Received: 24 May 2023 | Revised: 27 March 2024 | Accepted: 19 April 2024

DOI: 10.1111/ele.14440

ECOLOGY LETTERS

SYNTHESIS

Does spatial variation in insect herbivory match variations in plant quality? A meta-analysis

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Funding information
Biotieteiden ja Ympäristön Tutkimuksen Toimikunta, Grant/Award Number: 316182

Editor: Jonathan M. Chase

Abstract

Variation in herbivore pressure has often been predicted from patterns in plant traits considered as antiherbivore defences. Here, we tested whether spatial variation in field insect herbivory is associated with the variation in plant quality by conducting a meta-analysis of 223 correlation coefficients between herbivory levels and the expression of selected plant traits. We found no overall correlation between herbivory and either concentrations of plant secondary metabolites or values of physical leaf traits. This result was due to both the large number of low correlations and the opposing directions of high correlations in individual studies. Field herbivory demonstrated a significant association only with nitrogen: herbivore pressure increased with an increase in nitrogen concentration in plant tissues. Thus, our meta-analysis does not support either theoretical prediction, i.e., that plants possess high antiherbivore defences in localities with high herbivore pressure or that herbivory is low in localities where plant defences are high. We conclude that information about putative plant defences is insufficient to predict plant losses to insects in field conditions and that the only bottom-up factor shaping spatial variation in insect herbivory is plant nutritive value. Our findings stress the need to improve a theory linking plant putative defences and herbivory.

KEYWORDS

coevolution, field herbivory, meta-analysis, nitrogen, phenolics, physical leaf traits, plant defences, secondary metabolites, terrestrial ecosystems

INTRODUCTION

The evolution of plants and herbivores is tightly interlinked, although the extent and importance of this coevolution remain debatable (Endara et al., 2017; Suchan & Alvarez, 2015). The concept that many plant traits, especially secondary metabolites, evolved as adaptations aimed at reducing herbivory and, therefore, function as defences against herbivores is widely accepted in the ecological literature (Close & McArthur, 2002; Divekar et al., 2022; Karban & Baldwin, 1997; Mortensen, 2013). This concept has served as a basis for several hypotheses proposed to explain the spatial variation in plant damage imposed by herbivores or in the expression of antiherbivore defences in plants.

The expression of defences often varies between plants from different geographic localities, in particular along latitudinal and elevational gradients (Loughnan & Williams, 2019; Volf et al., 2022; Wang et al., 2016). If we assume that herbivory is driving the evolution of plant defences, then in localities and regions with higher herbivore pressure, plants should possess greater levels of defences (e.g., at low latitudes: Coley & Aide, 1991; MacArthur, 1972). Thus, we can predict a positive spatial correlation between the expression of plant defences and herbivory (Prediction 1). At the same time, it is generally accepted that plant defences reduce plant losses from herbivory because it is their main function (Johnson, 2011; Mortensen, 2013) and herbivory may be, therefore, expected to be lower in the localitites and regions with greater plant defences, resulting in negative correlation between herbivory and plant defences (Prediction 2).

Empirical data on the correlations between spatial variations in natural (field) herbivory and plant putative defences demonstrate support for both hypotheses. These correlations have been found to be both significantly negative, when low herbivory is associated with increased defences (Cui et al., 2022; Moreira et al., 2018) and significantly positive, when plants possess high levels of putative defences under high herbivore pressure (Andrew & Hughes, 2005; Volf et al., 2022). In addition, many studies have found no significant correlations between the expression of defensive traits in plants and their damage by herbivores (Garibaldi et al., 2011; Gaston et al., 2004). To our knowledge, the sources of variation in the direction and strength of these correlations have not been explored and no general pattern has been discovered to date in empirical findings.

Plant quality for herbivores depends not only on the expression of defensive traits but also on the concentrations of macronutrients (with nitrogen of prime importance), which change with resource availability (Chen et al., 2013; Reich & Oleksyn, 2004). Increased concentrations of essential nutrients in plants generally favour host plant preference and improve herbivore performance (Awmack & Leather, 2002; Mattson, 1980; Scriber & Slansky, 1981), as demonstrated by multiple experiments with herbivores feeding on fertilized plants (Lu et al., 2007; Strengbom et al., 2005) and by observations in edaphic gradients (Ramos et al., 2019; Silva et al., 2017). We therefore expect that, at the geographical spatial scale, herbivory will positively correlate with nutrient concentrations in their host plants (Prediction 3).

