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Johnson, S.N. orcid.org/0000-0002-8388-8345, Waterman, J.M. orcid.org/0000-0003-1782-827X, Hartley, S.E. orcid.org/0000-0002-5117-687X et al. (4 more authors) (2024) Plant silicon defences suppress herbivore performance, but mode of feeding is key. Ecology Letters, 27 (10). e14519. ISSN 1461-023X

https://doi.org/10.1111/ele.14519

Ecology Letters

WILEY

ECOLOGY LETTERS

SYNTHESIS OPEN ACCESS

Plant Silicon Defences Suppress Herbivore Performance, but Mode of Feeding Is Key

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Received: 28 February 2024 | **Revised:** 28 August 2024 | **Accepted:** 30 August 2024

Editor: Ted Turlings

Funding: This work was supported by the Australian Research Council (FT170100342 and LP220200872).

Keywords: grazers | herbivory | insects | mammals | meta-analysis | plant defence | silica | silicon

ABSTRACT

The performance of herbivorous animals depends on the nutritional and defensive traits of the plants they consume. The uptake and deposition of biogenic silicon in plant tissues is arguably the most basic and ubiquitous anti-herbivore defence used by plants, especially grasses. We conducted meta-analyses of 150 studies reporting how vertebrate and invertebrate herbivores performed when feeding on silicon-rich plants relative to those feeding on low-silicon plants. Silicon levels were 52% higher and 32% more variable in silicon-rich plants compared to plants with low silicon, which resulted in an overall 33% decline in herbivore performance. Fluid-feeding herbivore performance was less adversely impacted (−14%) than tissue-chewing herbivores, including mammals (−45%), chewing arthropods (−33%) and plant-boring arthropods (−39%). Fluid-feeding arthropods with a wide diet breadth or those feeding on perennial plant species were mostly unaffected by silicon defences. Unlike many other plant defences, where diet specialisation often helps herbivores overcome their effects, silicon negatively impacts chewing herbivores regardless of diet breadth. We conclude that silicon defences primarily target chewing herbivores and impact vertebrate and invertebrate herbivores to a similar degree.

1 | Introduction

The evolution of anti-herbivore defensive and nutritional traits is often proposed as the reason ‘why the world is green’ (Hartley and Jones 1997). Defensive traits include a myriad of chemicals (toxins and digestibility reducers) and physical structures (e.g., spines, tissue toughness) that deter herbivory and/or reduce herbivore performance (Denno and McClure 1983). Many plants accumulate significant amounts of biogenic silicon in their tissues, which is taken up from the soil via passive and active mechanisms (Ma and Yamaji 2015). For the Poaceae, of which three species (rice, wheat and maize) provide 42% of human calories (Deutsch et al. 2018), silicon concentrations are usually higher than any other inorganic constituent (Raven 1983b). While controversies remain about the role of silicon in plants, there is consensus that it alleviates a diverse range of biotic and abiotic stresses (Coskun et al. 2019) and is the key defence against both vertebrate (Hartley and DeGabriel 2016) and invertebrate herbivores (Reynolds, Keeping, and Meyer 2009; Alhousari and

Greger 2018). Defence mechanisms include silicon deposition between and within cell walls conferring physical resistance to herbivory (Massey and Hartley 2009). Silicon may also form discrete structures (e.g., opaline phytoliths) on the leaf surface which can interfere with feeding, wear down mouthparts and reduce nutrient acquisition by herbivores once ingested (Andama et al. 2020; Johnson et al. 2021). Silicon may also interact with herbivore defence phytohormonal pathways to optimise or enhance the production of a broader range of secondary metabolite defences (Ye et al. 2013; Hall et al. 2019).

There are many empirical studies reporting that plant silicon reduces herbivore performance, but there is considerable variation in how herbivores are affected, ranging from being highly negative (e.g., Nikpay et al. 2015), neutral (e.g., DoGramaci et al. 2013) and even beneficial when increased silicon supply stimulates plant growth and nutritional quality (e.g., Johnson et al. 2017). Moreover, some empirical studies reported that herbivores responded differently depending on the mode of feeding and speculated about the potential reasons (e.g., Massey, Ennos, and Hartley 2006; Johnson et al. 2021). Such empirical studies have been summarised in several descriptive reviews about plant silicon defences against invertebrate herbivores (e.g., Reynolds, Keeping, and Meyer 2009; Debona, Rodrigues, and Datnoff 2017; Alhousari and Greger 2018). There has, however, been no robust quantitative meta-analysis of silicon accumulation in plants and herbivore performance to establish patterns for different plant and herbivore functional groups. For example, it is unclear whether there are global models for how different types of herbivores (e.g., different feeding guilds or diet specialisation) respond to silicon defences or whether plant growth strategy (e.g., annual vs. perennial) matters when it comes to silicon defences. Nor is it known whether the body size of herbivores (e.g., mammalian grazers vs. invertebrates) influences the effectiveness of plant silicon defences.

Most studies considering plant defence traits and herbivore performance focus on the mean value and magnitude of both (Pearse, Paul, and Ode 2018). There is growing evidence, however, that variance in plant defences and traits (Wetzel et al. 2016; Pearse, Paul, and Ode 2018; Thiel et al. 2020) is an important, but largely overlooked, factor that reduces herbivore performance (Wetzel and Whitehead 2020). Variability in these traits, both at the individual plant and community level, could suppress herbivore fitness in several ways, including diversified chemical defences and increased frequency of non-host plants (Denno and McClure 1983). This variability primarily operates by reducing the selection pressure and opportunities for herbivores to develop and adapt to their effects. We therefore included variation in plant defence and herbivore performance in our meta-analysis. In summary, this is the first meta-analysis of plant silicon defences against herbivores and the first meta-analysis to incorporate variability in the broader area of plant–herbivore interactions.

The objective of this meta-analysis was to identify patterns in silicon defences, acting against both vertebrate and invertebrate herbivores, in a quantitative manner. We determined whether the effectiveness of silicon defences on herbivore performance differed depending on (1) herbivore feeding guild, (2) herbivore diet specialisation [specialist vs. generalist], (3) plant lifespan [annual vs. perennial] and (4) whether herbivores fed on Poaceae or non-Poaceae species. We also sought to examine variability in both silicon accumulation and herbivore performance to establish whether this potentially played a role in herbivore suppression. To achieve this, we considered both the mean effect sizes (the log response ratio [lnRR]) and the ratio of standard deviations (SDs) under comparison (log variation ratio [lnVR]) (Senior, Viechtbauer, and Nakagawa 2020) which, to our knowledge, has not been attempted in meta-analyses of plant–herbivore interactions. The conceptual framework for this approach, visualised in Figure 1, hypothesises that herbivore performance will decrease when

