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Population responses of omnivorous arthropods to plant alternative resources suppress prey populations: A meta-analysis

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Abstract

Omnivory is ubiquitous in ecological communities. Yet, we lack a consensus of how plant alternative resources impact the ability of omnivores to suppress prey populations. Previous work suggests that plant alternative resources can increase, decrease, or have no effect on the magnitude of omnivore−prey interactions. This discrepancy may arise from (1) the ability of omnivore populations to respond to plant alternative resources and (2) identity-specific effects of plant alternative resources. We used a meta-analysis to examine how omnivore population responses and the identity of plant alternative resources affect (1) omnivore predation rates (mainly reported as per capita predation rate) and (2) omnivore impacts on prey population density. Plant alternative resources reduced omnivore predation rate regardless of identity. The suppression of the predation rate by flowers and flowering plants was magnified when pollen alone was tested as the alternative resource. Surprisingly, plant alternative resource availability reduced prey density, suggesting that omnivore predation increased with plant alternative resources. This discrepancy (plant alternative resources not only decreased omnivore predation rates but also decreased prey density) resulted from experimental differences in the ability of omnivore populations to respond to plant alternative resources. In the presence of plant alternative resources, allowing omnivore population responses decreased prey density, while not allowing population responses increased prey density. Because omnivores commonly suppress prey density in the presence of plant alternative resources when population responses of omnivores are allowed, the effectiveness of biological control may depend upon the availability of such resources and the facilitation of population responses.

KEYWORDS
apparent competition, biological control, consumptive effects, diet mixing, food webs, population response, plant-provided foods, tritrophic signaling

INTRODUCTION

Omnivory is a common feeding strategy across multiple taxa (e.g., insects, birds, mammals, and fishes; Coll & Guershon, 2002; Eubanks et al., 2003; Polis & Strong, 1996) that can impact the structure and function of communities (Bruno & O'Connor, 2005; Polis & Strong, 1996). Omnivore impacts on prey can be determined by the availability of

alternative resources from plants (Eubanks & Denno, 2000; Janssen et al., 2003; Maselou et al., 2014; Mollot et al., 2012). Such resources can provide opportunities for diet mixing, predator refuges, and sites for mating aggregations (Hossain et al., 2002; Rinehart & Long, 2018, 2019). Although there is general agreement that plant alternative resources affect predation by omnivores, there is disagreement about the direction of these impacts on prey (Eubanks & Denno, 2000; Janssen et al., 2003; Maselou et al., 2014; Mollot et al., 2012). This discrepancy may result from experimental differences in the ability of omnivore populations to respond to plant alternative resources and the identity of plant alternative resources (e.g., pollen vs. seeds; Coll & Guershon, 2002; Cottrell & Yeargan, 1998; Eubanks & Denno, 1999; Musser & Shelton, 2003). Resolving this discrepancy may help identify when and where omnivores exert strong top-down control on their prey.

The indirect effects of plant alternative resources on prey populations via omnivores should depend on population responses of omnivores. On a per capita basis, omnivores may reduce predation as they include such resources in their diets. Although such decreases in predation rate could lead to higher prey densities, this may not be the case if omnivores display positive population responses to alternative resources that overwhelm per capita reductions in predation rate (Eubanks & Denno, 2000). Such aggregational and reproductive responses to plant alternative resources commonly occur for omnivores. For example, seaside ladybeetles (*Naemia seriata*) preferentially aggregate to habitat patches containing both cordgrass flowers and prey relative to patches containing prey alone (Rinehart & Long, 2018, 2019). Similarly, big-eyed bugs (*Geocoris punctipes*) numerically respond to bean pods, and thereby more strongly suppress lima bean pests (Eubanks & Denno, 1999, 2000). Given the potential for population responses to regulate the impact of omnivores on prey populations, there is a need to compare the impacts of alternative resources on omnivores in the presence and absence of such population responses.

In addition to population responses of omnivores, the identity of plant alternative resources may control their impact on omnivore−prey interactions. Identity-specific impacts of alternate resources may occur if plant alternative resources differ in nutritional quality (Calabuig et al., 2018; Coll & Guershon, 2002), defenses (Weiser & Stamp, 1998), or habitat/refuge quality (Hossain et al., 2002). For example, plant alternative resources with high protein content (cattail pollen) suppressed predation rates of phytoseiid mites on prey more than plant alternative resources with low protein content (pine pollen; Calabuig et al., 2018). Distinct types of plant alternative resources may also differ in the quantity of refuge habitat provided to omnivores, leading to differential survival over

winter and during disturbance events (Dennis et al., 1994; Griffiths et al., 2008; Liman et al., 2016). In addition to the effects on omnivores, plant alternative resources of different identities may affect the behavior of animal prey if they provide valuable food resources or refuge habitat from predation (Stephan et al., 2017). Regardless of the mechanism, the impact of these resources on predation by omnivores may be specific to plant resource identity.

