LETTER

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Variability in plant nutrients reduces insect herbivore performance

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The performance and population dynamics of insect herbivores depend on the nutritive and defensive traits of their host plants[1]. The literature on plant–herbivore interactions focuses on plant trait mean values[2–4], but recent studies showing the importance of plant genetic diversity for herbivores suggest that plant trait variance may be equally important[5,6]. The consequences of plant trait variance for herbivore performance, however, have been largely overlooked. Here we report an extensive assessment of the effects of within-population plant trait variance on herbivore performance using 457 performance datasets from 53 species of insect herbivores. We show that variance in plant nutritive traits substantially reduces mean herbivore performance via non-linear averaging of performance relationships that were overwhelmingly concave down. By contrast, relationships between herbivore performance and plant defence levels were typically linear, with variance in plant defence not affecting herbivore performance via non-linear averaging. Our results demonstrate that plants contribute to the suppression of herbivore populations through variable nutrient levels, not just by having low average quality as is typically thought. We propose that this phenomenon could play a key role in the suppression of herbivore populations in natural systems, and that increased nutrient heterogeneity within agricultural crops could contribute to the sustainable control of insect pests in agroecosystems.

Decades of research have established the importance of plant nutritive and defensive traits for herbivore performance and population dynamics[1]. Recent studies, showing that plant genetic diversity influences herbivore community patterns, suggest that plants influence herbivores not only through average trait values but also through variance in trait values[5,6]. The literature on plant defences and herbivore nutritional ecology, however, centres on mean relationships and mostly ignores the consequences of trait variance[2,3]. This narrow focus is an oversight as intraspecific plant trait variance pervades natural systems, from among tissues within individuals to among individuals within populations [4]. In modern agroecosystems, however, plant functional diversity has been replaced with extensive homogeneous monocultures of single crop varieties or genotypes[7]. How this loss of trait diversity influences higher trophic levels and ecosystem services, such as pest control, has been underexplored, considering how much is known about the consequences of genetic diversity[8,9]. Elucidation of the direct effects of variability in plant defensive or nutritive traits on herbivore performance could inform the management of agroecosystems, perhaps revealing ways to use crop heterogeneity for sustainable pest management, and advance our fundamental understanding of plant–insect interactions. Here we test for general patterns in the effects of plant trait variance on herbivore performance, using 457 datasets that relate plant traits to herbivore growth and survival for 53 species of phytophagous insects from 7 orders.

Plant variance could influence herbivores in several ways, such as reducing the opportunity for herbivore populations to adapt evolutionarily to plant defences[10]. We focused on the ecological effects that occur via non-linear averaging, a general phenomenon that potentially applies to all species and has been used successfully to understand diverse biological phenomena[11,12]. In this context, non-linear averaging (also known as Jensen's inequality[13]) allows us to predict the effects of plant variance on mean herbivore performance using the curvature of the relationship between plant trait values and herbivore performance (Fig. 1). If the function that relates herbivore performance to a plant trait is concave down (decelerating), then herbivore populations experiencing variance in that trait will exhibit lower mean performance relative to herbivores that experience constant levels of the trait at the same trait mean[3]. By contrast, variance enhances mean performance when herbivore performance functions are concave up (accelerating). When performance functions are linear, plant trait variance has no effect. Three reviews have attempted to generalize the effects of plant trait variance on herbivore performance by visually assessing and categorizing the curvature of herbivore performance functions in published studies[3,4,11]. They came to contradictory conclusions, perhaps because they had small sample sizes (less than 12 studies) and lacked objective methods for quantifying curvature.

We found 76 papers published between 1968 and 2014 that allowed us to estimate herbivore performance functions (Extended Data Fig. 1 and Supplementary Tables 1 and 2). These papers reported growth or survival of herbivores at least 4 values of a plant trait. Our search only included studies that directly manipulated trait values in a laboratory setting (for example, through artificial diet, or applying compounds to plant surfaces) to avoid inclusion of spurious correlations. We estimated a performance function for each dataset with a cubic spline (Fig. 2a, b). The spline from each dataset allowed us to quantify the effect of trait variance on herbivore performance—specifically the difference in performance in the presence and absence of plant trait variance (Jensen's effect). We predicted performance in the absence of variance using the value of the performance function at the mean of the plant trait levels in the dataset. We predicted performance in the presence of variance using the mean of the values of the performance function at each of the trait levels (Extended Data Fig. 2). This approach assumes that the original authors chose trait levels reflective of trait distributions encountered by herbivore populations in nature. Indeed, many studies reported field data justifying their range of values. In nature the magnitude, but not the sign, of Jensen's effect will depend on the plant trait distribution and resource selection behaviour; however, even herbivore populations with highly selective resource behaviour will experience plant variance owing to costs and limits of discrimination and intraspecific competition[4]. We tested the sensitivity of our conclusions to the shape of the trait distribution by repeating the entire analysis, assuming uniform and Gaussian distributions.

First, we investigated how the consequences of plant trait variance for herbivore performance differed for plant defensive traits (for example, concentrations of toxic secondary metabolites) versus plant

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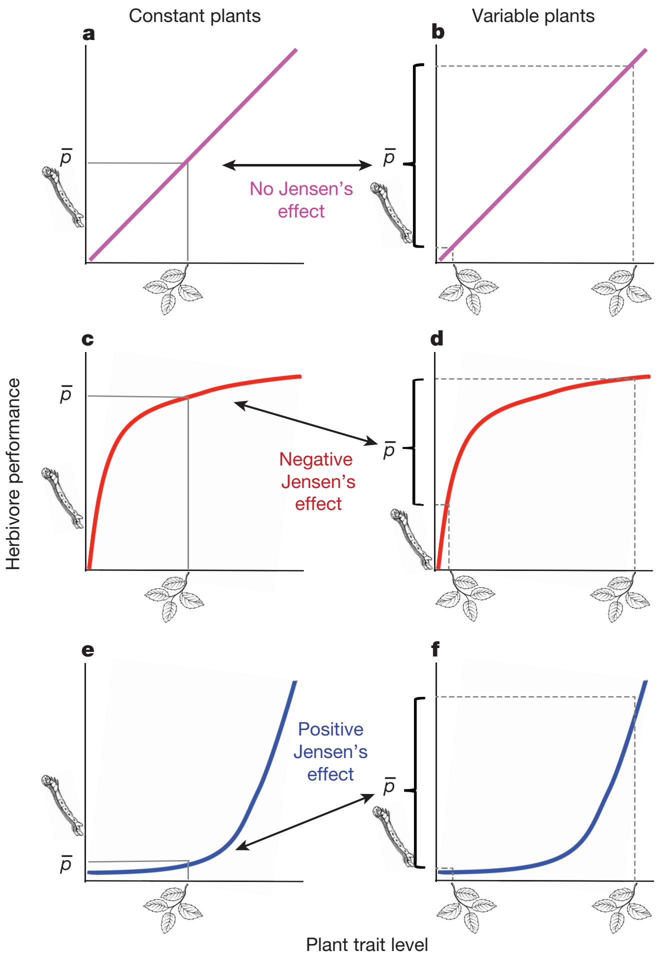

