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Review Article

Widespread experimental evidence of Allee effects in insects: a meta-analysis

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With 6 figures

Abstract: During the last two decades there has been growing recognition of the importance of Allee effects in population dynamics and applied ecology. The Allee effect, that is decreased fitness at lower population densities, has been recognized as potentially playing an important role in the conservation of endangered species, in the practice of biological control, and the eradication of invasive species. Although a number of theoretical studies have been devoted to the role of Allee effects in the population dynamics of insects and other terrestrial arthropods, experimental evidence documenting Allee effects is still scarce. Here, we reviewed the literature reporting on density-dependent relationships in low-density populations and conducted a meta-analysis of 191 case studies to identify the occurrence of Allee effects and associated species traits. Allee effects are not rare in terrestrial arthropods, as they were reported in 47% of the cases we reviewed, comprising 46 out of 68 species. Ample examples exist for both demographic Allee effects (28 out of 74 cases cases), and component Allee effects (61 out of 117 cases). Insufficient mating success, cooperative feeding, and enemy escape were the three main mechanisms associated with Allee effects in terrestrial arthropods. Insufficient reproductive success was the mechanism with the highest proportion of related Allee effects (71%). Voltinism and host specialization were common species traits behind demographic Allee effects. Host specialists with univoltine life cycles tended to have stronger Allee effects. The high frequency of Allee effects in terrestrial arthropods reported here and the identified mechanisms behind them have important implications for the selection of management strategies.

Keywords: Biological control; demography; eradication; extinction; fitness; growth rate; insect decline; specialization; species traits; voltinism

1 Introduction

The concept of an Allee effect refers to a decrease in the fitness of individuals, such as survival or fecundity, with decreasing population size (Drake & Kramer 2011). Conversely, this leads to a positive density-dependent relationship of increased population growth as population density increases. However, this effect only persists until reaching a particular upper threshold. Beyond this threshold, the positive effects of increasing density diminish, and the negative effects due to competition take over. Consequently, Allee effects manifest primarily at low population densities. As a consequence, instead of a monotonic decrease in growth rate with population density, as expected from the logistic growth model, growth rates are typically hump-shaped (Fig. 1). Allee and co-authors (1949) were the first to report growth rates exhibiting a hump-shape as a function of population density, in a laboratory population of the flour beetle *Tribolium confusum*. There is a further distinction between strong and weak Allee effects. In the case of strong Allee effects, a negative growth rate is observed below a certain threshold, whereas weak Allee effects generally indicate a gradual reduction in individual fitness and population growth as population density decreases, yet without reaching negative values (Fig. 1). Strong Allee effects can have important consequences in population dynamics because they lead to a critical population size, the “Allee threshold”, below which a population may not be able to sustain itself and thus collapses eventually. Nevertheless, even a weak Allee effect, when coupled with high or moderate environmental stochasticity increases

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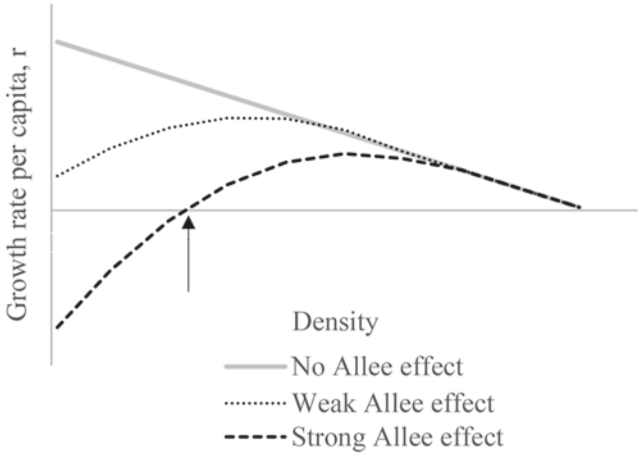

Fig. 1. The relationship of growth rate with population density when no demographic Allee effect is observed (linear response under a logistic growth model) and for a weak and strong demographic Allee effects as modeled in Amarasekare (1998). In the case of a strong Allee effect growth rates are negative for low population densities. The arrow indicates the Allee threshold below which a population will decline and collapse, given a strong Allee effect.

probability of extinction, which can pose a threat to populations of small sizes (Dennis 2002).

Allee effects can be further categorized as follows (Drake & Kramer 2011): 1) 'component Allee effects' expressed by a positive association between some component of fitness (e.g., mating success, juvenile survivorship, fecundity) and population size; 2) 'demographic Allee effects' expressed by a positive association between population size and population growth rate.

Component Allee effects may be associated with a number of different population processes. In arthropod populations, the best-known components are those related to mating success, several forms of cooperation (e.g., cooperative feeding enabling avoidance of host plant defenses, habitat modification, cooperative defence against predators), or escape from top-down regulation by satiation of natural enemies (Gascoigne et al. 2009; Kramer et al. 2009; Yamanaka & Liebhold 2009; Fauvergue 2013). The existence of one or multiple component Allee effects may result in a demographic Allee effect. A strong Allee effect can eventually lead to the extinction of small populations, unless immigrants can 'rescue' population levels above the Allee threshold. Low-density populations may also go extinct due to stochastic events, even if growth rates are positive, which should not be confused with an Allee effect, but may act in conjunction with Allee effects in contributing to local population extinction (Lande 1987; Liebhold & Bascompte 2003).

Allee effects have been observed in virtually all major plant and animal taxonomic groups. In the present study, we are specifically interested in the occurrence of Allee effects in terrestrial arthropods, mostly insects. A previous review on the ubiquity of Allee effects in animals by Kramer et al. (2009) reported the predominance of studies on vertebrates (birds, mammals, and fishes) compared with terrestrial arthropods. Arthropods, and particularly insects, might be expected to be less prone to Allee effects because of their efficient mate finding strategies and reproductive systems which, in some species, include facultative or obligate parthenogenesis (Vershinina & Kuznetsova 2016). In addition, the majority of arthropods have a high potential for recolonisation after local extinction events, due to their good flight or passive dispersal abilities, which could compensate for the reduction in population density levels as a result of Allee effects Still, Allee effects were reported in 77% (17 out of 22 cases) of the terrestrial arthropod study cases reviewed by Kramer et al. (2009) and in 52 cases of terrestrial invertebrates reported by Muir et al. (2024).

The relevance of Allee effects to the conservation of threatened arthropods received particular attention in recent years (Courchamp et al. 2008), especially with the increasing concern about the global decline in insect populations and the need to conserve endangered species when their populations reach low densities (Jactel et al. 2021; Wagner et al. 2021).