Here, we conducted a meta-analysis testing how the ability of omnivore populations to respond to plant alternative resources and the identity of these resources influences omnivore− prey interactions. We analyzed data from 37 publications reporting the effects of plant alternative resources on (1) omnivore predation rates (measure mainly as per capita predation rate) or (2) prey population density (in the presence of omnivores). We focused our analysis on studies of omnivorous terrestrial arthropods because most research focused on this taxon. We hypothesized that (1) plant alternative resources reduce omnivore per capita predation rates on prey, and (2) plant alternative resources reduce prey density when population responses are allowed. We also explored how omnivore impacts on prey density were influenced by the identity of plant alternative resources, omnivore taxon, experimental duration, and experimental spatial scale.

METHODS

Literature survey

We surveyed the literature using Google Scholar and the following search terms: ("omnivore") AND ("consumptive effects" OR "herbivore interactions" OR "alternative resources" OR "plant-provided foods" OR "non-prey foods" OR "pollen" OR "flowers"). The original search yielded 7030 results; however, Google Scholar limits the number of visible results to 1000 per search. To get around this, we searched each set of terms separately (e.g., "omnivore" AND "consumptive effects"; "omnivore" AND "herbivore interactions") and extracted up to 1000 of the most relevant papers for each set of search terms (Figure 1). This allowed us to obtain a total of 2985 potential manuscripts (2363 potential manuscripts after duplicate removal). We excluded any modeling studies and reviews/syntheses. Additionally, we included unpublished theses if no published manuscript containing the same data was available. The search was conducted on 24 October 2019. We used the preferred reporting practices outlined by preferred reporting items for systematic reviews and meta-analyses (PRISMA) to structure our overall literature search (Moher et al., 2009). For each potential manuscript, we read the title and abstract to determine if the study tested the

interactions between plant alternative resources and omnivorous terrestrial arthropods. Our initial goal was to include omnivores of all taxa; however, we obtained few (<5) manuscripts using non-terrestrial arthropod omnivores (e.g., gastropods) and thus we chose to focus only on terrestrial arthropods for this review. This screening yielded 426 papers that we read in full to determine if they were eligible for inclusion in our meta-analysis (see Figure 1). Studies were deemed eligible if they included direct (i.e., not simulated or modeled) measurements of omnivore top-down effects in the presence and absence of plant alternative resources. We targeted manuscripts that measured the effects of plant alternative resources on: (1) omnivore prey consumption and (2) prey density (in the presence of omnivorous predators). We focused on these two response variables because they were most consistently used by authors. Hereafter, these datasets will be referred to as the "animal prey consumption" and "prey density" datasets, respectively. Using these criteria, we identified 267 individual studies from 37 papers to include in our analysis (Figure 1). Most of the excluded studies tested the effects of plant alternative resources on omnivore performance (e.g., survival, fecundity, and body condition; see for example Eubanks & Denno, 1999; Rinehart & Long, 2018).