Figure 1 | An illustration of Jensen's inequality. a–f, The shape of the relationship between herbivore performance and a plant trait influences the consequences of trait variance for mean performance ($\bar{p}$) via non-linear averaging or Jensen's inequality. The left column (**a**, **c**, **e**) represents plant populations in which all plants have one trait value and no variance (plants at one location on the *x* axis). The right column (**b**, **d**, **f**) represents populations with trait variance, in which half of the plants have a high trait value and half have a low value (two plants on the *x* axis). The trait mean, however, is the same in the constant and variable populations. With any linear function, trait value changes result in proportional changes in performance. Mean herbivore performance is therefore equal in the absence or presence of variance (no Jensen's effect; compare **a** and **b**). With non-linear performance functions (**c**–**f**), however, trait value changes do not result in proportional performance changes, and mean performance will differ in the absence and presence of trait variance. When the relationship is concave down, mean performance will be lower in the presence of trait variance (negative Jensen's effect; compare **c** and **d**). When the relationship is concave up, mean performance will be higher in the presence of trait variance (positive Jensen's effect; compare **e** and **f**). Doubled-headed arrows show differences in mean performance with and without plant variance.

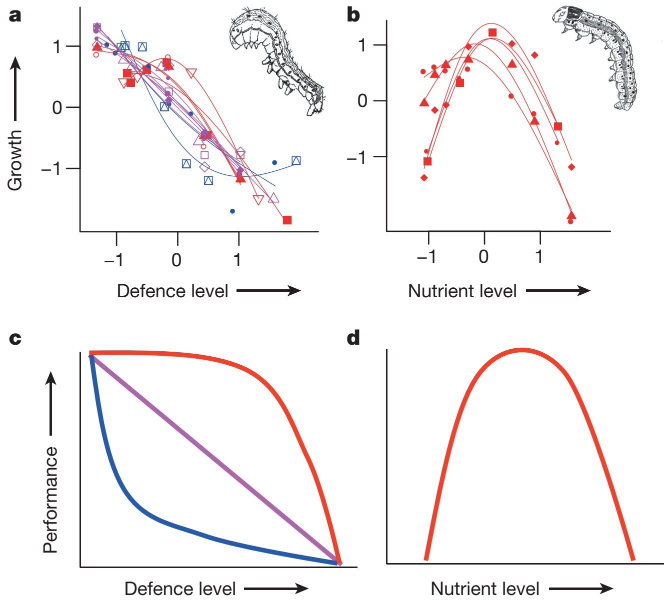

Figure 2 | Empirical and theoretical performance curves. a, **b**, Growth data from empirical studies and fitted growth curves for (**a**) *Heliothis virescens* (Lepidoptera: Noctuidae) across a range of levels of various plant secondary metabolites and (**b**) *Helicoverpa zea* (Lepidoptera: Noctuidae) across a range of levels of various plant nutrients. Data are standardized to zero mean and unit standard deviation. Red curves are significantly concave down, blue curves are concave up, and magenta curves are linear. Different symbols denote different experiments. **c**, **d**, Theoretical predictions for relationships between plant traits and herbivore performance. For simplicity, **d** shows one curve with an intermediate maximum, but curves that asymptote at high nutrients are also possible. Both shapes are concave down and would result in negative effects of nutrient variability.

nutritive traits (such as, protein concentration). Physiological theory predicts that the relationship between nutritive traits and herbivore performance should be concave down[14–17] (Fig. 2d), but makes less clear predictions about the relationship between defensive traits and performance[18,19] (Fig. 2c). Despite the importance of this relationship to insect physiology and to broader plant–insect interaction theory, we know of no other quantitative analyses of the shapes of empirical performance curves.

We found that the relationships between plant nutrients and herbivore growth and survival were consistently concave down, whereas the relationships between plant defences and herbivore growth and survival were close to linear on average. The curvature of nutrient–performance relationships led the experimentally generated variability in nutrients to reduce mean herbivore growth by half a standard deviation relative to plants with a similar mean nutrient value but zero nutrient variance. (Jensen's effect (95% CI) = −0.49 (−0.62, −0.35)) (Fig. 3a). The mean effect of nutrient variance was more than half a standard deviation more negative (−0.55 (−0.66, −0.44)) than the mean effect of defence variance, which was near to zero (0.063 (−0.055, 0.18); $\chi^2_1 = 92.6$, $P < 0.0001$). This difference suggests that there is less influence of variance in plant defences on herbivore performance compared to variance in nutritional content. Studies of herbivore survival had negative Jensen's effects for nutritive traits (–1.41 (−2.29, −0.53)) and effects near to zero (linear) for defensive traits (0.28 (−0.24, 0.81); $\chi^2_1 = 19.2$, $P < 0.0001$), mirroring the results for growth variables (Fig. 3b).

These results indicate that there are consistent constraints on herbivore physiology that lead to concave-down nutrient–performance relationships (Fig. 3d, f) and depressed growth and survival in the face of plant-nutrient variability (Fig. 3a, b). This finding supports the theoretical prediction that performance for most consumers increases with nutrient levels but then plateaus owing to diminishing returns, or even declines at high nutrient levels owing to nutrient toxicity[14,17]. By contrast, the generally linear decline observed in herbivore performance with increasing levels of plant defence indicate that defence variability has little effect on herbivores via non-linear averaging (Fig. 3c, e). This finding contradicts recent predictions concerning the ubiquity of hormesis—beneficial, stimulatory effects of low doses of toxins[18]—or indicates that hormesis may only occur at lower doses than were tested by the studies in our sample. It also suggests that defence thresholds, above which herbivore performance declines precipitously, are uncommon, and that increasing plant investment in a given defence will consistently decrease herbivore performance.