Another relevant research domain concerning the application of Allee effects in arthropods pertains to the management of invasive species. Recently, several studies recognized the importance of Allee effects in the ecology and management of invasive species (Liebhold & Tobin 2008). Non-native species are increasing globally and there is no sign of saturation (Seebens et al. 2017). Terrestrial arthropods, in particular insects, account for the majority of non-native animal species (Seebens et al. 2017). When non-native insect species successfully established in the introduced range, they typically spread into nearby suitable habitats. Many of these species become agricultural or forest pests or cause human health concerns in the invaded range, all of which are issues of global concern (Pimentel et al. 2001). However, only a minority of arriving populations of non-native species become established. Many introductions into a new environment do not result in established populations, primarily because of unfavorable environmental conditions, such as inadequate climate or lack of food resources. However, even if these conditions are appropriate, the existence of an Allee effect along with stochastic events can hinder the establishment of a founder population if it is too small in size (Liebhold & Bascompte 2003; Liebhold & Tobin 2008). To predict the likelihood of establishment, it is therefore important to know the relationship between the number of propagules and the probability of survival of a newly arrived insect population (Stringham & Lockwood 2021). Still, there are examples of terrestrial arthropods that become established at very low numbers and densities, suggesting the lack of Allee thresholds in some cases. For example, in *Vespa velutina* Lep. genetic studies of its invasion history indicate that the non-native population currently established in France was founded by a single multi-mated female (Arca et al. 2015).

One area where knowledge about Allee effects has provided practical insight is the selection of strategies for eradicating invading populations. Eradication refers to the total elimination of all individuals of a species from a given area. While this may seem like a daunting task, reducing populations density below the Allee threshold would drive populations to extinction with no need to kill all individuals (Liebhold & Tobin 2008; Liebhold et al. 2016). However, when eradication targets a new species about which little information is available, it may be difficult to determine whether a strong Allee effect may exist and what the value of its Allee threshold is. Furthermore, certain management tactics may be available for increasing the density threshold at which populations become extinct due to a demographic Allee effect (Liebhold & Tobin 2008) and this may facilitate eradication. Such tactics include mating disruption, improving host plant resistance, or increasing populations of generalist natural enemies (see Tobin et al. (2011) for a comprehensive analysis of these opportunities).

Knowledge about demographic and component Allee effect can also be useful for improving the efficiency of importation (=classic) biological control targeting both non-native plant pests and invasive plants as reviewed by Fauvergue et al. (2012). In this practice, natural enemies are imported from the pest or invasive plant's native range and released for the purpose of establishing a new population in the invaded environment. Globally, the success of classic biological control remains modest, at about 18%, which is partly explained by the relatively low success of biocontrol agent establishment, about 32% (Seehausen et al. 2021). There are several reasons for these failures, but one is when numbers of individuals released are insufficient to lead to successful establishment of a biological control agent. When information about Allee effects is available, this can help guide the identification of release sizes; presumably, it is necessary to exceed the Allee threshold in order to achieve establishment (Grevstad 1999; Williams et al. 2021).

Here, we focus particularly on insects. Although there is a considerable body of theoretical work considering the role of Allee effects on the population ecology of invading arthropod populations (e.g., Berec et al. 2001; Ryder et al. 2007; Goodsman et al. 2016), only a few experimental studies were found by a review by Kramer et al. (2009). There is also a lack of a clear and consistent understanding of which species traits best explain the existence of Allee effects. The purpose of this study is therefore to review the empirical evidence for Allee effect in insect species and other terrestrial arthropods. By performing a systematic review and a meta-analysis, our objective was to answer the following two questions: 1) How frequent and strong are Allee effects in insect species? 2) What are the most relevant population mechanisms (e.g. mating success, cooperation for habitat modification, etc.) or species traits explaining Allee effects?

2 Material and methods

2.1 Data acquisition

2.1.1 Literature search

Using ScienceDirect and Google Scholar, we searched the published scientific literature (published in English) for studies of insect populations on density dependent population growth or other population processes that could potentially provide empirical data on component or demographic Allee effects. We used the following keywords: "positive density-dependent" or "inverse density-dependent" or "density-dependent" and "insect" or "arthropod" in different combinations with one or more of the following words related to possible Allee components or demographic Allee effect: "mating", "reproduction", "fecundity", "survival", "winter survival", "predator", "parasit", "cooperation", "cooperative", "population growth", "resource exploitation", "low density", "Allee threshold", "biological control", "conservation". We used combinations of different key words in order to avoid missing relevant studies. Also, we did not use the term "Allee" in all of the combinations to avoid biased sampling. In total, 19 combinations of keywords were used, in all cases combined with "insect or arthropod" AND other keywords (see Suppl. Table S1 for a complete list). For each combination of keywords, the first 100 listed papers, sorted by relevance, were retrieved. The search was conducted up to the end of 2021 with no publication date restriction. We further used cross-references – i.e., those retrieved from selected relevant papers, combining systematic literature review with a snowballing approach which increases the efficiency and can be more reliable than a database search alone (Badampudi et al. 2015).

Using the ScienceDirect database we also retrieved the number of all published research papers from 1949 up to 2022 using the key words "arthropods" or "insects". This was used to estimate the proportion of research papers concerned with the analysis of Allee effects in the field of entomology.

2.1.2 Inclusion – exclusion criteria

We were particularly interested in studies using field, microcosm, mesocosm or laboratory experiments that analyzed density-dependent effects on arthropod population parameters. Theoretical and modeling studies were thus excluded. Review studies were only used for obtaining cross-references. Our aim was to take into account any positive relationship with population density, irrespective of the scale at which the population was studied. This included observations in Petri dishes, on groups of individuals (even siblings), in extended field samplings, or up to the metapopulation level.

Because we were searching for evidence of Allee effects, we focused on studies with low population levels. Therefore, any studies of density-dependent relationships conducted only at high-density populations (including outbreak events) were excluded. Among the retrieved papers, we selected reports from studies conducted on a gradient of at least 4 population densities to be able to perform linear regressions between a component (e.g. survival, body weight) or demographic parameter (e.g. net growth rate) and populations density. All other studies were excluded, including those indicating a potential Allee effect but lacking sufficient data to corroborate its presence.