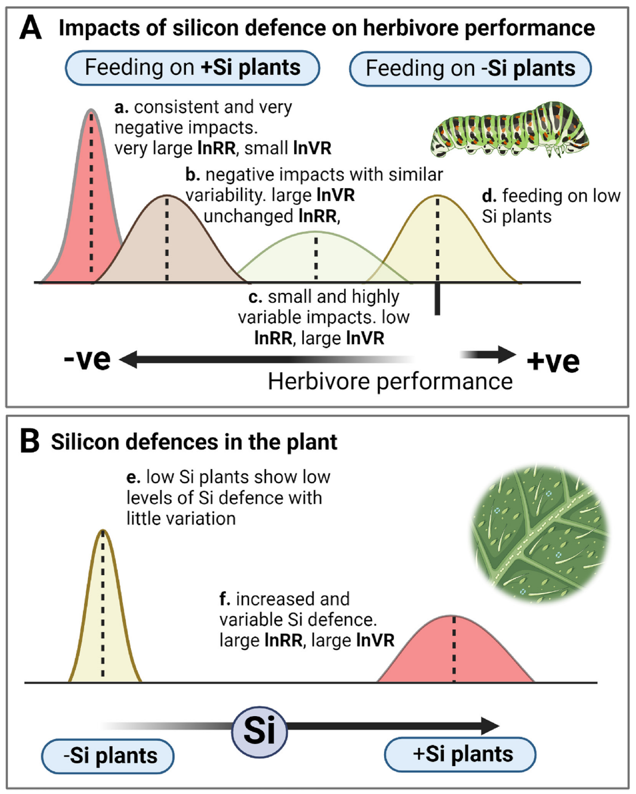

FIGURE 1 | (A) Schematic showing hypothetical impacts of silicon defence on herbivore performance, illustrating four hypothetical scenarios. Scenario d reflects herbivore performance when feeding on low-silicon plants (–Si) with a median ‘zero’ effect. In scenario a, high-silicon (+Si) plant defences have highly detrimental and consistent impacts on herbivore performance across the population, indicated by large (negative) lnRR values and small lnVR values. In (scenario b), silicon defences have negative impacts on performance (large lnVR), but some individuals are less affected than others, mirroring the variability (unchanged lnRR) when feeding on low-silicon plants (scenario d). In (scenario c), silicon defences are much less severe and have more variable impacts on herbivore performance, with some individuals in the population being substantially less affected than others, indicated with intermediate (but still negative) lnRR and large lnVR values. For silicon defences in plants (B), scenario e represents low-silicon (–Si) plants that have few silicon defences with very limited variation. In high-silicon (+Si) plants (scenario f), silicon defences are invariably higher than low-silicon plants, but some plants in the population may be better defended than others, as indicated by large lnRR and lnVR values.

feeding on silicon-rich (+Si) plants relative to when feeding on low-silicon (−Si) plants (scenario a; Figure 1A) with several patterns possible (scenarios b–d; Figure 1A). The potential impacts of silicon defence on herbivore performance range from being consistently very adverse with low variation (scenario b; Figure 1A) to being mild and highly variable throughout the population (scenario d; Figure 1A). Increasing silicon concentrations in the plant via manipulation or natural variation may be similarly represented in terms of mean effect size and variability (Figure 1B).

2 | Materials and Methods

Full details of Study Selection, Data Extraction and Compilation, outlined below, are given in the Supporting Information (figures and tables are prefixed with 'S'). Data for the meta-analysis, including R scripts, additional figures and tables are available in the Appendix (extended data figures and tables are prefixed 'E').

2.1 | Study Selection

We referenced and followed PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) and PRISMA-EvoEvo reporting guidelines (Moher et al. 2009; O'Dea et al. 2021) for reporting systematic study selection and data extraction (Supporting Information, Data S1). In brief, we conducted comprehensive searches using Web of Science and Scopus on 1 August 2021 and subsequently on 20 January 2023 using the search terms 'silic*' and 'plant*' (including NOT 'in silico') in combination with individual terms indicative of herbivory: 'herbiv*', 'insect', 'mammal' 'invertebrate', 'vertebrate' and 'consum*' (full search strategy given in Table S1). Once duplicates (519) were removed from the 1596 retrieved records, inspection of titles and abstracts of the remaining 1077 records identified 279 studies of potential relevance; 275 were obtained as full text for detailed inspection (Figure S1). Of these studies, only those that measured herbivore performance when feeding on plants with high and low plant silicon were retained. In most cases (95% of studies), this distinction was achieved using silicon supplementation of plants relative to a non-supplemented plant. Eight studies used natural variation in silicon concentrations (e.g., contrasting plant genotypes with high and low Si accumulation). Studies needed to report the extractible mean, SD and sample size (*n*) values to be included in analyses. Studies excluded at full-text screening stage are listed in Table S2 and depicted in Figure S1, alongside main exclusion reasons. In addition, 12 studies were identified through other sources (e.g., websites and online early notifications); of these 10 were then included in the analysis.

2.2 | Data Extraction and Compilation

During data extraction, herbivore performance was broadly defined to include any of the following: abundance/preference, feeding efficiency, growth/development, mortality/survivability and reproduction. Where reported, we also extracted values for silicon concentrations in the plants (mean, SD and sample size). In total, 150 studies, that produced 721 observations, were used for meta-analysis (see Appendix, Extended Data Table 1).

We extracted the following predictors for plant and herbivore characteristics: (1) whether the plant species belonged to the Poaceae (i.e., a grass) or was non-Poaceae, (2) plant lifespan category (annual or perennial), (3) the herbivores' feeding guild (fluid-feeding arthropods, cell-feeding arthropods, chewing arthropods (stem/stalk), boring arthropods, leaf-mining arthropods, rasping/grazing invertebrates, mammalian chewers) and (4) the herbivores' diet breadth (generalist vs. specialist). Additional information about the journal, publication year, plant and herbivore species, plant phylogeny and herbivore performance parameters are collated in the Appendix (Extended Data Table 1). Numerical data (herbivore performance and plant silicon concentration) were either directly extracted (e.g., when reported in tabular form) or extracted from plots using digitizer software (DigitizeIt, Braunschweig, Germany).

2.3 | Choosing Effect Size Statistics and Calculating Effect Sizes

Our data set showed strong positive mean–variance relationships. This relationship was observed in correlations between means and SDs of herbivore performance values in both high (experimental) and low (control) silicon plants (Figure E1A,B, respectively). Similarly, we found strong correlations between means and SDs of relative silicon contents (concentrations) in high- and low-silicon plants (Figure E1C,D, respectively). When such relationships are present it is preferable to use the logarithm of response ratio, lnRR, and its sampling variance (i.e., the inverse of effect-size specific weight) (Gurevitch and Hedges 1999) rather than the standardised mean difference (often known as Cohen's *d* or Hedges' *g*) because the latter assumes the homogeneity of variance. We also calculated the logarithm of variability (SD) ratio, lnVR, and its sampling variance (Nakagawa et al. 2015; Senior, Viechtbauer, and Nakagawa 2020). For most herbivore performance traits, smaller effect sizes indicate poorer performance (e.g., survival or reproduction). For some performance traits (17%), such as development time to adulthood, however, larger effect sizes represent poorer performance. In the latter case, lnRR was multiplied by −1. This sign change was not necessary for lnVR as the directionality of the effect size only applies to mean values and not variance (SD).