Second, we asked how these relationships differed among herbivore species with different resource-selection behaviours. Because the

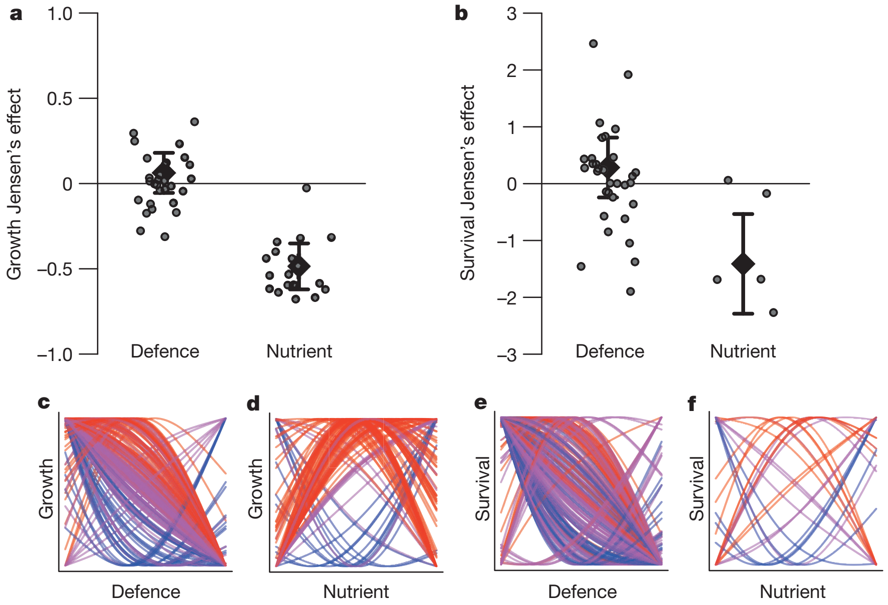

Figure 3 | The effect of variance in plant defensive and nutritive traits on herbivore growth and survival. a, **b**, Each point represents one herbivore species ($n=53$), jittered for visibility. Diamonds and error bars show mean values and 95% confidence intervals. Growth effects are standard deviations. Survival effects are log odds ratios. **c**–**f**, The empirically estimated functions that went into the analysis that yielded **a** and **b**. Red curves are significantly concave down (negative Jensen's effect). Magenta curves are linear (no Jensen's effect). Blue curves are significantly concave up (positive Jensen's effect). Curves are standardized to be on the same scale.

consequences of plant variance for an herbivore population depend not only on the shape of the herbivore performance function but also on the amount of plant variance encountered by the herbivore population, we proposed that the curve shapes may be different for herbivore species with different mobility and host breadth—two traits that influence how herbivore species encounter plant variance. We found, however, that mobility did not influence the patterns described above for growth (nutrients: $\chi_1^2=0.26$, $P=0.61$; defences: $\chi_1^2=0.10$, $P=0.75$) and survival (defences: $\chi_1^2=0.45$, $P=0.80$) (Extended Data Fig. 3). Herbivore host breadth was also not a significant predictor of Jensen's effect for growth (nutrients: $\chi_1^2=1.04$, $P=0.31$; defences: $\chi_1^2=0.18$, $P=0.67$) or survival (defences: $\chi_1^2=1.25$, $P=0.26$) (Extended Data Fig. 4). Sample sizes were too small to test the effect of nutrients on survival. These results suggest that the shapes of nutrient and defence performance curves are fundamental constraints regardless of insect life history traits.

Our findings indicate that plants may contribute to the suppression of herbivore populations, not only through low average quality but also through heterogeneity in nutrient levels. Concave-down nutrient performance functions may be an important link between herbivore physiology and the negative relationships commonly observed between plant diversity and herbivore density at the ecosystem scale[20]. A key implication is that agroecosystems may experience outbreaks of herbivores because herbivore performance is increased by artificially low plant heterogeneity owing to landscape simplification, reduced plant species diversity and crops that are bred to minimize variation. Increasing heterogeneity in plant nutrients in agroecosystems may be a key step towards the sustainable control of insect pests. Plant nutrient heterogeneity could be increased by planting greater numbers of crop varieties[21], by increasing genetic diversity within crop varieties, or by breeding varieties with increased constitutive or induced nutrient variance within the parts of the plant that are attacked by insect pests.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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1. Awmack, C. S. & Leather, S. R. Host plant quality and fecundity in herbivorous insects. *Annu. Rev. Entomol.* **47,** 817–844 (2002).
2. Adler, F. R. & Karban, R. Defended fortresses or moving targets? Another model of inducible defenses inspired by military metaphors. *Am. Nat.* **144,** 813–832 (1994).
3. Karban, R., Agrawal, A. A. & Mangel, M. The benefits of induced defenses against herbivores. *Ecology* **78,** 1351–1355 (1997).
4. Herrera, C. M. *Multiplicity in Unity: Plant Subindividual Variation & Interactions with Animals* (Univ. Chicago Press, 2009).
5. Crutsinger, G. M. *et al.* Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* **313,** 966–968 (2006).
6. McArt, S. H. & Thaler, J. S. Plant genotypic diversity reduces the rate of consumer resource utilization. *Proc. R. Soc. Lond. B* **280,** 20130639 (2013).
7. Esquinas-Alcázar, J. Science and society: protecting crop genetic diversity for food security: political, ethical and technical challenges. *Nat. Rev. Genet.* **6,** 946–953 (2005).
8. Díaz, S. & Cabido, M. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* **16,** 646–655 (2001).
9. Wood, S. A. *et al.* Functional traits in agriculture: agrobiodiversity and ecosystem services. *Trends Ecol. Evol.* **30,** 531–539 (2015).
10. Whitham, T. G. in *Variable Plants and Herbivores in Natural and Managed Systems* (eds Denno, R. F. & McClure, M. S.) 15–41 (Academic Press, 1983).
11. Ruel, J. J. & Ayres, M. P. Jensen's inequality predicts effects of environmental variation. *Trends Ecol. Evol.* **14,** 361–366 (1999).
12. Bolnick, D. I. *et al.* Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* **26,** 183–192 (2011).
13. Jensen, J. L. W. V. Sur les fonctions convexes et les inegalites entre les valeurs moyennes. *Acta Math.* **30,** 175–193 (1906).
14. Raubenheimer, D., Lee, K. P. & Simpson, S. J. Does Bertrand's rule apply to macronutrients? *Proc. R. Soc. Lond. B* **272,** 2429–2434 (2005).
15. Simpson, S. J. & Raubenheimer, D. A multi-level analysis of feeding behaviour: the geometry of nutritional decisions. *Philos. Trans. R. Soc. B* **342,** 381–402 (1993).
16. Mertz, W. The essential trace elements. *Science* **213,** 1332–1338 (1981).
17. Bertrand, G. On the role of trace substances in agriculture. *Eighth Int. Congr. Appl. Chem.* **28,** 30–40 (1912).
18. Calabrese, E. J. & Baldwin, L. A. Toxicology rethinks its central belief. *Nature* **421,** 691–692 (2003).
19. Ali, J. G. & Agrawal, A. A. Specialist versus generalist insect herbivores and plant defense. *Trends Plant Sci.* **17,** 293–302 (2012).
20. Andow, D. A. Vegetational diversity and arthropod population response. *Annu. Rev. Entomol.* **36,** 561–586 (1991).
21. Zhu, Y. *et al.* Genetic diversity and disease control in rice. *Nature* **406,** 718–722 (2000).