Several papers presented more than one experiment, targeting different species or studying different Allee components, or using different experimental conditions. In such cases, each experiment was analyzed separately, as a separate case study. A total of 1610 article abstracts were screened, of which 227 full texts were read for eligibility and $n = 75$ were eventually kept, providing $k = 191$ eligible case studies according to our criteria (Fig. 2. PRISMA diagram).

A demographic Allee effect was considered to exist when, for the lowest densities sampled, a statistically significant increase ($P < 0.05$) in individual fitness or population growth rate was observed increasing with population density (Fig. 3).

Because most Allee effects occur at low densities, we only used data from low population levels, stopping when the response curve reached a minimum or a maximum such as when it exhibited a parabola or dome shape (Fig. 3). The density cutoff was determined visually, if it was clear and unambiguous when only a few data points were available. Otherwise, when the inflection point of the response curve could correspond to 2 to 3 close densities, such as in Fig. 2, the cut-off was defined as the one that yielded the highest linear regression coefficient of determination r^2.

With regards to demographic Allee effects, we further distinguished studies showing a strong Allee effect, i.e. reporting negative growth rates in the lowest density range surveyed, from those showing a weak Allee effect, where growth rate was always ≥ 0 (Fig. 1).

2.1.3 Calculating effect size

To estimate the magnitude of the effect of arthropod population density on demographic components (e.g., survival, fecundity, mating probability or body condition; example in Fig. 3), we extracted the Pearson's coefficient of correlation (r) and the sample size (n) of their linear regression, which we used to calculate the Fisher's Z-score $Z = \frac{1}{2} \ln((1+r)/(1-r))$, and its variance $v(Z) = 1/(n-3)$. For the sake of convenience, we back-transformed z values to obtain correlation coefficients (r). Raw data were retrieved from tables or

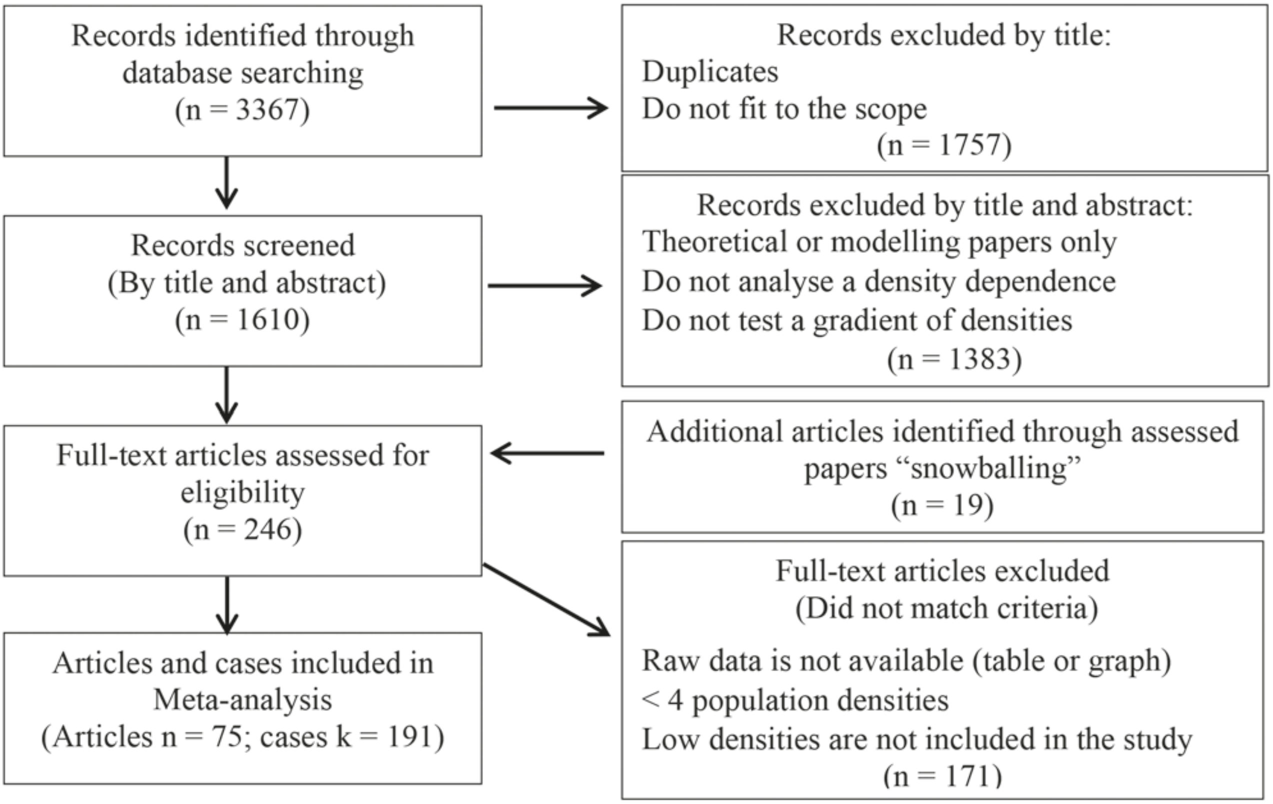

Fig. 2. PRISMA diagram (Preferred Reporting Items for Systematic Reviews and Meta-analyses) illustrating study cases selection process (O'Dea et al. 2021).

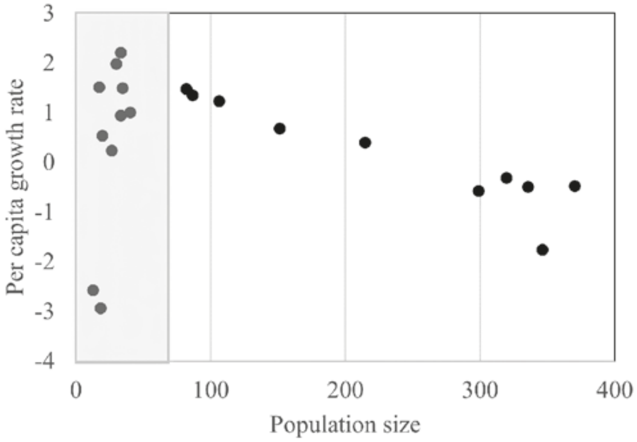

Fig. 3. Example of a study case with a density-dependent hump-shape (data from Vercken et al. 2021). The grey area corresponds to the data retrieved in this study for the meta-analysis.

graphs using WebPlotDigitizer (Rohatgi 2022). It should be noted that in the studies we considered, population density was expressed in several ways, such as average number per habitat (e.g., per plant, per leaf), average number of individuals per day of trapping, etc., over gradients of varying duration. Similarly, the response variable could take on various values and units, for example for the fitness of individuals or the growth of a population. Therefore, we did not attempt to carry out a meta-analysis of the values of the regression slopes, as this would have little meaning. However, it was possible to combine the values of the correlation coefficients, which are unitless and all vary from -1 to 1.