2.4 | Phylogenetic Tree and Correlation Matrix

We created a phylogenetic tree for plant species (Figure E2) and for herbivore species in our meta-analytic dataset using the R package rotl (Michonneau, Brown, and Winter 2016). We turned both of these trees into correlation matrices assuming the Brownian motion mode of evolution using the R package ape (Paradis and Schliep 2019). These correlation matrices were incorporated into subsequent meta-analyses to control for phylogenetic dependencies (see below; Nakagawa and Santos 2012).

2.5 | Meta-Analytic Models: lnRR And lnVR

We conducted meta-analyses on both herbivore performance and silicon content (i.e., running the intercept-only models) using the rma.mv function in the R package metafor (Viechtbauer 2010). We fitted variance–covariance matrices for the argument *V* which accounts for sampling variance and co-variance for sampling errors among effect sizes within studies (assuming shared measurements within a study); this is a conservative assumption (Noble et al. 2017). Also, we used adjustments for test statistics and confidence intervals (test = '*t*'), which is similar to (but not the exactly same as) those proposed by Hartung and Knapp (2003), reducing Type 1 errors compared to the default setting using the *z* distribution. For meta-analytic models (both for lnRR and lnVR) of herbivore performance, potential random effects included: (1) the publication (study) that effect size was extracted from, (2) the identity of herbivore species used in experiments (non-phylogenetic effect; e.g., species similarities due to their ecology), (3) the effect of the evolutionary relationship between herbivore species (estimated with correlation matrix based on a phylogenetic tree), (4) the identity of plant species used in experiments (non-phylogenetic effect), (5) the effect of the evolutionary relationship between plant species (estimated with correlation matrix based on a phylogenetic tree) and (6) effect size identity. For silicon content, the same random effects were tested, excluding herbivore species and phylogeny. We determined the optimal random effects structure based on Akaike information criterion (AIC) score comparison and the contributions of each variance component; we removed random effects that accounted for little variance (i.e., close to zero) and confirmed these removals did not decrease AIC values. The set of random effects that we used for subsequent meta-regression models of herbivore performance included study, herbivore species, herbivore phylogeny and effect size identity (note that we did not have any meta-regression models for plant silicon content).

2.6 | Meta-Regression Models and Model Selection

First, for the effects on herbivores (measured in lnRR and lnVR), we ran uni-moderator models for each of the key categorical variables in turn: (1) plant lifespan (annual vs. perennial), (2) plant type (Poaceae vs. non-Poaceae), (3) herbivore diet breadth (generalist vs. specialist) and (4) herbivore feeding guild. Then, we also identified the best model via an AIC-based model selection method implemented in the R package MuMIn (Barton 2009). We did not model all interaction terms for these four categorical variables because there was insufficient data for many combinations (56 possible permutations). Alluvial plots were used to visualize the degree of overlap between categories (i.e., levels within variables) for different pairs of categorical variables (Figure E12). In terms of meta-analytical effect size for the mean trait values (lnRR), the best model included herbivore feeding guild, which was the most important predictor by far (Tables E19 and E20). For variance (lnVR), plant type (Poaceae vs. non-Poaceae) was most important, followed by plant lifespan and diet breadth (Tables E21 and E22). Based on these findings, and the availability of observations that allowed meaningful comparisons to be made, we examined interactions between chewing and fluid-feeding arthropods and (1) plant lifespan, (2) plant type and (3) diet breadth, which are reported in Tables E13–E18.

2.7 | Publication Bias

We conducted three kinds of publication bias analyses: (1) contour-enhanced funnel plots (Peters et al. 2008) of residuals from a multivariate meta-regression model containing the four main predictor variables (moderators) listed above (Egger et al. 1997; Nakagawa and Santos 2012), (2) a multi-level type of Egger's regression on both uni- and multivariate meta-regression models to test for any deviations caused by funnel asymmetry (Egger et al. 1997; Moreno et al. 2009) and (3) a regression-based time-lag bias test to determine how effect sizes vary with date of publication (Nakagawa and Santos 2012). For Egger's regression, rather than using sampling variance, we used 'effective sample size' proposed by Nakagawa et al. (2022); this method can detect and also adjust for publication bias or, more precisely, a small-study effect where studies with small sample sizes have large effect sizes when such a bias exists (Sterne et al. 2011). Publication bias analyses are only appropriate for lnRR, as publication bias, by definition, cannot be caused by differences in variation (lnVR).

3 | Results

The meta-analysis was conducted on 150 studies that provided 721 observations from 46 plant species belonging to 14 plant families, with the Poaceae accounting for 79% of observations (Table S3). There were 62 herbivore species from 11 families with Hemiptera and Lepidoptera accounting for 37% and 49% of observations, respectively (Table S4).

3.1 | Collective Effects of Silicon on Herbivore Performance

Considering herbivore performance collectively, we observed that silicon significantly reduced herbivore performance by 33% (Figure 2A; Tables E1 and E2). There was a limited effect on variation in herbivore performance, which only decreased by 6% (Figure 2B; Tables E1 and E2). These effects are unlikely to be affected by publication bias because we did not see any obvious asymmetry in our contour-enhanced funnel plots (Figure E7). Also, uni-moderator analysis of lnRR (or sqrt [varlnRR]) statistically confirmed this pattern (Figure E8 and Table E23) along with equivalent multi-moderator models (Figure E9 and Table E24; see also E25). Although there was some evidence of a time-lag effect, with a significant decline in the magnitude of effect sizes over time (publication year), the effect seems to be relatively weak (Tables E26 and E27; Figures E10 and E11) (see also Costello and Fox 2022; Yang, Lagisz, and Nakagawa 2023).

When we contrasted the relative difference in the amounts of silicon in plants in high- and low-silicon plants, either resulting from silicon supplementation or natural variation, we found that, on average, the high-silicon plants had 52% more