The assumption that some plant traits decrease the loss of plant tissues due to herbivory is primarily supported by the adverse effects of plant secondary metabolites and/or physical leaf traits on the performance of insect herbivores and/or their food preferences in controlled experiments (reviewed by Carmona et al., 2011). However, these experiments are usually restricted to a single plant–herbivore system, whereas plant damage in nature is imposed by multiple herbivore species that often show idiosyncratic responses to defensive and nutritive plant traits (Karban & Baldwin, 1997). In particular, herbivores from different feeding guilds may respond differently to the same plant traits (Carmona et al., 2011; Moctezuma et al., 2014; Muola et al., 2010). We, therefore, anticipate that the direction and strength of the association between field herbivory and plant traits may differ among herbivore's feeding guilds (Prediction 4).

Finally, the differences between woody and herbaceous plants in modular architecture, longevity (generation time) and the type of herbivory they commonly experience (Haukioja & Koricheva, 2012), as well as in the impact of environmental factors on plant defences (Massad et al., 2011), may influence the association between herbivory and plant quality. Consequently, plant damage may show different associations with defensive and/or nutritive traits in woody and herbaceous species (Prediction 5).

Our aim in this article is to explore whether the variation in field herbivory among geographically distinct localities is associated with the variation in plant traits potentially affecting plant quality for insect herbivores. For this purpose, we tested five specific predictions (formulated above) and explored potential sources of variation in correlations between plant traits and herbivory related with research methodology, by meta-analysis of the outcomes of 51 publications simultaneously reporting data on spatial variation in plant traits and damage to these plants by insect communities in natural ecosystems. In this way, our meta-analysis will answer the burning question of whether information on plant quality, including macronutrient concentrations and the expression of putative defensive traits, allows a reliable prediction of herbivore pressure on plants in natural ecosystems. Knowledge regarding the validity of this prediction is critically important because global change research is focused on plants (Jamieson et al., 2012), and many projections on the level of future plant damage by herbivores are based (primarily or exclusively) on changes in plant traits (e.g., Holopainen et al., 2018; Jamieson et al., 2012; Zvereva & Kozlov, 2006).

METHODS

Search for and processing of studies

In our meta-analysis, we included studies reporting measurements of both natural damage imposed by insect herbivores and host plant traits reflecting their quality for herbivores (listed in Table SM1 in Zvereva et al., 2024). We selected studies that measured these variables in different geographic localities, particularly along natural environmental gradients. We considered plant traits which are widely accepted to function as chemical or physical antiherbivore defences (listed, e.g., in Hanley et al., 2007; Karban & Baldwin, 1997; Moles et al., 2011) and traits reflecting plant nutritive quality (Mattson, 1980; Scriber & Slansky, 1981). We first extracted 29 references from previously published meta-analyses of latitudinal and elevational patterns in trophic interactions (Zvereva & Kozlov, 2021, 2022) and then searched for additional publications in the ISI Web of Science core collection using the following combinations of the keywords: (gradient* OR geographical*) AND herbivor* AND ("plant defen*" OR "plant quality" OR "leaf nitrogen" OR "foliar nitrogen" OR "plant nitrogen" OR Si OR silicon). This search (completed on 21 March 2023) returned 347 publications, 29 of which were already extracted from previously published meta-analyses. The remaining 318 publications were checked against criteria specified below, and 12 of them were selected for meta-analysis. Additionally, 10 publications were found in reference lists of the selected papers and by a free web search using the keywords mentioned above.

We selected studies that fit the following criteria: (i) a study contains direct quantitative estimates of both the intensity of invertebrate herbivory (as reflected by the percentage of leaf area lost to herbivores, the proportion of damaged plants or plant parts [leaves, stems or seeds] or density of sap-feeders per unit of plant biomass) and an estimate of plant quality matching the herbivory data (i.e., obtained from the same sites and the same plant species or communities during the same time periods), (ii) the data were collected from natural ecosystems, (iii) the data were collected from at least four spatially distinct sites and (iv) the Pearson product–moment correlation coefficients (*r*) between herbivory and each relevant plant trait were reported in the publication or could be calculated from the data presented in the publication (including supplements) or available from a web-based repository or provided by the authors. Across plant traits, both a positive correlation between herbivory and nutrients or specific leaf area (SLA) and a negative correlation between herbivory and defensive traits other than SLA indicated that herbivory increased with an increase in plant quality. For correlations of herbivory with leaf mass per area (LMA), leaf dry mass concentration (LDMC) and the carbon:nitrogen (C:N) ratio, the sign was changed to match the remaining variables because increases in LMA, LDMC and C:N indicate an increase in defence. If the measurements conducted in different years were not combined by the authors, we selected the year with the highest level of herbivory. If the measurements were conducted several times during the season, we selected the last record, considering it as herbivory accumulated during the season. This selection was made for 10 effect sizes (out of 223) from five articles (out of 51).

