

RESEARCH ARTICLE

Environmental context and herbivore traits mediate the strength of associational effects in a meta-analysis of crop diversity

Philip G. Hahn  | Joseph H. Cammarano

Department of Entomology & Nematology, University of Florida, Gainesville, Florida, USA

Correspondence

Philip G. Hahn
Email: hahnp@ufl.edu

Funding information

National Science Foundation, Grant/Award Number: DEB-1901552; U.S. Department of Agriculture, Grant/Award Number: FLA-ENY-006018

Handling Editor: Lessando Gontijo

Abstract

1. Crop diversification offers a promising solution to meet expanding global food demands while maintaining ecosystem services. Diversification strategies that use mixed planting to reduce pest damage (e.g. intercropping), termed 'associational effects' (AE) in the ecological literature, can decrease (associational resistance) or increase (associational susceptibility) herbivore abundance on a focal plant. While application of AE to agroecosystems typically reduces pest abundance, the range of outcomes varies widely.
2. We conducted a meta-analysis using 272 estimates of insect herbivore abundance on crops neighbored by a conspecific or heterospecific from 44 studies undertaken on six continents. We focus on four agricultural crops well represented from sites across the globe to test hypotheses related to understanding how herbivore traits (diet breadth, feeding guild, origin), plant traits (crop type, phylogenetic distance to neighbour) and environmental context (climate, experimental design) contribute to variation in the outcomes of AE.
3. Overall, bicultures provided a strong reduction of insect abundance on the focal crop. Climate and interactions between herbivore traits, particularly diet breadth and origin, and plant traits or environmental context mediated the strength of AE.
4. Bicultures provided the strongest reductions in insect abundance at low latitudes, and this effect decreased at higher latitudes but only for insects with certain traits. Abundance of generalist herbivores and globally distributed pests tended to be most strongly negatively affected by bicultures, under certain contexts, whereas specialist herbivores and native pests were less affected by neighbours.
5. *Synthesis and application.* This meta-analysis highlights that crop diversification schemes have an overall strongly beneficial effect of reducing pest abundance. However, there was also variability in the outcomes that is determined in part by the interactive effects of herbivore traits and environmental context. The results provide guidance for incorporating beneficial ecological interactions into integrated pest management strategies.

KEYWORDS

agroecosystem, crop diversification, intercropping, IPM, neighbourhood effect, plant-insect interaction, push-pull, trap crop

1 | INTRODUCTION

Sustainable agricultural systems are required to meet the growing demand for food while minimizing environmental damage (Springmann et al., 2018). Crop diversification strategies that are inspired by ecological concepts hold great potential for maintaining ecosystem services and crop yield (Tamburini, Bommarco, et al., 2020). Associational effects (AE), which are a widespread type of indirect interaction that occur between plant neighbours and are mediated by herbivores (Agrawal et al., 2006; Barbosa et al., 2009), is one such ecological concept with potential to improve the ecological service of pest management. The utility of AE to reduce pest damage in agricultural systems has been recognized by indigenous people for centuries (Lewandowski, 1987) and have been shown experimentally to reduce damage and increase yield (Andow, 1991; Letourneau et al., 2011; Smith & McSorley, 2000). Recognized as an important ecological phenomenon over 60 years ago (Pimentel, 1961; Tahvanainen & Root, 1972), interest in AE has grown substantially in recent years, in part due to recent syntheses that show how AE can affect key ecological processes as well as the nature of evolution (Agrawal et al., 2006; Barbosa et al., 2009; Underwood et al., 2014). AE are conceptually appealing for both basic and applied research avenues because the framework spans a spectrum of ways in which neighbouring organisms could affect consumer attack on a focal organism, from reduced damage (associational resistance, AR) to increased damage (associational susceptibility, AS). However, despite the wide range of outcomes, from strongly negative to strongly positive (Barbosa et al., 2009; Mutz et al., 2022), predicting the direction and magnitude of AE remains challenging in both natural and agricultural systems.

Several hypotheses make predictions regarding how herbivore damage or abundance should vary in response to plant neighbours. The most prominent hypothesis, the resource concentration hypothesis (Root, 1973), predicts that plants growing in monocultures will support high abundance of specialist herbivores that cause high levels of damage to the plants. In contrast, in more diverse patches specialist herbivores will have more difficulty locating their preferred host plant resulting in less damage inflicted to plants when compared to monocultures (Andow, 1991; Moreira et al., 2016; Root, 1973). Therefore, the resource concentration hypothesis results in AR against specialists for the focal plant because the presence of neighbours results in reduced herbivory. AR can also occur via the 'repellent' hypothesis, where a neighbouring plant repels herbivores away from a patch (Atsatt & O'dowd, 1976) or via the 'attractant-decoy' hypothesis where herbivores preferentially attack a palatable neighbour (Agrawal, 2004; Atsatt & O'dowd, 1976). It is important to note that the attractant-decoy would result in AS for the neighbouring plant species (Agrawal, 2004; Atsatt & O'dowd, 1976). Alternatively, there are a number of hypotheses that predict AS. The 'spillover' hypothesis posits that high frequency of palatable neighbours attracts herbivores or supports high herbivore loads that then spillover onto the focal plant resulting in AS (Champagne et al., 2016; Hahn & Orrock, 2016). The diet mixing

hypothesis predicts that generalist herbivores will prefer diverse patches because they can better balance their nutrient intake when feeding on diverse plant species. Therefore, insect abundance and damage are predicted to be greater in more diverse compared with less diverse patches (Bernays et al., 1994; Moreira et al., 2016). This is not an exhaustive list of potential hypotheses, and other mechanisms can generate AE, such as induced defences or natural enemies (Moreira et al., 2016; Root, 1973).