Supplementary Information is available in the online version of the paper.

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Author Contributions W.W. conceived the project. All authors contributed to the development of the question, interpreted the results, and commented on the manuscript. W.W., H.K., and M.R. collected data and assembled the database. W.W. and M.H. developed the methods. W.W. and R.K. wrote the manuscript. M.R., H.K., and W.W. made the figures.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to W.W. (wcwetzel@cornell.edu).

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METHODS

Literature search. We located papers with data that relate plant traits to herbivore performance by conducting keyword searches in the Web of Science (https://apps.webofknowledge.com/) up to September 2014, collecting studies cited in relevant reviews[4,11,22], and searching papers known to the authors. Studies were included in our analysis if they met the following criteria: (i) a plant trait was experimentally manipulated and directly related to insect growth or survival; (ii) at least four levels of the plant trait were established; (iii) for all continuous response variables, some estimate of variance in herbivore performance was provided (for example, s.e.m.) along with the mean and sample size at each treatment level; (iv) for binomial survival response variables, studies provided an initial number of individuals at each treatment level and a count, proportion, or percentage that survived; and (v) data on traits and herbivore performance could be retrieved from a table, figure, text, or supplement[23]. See Supplementary Methods for additional methods.

Data collection. From each suitable paper, we recorded species, plant traits, and herbivore growth and survival variables measured. We categorized plant traits as defences or nutrients based on the original studies. (See Extended Data Fig. 1 for a summary of the database, including a list of all plant traits; see Supplementary Tables 1 and 2 for a list of the papers that met our criteria and a list of the herbivore species). For growth responses, we collected the mean and variability (for example, standard error) of the herbivore response and sample size at each level of the plant trait. For survival responses, we collected the initial number of herbivores and the count, proportion, or percentage that survived at each level of the plant trait.

Effect calculation. We used a bootstrapping approach to calculate a distribution of Jensen's effects for each empirical observation (Extended Data Fig. 2). Having a distribution of effects for each observation allowed us to estimate variance for each observation and quantify our uncertainty for each estimate. For survival responses, we used nonparametric bootstrapping. We resampled each survival dataset with replacement 10,000 times. We fit cubic splines to each bootstrap dataset using the mgcv package in R v.3.2.4 (refs 24–26) and calculated a Jensen's effect from each spline. We calculated Jensen's effect as the log odds ratio of the mean of the predicted survival probabilities at each plant trait level and the predicted survival probability at the mean plant trait level. The log odds ratio is widely used to express effect sizes in meta-analyses of response probabilities[27]; it is beneficial because it puts survival on the logit scale, which accurately represents survival as a multiplicative process.

For growth data, which were typically reported as mean and s.e.m. values at each plant trait level instead of raw data, we used parametric bootstrapping (Extended Data Fig. 2). We parameterized a log-normal distribution for herbivore growth at each level of the plant trait using the reported herbivore performance mean values and standard errors. We then drew values from each distribution until the length of our bootstrap response vectors equalled the sample sizes reported at each level of the plant trait. We repeated this procedure to obtain 10,000 bootstrap datasets and followed the curve-fitting methods described above, first log-transforming the responses and then using a Gaussian error distribution. We calculated Jensen's effect for growth by subtracting the predicted herbivore performance for the mean level of the plant trait (the expected herbivore performance in the absence of plant trait variance) from the mean of the predicted herbivore performances at each plant trait level (the expected herbivore performance accounting for trait variance and non-linear averaging). We standardized this difference by dividing it by the standard deviation of the bootstrapped herbivore performances to enable comparison across studies. This measure thus expresses the effect of non-linear averaging in terms of standard deviations of herbivore performance and is analogous to Hedges' d, one of the most widely used meta-analysis effect sizes[27]. See Supplementary Discussion for the computer code used in this analysis.

Effect of trait distribution. Our approach assumes that the values of the plant traits tested by the authors of each study reflect the natural distribution of trait values. We believe this is justified because most authors stated that they either chose trait levels that were representative of those in nature or provided data showing the correspondence between natural trait means and variances and experimentally chosen trait levels. Regardless, we also repeated the entire analysis assuming two different trait distributions: a uniform distribution between the minimum and maximum of the plant traits tested by the authors, and a Gaussian distribution with a mean equal to the midpoint of the doses chosen by the authors and a standard deviation that aligned the maximum author-chosen dose with 0.975 of the Gaussian cumulative probability function. The results were similar for each of the three trait distributions we tested, so in the main text we present the results based on the analysis that assumes a trait distribution defined by trait levels chosen by the author. See Supplementary Discussion for the results of the analyses with uniform and Gaussian distributions.