Classificatory variables

Plant traits were divided into defensive (concentrations of secondary metabolites and expression of physical traits) and nutritive (concentrations of primary nutrients), following the approach used in previous studies (Carmona et al., 2011; Descombes et al., 2020; Moles et al., 2011). Plant secondary metabolites were classified into different phenolic compounds (total phenolics, flavonoids, tannins, lignin) or other chemicals with presumed defensive functions (terpenoids, alkaloids, glucosides, latex). Plant traits classified as physical defences included SLA combined with LMA and LDMC, as well as leaf toughness, thickness, trichome density and cellulose content. Nutritive quality was reflected by mass concentrations of nitrogen, phosphorus, potassium and sugars in plant leaves. We also considered the plant C:N ratio, an index that combines the defensive and nutritive characteristics of plants. Plants were classified as woody or herbaceous, while herbivorous insects were classified as defoliators, miners, gallers, sap-feeders, predispersal seed eaters and borers. The moderators reflecting research methodology included the length (maximum distance between sampled sites) and the type of the ecological gradient, along which correlations between herbivory and plant traits were measured, as well as the way in which herbivory was quantified in publications.

Data analysis

Correlation coefficients and effect sizes

We classified correlation coefficients not exceeding 0.3 in absolute value as low, and we compared the proportions of greater (moderate and high) negative and positive correlation coefficients within each of the three groups of variables reflecting plant quality (i.e., secondary metabolites, physical traits and nutritive traits). This comparison was used to understand, whether the zero net effect results from a combination of consistently small correlations or from a combination of large correlations with opposite signs. We then transformed the correlation coefficients into *z*-score effect sizes (ES) following Rosenberg et al. (2000).

Between-study analysis

All analyses were conducted in R (version 4.3.2). We ran all meta-analytical models using the "metafor" package (Viechtbauer, 2010) and displayed the results with the "orchaRd" package (Nakagawa et al., 2023). We first estimated the grand mean ES and 95% confidence interval (CI95) across all studies to assess the overall strength of association between plant traits and insect herbivory, regardless of trait category or plant life form. The main purpose of this analysis was to estimate the degree of consistency among studies by quantifying (through the I^2 statistics) the proportion of total heterogeneity among ES that arose from between-study heterogeneity (Nakagawa et al., 2017). Based on predictions 1–3, we expected that the grand mean ES would not differ from zero, whereas between-study heterogeneity would be large, thus indicating that total heterogeneity could be accounted for by the use of appropriate moderators. To this end, we built an intercept-only multilevel (hierarchical) error model with the *rma.mv* and included the publication and

ES nested within the publication as random factors in order to account for non-independence among multiple ES drawn from a single publication.

Subgroup analysis

We modelled total heterogeneity (using the same hierarchical model structure) with two separate models. The first model incorporated trait category (secondary metabolites, physical traits, or nutritive traits), plant life form (woody vs. herbaceous) and their two-way interaction as fixed effects.

The second model incorporated the trait category, insect feeding guild (total folivores, defoliators, gallers, miners) and their two-way interaction as fixed effects. From this analysis, we removed data on borers ($k=1$ ES), sap-feeders ($k=6$ ES) and seed eaters ($k=8$ ES) to balance the distribution of ESs by traits within feeding guilds. When the interaction term was not significant, we removed it from the model for the sake of parsimony. For each model, we reported the Q_M statistic and associated p value for each moderator included in the simplified model, as well as model parameter estimates, CI95 and prediction interval (i.e., the interval within which the ES of a new study would fall if this study was selected at random from the population of studies already included in the meta-analysis) for each level of moderator.

Then, we checked whether methodological differences among studies may have affected the outcomes of our analyses. We ran two separate multi-level mixed-effects models with the trait category and (i) the type of ecological gradient, or (ii) the maximum distance between sites, as well as two-level interactions, as fixed effects. We limited this analysis to elevational and latitudinal gradients for which ESs were well-balanced among different plant traits. In the third model, we tested whether heterogeneity among ESs arose from the method in which herbivory was measured (the percentage of removed leaf area or the percentage of damaged leaves). To prevent misleading conclusions resulting from uneven distribution of ESs across herbivore guilds and herbivory metrics, we limited this analysis to correlations between plant secondary metabolites and herbivory by defoliators alone or by the entire community of folivores.