Conceptual models propose that AE outcomes can be predicted along two axes: (1) traits of the herbivores (e.g. diet breadth) and (2) traits of the focal plant or differences between the associating plants (Agrawal, 2004; Agrawal et al., 2006; Champagne et al., 2016). Differences between generalist and specialist herbivores have long been considered in the study of AE. For example, the resource concentration or dilution hypotheses are more likely to operate on specialist herbivores (Otway et al., 2005), whereas the spillover, repellent or diet-mixing hypotheses are predicted to operate on generalists (Bernays et al., 1994). Other herbivore traits are also likely to predict how they are influenced by AE, such as feeding guild and exotic status (Barbosa et al., 2009; Tamburini, Santoiemma, et al., 2020). Additionally, differences in traits between neighbouring plants are considered in some studies, although often only categorically (e.g. more vs. less palatable; Underwood et al., 2014) due in part to logistical difficulties in measuring meaningful functional traits (but see Mutz et al., 2022). An alternative to measuring plant traits directly is to use phylogenetic distances between neighbours as a proxy, which is often an ecologically meaningful metric of trait similarity that could be consistently used across studies (Webb et al., 2002). Phylogenetic relatedness integrates information on the similarity of functional traits that are phylogenetically conserved between a pair of co-occurring plant species (Webb et al., 2002). Examining interactions between herbivore traits and plant traits (or trait differences among neighbours) provides a promising (Moreira et al., 2016), although largely unexplored, way to examine how trait similarity may influence AE (Castagneyrol et al., 2014; Dinnage, 2013; Jactel et al., 2021).

Environmental context can strongly influence the strength of species interactions (Agrawal et al., 2007) and therefore may contribute to the variability in AE outcomes. However, environmental context is typically not considered in studies of AE. Herbivore pressure often increases across productivity or climatic gradients (Chase et al., 2000). Variation in herbivore pressure across environmental gradients may contribute to mediating the strength of AE (Louthan et al., 2014), although this has rarely been tested. Additionally, other aspects of environmental context, particularly factors that alter plant density and frequency may also contribute to affecting the strength of AE (Hahn & Orrock, 2016; Hambäck et al., 2014; Kim & Underwood, 2015). The precise definition of AE provided by Underwood et al. (2014, 2020) states that AE occur when a neighbouring plant influences herbivore effects on a focal plant at a given density of the focal plant and at a given spatial scale. Disentangling the effects of resource density and frequency is an important, but experimentally challenging, issue to identifying how neighbouring plants influence herbivore abundance

and damage (Hambäck et al., 2014). Additive experimental designs hold focal plant density constant and manipulate neighbouring plant density, resulting in a change only in plant frequency (Andow, 1991; Underwood et al., 2014), which allows for a direct evaluation of AE since the focal plant density remains constant within the study. Replacement designs replace some amount of the focal plant with a neighbour, resulting in a change in focal plant density and frequency (Andow, 1991; Underwood et al., 2014). In other words, replacement designs confound plant density and frequency (Andow, 1991; Underwood et al., 2014). Nevertheless, considering environmental context may increase the predictability of the strength and direction of AE.

In this study, we examined whether AE are mediated by herbivore traits (diet breadth, feeding guild and origin), plant traits (focal species or phylogenetic similarity to neighbour), climate or aspects of the experimental design. A synthesis of agricultural studies seems particularly well suited to address these questions because intercropping (i.e. planting another species with a cash crop) is an agricultural technique that aims to reduce pest damage and minimize inputs (Huss et al., 2022). Therefore, there are ample previous studies comparing insect abundance in monocultures versus bicultures established under a variety of environmental conditions using crops that are attacked by a variety of insect herbivore pests with different traits (Barbosa et al., 2009). We conducted a literature search and meta-analysis to address two questions: (1) which herbivore traits, plant traits and environmental context individually influence the strength of AE (i.e. the response of insect abundance in monocultures vs. bicultures) and (2) do herbivore traits and environmental context interact to affect the strength of AE? For each of these questions, if insect abundance is reduced in bicultures, this would provide support for either the resource concentration, repellence or decoy hypotheses, whereas if insect abundance increases in bicultures this would provide support for the spillover or diet mixing hypotheses.

2 | MATERIALS AND METHODS

2.1 | Literature search

We followed general guidelines for literature searches and meta-analysis (O'Dea et al., 2021). To address our questions, we focused on crop species with at least five publications conducted in multiple geographic locations. A preliminary screening of studies suggested only a few crops were represented by enough studies from different geographic locations, so we focused our search on four crop types: *Brassica*, two cucurbits (*Cucumis* and *Cucurbita*, which were pooled as one crop type), *Gossypium* and *Allium*. Additional information regarding the literature search and meta-analysis process, including our PRISM checklist (O'Dea et al., 2021) is available as Supporting Information (see Appendix S1). A full list of data sources used in the meta-analysis is available in the Data Sources section (Table S2).

2.2 | Screening

From our list of 107 papers plus the Barbosa and Letourneau studies, we screened for inclusion based on the following criteria. First, experimental treatments included monocultures and bicultures. In some cases, studies contained treatments that had multiple neighbouring species, which we excluded. Second, experiments were conducted in the field in managed agroecosystems where insects could naturally colonize the plants. We did not include lab, mesocosm or cage experiments. Third, insect herbivore abundance on the focal species was recorded at least once in both treatments, and treatment means, variances and sample sizes were available in text, tables, figures or supplements.