Most animal prey consumption studies quantified per capita predation rate of omnivores on animal prey in the presence and absence of plant alternative resources (161/196 studies or 82%; sensu Eubanks & Denno, 2000). We also included studies in our prey consumption analysis that reported (1) total predation rate for a known
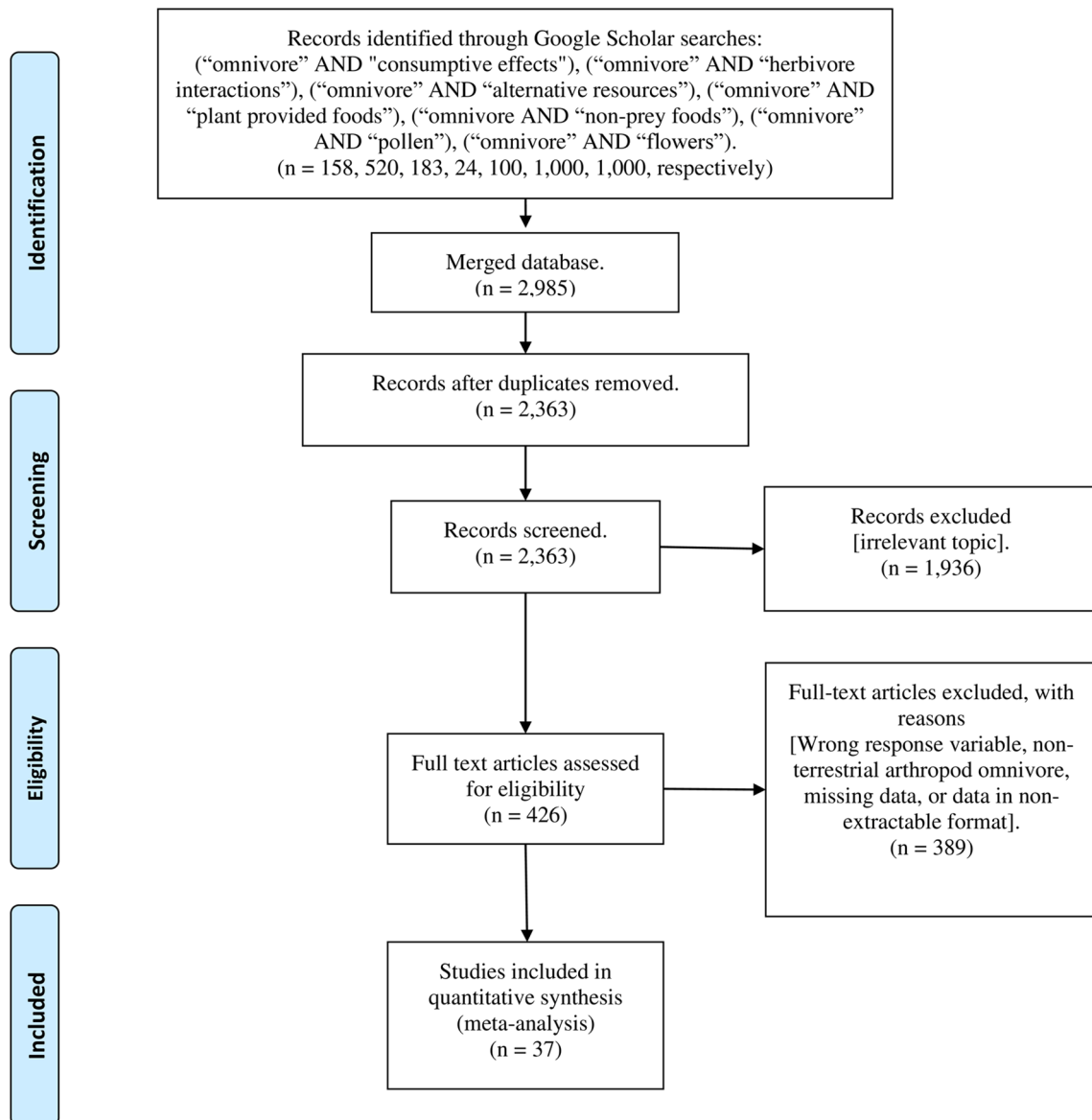
FIGURE 1 The PRISMA flow chart showing the workflow of manuscript and study selection

number of omnivores (sensu Calabuig et al., 2018) or (2) total predation rate for an unknown number of wild omnivores (sensu Rinehart & Long, 2019).

Studies of the impacts of extrafloral nectaries on predation by ants were rare in our literature search. We identified at least three explanations for this pattern. First, most of these studies were not included because they either failed to manipulate nectaries (e.g., Lange & Del-Claro, 2014; Oliveira et al., 1999; Rosumek et al., 2009; Stephenson, 1982) or they did not quantify the effects of nectaries on prey consumption/density (Bentley, 1976; Koptur et al., 2015; Kost & Heil, 2005; McLain, 1983; Rezende et al., 2014). There have also been three extensive meta-analyses evaluating the impacts of ants on herbivory and plant performance in the presence/absence of ants (see Chamberlain & Holland, 2009; Rosumek et al., 2009; Trager et al., 2010). Second, some studies were not included because they used system-specific terminology (e.g., ant−herbivore or ant−plant interactions). Regardless, extrafloral nectaries appear to have similar impacts on predation by ants as other plant alternative resources have on other omnivores. For example, when extrafloral nectaries are manipulated, they commonly decrease prey density when ants can exhibit population-level responses (Mathews et al., 2007, 2009, 2011), a finding consistent with one of our major conclusions.

Data collection

From each paper, we collected data on omnivore prey consumption and prey density in the presence and absence of plant alternative resources (Rinehart & Long, 2021). We extracted data from tables, text, and figures (using Web Plot Digitizer to extract data from figures; Rohatgi, 2015). For each relevant study, we extracted the sample size, mean, and variance (standard error or standard deviation). Because the mean was not reported for one manuscript (Robinson et al., 2008), we extracted the sample size, minimum, first quartile, median, third quartile, and maximum values of prey consumption for this study. We used this information to estimate the means and standard deviations for this manuscript's studies ($n = 3$; sensu Wan et al., 2014).