Finally, we ran a series of models to test the effect of different types of secondary metabolites (total phenolics, flavonoids, tannins, lignin, terpenoids, alkaloids and glucosides), physical (SLA + LMA + LDMC, leaf toughness, leaf thickness, trichome density and cellulose content) and nutritive (nitrogen and phosphorous content, sugars, C:N ratio) traits on the correlation between the values of these plant traits and insect herbivory. This analysis was conducted on three separate data subsets, one for each trait category. Two traits (latex production, potassium content) were each represented by one ES; we discarded the two corresponding ESs. The C:N ratio encapsulates both the effect of putative defences (C) and nutritive quality (N). To avoid confusion between defensive and nutritive traits, we re-ran the last model without ESs corresponding to the correlation between C:N ratio and herbivory. This exclusion did not affect the results of the analysis.

Publication bias

We tested for the existence of publication bias by regressing ES over the precision (SE) of each study (Nakagawa et al., 2022) in meta-regressions implemented with the function *rma.mv* in package "*metafor*" (Viechtbauer, 2010). As for previous models, we controlled for the hierarchical structure of the data with publication source and case studies as nested random factors.

RESULTS

Database

We extracted 223 correlation coefficients (studies, hereafter) from 51 articles published from 1987 to 2022 (Table SM1 in Zvereva et al., 2024). In the majority of these studies, the sites were located along environmental gradients: latitudinal (111 ES), elevational (66 ES), other climatic (17 ES) and edaphic (16 ES). The maximum distances among study sites ranged from 17 to 4500 km (median value: 1170 km). The number of sites in individual studies ranged from 4 to 43 (median value: 16 sites). Geographically, the identified studies covered all continents, excluding Antarctica (Europe: 96 ES; North America: 60 ES; South America: 40 ES; Asia: 14 ES; Australia and Oceania: 12 ES; Africa: 1 ES).

Species-specific data were collected from 22 herbaceous and 38 woody plant species; five publications provided community-wide values for both herbivory and plant traits. One-quarter of the studies (54 ES) reported plant damage caused by the entire herbivore community. In the remaining studies, herbivory was attributed to individual feeding guilds: defoliators (119 ES), gallers (11 ES), miners (24 ES), sap-feeders (6 ES), predispersal seed eaters (8 ES) and stem borers (1 ES).

The grand mean ES was not statistically different from zero (mean = 0.04; CI95 = −0.04 … 0.12), indicating that all leaf traits combined did not correlate with herbivory. We found a significant amount of residual heterogeneity ($Q_E = 407.1$, df = 222, $p < 0.001$), 40.5% of which (i.e., I^2) arising from between-study heterogeneity could further be accounted for by different moderators.

Regressing ES over their precision (SE) revealed that neither the intercept (mean = 0.03; CI95 = −0.09 … 0.14) nor the slope (mean = 0.18; CI95 = −0.69 … 1.04) were statistically different from zero. Thus, publication bias did not affect our results.

Between-study heterogeneity

Between-study heterogeneity was not explained by any of studied moderator describing biological features, including plant life form ($k = 223$, $Q_M = 0.03$, df = 1, $p = 0.86$, Figure 1a), herbivore feeding guild ($k = 208$, $Q_M = 1.59$, df = 3, $p = 0.66$, Figure 1b), or trait category ($k = 223$, $Q_M = 4.61$, df = 2, $p = 0.10$ in model with plant life form, Figure 1c; $k = 208$, $Q_M = 1.92$, df = 2, $p = 0.38$ in model with herbivore feeding guild). Contrary to our expectations, we found no evidence that the effect of plant traits on field herbivory differed among herbivore feeding guilds (Prediction 4, *Trait* × *Guild* interaction: $Q_M = 10.52$, df = 6, $p = 0.10$) or between woody and herbaceous species (Prediction 5, *Trait* × *Life form* interaction: $Q_M = 3.93$, df = 2, $p = 0.14$).

We found no evidence that the type of ecological gradient (latitudinal vs. elevational: $k = 177$; $Q_M = 3.10$; df = 1, $p = 0.08$), the maximum distance between sites ($k = 166$; $Q_M = 1.21$, df = 1, $p = 0.27$), or estimates of herbivory (proportion of damaged leaves vs. proportion of consumed leaf area: $k = 77$, $Q_M = 2.94$, df = 1, $p = 0.09$) explained between-study heterogeneity in ESs.

Subgroup analyses

Subgroup analyses revealed that between-study heterogeneity among ESs was not explained by the type of secondary metabolites ($k = 97$, $Q_M = 4.12$, df = 6, $p = 0.66$, Figure 2a) or physical traits ($k = 79$, $Q_M = 5.08$, df = 4, $P = 0.28$, Figure 2b), or by nutritive traits ($k = 45$, $Q_M = 3.66$, df = 2; $p = 0.30$, Figure 2c). When each trait was considered separately, only ES corresponding to the correlation between herbivory and the mass-based concentration of foliar nitrogen was significantly, and positively, different from zero (mean = 0.19; CI95 = 0.01 … 0.37). These results emerged due to similar proportions of large ($r < -0.30$ or $r > 0.30$) negative and positive correlations in plant defensive traits (secondary metabolites: 19 positive and 22 negative; physical traits: 20 negative and 20 positive), whereas in nutritive traits positive correlations dominated (14 positive and 4 negative).