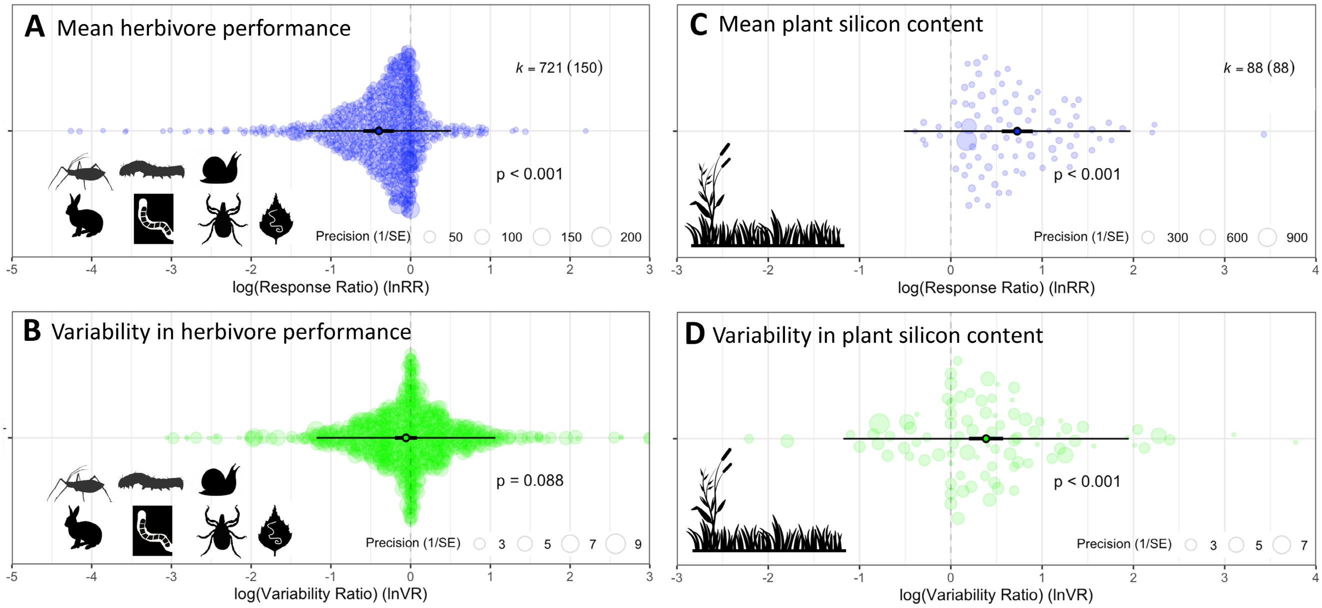

FIGURE 2 | Impact of plant silicification on (A) mean change (lnRR) and (B) change in variance (lnVR) in herbivore performance (−33% and −6%, respectively) and (C) mean change (lnRR) and (D) change in variance (lnVR) in plant silicon content between low- and high-silicon plants (+52% and +32%, respectively). The orchard plots show the meta-analytic mean estimate (mean effect size—open black circle) with its 95% confidence interval (thick horizontal whisker line) and 95% prediction interval (thin horizontal whisker line), with individual observed effect sizes as coloured circles scaled by their precision (1/SE). The number of effect sizes is denoted as *k* (the number of studies shown in parentheses). The icons represent herbivore-feeding guilds included in the study: Fluid-feeding arthropods (269), chewing arthropods (331), rasping/grazing invertebrates (2), mammalian chewers (29), boring arthropods (77), cell-feeding arthropods (12) and leaf-mining arthropods (1).

Si than the low-silicon plants (Figure 2C; Table E3). The high-silicon plants had 32% more variability in terms of silicon constituency (Figure 2D; Tables E3 and E4). There was a weak non-significant negative correlation between the magnitudes of herbivore performance effect sizes and magnitudes of effect sizes for differences in silicon levels in plants for lnRR ($r = -0.175$). Such a negative correlation is expected as higher amounts of silicon would reduce herbivore performance, but this weak correlation suggests that there is no simple linear relationship between relative silicon levels and relative effects on herbivores.

3.2 | Herbivore Feeding Strategy Determines How Adversely They Are Affected

When we examined whether the different predictors explained any differences in herbivore performance on plants with low- and high-silicon content, it was clear that feeding guild of the animal was the most important factor (see model selection; Tables E19–E22). In terms of changes in performance, the four feeding guilds with >15 observations that were negatively affected by Si defences included: mammalian chewers, chewing, (stem/stalk) boring and fluid-feeding arthropods (Figure 3; Table E11). Moreover, the mandibulate herbivores (mammals, chewing and boring arthropods) were more negatively impacted (−45%, −33% and −39%, respectively) compared to the more modest impacts on fluid-feeding arthropods (−14%) (Figure 3; Table E11). In terms of negative impacts on performance, mandibulate mammals, chewing and boring arthropods differed significantly from fluid-feeding arthropods ($p = 0.009$, 0.011 and 0.005, respectively). There was no evidence for differences in the effects on variability in herbivore performance for any of the feeding guilds (Table E12). The less well-represented feeding guilds (<15 observations) are shown in Appendix Figure E6 with corresponding results (Tables E11 and E12).

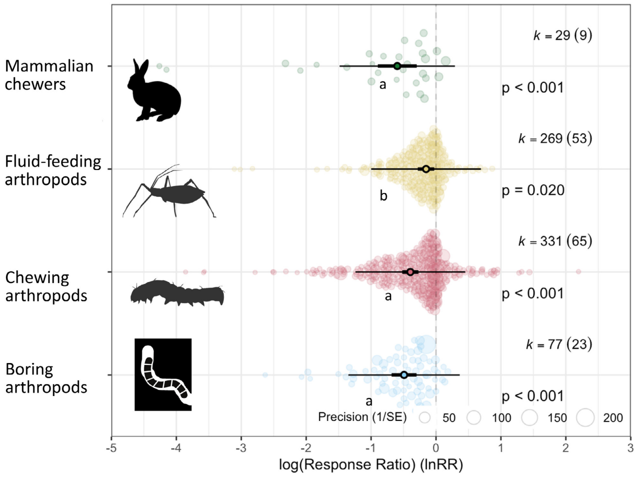

FIGURE 3 | Impacts of plant silicon on mean change (lnRR) in herbivore performance depending on herbivore feeding guild. Graphical details as per Figure 2. The four most represented feeding guilds (>15 observations) are shown (see Figure 2A,B for overall values across all guilds). The number of effect sizes is denoted as *k* (the number of studies shown in parentheses). Lowercase letters indicate significant differences between groups.

3.3 | Collective Impacts of Silicon Defences in Relation to Plant Lifespan, Grasses Versus Non-Grasses and Herbivore Diet Breadth

When herbivore performance was considered collectively, the impact of silicon defences was not significantly determined by plant lifespan, whether the plant was a grass or not, or the herbivores diet breadth. In terms of plant lifespan (annual or perennial), we found no differences in either effect on the mean performance or variation in herbivore performance (Figure E4; Tables E7 and E8, respectively). Likewise, the diet breadth of herbivores, (generalist vs. specialist) had no clear impact on how silicon defences affected herbivore performance (Figure E5; Tables E9 and E10). Silicon defences were equally effective in Poaceae and non-Poaceae (Figure E3; Table E5) and this factor also made no difference to variation in herbivore performance (Table E6). Chewing and fluid-feeding arthropods were the most studied herbivores (331 and 269 observations, respectively), so it was possible to look at their interactive effects with plant lifespan, Poaceae or non-Poaceae and diet breadth, as presented below.

3.4 | Impacts of Silicon Defences on Chewing Versus Fluid-Feeding Arthropods in Relation to Plant Lifespan, Grasses Versus Non-grasses and Herbivore Diet Breadth

In terms of Poaceae versus non-Poaceae species, we found that fluid feeders were weakly affected by silicon overall (Figure 4A; Table E15) and showed similar levels of variation (Table E16) on low and high-silicon plants; this pattern was similar when feeding on Poaceae and non-Poaceae species. Chewing arthropods were more adversely affected when feeding on Poaceae than non-Poaceae (Figure 4A; Table E15) but showed similar levels of performance variability (Table E16).