2.3 | Response variables, moderators and effect sizes

Our data extraction (Appendix S1) resulted in the following variables used to calculate effect sizes: (1) mean number of insects per plant and standard deviation in monoculture, (2) mean number of insects per plant and standard deviation in bicultures and (3) number of replications. For moderators, we used the following variables: (1) diet breadth (generalist or specialists), (2) feeding guild (chewing or piercing/sucking), and (3) origin (native, non-native, globally distributed with unknown origin or unknown in cases where the pest was not reported to species) of the insect species, (4) latitude as a surrogate for climate, (5) crop type (*Allium*, *Brassica*, *curcurbit* or *Gossypium*), (6) phylogenetic relatedness of the neighbouring plant species (in the same family or not), (7) plot size (m²), (8) plot arrangement (neighbours inside or around plot) and (9) experimental design (additive or substitutive). See Appendix S1 for details regarding selection of the moderators.

For each observation, we calculated Hedge's *g* effect sizes (Hedges, 1981). Negative values indicate that the presence of neighbours reduced insect abundance or provided AR, whereas positive values indicate that neighbours increased insect abundance or caused AS. We calculated effect sizes using the 'SMD' option (i.e. standardized mean difference, also known as Hedge's *g*: Hedges, 1981) with the *esalc()* function in the *metafor* package (v3.0-2; Viechtbauer, 2010) with sampling variances estimated assuming homoscedasticity between treatment groups.

2.4 | Statistical analysis

We constructed a linear mixed effect model using *metafor::rma.mv* in R. Because most papers contained multiple observations, we included paper ID as a random effect in the model. Effect sizes were weighted by their precision (i.e. inverse variance). We first estimated a grand mean (i.e. overall mean) effect size (i.e. Hedge's *g*) that included only an intercept and the paper ID random effect. We checked for publication bias by conducting a leave-one-out simulation, calculating Kendall's

tau for funnel plot asymmetry, Rosenberg's failsafe number and visually assessing funnel plots. Additionally, we tested for differences between the three sources of studies, Barbosa et al. (2009), Letourneau et al. (2011) and our literature search.

To address our first question—which factors individually influence the strength of AE—we added each of our nine variables individually as fixed effects to our base model described above ($n = 9$ models total). To address our second question—do herbivore traits and environmental context interact to affect the strength of AE—we constructed models that contained interactions between each herbivore trait and each metric of plant traits or environmental context (Table 1). We did not address any potential interactions between plant traits and environmental context or any three-way interactions because these were not directly relevant to our questions and in many cases there were missing combinations in the data. To compare heterogeneity among groups, we used Q statistics (Cochran's Q for the intercept only random effect and Q_M statistics for fixed effects). Data were visualized using the Orchard package (Nakagawa et al., 2021) or ggplot2 (Wickham, 2010). We interpreted magnitude of effect sizes as follows: no or neutral effect <0.2 , small ≥ 0.20 , medium ≥ 0.50 and large ≥ 0.80 (Cohen, 1988).

3 | RESULTS

3.1 | Test of overall strength of AE in all studies

Our search resulted in 272 individual observations from 44 studies (Appendix S1). Overall, pooled across all crop types, insect abundance was strongly reduced in bicultures compared with monocultures (Hedge's $g = -0.773$, [95% CI: $-1.02, -0.53$], $z = -6.2$, $p < 0.0001$, $k = 272$; Appendix S3) suggesting bicultures are providing AR. There was also considerable variability among studies (Test for heterogeneity: Cochran's $Q_{271} = 615.3$, $p < 0.0001$; $I^2 = 0.627$) and the prediction intervals, which estimate the range of effect sizes possible from future studies (Nakagawa et al., 2021), were large ($-2.23, 0.69$). A sensitivity analysis revealed that no studies had a disproportionate strong effect on the parameter estimates (Appendix S3). There was, however, some evidence of publication bias based on the funnel plot and a rank correlation test for funnel plot asymmetry showed moderate asymmetry (Kendall's $\tau = -0.356$, $p < 0.0001$; Appendix S3). Nevertheless, the data passed the Rosenberg failsafe test (Failsafe $N = 8015$, average effect size = -0.37 , observed significance level < 0.0001).

3.2 | Which factors individually influence the strength of AE?

There were effects of all three insect traits on the strength of AE. Diet breadths differed in the strength of AE ($Q_M = 5.9$, $p = 0.015$). Both generalists and specialists declined in abundance in bicultures compared with monocultures although the response of generalists was

TABLE 1 Summary of statistics for models that included interactions between moderating variables and herbivore traits. Q_M is the omnibus test statistic for each interaction. The heterogeneity statistic, Q_H , which represents the residual heterogeneity among studies, was similar and highly significant for all models ($p < 0.001$). Significant or marginally significant ($p < 0.06$) interactions are in bold.

Moderator	Herbivore trait	Q_M	df	p
Crop type	Diet breadth	14.7	2	0.0006
	Feeding guild	2.7	3	0.43
	Insect origin	27.0	4	0.0001
Related neighbour	Diet breadth	20.0	1	0.0001
	Feeding guild	0.1	1	0.75
	Insect origin	23.2	2	0.0001
Plot size	Diet breadth	8.9	1	0.003
	Feeding guild	0.11	1	0.74
	Insect origin	12.7	2	0.002
Latitude (absolute value)	Diet breadth	3.7	1	0.055
	Feeding guild	6.1	1	0.010
	Insect origin	14.3	2	0.001
Plot arrangement	Diet breadth	11.9	1	0.0006
	Feeding guild	0.3	1	0.57
	Insect origin	2.2	2	0.34
Experimental design	Diet breadth	28.7	1	0.0001
	Feeding guild	0.63	1	0.43
	Insect origin	21.4	2	0.0001

Note: Interactions were tested using the 'btt=' option to specify interactions coefficients.

stronger (Figure 2a). Feeding guilds differed only slightly ($Q_M = 3.3$, $p = 0.069$), with piercing/sucking insects responding slightly stronger than chewing insects (Figure 2b). Insect origin affected the strength of AE ($Q_M = 24.1$, $p < 0.001$), with native and globally distributed pests being most strongly affected by neighbours (Figure 2c). The hedge's g effect size increased slightly with (absolute) latitude, although this was not significant ($Q_M = 1.42$, $p = 0.233$; slope = 0.01 ± 0.008 SE, Figure 2d). Bicultures with the neighbouring species planted inside the plot boundary were more effective at providing AR than when neighbouring species were planted around the perimeter (Figure 2h), although both planting schemes were still effective. Other aspects of plants or the experimental design did not significantly affect the effect size (Figure 2e–g,i). However, there were also slight, although non-significant differences, among crop types ($Q_M = 4.5$, $p = 0.21$). *Brassica* and cucurbits enjoyed AR, while there was not strong AE for *Allium* or *Gossypium* (Figure 2e).