If manuscripts contained multiple relevant independent studies, we extracted each individual study. Several of the manuscripts that measured omnivore impacts on prey density recorded it across multiple, non-independent timepoints (e.g., repeated measures or time series data). For these studies, we extracted the final timepoint of the dataset for each relevant study. We chose to use the final timepoint, rather than using the average across timepoints for three

reasons. First, the final timepoint was the most comparable timepoint across all manuscripts because it was the only timepoint provided in 65% of the manuscripts and 85% of the individual studies included in our dataset. Second, almost every study in the animal prey consumption dataset provided only the final timepoint (except Choate & Lundgren, 2013). Third, we found no effect of timepoint (final vs. time-averaged) on our interpretation of plant alternative resource effects on prey density (see Appendix S1). This suggests that despite temporal variation in these data, the final timepoint is representative of the overall effect of plant alternative resources on prey density.

For each extracted study, we also recorded the (1) plant alternative resource identity (pollen, flowers, flowering plants, or seeds and pods), (2) ability of omnivores to display population responses, (3) temporal scale (i.e., days run), (4) experimental spatial scale [i.e., replicate size (m^2 or m^3)], and (5) omnivore taxon. Omnivores were able to display population responses if the experiment (1) allowed omnivorous predators born outside of the experimental area to freely immigrate into the experimental area (i.e., no barriers to omnivore dispersal, such as cages) and (2) contained >1 individual of the omnivore species of mixed/undetermined sex or introduced gravid females and allowed offspring to develop to predatory stages, where they can actively consume animal prey (i.e., the study did not remove eggs or larvae and ran long enough for development to occur, see Rinehart & Long, 2021).

Meta-analyses for effects of plant alternative resources on prey consumption and density

We conducted our meta-analysis using O$_{pen}$MEE software (Build date: 26 July 2016; Wallace et al., 2017). We used both the Hedges' d and the log response ratio (hereafter, d and LRR, respectively) to compare the effects of plant alternative resources (present/absent) on omnivore prey consumption and prey density (Hedges, 1981). We used these two measures of effect size to increase the robustness of our analysis because d is sensitive to differences in sample standard deviation and LRR can be biased by studies with small sample sizes (Lajeunesse & Forbes, 2003; Osenberg et al., 1997). For both effect sizes, a positive effect size indicates that plant alternative resources increased the response variable, while a negative effect size indicates that plant alternative resources decreased the response variable. The effect sizes of animal prey consumption and prey density should be inversely correlated, with negative effects on animal prey consumption manifesting positive effects on prey density.

We used separate meta-analyses (random-effect models with a DerSimonian and Laird's approach) to

determine the overall effect of plant alternative resources on omnivore prey consumption and prey density. To minimize the effects of small sample sizes, we excluded covariates (e.g., plant alternative resource identities) supported by less than three separate papers and five individual studies (sensu Rinehart & Hawlena, 2020). A synthesis of ecological meta-analyses suggested that a set of three papers is the minimum number of separate papers that should be included (Koricheva & Gurevitch, 2014).

Meta-regressions for the consequences of experimental methodology on the effect of plant alternative resources on prey consumption and density

We used meta-regressions (random-effect models with a restricted maximum likelihood approach) to understand the influence of our extracted covariates (e.g., plant alternative resource identity, the ability of omnivores to display population responses, experimental duration, experimental spatial scale, and omnivore taxonomy) on the effect of plant alternative resources on animal prey consumption and prey density. For the experimental spatial scale, we ran separate analyses for studies reporting experimental area and experimental volume. We considered extracted covariates eligible for meta-regressions if each subgroup in the analysis (e.g., pollen vs. flowering plants for plant alternative resource identity) was supported by at least three separate papers (sensu Rinehart & Hawlena, 2020).

Dataset variability, publication bias, and validation

For all meta-analyses and meta-regressions, we tested the heterogeneity of our dataset by calculating both Q (total heterogeneity) and I^2 (heterogeneity due to between-study variance). We tested for potential publication bias by calculating Kendall's Rank Correlations (T_b) between effect size and pooled variance within each dataset (Begg & Mazumdar, 1994). If potential bias was detected (T_b with $p < 0.05$), we used funnel plots to visually identify potential outliers (Begg & Mazumdar, 1994; Palmer, 1999). Additionally, we calculated Rosenthal's fail-safe number, N_{fs}, for all significant tests (Rosenberg, 2005; Rosenthal, 1979). Rosenthal's fail-safe number predicts the number of additional studies with neutral effect sizes (effect size = 0) that would need to be added to the dataset to lose significance. We calculated fail-safe numbers for all significant meta-analyses and classified fail-safe analyses as robust if they were $>5n + 10$, where n is the number of studies for a given response variable (Rosenberg, 2005).