DISCUSSION

No spatial correlation between herbivory and plant secondary metabolites

Overall, our meta-analysis did not reveal a significant correlation between field herbivory and any of the putative plant defensive traits, either chemical or physical. Thus, we found no support for either Prediction 1 (that plant defences are stronger in localities with high herbivore pressure) or Prediction 2 (that plant defences

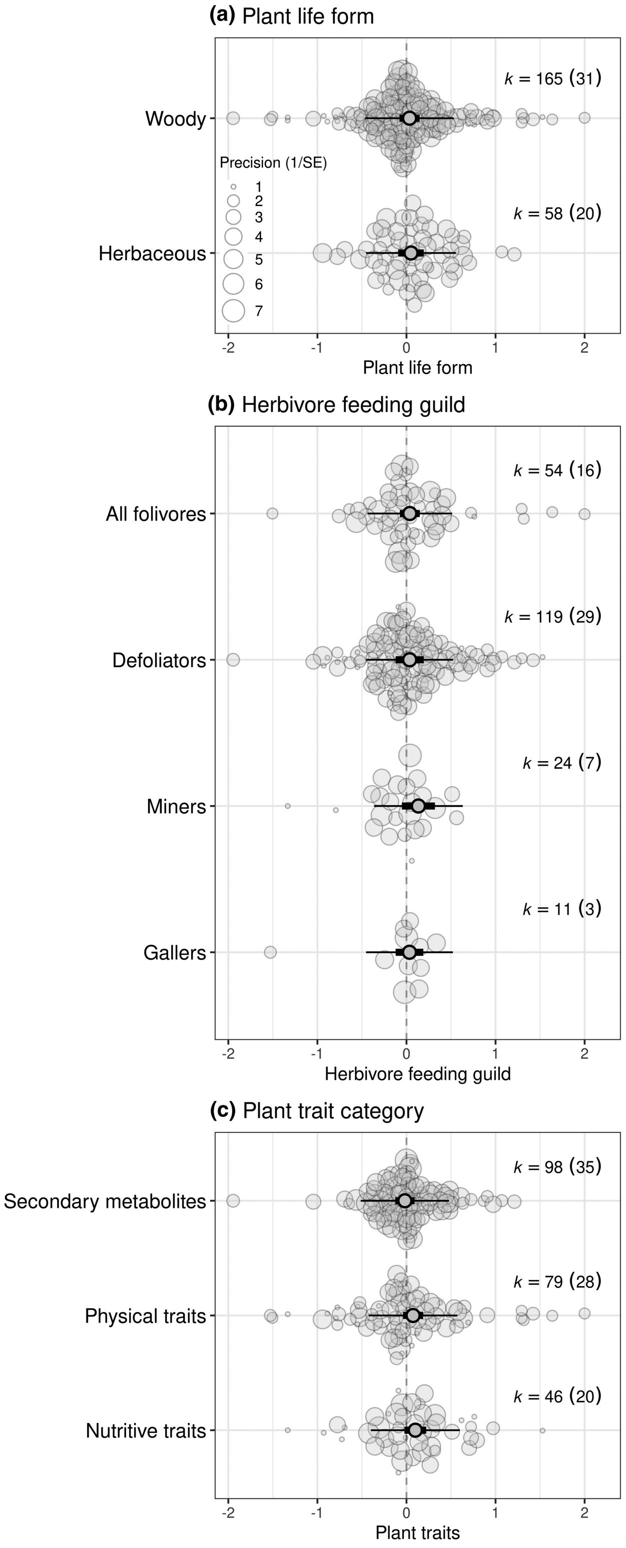

FIGURE 1 The strength of spatial association between field insect herbivory and leaf traits (a) for woody vs. herbaceous plants, (b) for herbivore feeding guilds and (c) for plant trait categories. Bubbles represent individual ES whose size is proportional to the precision of the effect size (ES) as shown on the insert to (a). Thick and thin lines represent a 95% confidence interval and prediction interval, respectively; central dots are mean ESs. Numbers refer to ESs (k) and publications they were extracted from (within brackets).