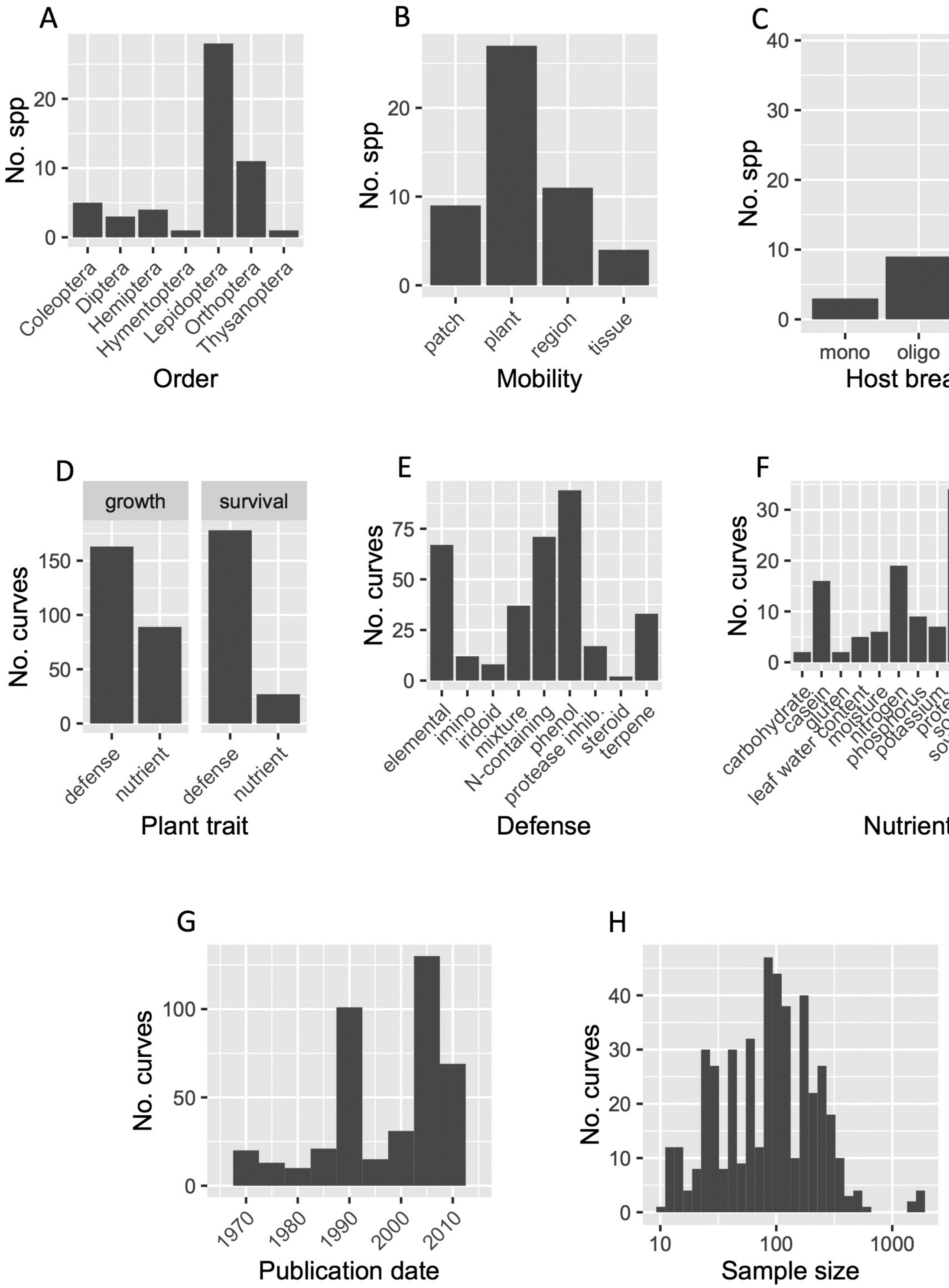
Statistical modelling. We tested our hypotheses using linear mixed effects models in the metafor package[28] in R v.3.2.4 (ref. 29). The response variable was the mean of the Jensen's effect distribution from each empirical dataset. We examined differences between variability in plant defensive and nutritive traits by fitting models with plant trait type (nutrient or defence) as an independent variable. We examined the effects of herbivore mobility and host breadth by including mobility and host breadth as independent variables. We tested the significance of trait type, mobility, and host breadth as predictors of Jensen's effects using an omnibus test based on a chi-squared distribution. We used random intercepts for herbivore family and genus to account for potential correlations due to the shared evolutionary history of genera within a family and of species within a genus. We used this approach because a reliable phylogenetic tree does not exist for this diverse group of insects. We used an additional random intercept to account for the non-independence of multiple Jensen's effects measured on the same species and included a random effect for each observation, following the standard practice of random effects meta-analysis[30]. Finally, the sampling variance of each observation was set equal to the estimated variance of the distribution of Jensen's effects generated by our bootstrapping procedure. We explored differences in Jensen's effect among insect orders and found them to be minimal (Supplementary Discussion).

Publication bias. Publication bias was unlikely to be an issue in our analysis because we used data for a different goal than the authors of the original studies did, none of whom estimated Jensen's effects or curvature. Regardless, we explored the potential for publication bias graphically and found no evidence suggesting particular curve shapes were more likely to be published than others (Extended Data Figs 5, 6 and Supplementary Discussion).