To further validate the robustness of our conclusions, we ran a separate analysis using only five manuscripts (hereafter, subset dataset) that quantified both omnivore prey consumption ($n = 14$ individual studies) and prey density ($n = 26$ individual studies). Specifically, we ran meta-analyses and meta-regressions to compare the outcomes of the full meta-analysis and the subset dataset for each response variable, as well as the impact of omnivore population responses. We were unable to evaluate the effects of population responses on prey consumption in these five manuscripts due to low sample size ($n = 1$ individual study). Our goal with this analysis was to validate that our findings in the broader meta-analysis are supported by studies that empirically evaluated these same relationships between prey consumption and prey density.

RESULTS

All but one of the papers used in our dataset examined agroecosystems (the exception was a single manuscript with two studies that focused on salt marshes; Rinehart & Long, 2019; 2021). Insecta was the most studied terrestrial arthropod omnivore taxon (74% of the full dataset; Rinehart & Long, 2021). Most studies used distinct species as both omnivore and animal prey; however, one study (Calabuig et al., 2018) looked at the effects of plant alternative resources on cannibalistic interactions between adult and larval Arachnida.

Effect of plant alternative resources on prey consumption

Of the 37 papers included in our full dataset, 24 manuscripts containing 196 studies examined the effects of plant alternative resources on animal prey consumption (Rinehart & Long, 2021). Plant alternative resources decreased omnivore prey consumption (Figure 2; Appendix S2: Table S1). This finding was supported by robust fail-safe calculations (Appendix S2: Table S2). We also observed high between-study variation (e.g., I^2 accounted for ~86%–95% of the between-study heterogeneity; Higgins et al., 2003; Appendix S2: Table S1).
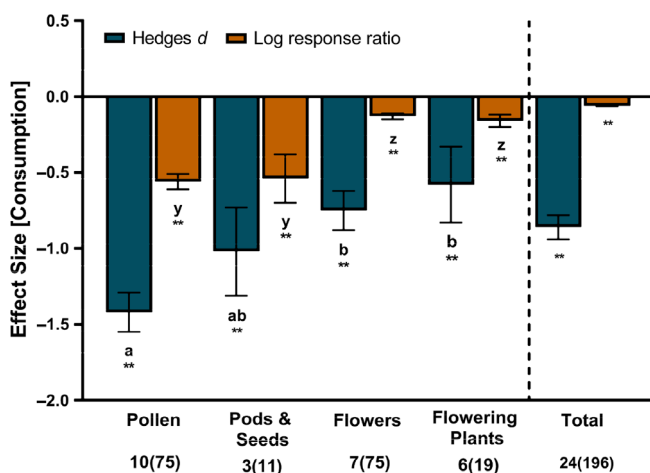
Although all plant alternative resources reduced predation by omnivores, the strength of this effect was identity-specific (d: $p = 0.001$; LRR: $p \leq 0.001$; Figure 2; Appendix S2: Table S3). Pollen and pods/seeds reduced omnivore prey consumption more than flowers or flowering plants (Appendix S2: Table S1). Flowers (whole flowers cut from stems) and pollen were the most abundant alternative resources in the prey consumption

dataset, each comprising 38% of the included studies (Rinehart & Long, 2021). We had to exclude somatic plant alternative resources from our analysis because only two papers, rather than the required three, used either non-reproductive plants or leaves (Rinehart & Long, 2021).

Effect of plant alternative resources on prey density

Because plant alternative resources decreased omnivore prey consumption, we predicted that plant alternative resources should increase prey density. Our search found 18 papers and 71 total studies of the effect of plant alternative resources on prey density in the presence of omnivorous predators (Rinehart & Long, 2021). In contrast to our prediction, plant alternative resources decreased prey density (Figure 3; Appendix S2: Table S1), suggesting that omnivorous predator populations consume more prey when plant alternative resources are available. This finding was supported by robust fail-safe calculations (Appendix S2: Table S2). Flowering plants and pollen were the main alternative resources in the prey density dataset, comprising 45% and 44% of the included studies, respectively (Rinehart & Long, 2021).

FIGURE 2   Mean (±SE) Hedges' *d* and log response ratio effect sizes for the impacts of plant alternative resources on prey consumption (mainly reported as per capita consumption) by omnivores. Negative effect sizes represent declines in omnivore prey consumption in the presence of plant alternative resources, while positive effect sizes would represent increases in omnivore prey consumption in the presence of plant alternative resources. For this figure, we only included plant alternative resources that had three or more comparisons. A double asterisk indicates an effect size significantly different from zero at $\alpha = 0.05$. Different letters represent significant differences between plant alternative resource identities within a given effect size calculation. Numbers below the x-axis labels represent the sample size with the number of manuscripts followed by the number of individual comparisons in parentheses

The remaining studies used flowers and pods/seeds; however, these alternative resources had to be excluded from our analysis due to their limited sample size (i.e., <3 papers or <5 studies). Alternative resource identity did not affect how alternative resources influence prey density (Figure 3; Appendix S2: Table S3). Between-study variation accounted for 79%–88% of the true heterogeneity (Appendix S2: Table S1).