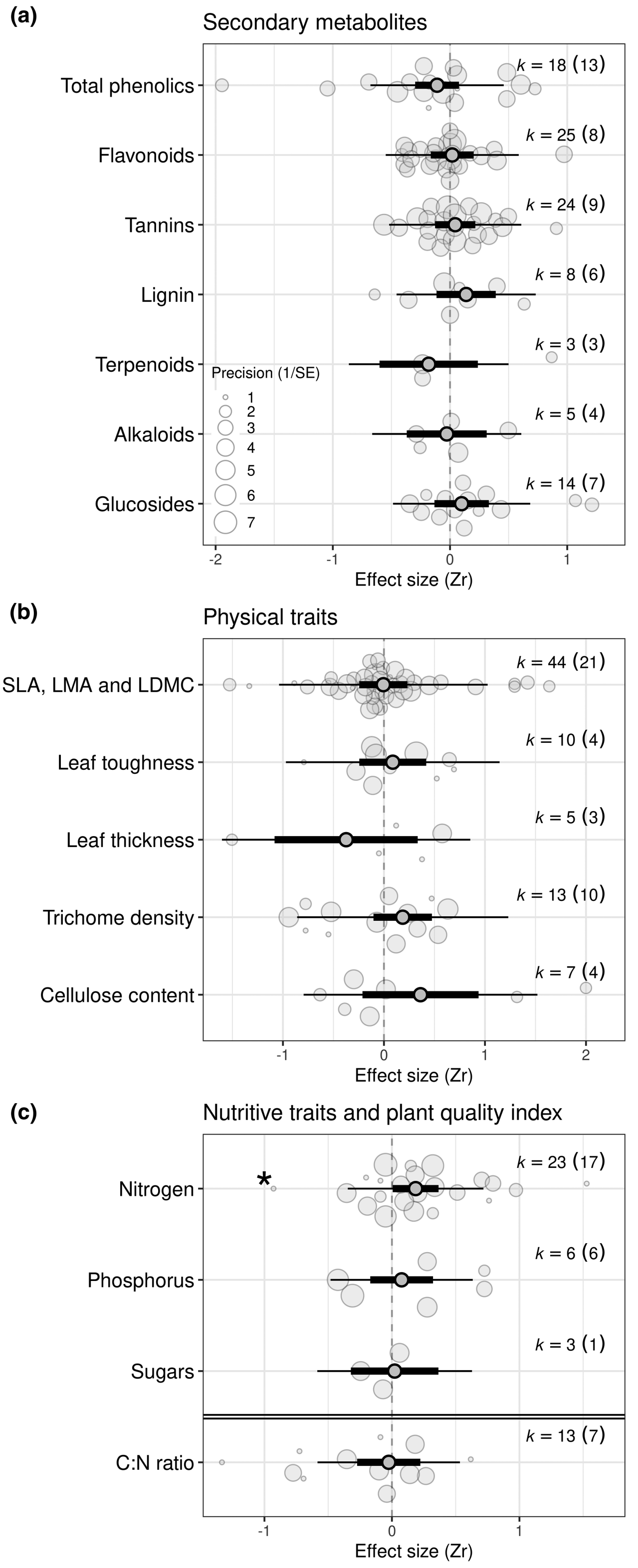

FIGURE 2 The strength of spatial association between field insect herbivory and (a) potentially defensive secondary metabolites, (b) potentially defensive physical traits (SLA, specific leaf area; LMA, leaf mass per area; LDMC, leaf dry mass content), (c) nutritive traits and (d) plant quality index. For explanations, see Figure 1.

reduce field herbivory). Consequently, our results indicate that field herbivory does not correlate with the local levels of defences in their host plants at the population level. This result appeared valid for both woody and herbaceous plants and for all feeding guilds of herbivores, thereby providing no support for our Predictions 4 or 5.

In our meta-analysis, the absence of an overall significant correlation between field herbivory and putative plant defences across geographically distinct localities arises from both the substantial proportion of low correlations and the similar proportions of greater negative and positive correlations between herbivory and plant defensive traits, both physical and chemical. This variation in both the sign and magnitude of the correlations may have several explanations.

First, specialist and generalist herbivores may respond differently to plant secondary metabolites (Zhang et al., 2018) and plant physical traits (Rotter et al., 2018). Compounds that are detrimental to generalist feeders may act as attractants and feeding stimulants for specialists, e.g. phenolic glucosides for some leaf beetles (Kolehmainen et al., 1995) and glucosinolates for crucifer specialists (Städler, 2002). This phenomenon can create a trade-off between the evolution of defences against generalist and specialist herbivores (Johnson et al., 2009). Contrasting responses of generalists and specialists to the same host plants have been clearly shown in many studies of introduced plant species (Zhang et al., 2018). Consequently, the correlation between field herbivory and a certain plant trait could change with the proportion of specialists in a local community of insect herbivores. However, available data do not allow for the testing of this hypothesis.