3.3 | Do herbivore traits and environmental or experimental context interact to affect the strength of AE?

We found strong evidence that herbivore traits, specifically diet breadth and insect origin but not feeding guild, interacted with

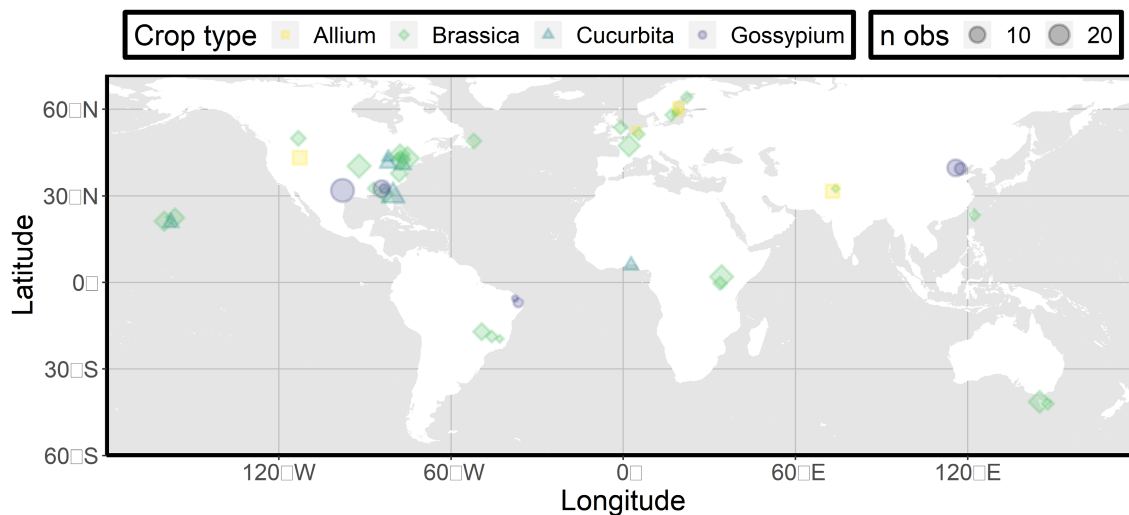


FIGURE 1 Locations of the 44 studies used in the meta-analysis mapped by crop type. Size of points represents the number of observations in the study.

several plant traits and experimental context variables to influence the strength of AE (Table 1). For diet breadth, the effect size for generalists was consistently negative across latitudes (Figure 3a), whereas the effect size for specialists increased from strong AR near the equator to neutral at high latitudes (Figure 3b). Additionally, generalists were more strongly negatively affected in bicultures when *Brassica* was the focal crop but not for other crop types (Figure 3c). Similarly, generalists were more strongly affected when the neighbour was related (within the same family), but not when the neighbour was unrelated (Figure 3d). Experiments that arranged the neighbouring plant around the perimeter of the study plots had no impact on specialist pests, although these designs reduced abundance of generalists (Figure 3e). Experiments that planted the neighbours among the focal plants equally reduced abundance of specialists and generalists (Figure 3e). Similar patterns were found for additive versus substitutive experimental designs. Substitutive design, in which focal plants are replaced by neighbours in bicultures thereby confounding density and frequency, were not effective against specialists but strongly reduced the abundance of generalists (Figure 3f). Additive designs, in which neighbouring plants are added to the same density of focal plants in bicultures thereby keeping focal plant density constant, were equally effective against generalists and specialists (Figure 3f).

For analyses with insect origin, we excluded observations where the pest species was reported above the species level (i.e. family or genus) because there was only a small number of cases ($n = 16$), which made testing interactions difficult. The effect of bicultures decreased across latitudes for globally distributed pests with unknown origin (Figure 4a), whereas they increased slightly for native (Figure 4b) and non-native (Figure 4c) pests. Globally distributed pests were most strongly negatively affected by bicultures, but only in *Brassica* and to a lesser degree in cucurbits (Figure 4d). Globally

distributed pests were also more strongly affected by bicultures than natives when the neighbouring plant was within the same family as the focal plant (Figure 4e). Experimental designs that planted neighbours among (inside the plot) the focal plant only moderately affected native pests, whereas non-native and globally distributed pests were more strongly affected (Figure 4f). Experimental designs that arranged the neighbours in a perimeter around the plots only moderately affect pest abundance regardless of origin (Figure 4f). Substitutive design, in which focal plants are replaced by neighbours in bicultures thereby confounding density and frequency, were not effective against native pests but weakly reduced the abundance of non-native pests and strongly reduced the abundance of globally distributed pests (Figure 4g). Additive designs, in which neighbouring plants are added to the same density of focal plants in bicultures thereby keeping focal plant density constant, were equally effective against pests regardless of origin (Figure 4g). There were also interactions between insect origin and plot size and between feeding guild and latitude, although these effects were very weak (Appendix S4).