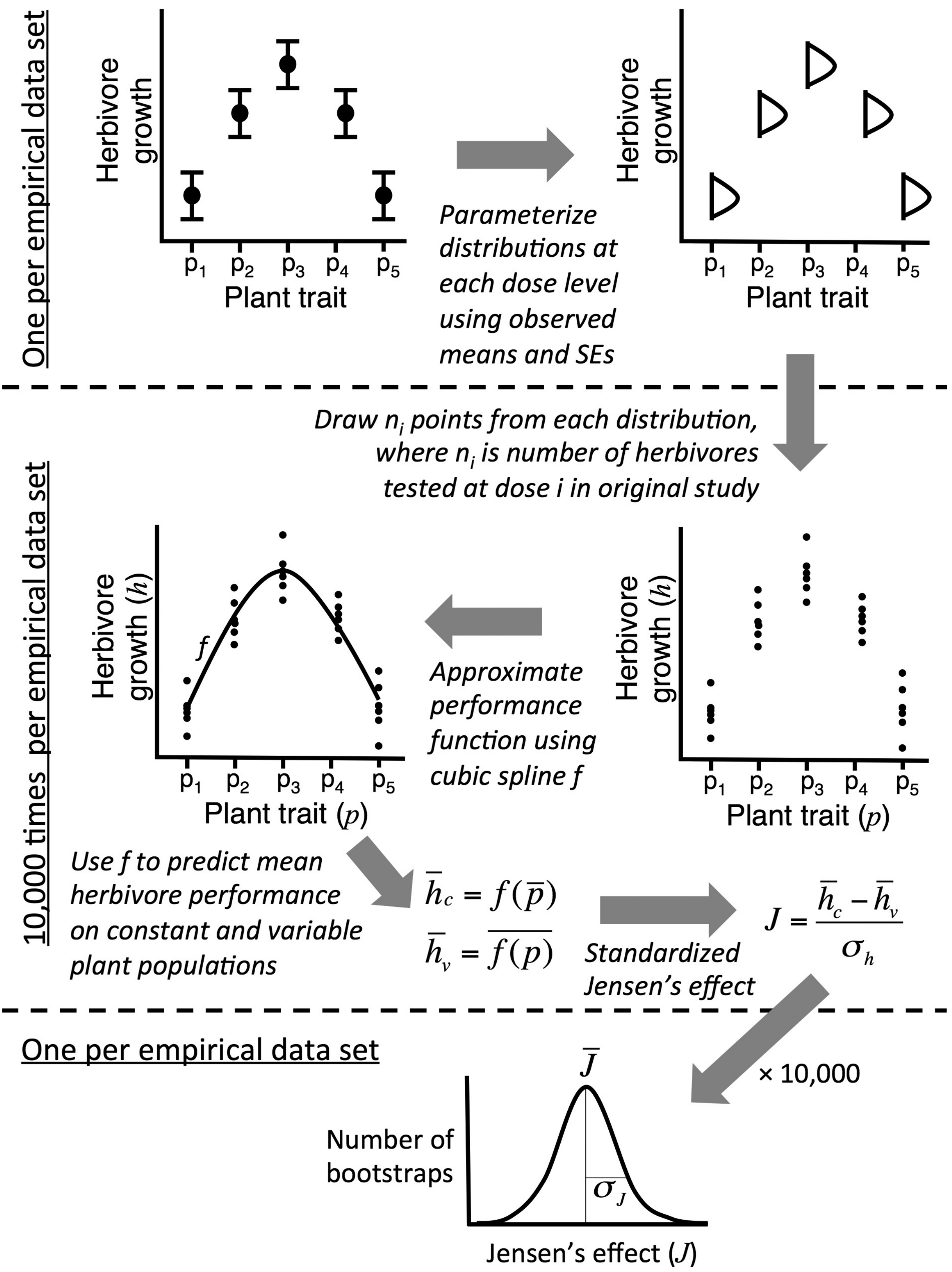
Code availability. Computer code used in the analysis is available in the Supplementary Information.

Data availability. Data used in the analysis have been deposited at http://dx.doi.org/10.6084/m9.figshare.3792117.

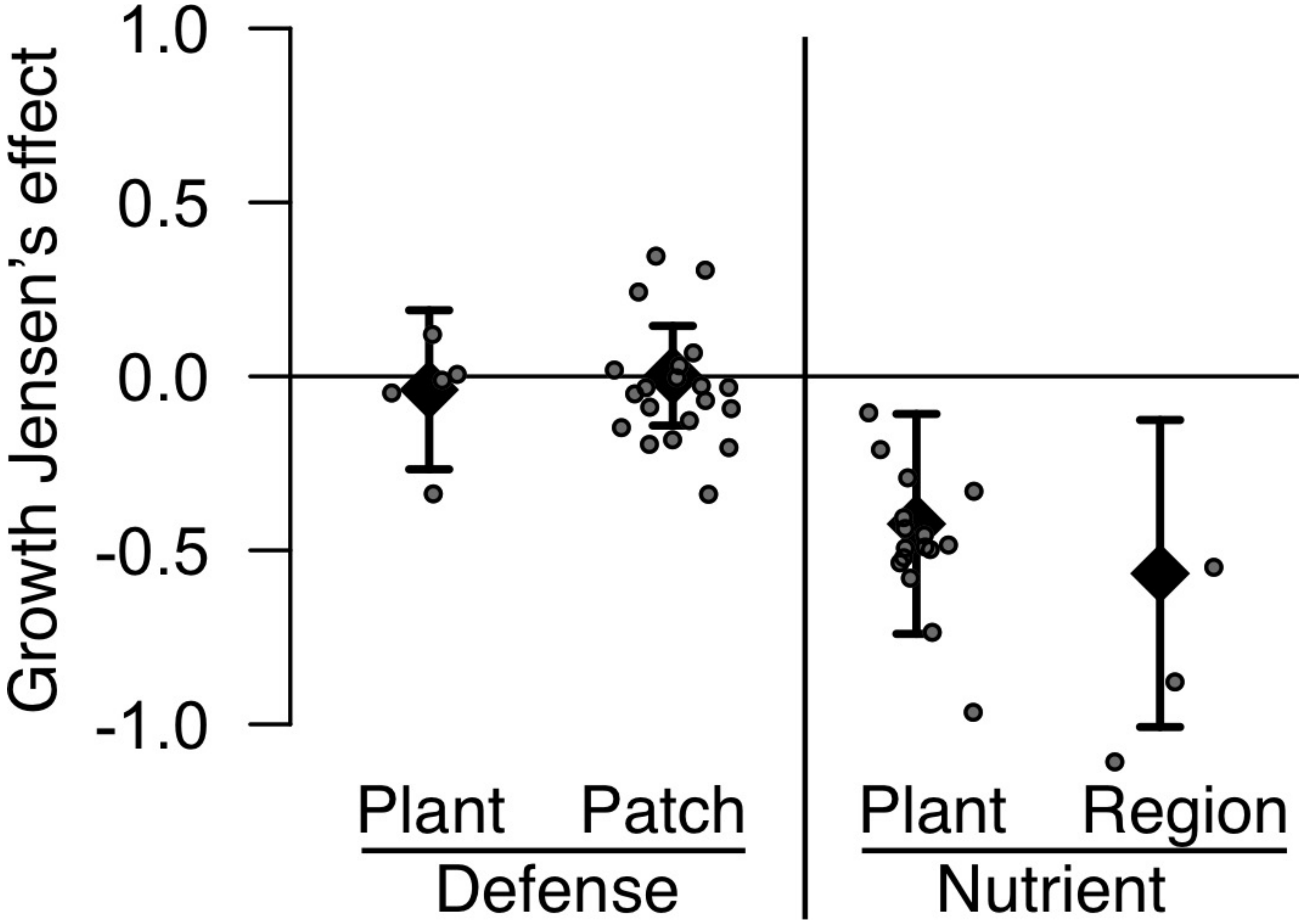
22. Carmona, D., Lajeunesse, M. J. & Johnson, M. T. J. Plant traits that predict resistance to herbivores. *Funct. Ecol.* **25,** 358–367 (2010).
23. Curtis, P. S., Mengersen, K., Lajeunesse, M. J., Rothstein, H. R. & Stewart, G. B. in *Handbook of Meta-analysis in Ecology and Evolution* (eds Koricheva, J., Gurevitch, J. & Mengersen, K.) 52–60 (Princeton Univ. Press, 2013).
24. Wood, S. N. *Generalized Additive Models: An Introduction with R* (Chapman and Hall/CRC, 2006).
25. R Core Team. *R: A Language and Environment for Statistical Computing.* http://www.R-project.org/ (2015).
26. Schluter, D. Estimating the form of natural selection on a quantitative trait. *Evolution* **42,** 849–861 (1988).
27. Rosenberg, M. S., Rothstein, H. R. & Gurevitch, J. in *Handbook of Meta-analysis in Ecology and Evolution* (eds. Koricheva, J., Gurevitch, J. & Mengersen, K.) 61–71 (Princeton Univ. Press, 2013).
28. Viechtbauer, W. Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* **36,** 1–48 (2010).
29. Bates, D., Maechler, M., Bolker, B. M. & Walker, S. lme4: Linear mixed-effects models using Eigen and S4. *R package version* 1.7 (2014).
30. Koricheva, J., Gurevitch, J. & Mengersen, K. (eds) *Handbook of Meta-analysis in Ecology and Evolution* (Princeton Univ. Press, 2013).