Effects of experimental duration, spatial scale, and omnivore taxonomy

Studies testing the effects of alternative resources on prey density lasted 17 times longer than prey consumption studies (38.7 ± 3.8 days vs. 2.2 ± 0.5 days, respectively; mean ± SE; Rinehart & Long, 2021), but experimental duration ultimately did not influence omnivore prey consumption or prey density (Appendix S3: Table S1). The effect of alternative resources on prey consumption by omnivores depends upon omnivore taxa (*d*: $p < 0.001$; LRR: $p = 0.005$). Specifically, alternative resources decreased prey consumption by Arachnida more so than it did prey consumption by Insecta (Appendix S3: Table S2 and Table S3). In contrast, the effect of alternative resources on prey density did not depend upon omnivore taxa (Appendix S3: Table S2).

The area and volume of the experimental replicates did not influence the effect of alternative resources on omnivore prey consumption (Appendix S3: Table S4). However, studies with larger experimental replicates [area (m^2) and volume (m^3)] resulted in greater suppression of prey density than studies conducted in smaller experimental replicates. This effect was present in our *d* analysis for studies reporting experimental size as area ($p < 0.001$) and volume ($p < 0.001$), as well as our LRR analysis of volume ($p < 0.001$; Appendix S3: Table S4). We found no effect of arena area in our LRR analysis ($p = 0.871$). Insignificance in the LRR analysis of the arena area is not surprising, since our sample sizes were relatively small ($n = 14$ studies) and LRR can be inaccurate for analyses with small sample sizes (Lajeunesse & Forbes, 2003; Osenberg et al., 1997).

Effect of population responses

Most studies on the impacts of alternative resources on omnivore consumption of prey (98% of studies) prevented omnivore population responses. In fact, only four studies, in three papers, allowed for population responses to occur. While this is a small sample size, we chose to proceed with a meta-regression to explore the possible effects of population responses on the impacts of alternative
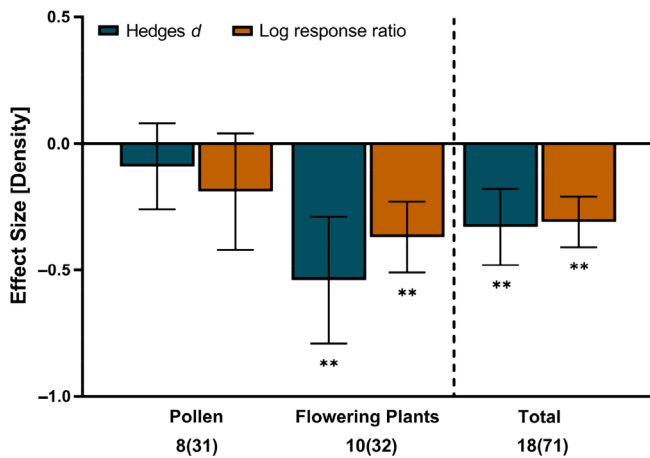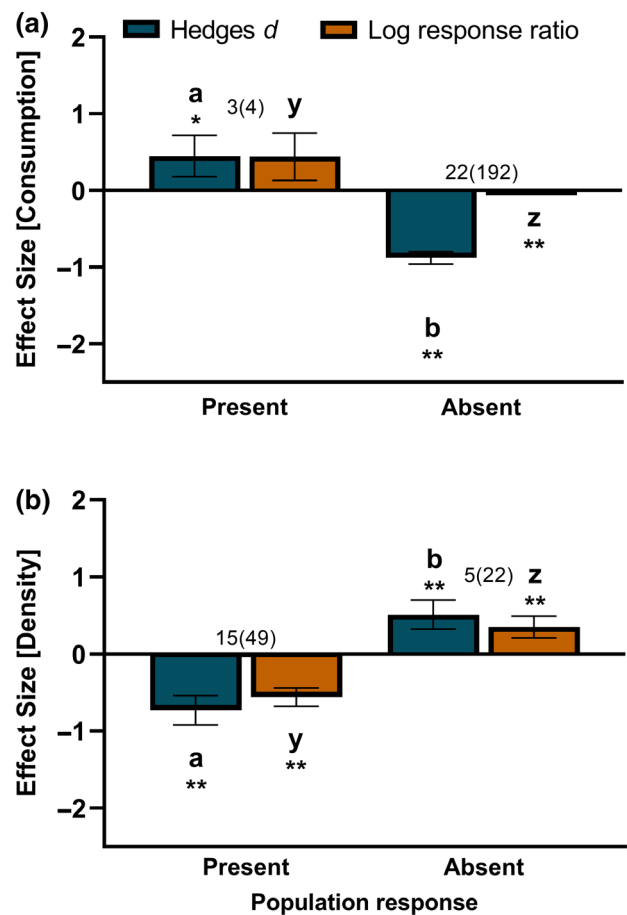
FIGURE 3 Mean (±SE) Hedges' d and log response ratio effect sizes for the impacts of plant alternative resources on prey density in the presence of omnivorous predators. Negative effect sizes suggest that plant alternative resources decrease prey density (i.e., increased predation pressure), while positive effect sizes suggest that plant alternative resources increase prey density (i.e., decreased predation pressure). For this figure, we only included plant alternative resources that had three or more comparisons. A double asterisk indicates an effect size significantly different from zero at $\alpha = 0.05$. Numbers below the x-axis label represent the sample size with the number of manuscripts, followed by the number of individual comparisons in parentheses. We observed no differences between plant alternative resource identities

