important demographic rates for perennial plants (Silvertown et al. 1993). Thus, it stands to reason that seed predation has less of an impact than other types of herbivory. However, it should be noted that studies which focused on seed predators were also more likely to be observational than experimental, and were more likely to focus on only one species of herbivore.

Knowledge gaps

This synthesis has documented that invertebrate herbivores can and often do have large effects on plant populations; however, the extent to which herbivory regulates plant populations remains unknown. Although a few studies reported information on changes in plant density and herbivory rates over time or over space (e.g., Fagan and Bishop 2000; Fröberg and Eriksson 2003; Rose et al. 2011), most did not. Density dependence is only infrequently included in plant population growth models that quantify the impacts of herbivory (Halpern and Underwood 2006; Ramula and Buckley 2009). By including plant and herbivore density (Halpern and Underwood 2006), future studies may be able to more directly connect herbivores to plant population regulation.

It should also be noted that particular systems remain understudied; of the studies reviewed, only two focused on annual plants, none studied trees, and only three studied exotic herbivores. While phylogeny has not been found to be a strong driver of population growth rates (Buckley et al. 2010), additional studies on underrepresented functional groups will help to fill in gaps. Another gap is that none of these studies measured belowground herbivory, despite its importance to individual plants and entire communities (Van der Putten 2003). Finally, the results from these studies are not representative of the true effects of herbivores on plant populations for two reasons. First, the types of herbivory recorded and experimentally manipulated in these studies represent only a fraction of total herbivory experienced by these plants; herbivory is almost never monitored in every single plant organ over every single life stage. Second, a focus on existing plant populations means that cases where herbivores have extirpated a population or kept it from establishing in the first place are largely undocumented. There are many examples of herbivores preventing their host plants from colonizing particular habitats, such as serpentine soils (Fine et al. 2004, 2006; Lau et al. 2008), well-lit areas (Louda and Rodman 1996), or particular

elevation zones (Parker and Root 1981; Rand 2002), implying that the studies included in this analysis underrepresent extreme effects of invertebrate herbivores on plant population growth rates.

Acknowledgments Thanks are due to Inés Ibáñez for excellent advice and support throughout this project, and to Don Zak, Mark Hunter, Knute Nadelhoffer, Ben Lee, Teegan McClung, Natalie Tonn, and two anonymous reviewers for their helpful comments on an earlier version of this manuscript. The author was supported in part by a graduate research fellowship from the National Science Foundation.

Author contribution statement DSWK conceived, designed, and executed this study and wrote the manuscript. No other person is entitled to authorship.

Compliance with ethical standards

Conflict of interest The author declares that he has no conflict of interest.

References

- Buckley YM, Ramula S, Blomberg SP et al (2010) Causes and consequences of variation in plant population growth rate: a synthesis of matrix population models in a phylogenetic context. *Ecol Lett*. doi:10.1111/j.1461-0248.2010.01506.x
- Caswell H (1989) Matrix population models construction, analysis, and interpretation. Sinauer Associates, Sunderland
- Chun YJ, van Kleunen M, Dawson W (2010) The role of enemy release, tolerance and resistance in plant invasions: linking damage to performance. *Ecol Lett*. doi:10.1111/j.1461-0248.2010.01498.x
- Crawley MJ (1989) Insect herbivores and plant population dynamics. *Annu Rev Entomol*. doi:10.1146/annurev.en.34.010189.002531
- Crone EE, Menges ES, Ellis MM et al (2011) How do plant ecologists use matrix population models? *Ecol Lett* 14:1–8. doi:10.1111/j.1461-0248.2010.01540.x
- Dauer JT, McEvoy PB, Van Sickle J (2012) Controlling a plant invader by targeted disruption of its life cycle. *J Appl Ecol* 49:322–330. doi:10.1111/j.1365-2664.2012.02117.x
- Easterling M, Ellner S, Dixon P (2000) Size-specific sensitivity: applying a new structured population model. *Ecology* 81:694–708
- Egan JF, Irwin RE (2008) Evaluation of the field impact of an adventitious herbivore on an invasive plant, yellow toad-flax, in Colorado, USA. *Plant Ecol* 199:99–114. doi:10.1007/s11258-008-9415-0
- Ehrlén J (1995) Demography of the perennial herb *Lathyrus vernus*. II. Herbivory and population dynamics. *J Ecol* 83:297–308
- Ehrlén J (1996) Spatiotemporal variation in predispersal seed predation intensity. *Oecologia* 108:708–713
- Ehrlén J (2002) Assessing the lifetime consequences of plant-animal interactions for the perennial herb *Lathyrus vernus* (Fabaceae). *Perspect Plant Ecol Evol Syst* 5:145–163. doi:10.1078/1433-8319-00031
- Ehrlén J (2003) Fitness components versus total demographic effects: evaluating herbivore impacts on a perennial herb. *Am Nat* 162:796–810. doi:10.1086/379350
- Elder BD, Doak DF (2006) Comparing the direct and community-mediated effects of disturbance on plant population dynamics: flooding, herbivory and *Mimulus guttatus*. *J Ecol* 94:656–669. doi:10.1111/j.1365-2745.2006.01115.x