2.1.4 Moderators

For each case study, we extracted the following moderators, i.e., the covariates that might influence the relationship between population density and components of the Allee effect: i) type of Allee effect, i.e. demographic (population growth rate or probability of persistence) vs component (adult body size/weight, larval body size/weight, female fecundity, egg survival, larval survival, adult survival, fitness or mating success); ii) species voltinism (number of generations per year, which we then separated into either univoltine (which merges univoltine and semi-voltine) vs. multivoltine), and iii) the degree of host specialization (specialist, that is feeding on a single genus or family vs. generalist, feeding on species from several families). We also collected information about the feeding guild (folivorous, second order consumer [hereafter considered predators *sensu lato*], fruit- or seed-feeding consumer, detritivore, bark & wood borer, sap feeder, gall maker, root borer); main reproductive mode (parthenogenetic, sexual); type of study (laboratory, field sampling, field manipulative); and habitat (forest, agriculture, other) (Appendix S1). However, the low number of cases for some classes prevented us from testing all of these moderators (see below regarding the need to follow a hierarchical approach of moderators' effects).

In addition to moderators, each study case was attributed a single identifier (Case ID) and assigned to one original paper (Paper ID).

2.2 Statistical analyses

We estimated the grand mean effect size using the complete data set to assess whether there was an overall effect of increasing population density on Allee effect components (demographic of fitness response variables). This effect was considered significant if the 95% confidence interval around the grand mean effect size did not include zero. We calculated the between-study heterogeneity (τ^2) (i.e., how studies were distributed around the grand mean effect size), and the standardized estimate of total heterogeneity (I^2) ranging from 0 to 1, indicating how much of the variation in effect sizes was due to the between-study variance (τ^2) (Koricheva et al. 2013; Nakagawa et al. 2017). Total heterogeneity around the grand mean effect size was addressed by testing the effect of moderators on individual effect sizes in a second step. To avoid confounding factors, moderators were tested using a hierarchical approach (Castagneyrol & Jactel 2012; Ferreira et al. 2015). Thus, the effect of the second moderator on effect sizes was tested in each of the categories of the first moderator analyzed (and so on), taking care that it was well distributed in terms of the number of case studies between the different modalities of the different moderators (see Fig. 6 for the structure of the database used to test the three moderators of interest).

For each model, we used Case ID nested within Study ID as random factor to account for correlation among multiple case studies within the same article (primary study). We ran each model using the *rma.mv* function of the "*metafor*" package in R (Viechtbauer 2010). Finally, we used complementary analyses to evaluate the sensitivity and robustness of our results to several sources of bias, such as the Funnel plot of the grand mean effect size, and calculation of Rosenthal's fail-safe number (see details in Appendix A2). To assess the robustness of our findings, we selected only one case study per article and used this selection to run a meta-analysis. We then re-ran the selection 100 times, since some studies had more than one case study and evaluate the mean grand mean effect size ± 95 % CI. We used the same approach to account for unequal numbers of articles (studies) per insect species. We randomly selected a single study for each of the 69 species and performed the meta-analysis on these 69 studies. We repeated the selection 2000 times. In addition, as *Lymantria dispar* (L.) was the most frequent species in our dataset (11% of case studies), we tested the effect of removing all data based on this particular species on the analysis. We reapplied the same models to estimate the magnitude of effect sizes and the effect of moderators on this subset of the data. All statistical analyses were performed using the *R* software, version 4.2.0 (R Core Team 2022).

3 Results

3.1 Allee effects reported in the literature

From the literature search, we retrieved 75 papers that fulfilled the criteria. They produced 191 case studies included in the meta-analysis, which involved 68 different species of arthropods, 66 were hexapods, one mite and one spider (Suppl. Table S2).

Overall, an Allee effect was found in at least one case study in 47% of the cases. During the last three decades, the proportion of case studies showing an Allee effect has been fairly constant at around 50% (Fig. 4). In 32% of the papers, some type of Allee effect could be observed for some case studies, such as specific component Allee effects or under certain conditions (e.g., certain habitats, host plants, etc.), but not for other conditions or for other types of Allee effects.

In most of the retrieved papers (48 papers, 64%), the scope of the study did not specifically include a search for an Allee effect. However, the number of publications explicitly dealing with Allee effects consistently increased during the last decades (Fig. 4).

Allee effects were observed in 46 out of the 68 species identified. However, in 25 of these 46 species, Allee effects were evident in certain experiments or parameters but not in others. These effects were found across various orders, including Lepidoptera, Hymenoptera, Diptera, Coleoptera, and Hemiptera, and were found in different families within each order (Suppl. Table S2). The presence of Allee effects could be observed in all feeding guilds (Fig. 5). However, the proportion of papers reporting an Allee effect was highest for bark and wood borers, folivorous species and sap feeders (73%, 62% and 53%, respectively). The proportion was lower, for species feeding internally on fruit, seeds and in galls (37%). For predators (*sensu lato*) and decomposers, this proportion decreased to 19% and 25%, respectively. The remaining guilds were represented by only a few studies which prevented drawing definitive conclusions.

From the 191 case studies, 111 were field studies (including field observations, field manipulative experiments, and releases of natural enemies). The other 80 case studies were laboratory or mesocosm experiments. In 71 studies, a demographic parameter, population growth, or population establishment success were analyzed and potentially indicative of a demographic Allee effect, whereas in 120 studies individual fitness components were recorded which would potentially be indicative of component Allee effects. The proportion of studies documenting a component Allee effect was higher (52%, 61 out of 117) than the proportion of those reporting a demographic effect (38%, 28 out of 74). Where a demographic Allee effect was detected, strong Allee effects were about 4.6 times more prevalent than weak Allee effect.