FIGURE 4 Mean (±SE) Hedges' d and log response ratio effect sizes for the impacts of plant alternative resources on (a) prey consumption and (b) prey density when omnivore population responses are present and absent. For prey consumption, negative effect sizes suggest that plant alternative resources decrease prey consumption, while positive effect sizes suggest that plant alternative resources increase prey consumption. However, for prey density, negative effect sizes suggest that plant alternative resources decrease prey density (thus, increasing omnivore prey consumption), while positive effect sizes suggest that plant alternative resources increase prey density (thus, decreasing omnivore prey consumption). A single asterisk indicates an effect size significantly different from zero at $\alpha = 0.10$ and a double asterisk indicates an effect size significantly different from zero at $\alpha = 0.05$. Different letters represent significant differences between population response treatments within a given effect size calculation. The numbers above bars represent the sample size with the number of manuscripts followed by the number of individual comparisons in parentheses [Correction statement added on 18 April 2022 after first publication. The x-axis label of Figure 4 has been corrected in this version.]

resources on omnivore prey consumption. Omnivore population responses mediated the impact of alternative resources on omnivore prey consumption (d: $p = 0.048$; LRR: $p = 0.033$; Figure 4a; Appendix S4: Table S1), with population responses shifting the impact of alternative resources on omnivore prey consumption from negative to positive (Appendix S4: Table S2). However, this conclusion should be interpreted with caution, given the low sample size of studies, allowing population responses to occur in our prey consumption dataset.

In contrast to the animal prey consumption dataset, most studies in the prey density dataset allowed for omnivore population responses to occur (69% of studies, Rinehart & Long, 2021). The impact of population responses on the interactions between plant alternative resources and prey density was supported by both effect size calculations (d: $p < 0.001$; LRR: $p < 0.001$; Figure 4b; Appendix S4: Table S1). Specifically, prey density always decreased in the presence of alternative resources and omnivore population responses (d: $p < 0.001$; LRR: $p < 0.001$; Appendix S4: Table S2).

Publication bias and validation

We found no evidence of publication bias in our Kendall's Rank Correlations on omnivore prey

consumption (d: $T_b = 0.03$, $p = 0.570$; LRR: $T_b = 0.02$, $p = 0.745$) or prey density (d: $T_b = -0.108$, $p = 0.182$; LRR: $T_b = -0.112$, $p = 0.168$).

Our validation analysis, using the five-manuscript subset, confirmed our finding that plant alternative resources

decrease omnivore prey consumption (d: $p = 0.184$; LRR: $p = 0.304$; Appendix S5: Table S1). Additionally, the subset dataset supported our broader finding that plant alternative resource effects on prey density depend on the ability of omnivore population responses (Appendix S5: Table S2, S3; Appendix S5: Figure S1). This validation analysis increased the robustness of our full meta-analysis by showing that our conclusions are supported by empirical studies that tested both response variables within a single system.

DISCUSSION

Consistent with previous studies, our meta-analysis found a major discrepancy between studies regarding the influence of plant alternative resources on omnivorous terrestrial arthropods and their prey, alternative resources impact on prey varied from positive to negative. This discrepancy did not arise because of the differences in alternative resource identity. All plant resources included in our survey (pollen, seeds/pods, flowers, and flowering plants) decreased prey consumption by omnivores (Figure 2). In contrast, the discrepancy was related to experimental differences in the ability of omnivore populations to respond to plant alternative resources.