4 | DISCUSSION

AE can have strong impacts on species abundances, community structure and evolutionary processes and can strongly impact crop yield in agricultural systems. However, predicting the direction and magnitude of AE has been difficult. Using a meta-analysis of agricultural experiments, we found that bicultures provided moderately strong AR when pooling across all studies (overall Hedge's g effect size: -0.77 ; 95% CI: $[-1.02, -0.53]$). These findings reinforce the use of bicultures as a tool to reduce pest abundance in agroecosystems where pest damage can reduce yield (Letourneau et al., 2011; Smith & McSorley, 2000). There was also high heterogeneity among studies,

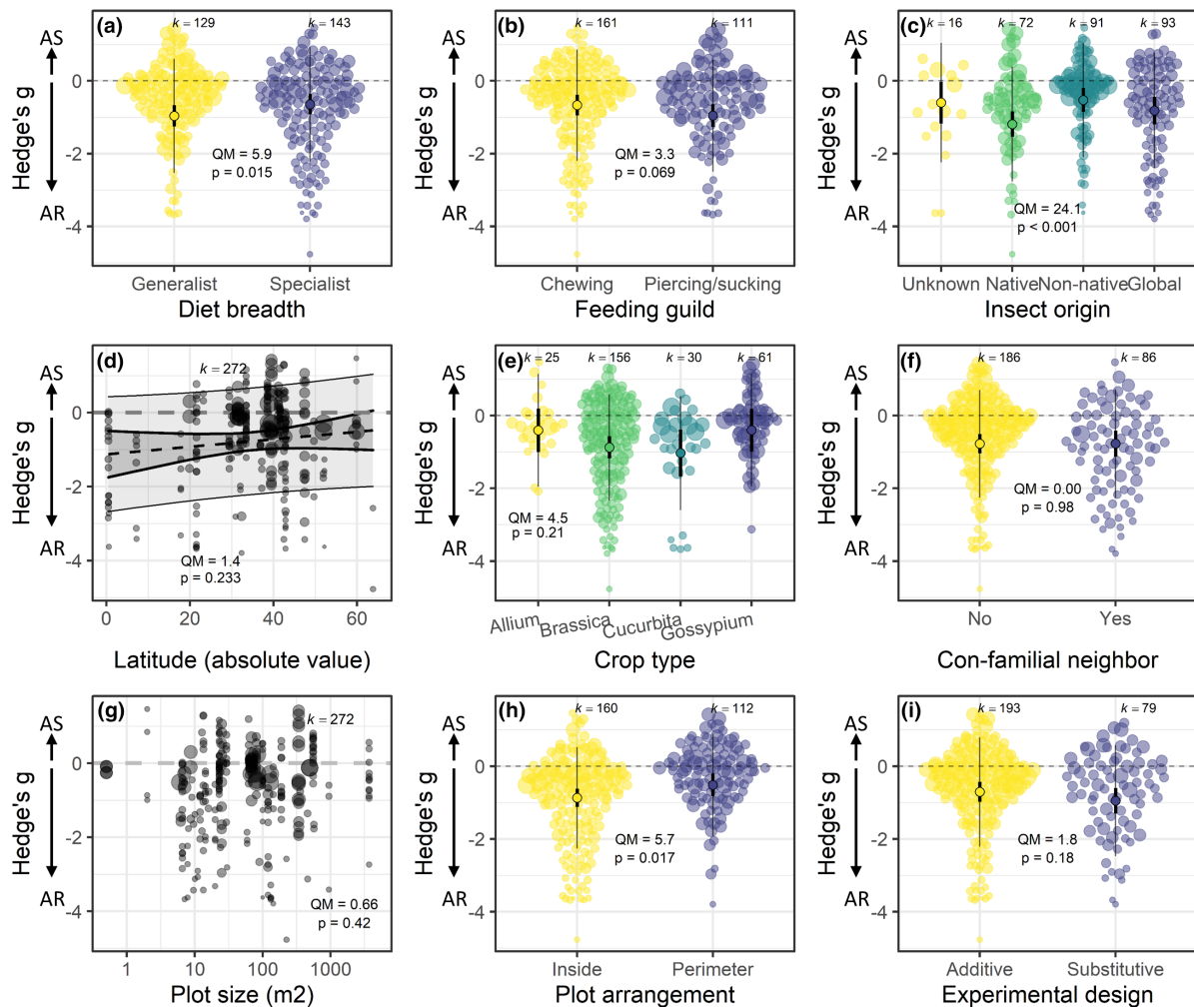


FIGURE 2 Effect size (Hedge's g) of insect abundances on a focal plant in the presence of a neighbouring plant (i.e. bicultures) versus growing in monocultures separated by different herbivore traits (a–c), plant traits (d–f) or experimental context (g–i). Large points show means. Transparent circle points show individual data points sized by study precision. Thick bars (or bands) are 95% confidence intervals and thin bars (or bands) are 95% prediction intervals (i.e. the range of expected values a new study might find). AR, associational resistance; AS, associational susceptibility.

as the prediction intervals for the overall effect size ranged from strongly negative to moderately positive ($-2.23, 0.69$; [Figure S3.2](#)), suggesting future studies may expect any outcome from AR to AS. However, we also show that the strength of AE is contingent on latitude, herbivore traits (diet breadth or origin) and aspects of the experimental design (plot arrangement or additive vs. substitutive designs), as well as interactions among these variables and plant traits (crop type or phylogenetic proximity to the neighbour). We focused specifically on crops that are well represented across the globe and grown in different climates. While this allowed us to test unique factors, such as latitude, crop type and interactions, it did limit the scope from examining all possible studies with monocultures versus bicultures. However, our focused approach allowed us to make more ecologically useful comparisons and also compare our results with other similar system-specific meta-analyses (see below for comparisons with Castagneyrol et al., 2014; Jactel et al., 2021). Although we did find some evidence of publication bias (see [Appendix S3](#)), our

focused meta-analysis provides insight into several key mechanisms that generally regulate the strength of AE and provides several key insights for improving the efficacy of bicultures in crop diversification schemes, which we discuss below.