Parameters measuring components of individual fitness were highly variable, but can be categorized into three main groups: i) physic or physiological condition (including body size, body weight, physiological resistance, development time), ii) survival rate (egg or larval), and iii) reproductive success (e.g., mating probability, fecundity, number of brood galleries). The individual components of fitness most frequently identified were mating, cooperative feeding, and enemy escape by predator/parasitoid satiation (Suppl. Table S3). Mating type was investigated in papers reporting reproductive success or a demographic Allee effect. Cooperative feeding was related to individual survival and body size. Enemy escape was related mainly to the survival component

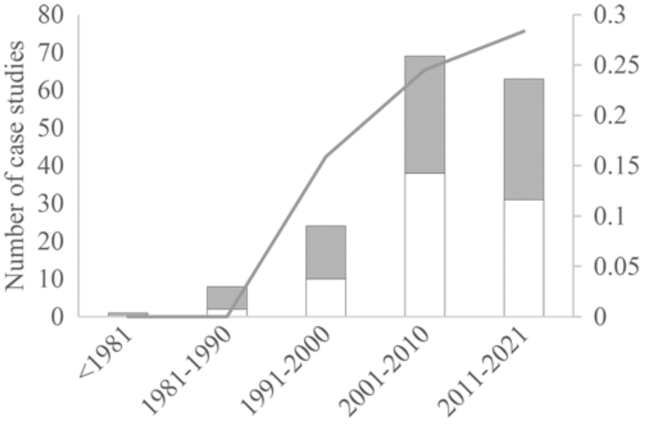

Fig. 4. Number of case studies from 1949 to 2021 in which an Allee effect was detected (Yes) or not (No). The line indicates the percentage of research papers (out of all published research papers on arthropods or insects) that were experimentally searching for the existence of an Allee effect.

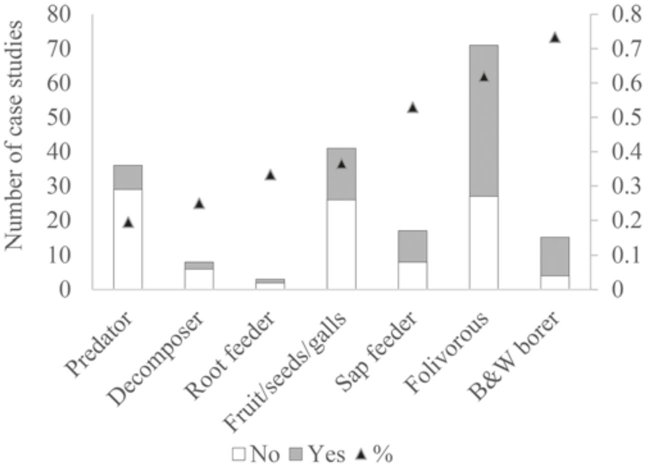

Fig. 5. Number of case studies retrieved in which an Allee effect was detected (Yes) or not (No), per feeding guild. The "Predator" guild includes predators and parasitoids. Triangles correspond to the proportion of studies in which an Allee effect was present in each guild.

of Allee effects. In many cases the mechanisms associated with a demographic Allee effect were unknown or there were multiple mechanisms (Suppl. Table S3).

Some of the reviewed studies reported on laboratory experiments in which a fixed number of individuals could be controlled, while other studies were based on field sampling. In the field surveys, the variety of sampling methods, as well as the metrics used, were large. The most common metrics were density expressed per unit area, per unit of habitat (e.g., per tree, twig, leaf, plot, bud, fruit), per unit of observation period, and the number of catches per trap (Suppl. Table S2). The presence of an Allee effect was significantly higher when pheromone traps were used, observed in 20 out of 22 cases (91%), in comparison with other density metrics, in which an Allee effect was observed only in 69 out of 169 of the cases (41%) ($\mathrm{Chi}^2 = 5.713$, p-value = 0.016).

3.2 Meta-analysis

The grand mean effect size calculated with the full data set ($k = 191$) was significantly positive and equaled $r = 0.39$ (confidence interval 0.26 to 0.50) (Fig. 6), indicating a positive correlation between component or demographic Allee effects and insect population density, or reciprocally that these variables significantly decrease as populations decrease to low densities, towards near zero values.

The robustness analysis, based on selection of only one case study per article, showed that the result was still positively significant (confidence interval does not bracket zero, Suppl. Fig. S4.1). Also, when using the classical "leave one out" approach, where we removed one paper at a time (Willis & Riley 2017), the mean effect size was still significantly positive (Suppl. Fig. S4.2). When we randomly selected only one paper per species, we still found a significantly positive grand mean effect size, indicating that the unbalanced number of reported studies per species did not affect the results of the meta-analysis (Suppl. Fig. S4.3). Furthermore, when we removed all data from studies on *L. dispar*, we found similar outcomes of the models as with the full dataset, indicating that the over-representation of this species did not bias our results (Suppl. Table S5).

The funnel plot was roughly symmetrical and most of the points fell on the pseudo-confidence region (Suppl. Fig. S4.4). The cumulative meta-analysis also showed that the mean effect size stabilized from the 2000s onwards. (Suppl. Fig. S4.5). Publication bias was thus unlikely. The Rosenthal's fail-safe number to change our result would have been 12,218, much larger than the threshold of $5n+10=965$ case studies.

Total heterogeneity was high ($\tau^2 = 0.84$, $I^2 = 0.40$) suggesting that covariates (moderators) could explain much of the variance. We thus successively tested individual moderators. The effect of voltinism on effect sizes (correlations between an Allee effect component or demographic and population density) was significant ($Q_B = 8.60$, p-value = 0.003) with a higher magnitude of the Allee effect for univoltine insect species (Suppl. Fig. S4.6). There was no effect of host specialization on effect sizes ($Q_B = 0.30$, p-value = 0.58), with significantly positive Allee effects for both specialists and generalists. There was no significant difference between mean Allee demographic and component effects ($Q_B = 0.14$, p-value = 0.71), which were both significantly positive (Suppl. Fig. S4.7). Finally, we found a significant Allee effect for species with sexual reproductive system whereas the effect was non-significant for parthenogenetic species (QB = 7.58, p-value = 0.006) (Suppl. Fig. S4.8). However, we also found significant interactions between voltinism and host specialization ($Q_B = 39.69$, p-value < 0.0001), voltinism and Allee effect component ($Q_B = 35.20$, p-value < 0.0001), reproduction type and host specialization ($Q_B = 32.12$, p-value < 0.0001) but not between component and host specialization ($Q_B = 0.85$, p-value = 0.84).