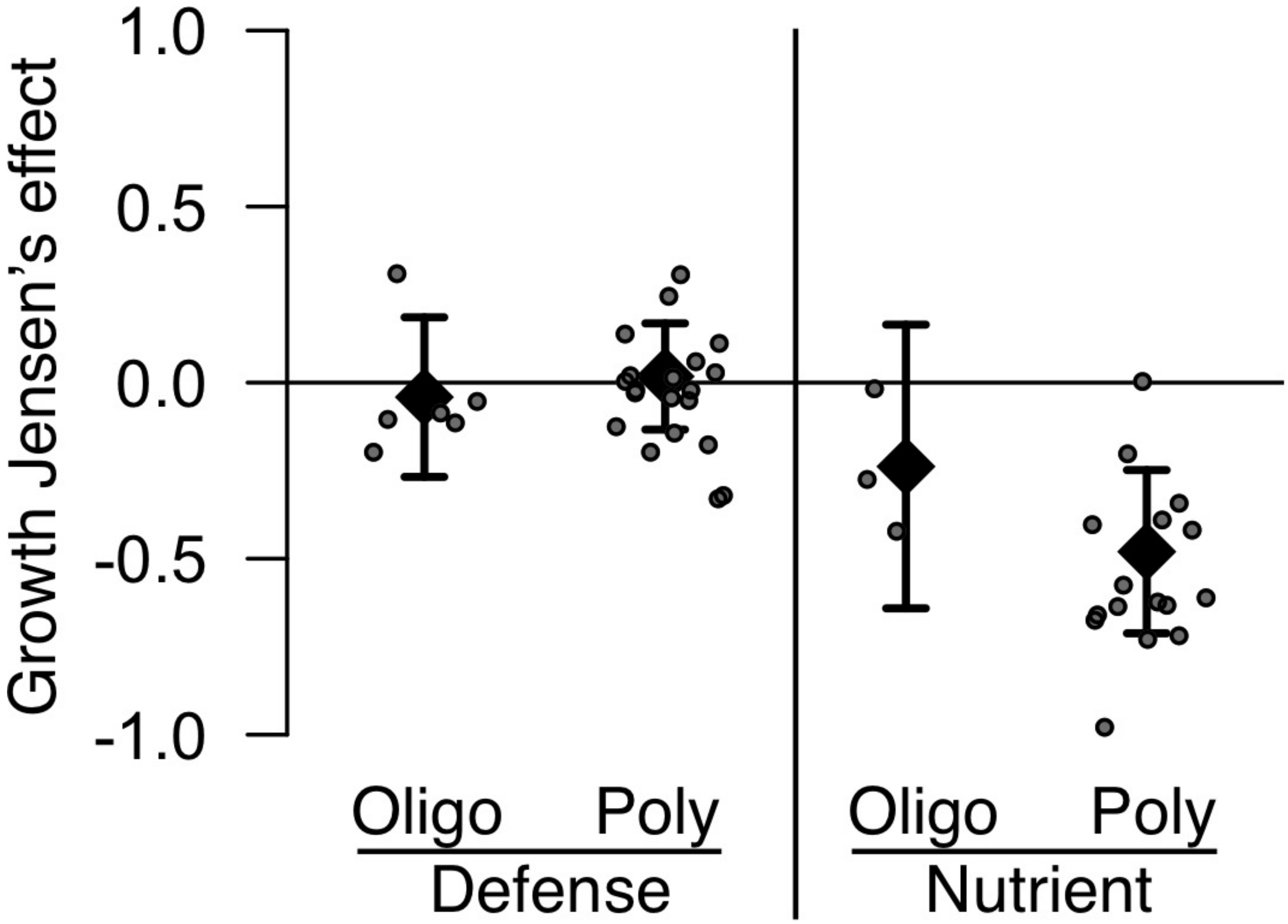
Extended Data Figure 1 | Graphical summary of database. a–c, Number of herbivore species per order (**a**), mobility of feeding stage (**b**), and host breadth (**c**). **b**, Each mobility level indicates the maximum extent at which the feeding stage of an herbivore commonly moves. For example, species in the 'plant' category move within plant individuals but do not typically move between plants. Species within the 'patch' category readily move among neighbouring plant individuals but do not typically move between patches of plants. Species in the 'tissue' category are restricted to a single organ within an individual plant (for example, leaf or root). Species in the 'region' category readily move among plant patches across entire geographic regions. **c**, Host breadth categories monophagous (mono), oligophagous (oligo), and polyphagous (poly) indicate that an herbivore species feeds on plant species in one genus, plant species across multiple genera within one plant family, and plant species across two or more plant families, respectively. **d–h**, Number of herbivore performance curves per trait type (**d**), defence class (**e**), nutrient class (**f**), date of publication (**g**), and study sample size (**h**).