In terms of plant lifespan, fluid-feeding arthropods performed slightly worse when feeding on silicon-rich annual plants compared to perennial plants (Figure 4B; Table E13). Chewing arthropods were adversely affected by silicon defences, regardless of whether feeding on annual or perennial plants (Figure 4B; Table E13). Variation in herbivore responses was mostly unaffected (Table E14).

Fluid-feeding arthropods with a generalist diet breadth were unaffected by silicon defences, with specialists only being minimally affected (Figure 4C; Table E17). Chewing arthropods were very negatively impacted regardless of their diet breadth (Figure 4C; Table E17). Neither feeding guild showed statistically significant effects on variability in performance regardless of whether they had generalist or specialist diets (Table E18).

4 | Discussion

4.1 | Global Differences Between Feeding Guilds

Why are fluid-feeding arthropods less affected by silicon defences than other herbivores? There are several possible reasons why silicon defences (physical and chemical) may be generally less effective against fluid-feeding herbivores than mandibulate herbivores (i.e., chewing and boring arthropods and mammalian herbivores). Firstly, silicon may be deposited on or within plant tissues in a way that does not present a physical barrier to stylet (feeding tubes used to withdraw plant fluids) penetration (e.g., Massey, Ennos, and Hartley 2006; Rowe et al. 2020). For example, discrete opaline phytoliths on the leaf surface or within the cell itself are less likely to inhibit feeding by fluid-feeding herbivores. Furthermore, fluid feeders do not ingest silicon fragments from the leaf surface in the same way as herbivores with mandibles, so this type of silicon deposition is unlikely to inhibit nutrient acquisition. Deposition in the cell wall might, however, narrow intercellular spaces, reduce flexibility and inhibit successful stylet penetration.

Secondly, silicon defences are controlled by the defensive phytohormonal pathways, specifically the jasmonic acid (JA) pathway (Hall et al. 2019), which is linked to the production of other secondary metabolite defences (Erb, Meldau, and Howe 2012). With a few specific exceptions, fluid-feeding herbivores,

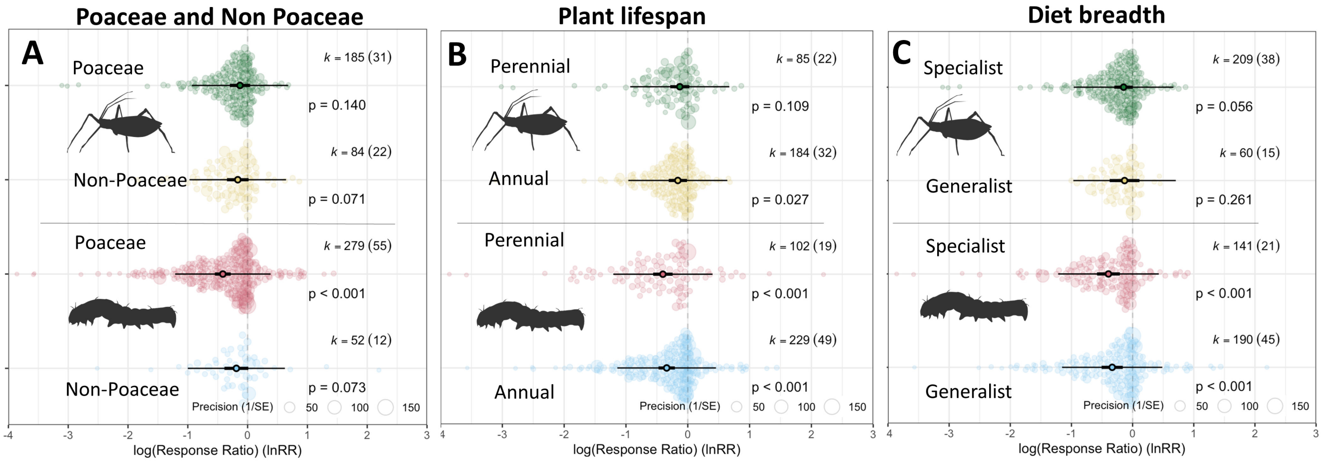

FIGURE 4 | Comparing impacts of silicon defences on the mean change (lnRR) in arthropod fluid-feeding and chewing herbivores performance when feeding on (A) Poaceae versus non-Poaceae, (B) annual versus perennial plants and (C) and in terms of herbivore diet breadth (specialist versus generalist). Graphical details as per Figure 2.

such as aphids, trigger the salicylic acid (SA) pathway, potentially as a strategy to suppress JA-related defences (Züst and Agrawal 2016). The SA and JA pathways utilise separate compounds for signal transduction (Thaler, Humphrey, and Whiteman 2012) and activation of the SA pathway often suppresses the JA pathway, and vice versa, via antagonistic cross-talk at several biosynthetic nodes (Bostock et al. 2001; Thaler, Humphrey, and Whiteman 2012). This cross-talk adjusts the defensive responses against specific attackers, especially in terms of herbivore feeding guild (Schweiger et al. 2014). We recently showed that aphids neither stimulated the JA pathway (but triggered the SA pathway) nor induced silicon uptake and were unaffected by silicon defences in the model grass *Brachypodium distachyon* (Johnson et al. 2021). Chewing herbivores, in contrast, activated the JA pathway, increased silicon uptake and were negatively impacted by increased silicon levels in the plant.

The third possible reason is that many of the defensive compounds whose production may be enhanced by silicon supplementation may be less effective against fluid-feeders than mandibulate herbivores. Defensive compounds that inhibit digestive proteolysis (e.g., protease inhibitors), for example, are generally thought to affect chewers much more than aphids (Zhu-Salzman and Zeng 2015). Moreover, plant toxins and digestive inhibitors are located in the apoplast and cell vacuole where they are excluded from phloem sieve elements (Douglas 2003), and any secondary metabolites which do occur in phloem fluid (e.g., glucosinolates, cardenolides, alkaloids, pyrrolizidines) occur in lower concentrations than in most other plant tissues (Raven 1983a; Douglas 2003).

4.2 | Differences in How Feeding Guilds Are Affected by Plant Family, Plant Lifespan and Diet Breadth

The meta-analysis showed that there were differences in how fluid-feeding and chewing arthropods responded to plant silicon defences, depending on whether their host plant was grass or not (i.e., Poaceae vs. non-Poaceae), the lifespan of the plant (i.e., annual vs. perennial) and the diet breadth of the herbivore (generalist vs. specialist). Firstly, chewing arthropods were more adversely affected when feeding on Poaceae than when feeding on non-Poaceae plant species. Given that the Poaceae are the highest accumulators of silicon, this seems logical and may suggest that silicon is primarily a physical defence whereby high levels of silicon accumulation are needed for herbivore resistance. In contrast, if the presence of silicon in low concentrations (more typical of the non-Poaceae; Hodson et al. 2005) stimulated the production of secondary metabolite defences, it might be expected that the non-Poaceae would be equally defended.