We therefore calculated mean effect sizes according to a hierarchical structure of three moderators, type of Allee effect, host specialization and voltinism (Fig. 6). We had no enough data to add the effect of the reproduction type. This analysis confirmed that Allee effects were more detectable in univoltine than multivoltine insects. Generalist species also had more detectable Allee effects than specialists among univoltine species, while the opposite was true for multivoltine species. The magnitude of Allee effects did not differ between component and demographic Allee effects but in multivoltine generalist species. For the multivoltine generalist species the regression was in fact negative, suggesting non-existence of an Allee effect but, instead, a negative density-dependent shape as in the logistic curve. The group of multivoltine species mostly included small sized arthropods with short generations from different guilds such as detritivorous collembola (*Folsomia candida*), aphids (*Aphis glycines*), parasitoid wasps (*Trichogramma* spp.) and mites (*Tetranychus urticae*). Finally, the largest (highest r^2) Allee effect was found among demographic effects of univoltine, generalist insects ($r = 0.95$). These were mainly represented by forest defoliating Lepidoptera, sampled with pheromone traps, such as the spongy moth *L. dispar*.

4 Discussion

4.1 How common is the Allee effect in terrestrial arthropods and why is it important?

More than 70 years after the first description of an Allee effect, it is still unclear how ubiquitous Allee effects are in populations of terrestrial arthropods, particularly insects. Previous studies reported a scarcity of experimental studies addressing this phenomenon, especially in terrestrial invertebrates (Kramer et al. 2009).

Based on an extensive literature review, we compiled 191 study cases on insects, spiders and mites from which an Allee effect was demonstrated in 89 cases (47%), mainly with insects. Allee effects were observed in 46 out of the

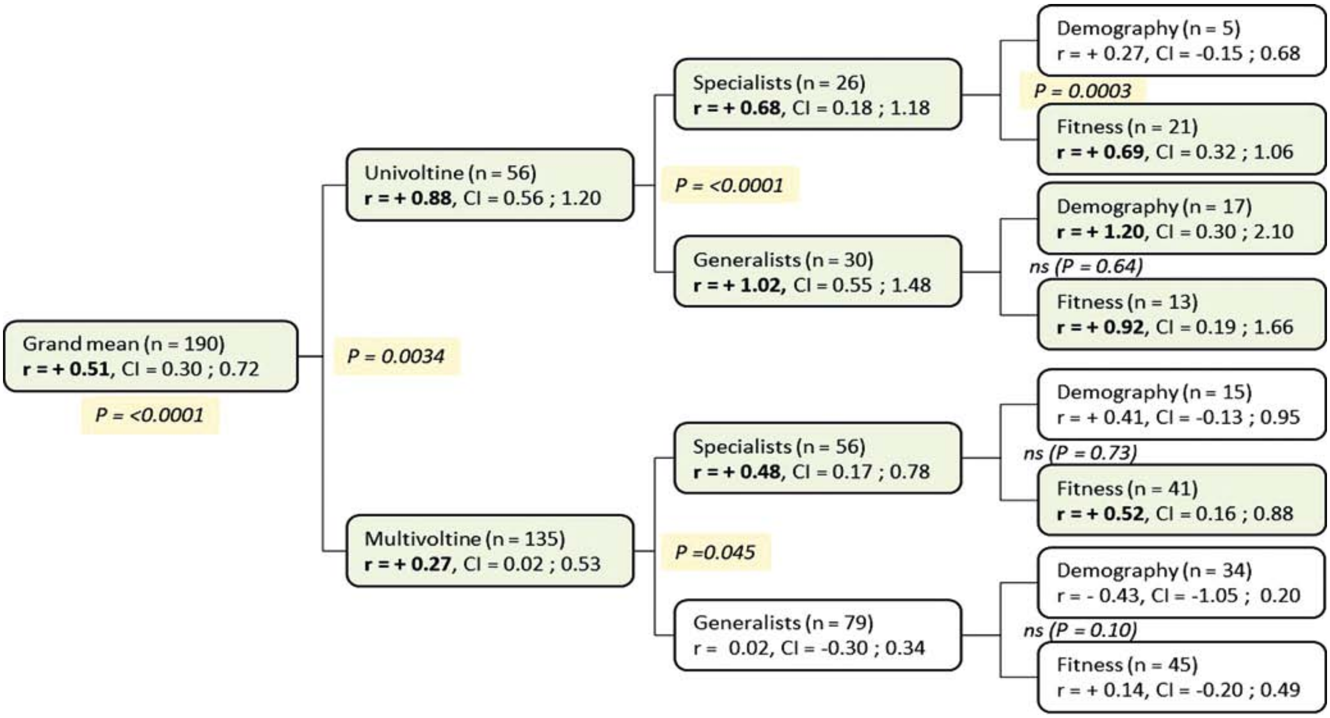

Fig. 6. Summary of meta-analysis outcomes with the hierarchical structure of the tests where voltinism, diet breadth and Allee effect components were successively tested. *r* values were obtained by the back transformation of *Z*-scores. *CI* = 95% Confidence Interval. The variable *n* is the sample size.

68 species that were studied. It is also worth noting that these effects covered five orders and were found in different families within each order. These results show that Allee effects are widespread in insect populations and also occur in other terrestrial arthropods. The number of experimental studies demonstrating the existence of Allee effects in terrestrial arthropods has increased significantly over the last two decades being observed about 20 in the last decades. This in part justifies the increasing number of cases from 17 (in Kramer et al. 2009) to 89 (in this review). Although we included multiple case studies from the same paper in several instances (a practice not adopted by Kramer et al. 2009), our selection process was generally more rigorous. We only selected cases that provided density-dependent data and had at least four observation points for regression analysis, with the magnitude of effect determined by the regression coefficients. Because of this selection process, we excluded some cases that showed an Allee effect but did not meet our criteria, including some highlighted by Kramer et al. 2009. In a recent study from Muir et al. (2024), Allee effect were reported in 52 experimental cases of terrestrial invertebrates, corroborating the fact that Allee effects are widespread in this group. Component Allee effects were detected in a higher number of cases (61) than demographic Allee effects (28). Nevertheless, a strong demographic Allee effect was evidenced in a number of cases (25), indicating that these species would become extinct or not established below a minimum threshold of population density.

The impact of a demographic Allee effect on the local extinction of small populations and its importance for the conservation of threatened populations has been widely emphasized (Stephens & Sutherland 1999). The focus on the role of Allee effects on endangered organisms has historically been on large mammals and plants (Kramer et al. 2009). Because most insects have short life cycles and high fecundities, it can be expected that they have rapid growth rates, which, combined with efficient mate finding systems, would make them less vulnerable to extinction than larger animals. However, in the last few decades, many studies have reported a decline in insect populations globally (Simmons et al. 2019; Wagner et al. 2021) which elevated concerns about insect extinctions. Connections between insect extinctions and Allee effects are rarely suggested (2021). In the present review, although we found an increasing number of studies reporting Allee effects, none of them specifically addressed conservation objectives.