Our meta-analysis revealed that latitude (a surrogate of climate; [Appendix S1](#)) was important for mediating the strength of AE, although the strength of this effect depended on insect traits. We show overall that the benefits of bicultures (i.e. AR) were greatest at low-latitude locations and the effect size tended to decrease in strength slightly with increasing latitude ([Figure 2d](#)). This effect was strongest for specialist herbivores ([Figure 3b](#)), piercing-sucking herbivores ([Figure S4.1](#)), and for native insects ([Figure 4b](#)). Changes in pest pressure associated with latitude is one potential explanation for this finding. For example, at lower-latitude sites, with warmer and less variable climates, abundance and diversity of pest species, particularly specialists, tends to be greater (Salazar & Marquis, 2012). Increased pest pressure and/or diversity may increase the likelihood

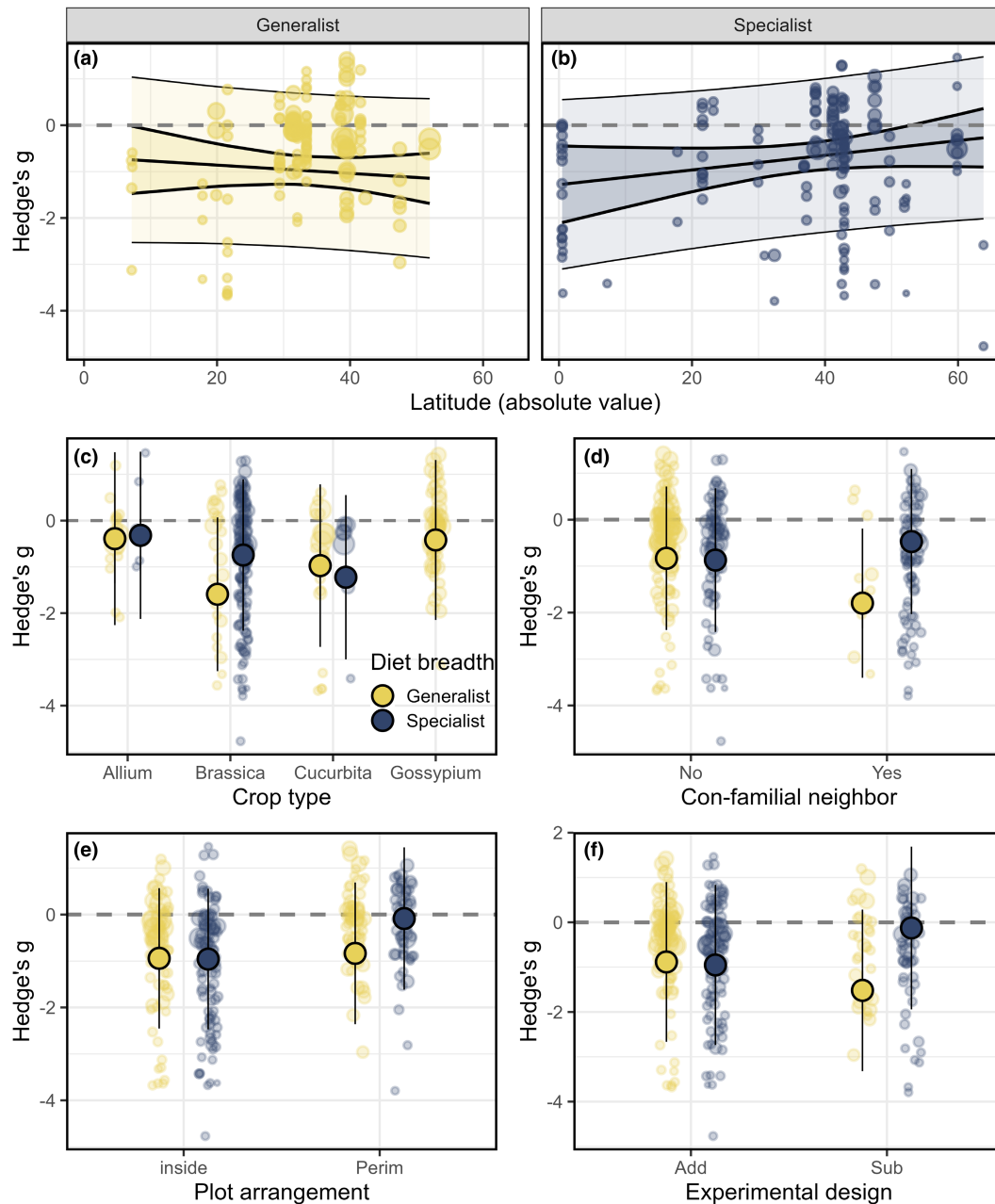


FIGURE 3 Effect size (Hedge's g) of insect abundances on a focal plant in the presence of a neighbouring plant (i.e. bicultures) versus growing in monocultures separated by diet breadth (in a) generalist versus (b) specialist across latitude and (c) crop type, (d) whether the neighbour is in the same family as the focal plant, (e) arrangement of the neighbouring plant relative to the focal plant and (f) experimental design where neighbours were either added to the focal plants keeping density constant or substituting some focal plant with neighbours thereby confounding density and frequency. Large points show means; thick bars are 95% confidence intervals; thin bars are 95% prediction intervals; transparent circle points show individual data points sized by study precision.

of AR occurring either through a sampling effect (i.e. increased probability of an insect species that is particularly susceptible to the influence of a neighbouring plant), similar responses of multiple herbivore species to neighbouring plants or both. In a laboratory study, the strength of AE increased with increasing herbivore abundance, at least up to a point until herbivores overwhelmed the ability of neighbours to provide AE (Merwin et al., 2017). Although we do not know the exact mechanism, our meta-analysis, which focused on four crops well represented across the globe (Figure 1), revealed

interesting patterns regarding how the strength of AE changes across environmental gradients that deserve continued investigation.