Second, the detected lack of correlation between herbivory and the concentrations of certain groups of secondary metabolites could have resulted from insufficient resolution of chemical analyses. The majority of publications included in our meta-analysis reported only combined concentrations of multiple individual compounds (e.g., phenolics as a class of chemicals). However, herbivores may demonstrate differential, and sometimes opposite, responses to individual substances belonging to the same class (Haviola et al., 2007; Moctezuma et al., 2014), thereby yielding a zero net effect of a group of substances. Furthermore, the most biologically important component may constitute only a small percentage of the total concentration of a chemical class, making any effect of its variation on herbivory difficult (or even impossible) to detect.

Third, the lack of an association between field herbivory and plant traits could result from the rapid evolution of both plant defences and the herbivore's ability to overcome these defences, as stated by an arms race hypothesis (Feeny, 1976; Rhoades & Cates, 1976). Newly established plant species generally suffer less herbivory in their invasive range than in their native range (Hinz & Schwarzlaender, 2004; and references therein); however, soon after their establishment, herbivory becomes similar in the invasive and native ranges (Hawkes, 2007). Selection experiments and field observations show that the responses of insects to their host plants can be altered in only 10–16 generations (Bernays & Graham, 1988) and that native herbivores adapt quite rapidly to novel plants and their defences, sometimes within less than a decade (Santamaría et al., 2022). In turn, plant defences can also change within 10–100 years after changes in herbivory level (Sakata, 2022; and references therein). This means that the co-evolution of plants and herbivores is quite dynamic within a short time scale and that plant populations in different localities may be at different stages of their arms race–driven co-adaptation with local herbivore communities. The end result is then an overall lack of spatial correlation between plant defences and herbivore damage. This zero net correlation revealed by our meta-analysis may indicate that an eco-evolutionary equilibrium is a typical state of plant–herbivore systems.

Fourth, the expression of plant antiherbivore defences, both chemical and physical, can be modified by environmental factors, such as climate, resource availability and UV radiation (Loughnan & Williams, 2019; Moles et al., 2014). The effects of these abiotic factors may distort the spatial association between field herbivory and plant defences, should it exist. Finally, the zero net effect may indicate that herbivory is not the main selection factor driving the evolution of plant traits classified as putative defences. This result provides additional motivation for the development of experimental approaches to studies of co-evolution between plants and herbivorous insects.

Secondary metabolites as antiherbivore defences

The hypothesis that the primary role of secondary metabolites (i.e., their '*raison d'être*') is plant defence from herbivores was coined some 65 years ago (Fraenkel, 1959) and gave rise to multiple ecological, evolutionary and physiological hypotheses, collectively known as the plant defence theory (Coley et al., 1985; Feeny, 1976; Herms & Mattson, 1992; McKey, 1974; Stamp, 2003). Within the framework of this theory, plant secondary metabolites are assumed to be the result of selection imposed by herbivory (Pearse & Hipp, 2012; and references therein). This assumption has been questioned for decades (Hamilton et al., 2001; Jermy, 1984; Matsuki, 1996); nevertheless, it remains widely accepted and is included in a plethora of ecological and evolutionary textbooks.

The knowledge accumulated to date has revealed that secondary metabolites mediate multiple plant–environment interactions (Erb & Kliebenstein, 2020). Plant phenolic compounds act as antioxidants (flavonoids and phenolic acids), structural polymers (lignin), attractants (flavonoids and carotenoids), UV screens (flavonoids), signal compounds (salicylic acid and flavonoids) and defence response chemicals (tannins and phytoalexins) (Lin et al., 2016; Zhang et al., 2018). The levels of many phenolics positively correlate with the risk of photodamage, suggesting that protection from photodamage might be their primary role (Close & McArthur, 2002). If the latter suggestion is true, then herbivory may not exert as much selective pressure on plant secondary metabolites as is often assumed (Close & McArthur, 2002; Matsuki, 1996).

The evidence questioning the leading role of plant secondary metabolites in antiherbivore defence is accumulating rapidly. In particular, a meta-analysis by Carmona et al. (2011) detected a lack of genetic within-species correlation between concentrations of secondary compounds and plant susceptibility to herbivores. Similarly, little connection was found between secondary chemicals and herbivory across related plant species (Agrawal & Weber, 2015). Consistently, our meta-analysis of correlations between secondary compounds and field herbivory across geographically distinct populations supports the view that the importance of secondary metabolites in plant antiherbivore defence has been generally overstated (Agrawal & Weber, 2015). In line with meta-analysis by Carmona et al. (2011) we conclude that concentrations of secondary metabolites in plants are poor predictors of deterrence for herbivores. At the same time, the presence of secondary metabolites in wide range of concentrations can play the signalling role for herbivores. This role, which is likely to drive niche differentiation among herbivorous insects (Hardy et al., 2020), remains underexplored.