A few of the studies covered by our analysis mentioned implications of Allee effects on importation biological control, in which establishment success may be limited by small initial population sizes of released organisms (Hopper & Roush 1993; Grevstad 1999). On the other hand, there were a larger number of studies (more than 15) concerning non-native insect species. Indeed, several reviews and theoretical studies have considered how a demographic Allee effects may be exploited for the eradication of invasive insect pests (Liebhold & Bascompte 2003; Liebhold et al. 2016; Tobin et al. 2011; Barron et al. 2020).

4.2 Allee components in terrestrial arthropods

Which Allee effect components are mostly found in terrestrial arthropods is a relevant question for practical applications. Three main components emerged in our review as the most important for the existence of an Allee effect in terrestrial arthropods: mating success (31%), enemy escape (25%) and cooperative feeding (19%). Other known factors were of minor relevance. In 23% of the cases, the Allee component was unknown – i.e., in studies where only population growth was quantified. Also, in some of these cases, multiple Allee components were found acting in synergy (Berec et al. 2007; Gascoigne et al. 2009).

Mating success was the most relevant component recorded. Furthermore, a demographic or component Allee effect was found in 67% (28 out of 42) of the studies measuring density-dependent mating success. Many other studies have shown that mating success is the most important Allee component for insect populations, as reviewed by Gascoigne et al. (2009) and Rhainds (2019). Mate limitation was also one of the most common Allee mechanisms reported by Muir et al. (2024). Therefore, the reproductive system (sexual vs parthenogenesis) can be expected to have a large impact on the existence of demographic Allee effects (Queffelec et al. 2021). For example, it was found that the establishment of invading populations was facilitated in species with inbreeding mating systems, such as some bark and ambrosia beetle species (Kirkendall & Faccoli 2010; Lantschner et al. 2020). In our study, species that reproduce both sexually and parthenogenetically were less susceptible to Allee effect than those that reproduce only sexually. Among the species with both modes of reproduction, an Allee effect was detected in only three species out of ten, and even then, it was observed in only a small number of cases for each of the three species.

Cooperative feeding was found in 19% of the observed Allee effects. This mechanism could affect individual fitness, reproductive success, or survival. Cooperative feeding was observed in insect guilds where the presence of conspecifics facilitated feeding activity, via overcoming interspecific competition, facilitation of pre-ingestive enzymatic activity, or overcoming host plant defense. This component has been reported in fruit flies (e.g., Rohlfs et al. 2005), in decomposers such as blowflies (Saunders & Bee 2013), in defoliators (Nahrung et al. 2001; Hambäck 2010), and in bark beetles (e.g., Friedenberg et al. 2007; Chase et al. 2023). For many bark beetle species, it is well known that a minimum population attack threshold per tree is needed to overcome tree defense and become established. This can generate an Allee effect and, therefore, pressure load is important for their establishment in a new location (Goodsman et al. 2016; Lantschner et al. 2020).

Enemy satiation emerged as a frequent Allee component (25% of the cases). It was found in almost half of the cases (20 out of 43) in which a predator/parasitoid density-dependent response was studied. This result seems to contradict previous studies on predator/parasitoid density-dependent response. In a review, Walde & Murdoch (1988) found that most parasitoids responded in a positive density-dependent fashion, i.e., a positive correlation between host density and parasitism rate. Also, in a meta-analysis on the response of parasitism rates to host densities, Gunton & Pöyr (2016) found a positive density-dependent relationship, that is increasing parasitism rates with host population density, in 59% of cases (151), whereas negative density-dependent parasitism, which would cause an Allee effect, was observed in only 13% of cases. This figure contrasts with our results, in which a decrease in parasitism rates with increasing host density causing an Allee effect was observed in 47% of the cases. The discrepancy between our results and previous studies may be explained by the fact that we focused on data ranges for the lowest population densities (see Fig. 2), where Allee effects are noticeable.

Generalist predators are more likely to cause Allee effect because their growth rate is not dependent on a particular prey species. An example from the cases found in our review is the inverse density-dependent predation rate by small mammals on *L. dispar* pupae (Elkinton et al. 2004). Due to this mechanism, generalist natural enemies introduced in a new range may contribute to the extinction of local, non-target prey species (Tobin et al. 2009). Another example is provided by the generalist parasitoid *Compsilura concinnata* (Meigen) introduced to control the non-native moth *L. dispar*, but then also attacked brown-tail moth *Euproctis chrysorrhoea* (L.)., with a greater impact on the later. Introduction of this parasitoid was considered responsible for the population decline of *E. chrysorrhoea* leading to its substantial range retraction and local extinction (Elkinton et al. 2006). The same parasitoid is also affecting north American native Lepidoptera (Elkinton et al. 2012). The introduction of invasive generalist predators or parasitoids can thus lead to Allee effects, which potentially risk for the conservation of native endangered species.

Other Allee components, such as habitat conditioning, inverse density-dependent dispersal, and immuno-resistance, were less well represented. For social and gregarious insects, the presence of conspecifics is necessary for development and survival (Angulo et al. 2018). This was reported in two studies on two pine processionary moths, *Thaumetopoea pityocampa* and *Thaumetopoea pinivora*. For both species, individual fitness increased with population density (Ronnås et al. 2010; Pérez-Contreras et al. 2003), and for *T. pityocampa* an increase in larval survival was further observed (Pérez-Contreras et al. 2003; Aimi et al. 2008). This is a result of their ability to modify the quality of the habitat through the collective construction of silky tents, which protects these species from adverse weather conditions and predators (Poitou et al. 2021).

Density-dependent dispersal is a biological phenomenon in which individuals change their dispersal patterns in response to the density of conspecifics. In most cases, individuals tend to disperse when population density is high, thereby reducing competition for resources (Harman et al. 2020). Inverse density-dependent dispersal (IDD) is considered a relatively rare phenomenon in which individuals disperse from areas with low population density to areas with high density. In these cases, IDD can trigger an Allee effect. In a review, Harman et al., (2020) found 9 cases of IDD out of 55 cases in terrestrial arthropods, suggesting that IDD is far less common than positive density-dependent dispersal. Finally, one case of increasing immune-resistance with increasing larval density, through the phenomenon termed "density-dependent prophylaxis", was reported for the larvae of *Plutella xylostella* reared in laboratory conditions (Kong et al. 2020).