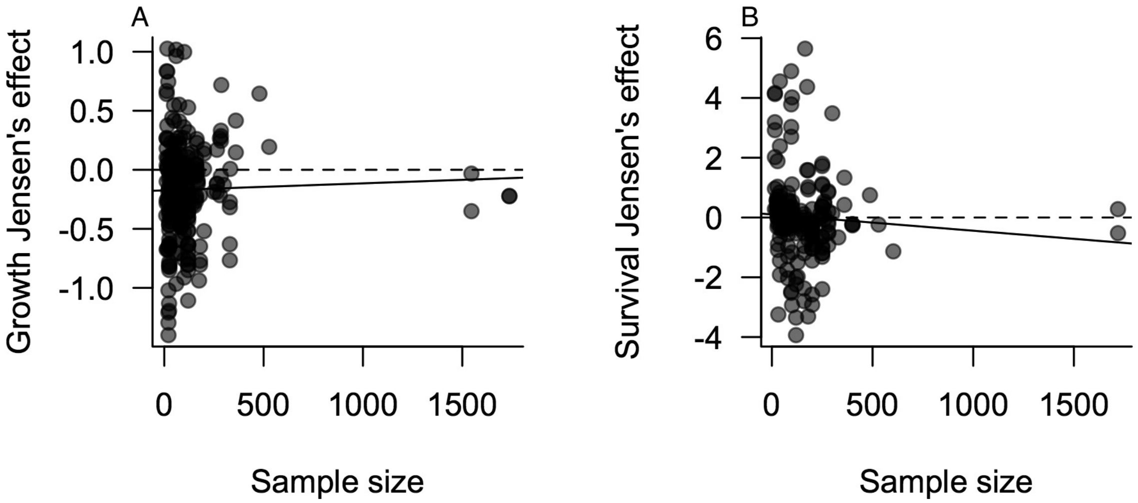
Extended Data Figure 2 | Visual representation of quantitative methods. Diagram summarizes the bootstrapping algorithm used to calculate a distribution of Jensen's effects for each empirical dataset for herbivore growth. For more details and for differences in methods between growth and survival, see Methods and Supplementary Methods.



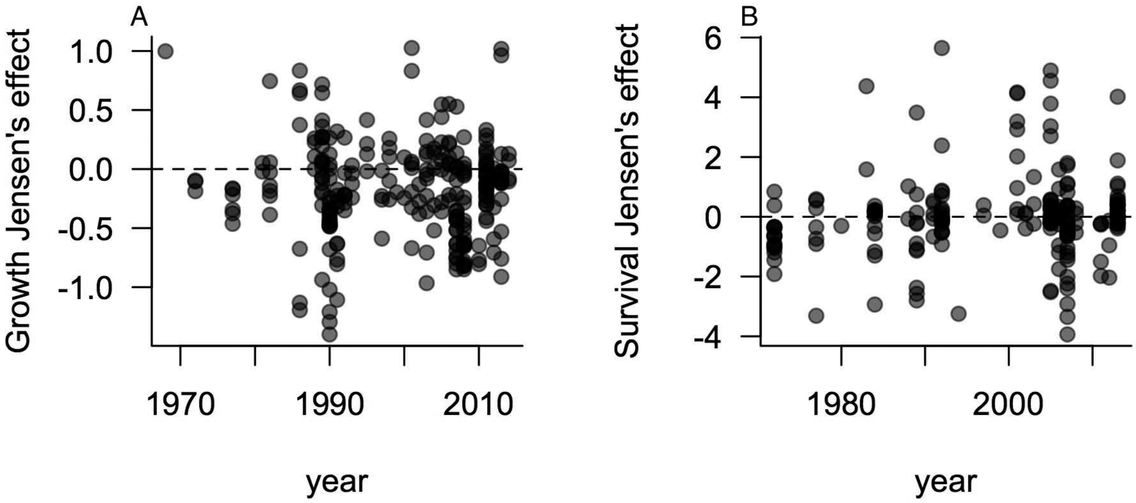
Extended Data Figure 3 | Jensen's effects by plant trait type (defences and nutrients) and mobility of the feeding stage. Defence variance had mean effects near to zero and nutrient variability had generally negative effects regardless of the mobility of the feeding stage of the herbivore species. Species in the 'plant' category move within plant individuals but do not typically move between plants. Species within the 'patch' category readily move among neighbouring host plants but do not typically move between patches. Species within the 'region' category commonly move among host plant patches. Each point is one herbivore species, jittered for visibility. Diamonds and error bars show mean values and 95% confidence intervals. See Supplementary Methods for more details.



Extended Data Figure 4 | Jensen's effects by plant trait type (defences and nutrients) and host breadth. Defence variance had mean effects near to zero and nutrient variability had generally negative effects regardless of the host breadth of the herbivore species. Oligophagous species ('oligo') feed on plant species in multiple genera but are restricted to one plant family. Polyphagous species ('poly') feed on plant species across two or more plant families. Each point represents one herbivore species, jittered for visibility. Diamonds and error bars are mean values with 95% confidence intervals. See Supplementary Methods for more details.



Extended Data Figure 5 | Funnel plots for growth and survival. a, **b**, The lack of a relationship between the sample size of a study and its Jensen's effect for growth (**a**) or survival (**b**) suggests that publication bias did not have a major influence on the results. Dashed line shows zero. Solid lines show linear regressions for growth ($F_{1,248} = 0.23$, $P = 0.63$, $R^2 = 0.0$) and survival ($F_{1,203} = 1.04$, $P = 0.31$, $R^2 = 0.0$).



Extended Data Figure 6 | Jensen's effect for each observation by the year of publication for growth and survival. a, **b**, The lack of temporal trends in Jensen's effects for growth (**a**) or survival (**b**) suggests that publication bias did not play a major role.