Secondly, fluid-feeding arthropods performed slightly worse when feeding on silicon-rich annual plants than when feeding on silicon-rich perennial plants. Longer-lived plant tissues, and by extension longer-lived plants (e.g., perennial species), often invest in 'more expensive' plant defences than fast-growing plants (e.g., annuals) (Coley, Bryant, and Chapin 1985). This reflects their longer exposure to herbivory, the relatively high costs of replacing slow-growing tissues lost to herbivory and that the investment in defences is recovered over a longer lifespan (Coley, Bryant, and Chapin 1985). Silicon is sometimes regarded as a metabolically 'cheaper' herbivore defence than some other plant defences (Raven 1983b; Quigley and Anderson 2014; Simpson et al. 2017), so might have greater utility in annual species compared with perennial species. Cooke and Leishman (2011) found strong empirical support for this idea in their assessment of 155 plant species.

Finally, two notable patterns were apparent when we considered diet breadth: (1) specialist and generalist chewing arthropods were equally affected by silicon defences and (2) fluid-feeding arthropods with generalist diet breadth were unaffected by silicon defences and the impacts on specialists were weak. Most plant defence theories predict that herbivores specialising in a smaller number of host plants (i.e., specialists) are better adapted to the defences of their host plants than those that feed on a broader range of host plants (i.e., generalists) (Whittaker and Feeny 1971; Stamp 2003). Specialist herbivores (especially chewing arthropods) were clearly not evading plant silicon defences in the same way as they frequently do for many secondary metabolite defences (Rothwell and Holeski 2020). Silicon physical defences may impose more generic damage to herbivore body parts and may be more challenging to adapt to than specific secondary metabolites (Caldwell, Read, and Sanson 2016). Herbivores often possess adaptations for overcoming the effects of secondary metabolites, including effective biochemical adaptations such as enzymatic detoxification, expedited excretion and sequestration (War et al. 2018). Herbivores may be able to similarly adapt to physical defences to some extent, for instance, by evolving larger heads, changing mandible morphology or passing through extra moults to replace mouthparts (Isley 1944; Bernays 1986; Kvedaras et al. 2009). These are, however, physiologically constrained, and likely to impose high fitness costs (Caldwell, Read, and Sanson 2016). For the fluid feeders, Ali and Agrawal (2012) make the point that generalist fluid feeders may adopt a strategy of suppressing the generic JA pathway rather than tolerating or adapting to specific metabolites. As discussed above, suppression of the JA pathway may limit the induction of silicon defences and may explain why generalist fluid-feeding arthropods are unaffected by silicon defences.

4.3 | Herbivore Body Size and Variability in Silicon Defence and Herbivore Performance

It was noteworthy that mammalian herbivores were as adversely affected by silicon as mandibulate arthropod herbivores. It has long been argued herbivores with larger body sizes can cope with a poorer quality diet because they can digest plant material more thoroughly due to longer gut retention time (Demment and Vansoest 1985). This has since been challenged, and other factors such as intake rate, pre-digestion food processing and gut morphology have been proposed to be more important (Steuer et al. 2014). With much fewer observations for vertebrate herbivores than invertebrate herbivores, definitive conclusions about the similarity of plant silicon effects on vertebrate and invertebrate herbivores are perhaps premature, but this finding challenges the prediction made by Johnson, Hartley, and Moore (2021) that increasing body size may mitigate the impacts of silicon-rich diets.

The meta-analysis showed that an increase in plant silicon was associated with increased variability in the extent of silicification, resembling scenario f in Figure 1B which may, in part, underpin their effectiveness in reducing herbivore performance, similar to what has been reported for secondary metabolite defences (Pearse, Paul, and Ode 2018). We showed that herbivore performance declined considerably when feeding on silicon-rich plants but the variability in the performance did not significantly change, best represented by scenario c in Figure 1A. This indicates consistency in the impacts of silicon defence and that these defences are potentially harder to adapt to than secondary metabolite defences.

5 | Conclusions

While there are numerous specific examples of fluid-feeding arthropods being negatively impacted by silicon defences, included as contributing studies in this meta-analysis, the overall trend is that silicon defences affect fluid-feeding arthropods less than herbivores that chew plants. Early experimental work by Massey, Ennos, and Hartley (2006) suggested that phloem-feeding aphids might be less adversely affected than leaf-chewing arthropods, but until now, there was no systematic test of this. Narrative reviews that cover plant silicon defences against herbivores imply that herbivore feeding guilds are impacted equally, or at least that the mode of feeding is not a point of significant distinction (Reynolds et al. 2016; Debona, Rodrigues, and Datnoff 2017). Our results suggest that this distinction should be made if we are to accurately understand the evolutionary and ecological role of silicon in plant defence theory.

Author Contributions

Scott N. Johnson, Susan E. Hartley and Julia Cooke conceived the ideas for the meta-analysis. Scott N. Johnson conducted the search, extracted the data and built the database. Scott N. Johnson conducted the initial analysis with the assistance of Julia Cooke and James M. W. Ryalls; Jamie M. Waterman and Shinichi Nakagawa conducted the final meta-analysis and produced the code and outputs. Malgorzata Lagisz conducted quality checks and initial input to the writing of the manuscript. Scott N. Johnson produced the initial draft of the manuscript, which received input from all authors. All authors agreed to the submitted version of the manuscript.

Acknowledgements

This work was funded by a Future Fellowship grant from the Australian Research Council (FT170100342) awarded to Scott N. Johnson. We thank Jane DeGabriel, Adam Frew and Olivia Reynolds for early discussions about potential questions for a meta-analysis. Open access publishing facilitated by Western Sydney University, as part of the Wiley - Western Sydney University agreement via the Council of Australian University Librarians.

Data Availability Statement

The data set and coding, together with supplemental material and PRISMA details, are available at the Fig Share Digital Repository: https://doi.org/10.6084/m9.figshare.25303366.v5.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14519.

References

Alhousari, F., and M. Greger. 2018. “Silicon and Mechanisms of Plant Resistance to Insect Pests.” *Plants* 7: 33.

Ali, J. G., and A. A. Agrawal. 2012. “Specialist Versus Generalist Insect Herbivores and Plant Defense.” *Trends in Plant Science* 17: 293–302.

Andama, J. B., K. Mujiono, Y. Hojo, T. Shinya, and I. Galis. 2020. “Non-Glandular Silicified Trichomes Are Essential for Rice Defense Against Chewing Herbivores.” *Plant, Cell & Environment* 43: 2019–2032.

Barton, K. 2009. “MuMIn: Multi-Model Inference.” https://cran.r-project.org/web/packages/MuMIn/index.html

Bernays, E. A. 1986. “Diet-Induced Head Allometry Among Foliage-Chewing Insects and Its Importance for Graminivores.” *Science* 231: 495–497.