Interestingly, differences could be observed between populations of the same species. In an experimental study by Vercken et al. (2021) analyzing the growth rate of *Trichogramma* ssp. populations reared on *Ephestia kuehniella* eggs, a demographic Allee effect was found in only 8 of the 30 populations. Populations with an Allee effect compared to those without an Allee effect were characterized by lower per capita growth rates and lower maximum population size, demonstrating a correlation between the presence of an Allee effect and reduced demographic performance.

4.3 Meta-analysis of species traits most associated with Allee effects

With the meta-analysis, we were able to show that the main factor explaining the occurrence of an Allee effect in arthropods is their degree of voltinism, with on average a strong dependence of fitness or demographic components on population density in univoltine species but no such correlation in multivoltine species. Overall, the ability of species to better exploit resources or adapt to a changing environment may be facilitated by increased voltinism, since the succession of generations in a single year increases the chances that at least one of them will benefit from favorable weather conditions or abundant food resources as long as these resources are still available (Altermatt 2010).

Asynchrony or phenological mismatch in biotic interactions is more likely in univoltine species than in multivoltine species, particularly those with overlapping generations such as is the case with several bark beetle species (Friedenberg et al. 2007). In addition, it has also been suggested that multivoltine species are more resistant to phenological shifts and adapt better to changes in seasonality (Shama et al. 2011), because of the reconstitution of population size and genetic diversity after each mismatch event (Knell et al. 2016). Yet, asynchrony in the life cycle, such as during adult emergence, can lead to a reduction in mating success, thus reinforcing the Allee effect (Robinet et al. 2007). Reproductive stages are present for only a brief period in most univoltine insects, but they are typically present for longer periods in multivoltine insects; as such, developmental synchronization is much more important to mating success in univoltine insects and populations may be more likely limited by mating success (Yamanaka & Liebhold 2009).

The second most important driver of an Allee effect was diet breadth, with overall stronger evidence for a demographic or component Allee effect in low population densities of host specialists. As with multivoltinism, a broad diet range offers more opportunities to escape quantitative or temporal constraints requiring cooperation for the availability of food resources which would lead to Allee effects. For example, the need for cooperative feeding that allows some species to overcome host plant defenses can be expected to be more common for host specialist than generalist herbivores. However, this could interfere with the spatial distribution of organisms and their resources. Generalist insects, which have a wider choice of hosts, could be less spatially concentrated, leading to an increase in mate-finding failures and therefore a greater risk of being affected by Allee effects (Robinet et al. 2008). Specialists might have more difficulty finding isolated resources, but once these resources have been colonized, they would be closer to their conspecifics, increasing the chances of mating (Tobin et al. 2009). These complex and probably species-specific effects would explain why the influence of specialization on the intensity of the Allee effect varies between univoltine and multivoltine species categories in our meta-analysis. It is important to acknowledge that the spatial arrangement of habitats can significantly affect the likelihood of recolonization from neighbouring patches, which act as sources for colonisers (Öckinger et al. 2018). Highly fragmented landscapes and low dispersal capacity can then exacerbate the impact of Allee effects on stenotopic species. In most cases voltinism and specialization have similar outcomes for both demographic and component Allee effects (as measured by r^2), suggesting similar effects on both dimensions of the Allee effect or a close correlation between the two types of Allee effects.

It should be mentioned that some species were overrepresented in our dataset (e.g., *L. dispar*) which might have influenced the results regarding the influence of species traits. We used statistical methods to check that this had not biased the results of our meta-analysis. Nevertheless, it is clear that while Allee effects seem widespread in arthropods, only a few studies have systematically investigated this phenomenon experimentally. Further research is therefore needed, involving a wider range of species, so that detailed analyses of the role of species traits and the significance of their phylogenetic relationships can be carried out.

4.4 Detectability of the Allee effect

It is possible that in some cases demographic Allee effects exist but are limited to very low population size at which sampling error becomes proportionally high and, consequently, Allee effects may not be detected. Although we have limited our analysis to the lowest reported sampled densities, it is possible that these observed densities were still above the range of densities at which Allee effects are expressed. Insects and other terrestrial arthropods are generally small and can be easily hidden, making them difficult to detect using conventional sampling methods (Gregory et al. 2010). Compared with other methods, pheromone-based trap catches stand out for their high sensitivity, i.e., ability to detect of insects even at very low density (Witzgall et al. 2010; Larsson 2016). This may explain why an Allee effect was observed in 91% of the cases using pheromone traps with long-range attraction, compared to 41% using other sampling methods. While we need to be cautious in interpreting this outcome, given the limited number of case studies using pheromone traps (employed for only three species, two Lepidoptera and one Coleoptera), we postulate that using more effective sampling methods could reveal a higher proportion of Allee effects. It should also be noted that the detectability of an Allee effect depends on the spatial scale at which the population is observed. Both habitat type and spatial scale can modify the density-dependent relationship, as demonstrated by Segoli (2016).

5 Conclusions

By conducting a systematic search, we were able to compile 191 experimental studies on density dependence in population growth of terrestrial arthropods, with 89 cases where an Allee effect was detectable and measurable. This proportion (47%) is lower than the 77% rate reported in the previous study by Kramer et al. (2009), which is probably explained by our choice to include all study cases linking potential Allee effect components with low population densities, and not only those studies that explicitly investigated the presence of Allee effects. Further we restricted our confirmation of Allee dynamics to cases with only a significant increase in fitness or growth rate with population size. Still, we could confirm a high prevalence of Allee effects in terrestrial arthropods, with promising practical implications for the management of their populations, either for the conservation of endangered species, for the release of biological control agents or for the eradication of invasive species.

Reduced mating success emerged as the most prevalent mechanism behind demographic Allee effects, followed by enemy satiation and cooperative behaviors (mostly for feeding), in accordance with previous studies focusing on the use of Allee effects for the management of invasive insect pests (Tobin et al. 2011). Voltinism and feeding specialization emerged as key species traits that explain variation in the expression of demographic Allee effects, but not as much on component Allee effects. Our results also indicate that the detectability of Allee effects is likely to depend on the sampling methods used in field studies. Additional data on demographic values would be useful for estimate Allee thresholds beyond which arthropods species may become locally extinct in relation to the sampling effort. This information will be most useful for prediction of extinction in the context of conservation of endangered insect species, biological control and eradication of invasive species.

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Table S1–S5, Figure S1–S8