- Fagan W, Bishop J (2000) Trophic interactions during primary succession: herbivores slow a plant reinvasion at Mount St. Helens. *Am Nat* 155:238–251. doi:[10.1086/303320](https://doi.org/10.1086/303320)
- Fine PVA, Mesones I, Coley PD (2004) Herbivores promote habitat specialization by trees in Amazonian forests. *Science* 305:663–665
- Fine PVA, Miller ZJ, Mesones I et al (2006) The growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology* 87:150–162
- Fröberg H, Eriksson O (2003) Predispersal seed predation and population dynamics in the perennial understorey herb *Actaea spicata*. *Can J Bot* 81:1058–1069. doi:[10.1139/b03-099](https://doi.org/10.1139/b03-099)
- Geman S, Geman D (1984) Stochastic relaxation, Gibbs distributions, and the Bayesian restoration of images. *IEEE Trans Pattern Anal Mach Intell* 6:721–741. doi:[10.1109/TPAMI.1984.4767596](https://doi.org/10.1109/TPAMI.1984.4767596)
- Green PT, Harms KE, Connell JH (2014) Nonrandom, diversifying processes are disproportionately strong in the smallest size classes of a tropical forest. *Proc Natl Acad Sci USA*. doi:[10.1073/pnas.1321892112](https://doi.org/10.1073/pnas.1321892112)
- Greenland S (1987) Quantitative methods in the review of epidemiologic literature. *Epidemiol Rev* 9:1–30
- Gurevitch J, Hedges LV (2001) *Meta-analysis: combining the results of independent experiments*, 2nd edn. Oxford University Press, Oxford
- Halpern SL, Underwood N (2006) Approaches for testing herbivore effects on plant population dynamics. *J Appl Ecol* 43:922–929. doi:[10.1111/j.1365-2664.2006.01220.x](https://doi.org/10.1111/j.1365-2664.2006.01220.x)
- Hartley SE, Jones CG (1997) Plant chemistry and herbivory, or why the world is green. In: Crawley M (ed) *Plant ecology*. Blackwell Scientific, Cambridge, pp 284–324
- Hawkes CV, Sullivan JJ (2001) The impact of herbivory on plants in different resource conditions: a meta-analysis. *Ecology* 82:2045–2058
- Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156
- Huwaldt J, Steinhilber S (2013) Plot Digitizer. Available at: <http://plot-digitizer.sourceforge.net/>
- Ibáñez I, Katz DSW, Peltier D et al (2014) Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess-multiresponse dynamics. *J Ecol* 102:882–895. doi:[10.1111/1365-2745.12223](https://doi.org/10.1111/1365-2745.12223)
- Jongejans E, Sheppard AW, Shea K (2006) What controls the population dynamics of the invasive thistle *Carduus nutans* in its native range? *J Appl Ecol* 43:877–886. doi:[10.1111/j.1365-2664.2006.01228.x](https://doi.org/10.1111/j.1365-2664.2006.01228.x)
- Koricheva J, Gurevitch J, Mengersen K (2013) *Handbook of meta-analysis in ecology and evolution*. Princeton University Press, Princeton
- Lajeunesse M (2013) Recovering missing or partial data from studies: a survey of conversions and imputations for meta-analysis. In: Koricheva J, Gurevitch J, Mengersen K (eds) *Handbook of meta-analysis in ecology and evolution*. Princeton University Press, Princeton, pp 196–206
- Lau JA, McCall AC, Davies KF et al (2008) Herbivores and edaphic factors constrain the realized niche of a native plant. *Ecology* 89:754–762
- Louda SM, Rodman JE (1996) Insect herbivory as a major factor in the shade distribution of a native crucifer (*Cardamine Cordifolia* A. Gray, Bittercress). *J Ecol* 84:229–237. doi:[10.2307/2261358](https://doi.org/10.2307/2261358)
- Maron JL, Crone E (2006) Herbivory: effects on plant abundance, distribution and population growth. *Proc R Soc B* 273:2575–2584. doi:[10.1098/rspb.2006.3587](https://doi.org/10.1098/rspb.2006.3587)
- Miller TEX, Louda SM, Rose K, Eckberg JO (2009) Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient. *Ecol Monogr* 79:155–172. doi:[10.1890/07-1550.1](https://doi.org/10.1890/07-1550.1)
- Morris WF, Hufbauer R, Agrawal A et al (2007) Direct and interactive effects of enemies and mutualists on plant performance: a meta-analysis. *Ecology* 88:1021–1029. doi:[10.1890/06-0442](https://doi.org/10.1890/06-0442)
- Nelson ESD, Harris S, Soulsbury CD et al (2010) Uncertainty in population growth rates: determining confidence intervals from point estimates of parameters. *PLoS One* 5:e13628. doi:[10.1371/journal.pone.0013628](https://doi.org/10.1371/journal.pone.0013628)