Bostock, R. M., R. Karban, J. S. Thaler, P. D. Weyman, and D. Gilchrist. 2001. “Signal Interactions in Induced Resistance to Pathogens and Insect Herbivores.” *European Journal of Plant Pathology* 107: 103–111.

Caldwell, E., J. Read, and G. D. Sanson. 2016. “Which Leaf Mechanical Traits Correlate With Insect Herbivory Among Feeding Guilds?” *Annals of Botany* 117: 349–361.

Coley, P. D., J. P. Bryant, and F. S. I. Chapin. 1985. “Resource Availability and Plant Antiherbivore Defense.” *Science* 230: 895–899.

Cooke, J., and M. R. Leishman. 2011. “Silicon Concentration and Leaf Longevity: Is Silicon a Player in the Leaf Dry Mass Spectrum?” *Functional Ecology* 25: 1181–1188.

Coskun, D., R. Deshmukh, H. Sonah, et al. 2019. “The Controversies of Silicon's Role in Plant Biology.” *New Phytologist* 221: 67–85.

Costello, L., and J. W. Fox. 2022. “Decline Effects Are Rare in Ecology.” *Ecology* 103: e3680.

Debona, D., F. A. Rodrigues, and L. E. Datnoff. 2017. “Silicon's Role in Abiotic and Biotic Plant Stresses.” *Annual Review of Phytopathology* 55: 85–107.

Demment, M. W., and P. J. Vansoest. 1985. “A Nutritional Explanation for Body-Size Patterns of Ruminant and Nonruminant Herbivores.” *American Naturalist* 125: 641–672.

Denno, R. F., and M. S. McClure, (Eds.). 1983. *Variable Plants and Herbivores in Natural and Managed Systems*. Michigan, USA: Academic Press.

Deutsch, C. A., J. J. Tewksbury, M. Tigchelaar, et al. 2018. “Increase in Crop Losses to Insect Pests in a Warming Climate.” *Science* 361: 916–919.

DoGramaci, M., S. P. Arthurs, J. J. Chen, and L. Osborne. 2013. “Silicon Applications Have Minimal Effects on *Scirtothrips dorsalis* (Thysanoptera: Thripidae) Populations on Pepper Plant, *Capsicum annum* L.” *Florida Entomologist* 96: 48–54.

Douglas, A. E. 2003. “The Nutritional Physiology of Aphids.” *Advances in Insect Physiology* 31: 73–140.

Egger, M., G. D. Smith, M. Schneider, and C. Minder. 1997. “Bias in Meta-Analysis Detected by a Simple, Graphical Test.” *BMJ* 315: 629–634.

Erb, M., S. Meldau, and G. A. Howe. 2012. “Role of Phytohormones in Insect-Specific Plant Reactions.” *Trends in Plant Science* 17: 250–259.

Gurevitch, J., and L. V. Hedges. 1999. “Statistical Issues in Ecological Meta-Analyses.” *Ecology* 80: 1142–1149.

Hall, C. R., J. M. Waterman, R. K. Vandegeer, S. E. Hartley, and S. N. Johnson. 2019. “The Role of Silicon in Phytohormonal Signalling.” *Frontiers in Plant Science* 10: 1132.

Hartley, S. E., and J. L. DeGabriel. 2016. “The Ecology of Herbivore-Induced Silicon Defences in Grasses.” *Functional Ecology* 30: 1311–1322.

Hartley, S. E., and C. G. Jones. 1997. "Plant Ecology and Diversity." In *Plant Chemistry and Herbivory, or Why the World Is Green*, In *Plant Ecology* edited by M. J. Crawley, 284–324. Oxford: Blackwell Science. https://doi.org/10.1002/9781444313642.ch10

Hartung, J., and G. Knapp. 2003. "An Alternative Test Procedure for Meta-Analysis." In *Meta-analysis: New Developments and Applications in Medical and Social Sciences*, edited by R. Schulze, H. Holling, and D. Böhning, 53–69. Ashland, OH, USA: Hogrefe & Huber Publishers.

Hodson, M. J., P. J. White, A. Mead, and M. R. Broadley. 2005. "Phylogenetic Variation in the Silicon Composition of Plants." *Annals of Botany* 96: 1027–1046.

Isley, F. B. 1944. "Correlation Between Mandible Morphology and Food Specificity in Grasshoppers." *Annals of the Entomological Society of America* 37: 47–67.

Johnson, S. N., S. E. Hartley, and B. D. Moore. 2021. "Silicon Defence in Plants: Does Herbivore Identity Matter?" *Trends in Plant Science* 26: 99–101.

Johnson, S. N., S. E. Hartley, J. M. W. Ryalls, et al. 2017. "Silicon-Induced Root Nodulation and Synthesis of Essential Amino Acids in a Legume Is Associated With Higher Herbivore Abundance." *Functional Ecology* 31: 1903–1909.

Johnson, S. N., S. E. Hartley, J. M. W. Ryalls, A. Frew, and C. R. Hall. 2021. "Targeted Plant Defense: Silicon Conserves Hormonal Defense Signaling Impacting Chewing but Not Fluid-Feeding Herbivores." *Ecology* 102: e03250.

Kvedaras, O. L., M. J. Byrne, N. E. Coombes, and M. G. Keeping. 2009. "Influence of Plant Silicon and Sugarcane Cultivar on Mandibular Wear in the Stalk Borer *Eldana saccharina*." *Agricultural and Forest Entomology* 11: 301–306.

Ma, J. F., and N. Yamaji. 2015. "A Cooperative System of Silicon Transport in Plants." *Trends in Plant Science* 20: 435–442.

Massey, F. P., A. R. Ennos, and S. E. Hartley. 2006. "Silica in Grasses as a Defence Against Insect Herbivores: Contrasting Effects on Folivores and a Phloem Feeder." *Journal of Animal Ecology* 75: 595–603.

Massey, F. P., and S. E. Hartley. 2009. "Physical Defences Wear You Down: Progressive and Irreversible Impacts of Silica on Insect Herbivores." *Journal of Animal Ecology* 78: 281–291.

Michonneau, F., J. W. Brown, and D. J. Winter. 2016. "Rot1: An R Package to Interact With the Open Tree of Life Data." *Methods in Ecology and Evolution* 7: 1476–1481.

Moher, D., A. Liberati, J. Tetzlaff, and D. G. Altman. 2009. "Preferred Reporting Items for Systematic Reviews and Meta-Analyses: The PRISMA Statement." *BMJ* 339: b2535.

Moreno, S. G., A. J. Sutton, A. Ades, et al. 2009. "Assessment of Regression-Based Methods to Adjust for Publication Bias Through a Comprehensive Simulation Study." *BMC Medical Research Methodology* 9: 2.

Nakagawa, S., M. Lagisz, M. D. Jennions, et al. 2022. "Methods for Testing Publication Bias in Ecological and Evolutionary Meta-Analyses." *Methods in Ecology and Evolution* 13: 4–21.