Nutritive traits shape spatial variation in herbivory

Our database clearly demonstrates that the contribution of primary metabolites (which are closely engaged in the growth, development and reproduction of plants) to shaping spatial variation in field herbivory is understudied compared to putatively defensive traits. The number of correlations between field herbivory and concentrations of primary metabolites extracted from discovered publications (33) comprised one-third of the number of correlations between field herbivory and concentrations of secondary metabolites (98) and one-half of the number of correlations between field herbivory and plant physical traits (79).

Nitrogen is the most important essential nutrient for insects, and plants are the only source of nitrogen for herbivores (Mattson, 1980). Consistently, of the three primary nutrients included in our meta-analysis, only the nitrogen concentration in leaves showed a significant and positive correlation with field herbivory, thus supporting Prediction 3. This result identifies plant nitrogen as the only predictor of spatial variation in field herbivory at the current level of knowledge. It also supports the idea that the high nutritive quality of plant tissues may override the defences of these tissues, leading to their substantial damage (Moles et al., 2011).

Despite the significant association between herbivory and foliar nitrogen, we did not find any statistically significant relationship between herbivory and the C:N ratio in host plant leaves. The C:N ratio is often used as an index of plant quality (Herms & Mattson, 1992; Lincoln et al., 1993), and an increase in this index is supposed to reduce herbivore performance via the dilution of foliar nitrogen due to the increase in carbon-based secondary compounds and fibre (Lincoln et al., 1993). However, our results indicate that the absolute concentration of nitrogen is more important than the C:N ratio as a factor shaping the spatial variation in field herbivory.

Our findings regarding the importance of foliar nitrogen in shaping spatial variation in herbivory may be valid at the global scale. Previously, we demonstrated that insect herbivory peaks in temperate forests, decreasing both towards the equator and the poles (Kozlov et al., 2015). Leaf nitrogen in the dominating plant species follows a similar pattern: it increases from the tropics to the cooler and drier mid-latitudes and then plateaus or decreases at high latitudes (Reich & Oleksyn, 2004). This concordance suggests that the latitudinal pattern in foliar nitrogen may contribute to the dome-shaped latitudinal pattern in insect herbivory.

CONCLUSIONS

At the geographical spatial scale, our meta-analysis did not detect any association in the variation between field herbivory levels and either plant secondary metabolites or physical leaf traits with presumed antiherbivore functions. Thus, we found no support for either of the opposing theoretical predictions that plants should possess high antiherbivore defences in localities with high herbivore pressure or that herbivory should be low in localities where plant defences are high. In combination with the meta-analysis by Carmona et al. (2011), and given the lack of the effects of methodology of primary studies on the outcomes of meta-analysis, our conclusions cast doubt on the longstanding concept that secondary metabolites function as antiherbivore defence because no correlation has been found between the concentrations of these compounds and plant susceptibility or herbivory at either the genetic (Carmona et al., 2011) or spatial (current study) scales.

We conclude that information about putative plant defences, either chemical or physical, is insufficient for predicting field herbivory levels. This conclusion raises questions regarding the accuracy of predictions about either contemporary spatial variations or the future levels of insect herbivory (in particular, those by Holopainen et al., 2018; Jamieson et al., 2012; Zvereva & Kozlov, 2006) when they are based primarily or exclusively on the information about effects of abiotic drivers of global change on putative plant defences. Our findings stress the need for an improvement of a theory linking plant putative defences and herbivory.

AUTHOR CONTRIBUTIONS

ELZ and MVK formulated goals, designed methodology and searched for suitable publications, ELZ extracted data for meta-analysis and wrote the first draft of the manuscript, BC conducted meta-analysis, MVK and BC participated in the writing of later drafts.

ACKNOWLEDGEMENTS

We are grateful to the authors of several publications for supplying primary data and to three anonymous reviewers for inspiring suggestions to an earlier draft of the manuscript. The study was funded by the Academy of Finland (project 316182).

DATA AVAILABILITY STATEMENT

The dataset and R codes used for the analyses are archived in Figshare (https://doi.org/10.6084/m9.figshare.25108460.v2).

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How to cite this article: Zvereva, E.L., Castagneyrol, B. & Kozlov, M.V. (2024) Does spatial variation in insect herbivory match variations in plant quality? A meta-analysis. *Ecology Letters*, 27, e14440. Available from: https://doi.org/10.1111/ele.14440