- Ogle K, Pathikonda S, Sartor K et al (2014) A model-based meta-analysis for estimating species-specific wood density and identifying potential sources of variation. *J Ecol* 102:194–208. doi:[10.1111/1365-2745.12178](https://doi.org/10.1111/1365-2745.12178)
- Orwin RG (1983) A fail-safe N for effect size in meta-analysis. *J Educ Behav Stat* 8:157–159. doi:[10.3102/10769986008002157](https://doi.org/10.3102/10769986008002157)
- Parker MA, Root RB (1981) Insect herbivores limit habitat distribution of a native composite, *Machaeranthera canescens*. *Ecology* 62:1390–1392
- Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Available at: <http://mcmc-jags.sourceforge.net/>
- Plummer M (2014) rjags: Bayesian graphical models using MCMC. Available at: <https://cran.r-project.org/web/packages/rjags/rjags.pdf>
- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ramula S, Buckley YM (2009) Multiple life stages with multiple replicated density levels are required to estimate density dependence for plants. *Oikos* 118:1164–1173. doi:[10.1111/j.1600-0706.2009.17595.x](https://doi.org/10.1111/j.1600-0706.2009.17595.x)
- Ramula S, Rees M, Buckley YM (2009) Integral projection models perform better for small demographic data sets than matrix population models: a case study of two perennial herbs. *J Appl Ecol* 46:1048–1053. doi:[10.1111/j.1365-2664.2009.01706.x](https://doi.org/10.1111/j.1365-2664.2009.01706.x)
- Rand T (2002) Variation in insect herbivory across a salt marsh tidal gradient influences plant survival and distribution. *Oecologia* 132:549–558. doi:[10.1007/s00442-002-0989-2](https://doi.org/10.1007/s00442-002-0989-2)
- Rose KE, Russell FL, Louda SM (2011) Integral projection model of insect herbivore effects on *Cirsium altissimum* populations along productivity gradients. *Ecosphere* 2:1–19. doi:[10.1890/ES11-00096.1](https://doi.org/10.1890/ES11-00096.1)
- Schmidt IB, Mandel L, Tickin T, Gaoue OG (2011) What do matrix population models reveal about the sustainability of non-timber forest product harvest? *J Appl Ecol* 48:815–826. doi:[10.1111/j.1365-2664.2011.01999.x](https://doi.org/10.1111/j.1365-2664.2011.01999.x)
- Schutzenhofer MR, Valone TJ, Knight TM (2009) Herbivory and population dynamics of invasive and native *Lespedeza*. *Oecologia* 161:57–66. doi:[10.1007/s00442-009-1354-5](https://doi.org/10.1007/s00442-009-1354-5)
- Silvertown J, Franco M, Pisanty I, Mendoza A (1993) Comparative plant demography—relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J Ecol* 81:465–476
- Spiegelhalter DJ, Best NG, Carlin BP, van der Linde A (2002) Bayesian measures of model complexity and fit. *J R Stat Soc* 64:583–639. doi:[10.1111/1467-9868.00353](https://doi.org/10.1111/1467-9868.00353)
- Stephens AE, Westoby M (2015) Effects of insect attack to stems on plant survival, growth, reproduction and photosynthesis. *Oikos* 124:266–273. doi:[10.1111/oik.01809](https://doi.org/10.1111/oik.01809)
- Turcotte MM, Davies TJ, Thomsen CJM et al (2014) Macroecological and macroevolutionary patterns of leaf herbivory across vascular plants. *Proc R Soc B* 281:1–7. doi:[10.1098/rspb.2014.0555](https://doi.org/10.1098/rspb.2014.0555)
- Van der Putten W (2003) Plant defense belowground and spatiotemporal processes in natural vegetation. *Ecology* 84:2269–2280
- Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. *J Stat Softw* 36:1–48
- von Euler T, Ågren J, Ehrlén J (2014) Environmental context influences both the intensity of seed predation and plant demographic sensitivity to attack. *Ecology* 95:495–504

- Wickham H (2009) *ggplot2: elegant graphics for data analysis*. Springer SBM, New York
- Zhu Y, Comita LS, Hubbell SP, Ma K (2015) Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. *J Ecol* 103:957–966. doi:[10.1111/1365-2745.12414](https://doi.org/10.1111/1365-2745.12414)
- Zvereva EL, Lanta V, Kozlov MV (2010) Effects of sap-feeding insect herbivores on growth and reproduction of woody plants: a meta-analysis of experimental studies. *Oecologia* 163:949–960. doi:[10.1007/s00442-010-1633-1](https://doi.org/10.1007/s00442-010-1633-1)