Nakagawa, S., R. Poulin, K. Mengersen, et al. 2015. "Meta-Analysis of Variation: Ecological and Evolutionary Applications and Beyond." *Methods in Ecology and Evolution* 6: 143–152.

Nakagawa, S., and E. S. A. Santos. 2012. "Methodological Issues and Advances in Biological Meta-Analysis." *Evolutionary Ecology* 26: 1253–1274.

Nikpay, A., E. Soleyman-Nejadian, S. Goldasteh, and H. Farazmand. 2015. "Response of Sugarcane and Sugarcane Stalk Borers *Sesamia* spp. (Lepidoptera: Noctuidae) to Calcium Silicate Fertilization." *Neotropical Entomology* 44: 498–503.

Noble, D. W. A., M. Lagisz, R. E. O'dea, and S. Nakagawa. 2017. "Nonindependence and Sensitivity Analyses in Ecological and Evolutionary Meta-Analyses." *Molecular Ecology* 26: 2410–2425.

O'Dea, R. E., M. Lagisz, M. D. Jennions, et al. 2021. "Preferred Reporting Items for Systematic Reviews and Meta-Analyses in Ecology and Evolutionary Biology: A PRISMA Extension." *Biological Reviews* 96: 1695–1722.

Paradis, E., and K. Schliep. 2019. "Ape 5.0: An Environment for Modern Phylogenetics and Evolutionary Analyses in R." *Bioinformatics* 35: 526–528.

Pearse, I. S., R. Paul, and P. J. Ode. 2018. "Variation in Plant Defense Suppresses Herbivore Performance." *Current Biology* 28: 1981–1986.

Peters, J. L., A. J. Sutton, D. R. Jones, K. R. Abrams, and L. Rushton. 2008. "Contour-Enhanced Meta-Analysis Funnel Plots Help Distinguish Publication Bias From Other Causes of Asymmetry." *Journal of Clinical Epidemiology* 61: 991–996.

Quigley, K. M., and T. M. Anderson. 2014. "Leaf Silica Concentration in Serengeti Grasses Increases With Watering But Not Clipping: Insights From a Common Garden Study and Literature Review." *Frontiers in Plant Science* 5: 568.

Raven, J. A. 1983a. "Phytophages of Xylem and Phloem–A Comparison of Animal and Plant Sap-Feeders." *Advances in Ecological Research* 13: 135–234.

Raven, J. A. 1983b. "The Transport and Function of Silicon in Plants." *Biological Reviews* 58: 179–207.

Reynolds, O. L., M. G. Keeping, and J. H. Meyer. 2009. "Silicon-Augmented Resistance of Plants to Herbivorous Insects: A Review." *Annals of Applied Biology* 155: 171–186.

Reynolds, O. L., M. P. Padula, R. S. Zeng, and G. M. Gurr. 2016. "Silicon: Potential to Promote Direct and Indirect Effects on Plant Defense Against Arthropod Pests in Agriculture." *Frontiers in Plant Science* 7: 744.

Rothwell, E. M., and L. M. Holeski. 2020. "Phytochemical Defences and Performance of Specialist and Generalist Herbivores: A Meta-Analysis." *Ecological Entomology* 45: 396–405.

Rowe, R. C., P. Trębicki, A. Gherlenda, and S. N. Johnson. 2020. "Cereal Aphid Performance and Feeding Behaviour Largely Unaffected by Silicon Enrichment of Host Plants." *Journal of Pest Science* 93: 41–48.

Schweiger, R., A. M. Heise, M. Persicke, and C. Müller. 2014. "Interactions Between the Jasmonic and Salicylic Acid Pathway Modulate the Plant Metabolome and Affect Herbivores of Different Feeding Types." *Plant, Cell & Environment* 37: 1574–1585.

Senior, A. M., W. Viechtbauer, and S. Nakagawa. 2020. "Revisiting and Expanding the Meta-Analysis of Variation: The log Coefficient of Variation Ratio." *Research Synthesis Methods* 11: 553–567.

Simpson, K. J., R. N. Wade, M. Rees, C. P. Osborne, and S. E. Hartley. 2017. "Still Armed After Domestication? Impacts of Domestication and Agronomic Selection on Silicon Defences in Cereals." *Functional Ecology* 31: 2108–2117.

Stamp, N. 2003. "Out of the Quagmire of Plant Defense Hypotheses." *Quarterly Review of Biology* 78: 23–55.

Sterne, J. A. C., A. J. Sutton, J. P. A. Ioannidis, et al. 2011. "Recommendations for Examining and Interpreting Funnel Plot Asymmetry in Meta-Analyses of Randomised Controlled Trials." *BMJ* 343: d4002.

Steuer, P., K.-H. Südekum, T. Tütken, et al. 2014. "Does Body Mass Convey a Digestive Advantage for Large Herbivores?" *Functional Ecology* 28: 1127–1134.

Thaler, J. S., P. T. Humphrey, and N. K. Whiteman. 2012. "Evolution of Jasmonate and Salicylate Signal Crosstalk." *Trends in Plant Science* 17: 260–270.

Thiel, T., S. Gaschler, K. Mody, N. Blüthgen, and B. Drossel. 2020. "Impact of Plant Defense Level Variability on Specialist and Generalist Herbivores." *Theoretical Ecology* 13: 409–424.

Viechtbauer, W. 2010. "Conducting Meta-Analyses in R With the Metafor Package." *Journal of Statistical Software* 36: 1–48.

War, A. R., G. K. Taggar, B. Hussain, M. S. Taggar, R. M. Nair, and H. C. Sharma. 2018. "Plant Defence Against Herbivory and Insect Adaptations." *AoB Plants* 10: ply037.

Wetzel, W. C., H. M. Kharouba, M. Robinson, M. Holyoak, and R. Karban. 2016. "Variability in Plant Nutrients Reduces Insect Herbivore Performance." *Nature* 539: 425–427.

Wetzel, W. C., and S. R. Whitehead. 2020. "The Many Dimensions of Phytochemical Diversity: Linking Theory to Practice." *Ecology Letters* 23: 16–32.

Whittaker, R. H., and P. P. Feeny. 1971. "Allelochemics: Chemical Interactions Between Species." *Science* 171: 757–770.

Yang, Y., M. Lagisz, and S. Nakagawa. 2023. "Decline Effects Are Rare in Ecology: Comment." *Ecology* 104: e4069.

Ye, M., Y. Y. Song, J. Long, et al. 2013. "Priming of Jasmonate-Mediated Antiherbivore Defense Responses in Rice by Silicon." *Proceedings of the National Academy of Sciences of the United States of America* 110: E3631–E3639.

Zhu-Salzman, K., and R. Zeng. 2015. "Insect Response to Plant Defensive Protease Inhibitors." *Annual Review of Entomology* 60: 233–252.

Züst, T., and A. A. Agrawal. 2016. "Mechanisms and Evolution of Plant Resistance to Aphids." *Nature Plants* 2: 15206.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.