Studies focusing on consumption rate that found a positive impact of alternative resources on prey (i.e., reduced consumption) generally did not allow omnivore population responses, but studies focusing on prey density that found a negative impact of alternative resources on prey generally allowed population responses. Allowing population responses by omnivorous terrestrial arthropods switched the effect of alternative resources on prey density from positive to negative. Such population responses to plant alternative resources may lead to higher predation pressure on prey, thereby overwhelming reductions in per capita predation rates. Importantly, our analysis of empirical studies is consistent with theoretical models that predict that alternative resources increase omnivore predation pressure by promoting omnivore population responses (Harmon & Andow, 2004).

Omnivore population responses to plant alternative resources likely arise for several reasons. Plant alternative resources may increase omnivore immigration into patches because they contain valuable food resources (Frank et al., 2011), habitat refuges (Hossain et al., 2002), and opportunities for intraspecific interactions (e.g., mating; Rinehart & Long, 2019). These resources can enhance omnivore fitness, especially when only a few prey or low-quality resources are available (Eubanks & Denno, 1999; Jonsson et al., 2009; Rinehart & Long, 2018). For example, ladybeetles

provided only prey diets suffered spermatogenic failure that could be restored when beetles were supplemented with either plant resources or phytosterols and cholesterol (Ugine et al., 2019). While the nutritional benefits of plant alternative resources for omnivorous terrestrial arthropods have been well-documented (Coll & Guershon, 2002; Ugine et al., 2019), there have been fewer attempts to evaluate how other mechanisms, like refuge, can benefit omnivores.

In addition to increasing omnivore immigration rates, plant alternative resources may enhance local omnivore density by reducing emigration rates. For example, plots supplemented with seeds increased omnivore residence time by 37% and 111% relative to plots supplemented with prey or non-supplemented plots, respectively (Frank et al., 2011). Population responses could also have some negative impacts on omnivores populations over time if it increases cannibalistic behaviors. Thus, understanding the ecological and evolutionary consequences of population responses of omnivores to plant alternative resources is an important area of future research.

For example, population responses of omnivores that reduce pest density could influence the evolution of plant traits involved in indirect defense (i.e., plants benefiting from pest control by higher trophic levels). Plants may receive an adaptive benefit if their seeds, flowers, and pollen facilitate aggregations of pest-controlling omnivores, like the benefits they receive by providing omnivorous ants with food rewards via extrafloral nectar. However, the role of non-ant omnivores in such interactions remains unclear for several reasons. First, most studies of tritrophic signaling have focused on carnivores (Heil, 2008; Vet & Dicke, 1992). Second, food webs containing generalist consumers (e.g., omnivores) may be less likely to contain tritrophic signaling because generalists spend less time searching for prey than specialists (Vet & Dicke, 1992). Although sometimes present, tritrophic signaling is rare in food webs containing generalist herbivores and their generalist consumers (Dolecal & Long, 2014; Steidle & van Loon, 2003). Third, pest control by omnivores comes at the cost of signaling a consumer that also eats the plant receiving the benefit (Puentes & Björkman, 2017). Because our analysis suggests that omnivores commonly reduce prey density on plants, it would be worthwhile to continue to examine the costs and benefits omnivores represent for plants (Heil, 2008).

All plant alternative resources we compared (pollen, pods/seeds, flowers, and flowering plants) reduced omnivore consumption of prey. Although some alternative resources had a stronger effect on predation by terrestrial arthropod omnivores (e.g., pollen and pods/seeds had the strongest effects), our analysis found no differences in

prey density due to variation in plant alternative resource identity. Because population responses by omnivores to plant alternative resources appear critical, we hypothesize that plant resources that facilitate population responses will have the strongest effects on prey density in the presence of omnivores. For example, flowering plants may have stronger impacts on prey density because they serve as hubs for omnivore aggregations (Rinehart & Long, 2019), perhaps because of their apparency and the nutritional value of their pollen.

Population responses to plant alternative resources allow omnivores to suppress prey density despite per capita reductions in predation rates. There are at least three consequences of this finding. First, understanding the impact of plant alternative resources on omnivore—prey dynamics requires experiments that allow omnivores to aggregate and reproduce. Second, omnivores have the potential to serve as targets of conservation biological control efforts that seek to modify habitats via resource supplementation with the goal of enhancing natural enemy efficacy (Eilenberg et al., 2001). Third, such biocontrol may be most effective when it elicits strong population responses of omnivores. Biocontrol success may be achieved by using plant alternative resources that have strong visual or olfactory cues to attract or retain omnivores, or that promote omnivore fitness via reduced predation or enhanced survival and fecundity.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
Both authors conceived the project, designed the study, and wrote the manuscript. Shelby Rinehart preformed the literature survey and analyzed the data.

DATA AVAILABILITY STATEMENT
Data (Rinehart & Long, 2021) are available on Dryad: https://doi.org/10.25338/B8KP8P.

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