We found that herbivore traits, specifically diet breadth and origin but not feeding guild, interacted with several factors to mediate the strength of AE. Unrelated neighbours provided AR equally against all pests regardless of diet breadth (Figure 3d) or origin (Figure 4e), which is consistent with the 'repellent' hypothesis. The use of unpalatable, aromatic neighbouring crops are often used in polyculture systems (Finch et al., 2003; Smith & McSorley, 2000), so this finding may reflect

that the neighbouring plants are specifically selected to act as repellent plants. For example, one study in our meta-analysis found strong AR on the abundance of cabbage aphids when spring onions (*Allium cepa*) were intercropped with *Brassica* (Mutiga et al., 2010). Another potential explanation for this finding is that very distantly related plant species may share very few herbivores, regardless of their diet breadth or origin, and thus work to 'repel' each other's pests. For example, studies that intercropped species from distantly related families, such as

mustards or cucurbits intercropped with legumes (Broad et al., 2008), grasses (Pitan & Filani, 2014), mustards and solanaceous plants (Le Guigo et al., 2012), tended to result in very strong AR. However, when neighbours were closely related to the focal plant, the results differed among diet breadth guilds and origins. Generalist herbivores were most strongly negatively affected by a related neighbour, whereas specialist herbivores were not as strongly affected by neighbours (Figure 3d). Related neighbours that were more palatable than the focal plant

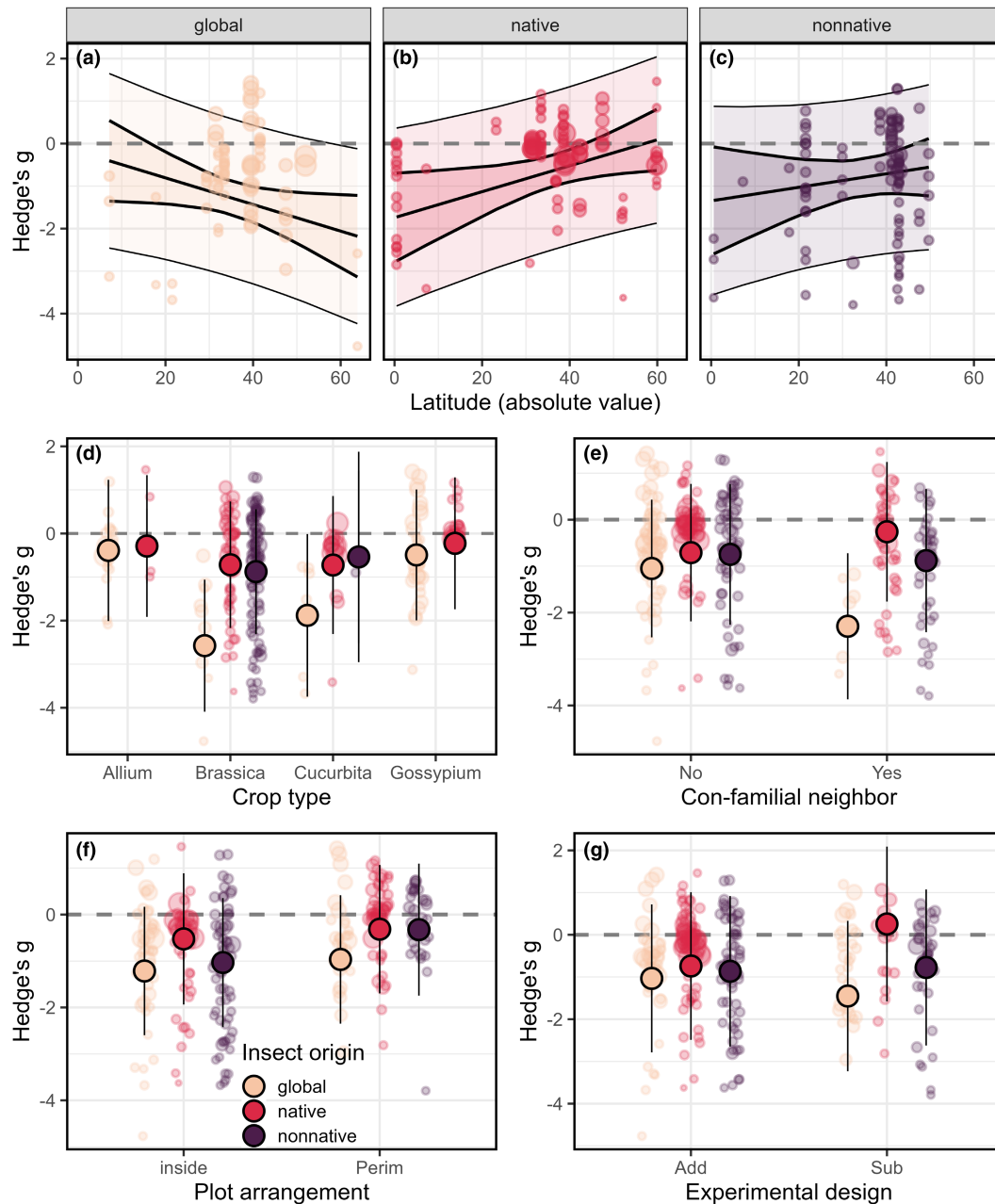


FIGURE 4 Effect size (Hedge's g) of insect abundances on a focal plant in the presence of a neighbouring plant (i.e. bicultures) versus growing in monocultures separated by insect origin across latitude in (a) native, (b) non-native or (c) unknown and by (d) crop type, (e) whether the neighbour is in the same family as the focal plant, (f) arrangement of the neighbouring plant relative to the focal plant and (g) experimental design where neighbours were either added to the focal plants keeping density constant or substituting some focal plant with neighbours thereby confounding density and frequency. Note that pests that were only identified above the species level are not shown due to only a small number of these studies in the database. Large points show means; thick bars are 95% confidence intervals; thin bars are 95% prediction intervals; transparent circle points show individual data points sized by study precision.

may have acted as attractant-decoy plants particularly to generalists (Figure 3d). For example, studies that used trap crops aimed at attracting (and trapping) insects appear to be most beneficial against generalists with related neighbours (Bohinc & Trdan, 2012; Wallingford et al., 2013) but less effective against specialists, although these cases were represented by only a few effect sizes (Figure 3d). Similarly, globally distributed pests with unknown origins, and to a lesser degree non-native pests, were strongly negatively affected by related neighbours, whereas native pests were not impacted (Figure 4e). Although it is less clear what may be driving differences between insects with different origin status, mechanisms similar to diet breadth may apply.

Our findings for how diet breadth and phylogenetic distance of the neighbouring plant affect the strength of AR differ somewhat from three previous meta-analyses. Castagneyrol et al. (2014) and Jactel et al. (2021), meta-analyses on studies conducted in forested ecosystems, only found AR to generalists when the neighbouring plants were distantly related, whereas we found strong AR to generalists when neighbouring plants were within the same family (Figure 3d). Unrelated neighbours in forested systems typically are conifers and broadleaved trees, which may have repelled each other's generalist herbivores and represent a much larger phylogenetic distance than examples in our studies (Castagneyrol et al., 2014; Jactel et al., 2021). The broader Barbosa et al. (2009) meta-analysis focused on both natural and managed systems, including agricultural and forestry systems, which perhaps obscured patterns due to opposing findings regarding phylogenetic relatedness and diet breadth in different systems. It is important to reiterate that all three previous meta-analyses, as well as ours, found strong AR overall, but that the strength of AE are highly variable and context-dependent. Collectively, these findings suggest that generalists may be more strongly influenced by neighbours than specialist insects (Figures 2a and 3), at least in forested and agricultural systems, but habitat-specific differences between forests and agricultural systems are also important for determining specifically how these interactions play out. On the other hand, the effect of feeding guild (chewers vs. piercing-sucking) was consistently negative and did not vary with other factors (Table 1).

The definition of AE requires that insect abundance (or damage) is affected by changes in focal plant frequency (Underwood et al., 2014). One strength of our meta-analysis is that most of the studies held focal plant density constant while manipulating the presence/absence of a neighbouring plant using additive designs, although several studies used substitutive designs that confound density and frequency (195 vs. 79 effect sizes, respectively). While we did not find any overall differences between additive and substitutive designs (Figure 2i), we again found interactive effects between experimental design and herbivore diet breadth and origin (Table 1), which may provide insight into the degree of density- versus frequency dependence based on herbivore traits. For generalists, the strength of AR was stronger for substitutive than additive designs. Additive designs equally reduced the abundance regardless of both diet breadth (Figure 3d) or origin (Figure 4e). For substitutive

experiments, generalists experience strong AR, whereas specialists are not affected by neighbours (Figure 3f). Similarly, globally distributed pests with unknown origin also experience strong AR, and to a less degree non-native pests, whereas native herbivores are unaffected by neighbours (Figure 4g). Thus, these findings that generalists and globally distributed pests are more strongly influenced by substitutive designs may suggest that generalists are more affected by plant frequency, whereas specialists and native pests may be more affected by plant density.

5 | CONCLUSIONS

Our meta-analysis reinforces the use of bicultures as a pest management tool (Huss et al., 2022), although with several contingencies. Most agricultural crops have well-resolved relationships between pest abundance and damage levels that are used as 'economic thresholds' for when to apply management action (Oerke, 2006; Pedigo et al., 1986). While our meta-analysis clearly shows strong benefits of neighbouring plants in reducing pest abundance, the variability we found suggests incorporating AE into economic decision-making tools, such as economic thresholds, will require site- and crop-specific information. For example, only two of our four focal crops strongly benefitted from pest reduction in bicultures (*Brassica* and cucurbits; Figure 2e). Techniques where the neighbouring plant was planted within the plot boundaries were more effective than neighbours planted around the perimeter of the focal crop (Figure 2h). Plot size did not affect the strength of AE (Figure 2g), suggesting that the benefits of bicultures are scalable at least given the contingencies described above. Our use of herbivore traits and phylogenetic distance of the neighbouring plants provides a generalizable framework that may aid in decision-making for assessing the potential ecological-economic trade-offs of crop diversification.

AUTHOR CONTRIBUTIONS

Philip G. Hahn conceived the ideas, designed methodology, analysed data and wrote the manuscript. Joseph H. Cammarano designed methodology, collected data and edited the manuscript. Both authors gave final approval for publication.

ACKNOWLEDGEMENTS

We thank J. Kaur, M. Kuhlman, E. Calixto, B. Inouye and N. Underwood for helpful discussions and comments. Funding was provided by NSF DEB-1901552 and McIntire-Stennis FLA-ENY-006018 to PGH.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.rm8pk0pgq> (Hahn & Cammarano, 2023).

ORCID

Philip G. Hahn  <https://orcid.org/0000-0001-9717-9489>

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How to cite this article: Hahn, P. G., & Cammarano, J. H. (2023). Environmental context and herbivore traits mediate the strength of associational effects in a meta-analysis of crop diversity. *Journal of Applied Ecology*, 60, 875–885. <https://doi.org/10.1111/1365-2664.14382>