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Meta-analysis

The magnitude of Allee effects varies across Allee mechanisms, but not taxonomic groups

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The Allee effect is a density-dependent phenomenon in which individual fitness increases as population density increases at low population densities. Over the past few decades, a growing number of studies have identified Allee effects in populations using experimental approaches and statistical modeling techniques. These studies have investigated multiple Allee mechanisms (e.g. mate-finding, predation, resource limitation), across a range of systems and taxa (e.g. plants, vertebrates, invertebrates). This meta-analysis aims to synthesize studies that experimentally manipulated population density and measured either per capita population growth or fitness components, with the goal of determining whether the 'magnitude' of the Allee effect (defined here as the positive correlation between population density and population growth or fitness) varies with Allee mechanism across taxonomic groups. A total of 2305 studies were screened, and 62 of these studies met our meta-analysis inclusion criteria. Within these 62 studies, 155 effect sizes encompassing nine different Allee mechanisms were identified across five broad taxa. When grouped by Allee mechanism and taxa, the magnitude of the Allee effect differed across mechanisms, whereas taxonomic group was less useful at explaining variation in the magnitude of Allee effects. Of the nine Allee mechanisms identified, interspecific competition was associated with the largest Allee effects, followed by fear, pollen limitation and mate limitation. These findings suggest that Allee effects may be more dependent on mechanism than taxa and may function similarly within different taxonomic groups. However, as the majority of experimental Allee effect studies included in this meta-analysis focused on plants and invertebrates, more research is needed on Allee effects in other taxonomic groups to confirm this conclusion. This first quantitative synthesis of Allee effect research in ecology offers novel

Synthesis

This meta-analysis provides a quantitative synthesis of experimental research on Allee effects, shedding light on factors influencing the strength of positive density dependence in populations. By standardizing diverse effect sizes into a common metric, we were able to include a wide range of taxa and Allee mechanisms in our synthesis, highlighting how the magnitude of Allee effects can vary amongst different groups. This work advances our understanding of Allee effects in ecology – the findings identify crucial knowledge gaps in Allee effect research and suggest that certain Allee mechanisms, such as mate limitation, may be particularly potent drivers of Allee effects.

insight into how Allee mechanisms affect the manifestation of Allee effects in populations, providing important information for ecologists and conservationists.

Introduction

In recent years, an increasing number of organisms have experienced significant declines in population size. These declines have resulted in widespread ramifications for many ecological communities (Ceballos et al. 2017, Simmons et al. 2019), making research on the dynamics of small or declining populations an area of critical importance in the fields of ecology, conservation, and wildlife management (Purvis et al. 2000, Kramer et al. 2018, Wittmann et al. 2018). One intrinsic challenge faced by small populations of sexually reproducing organisms is the difficulty finding a mate when population densities are low. This is because when there are a limited number of potential mates within the environment, reduced encounter probability can result in poor reproductive success (Dennis et al. 1989, Gascoigne et al. 2009). Other issues experienced by small populations can include increased risk of predation (Kramer and Drake 2010, Pavlová et al. 2010), inability to adequately perform cooperative behaviors in social species (Angulo et al. 2017), difficulty obtaining sufficient resources (Noel et al. 2006, Neiman et al. 2013), and decreased genetic diversity (Wittmann et al. 2018). These ecological situations can generate what is known as the Allee effect, a density dependent phenomenon in which individual fitness increases as population density increases (Allee 1931, Stephens et al. 1999, Courchamp et al. 2008, Kramer et al. 2009).

Despite an increase in research interest, relatively little is known about the prevalence of Allee effects in wild populations (Gregory et al. 2010). However, over recent years, a growing number of theoretical and experimental studies have contributed to ecological knowledge in this area (Kramer et al. 2018). This accumulation of research has necessitated the need for research synthesis and meta-analysis. As more studies aim to identify Allee effects in populations, between-study patterns and trends can be investigated to improve practical and theoretical understanding of how this ecological phenomenon presents and functions across different groups. Improving this understanding is important because research on Allee effects is diverse (different methods, different taxa, different Allee mechanisms), meaning it is difficult to form general conclusions when comparing the results of these studies.

The conceptual focus of this accumulating research on Allee effects is quite variable. Much of the theoretical literature on Allee effects has focused on demographic Allee effects, defined as a positive relationship between per capita population growth and population density. These studies usually involve identifying the critical Allee threshold, which is the population size at which population growth changes from positive to negative. This is commonly referred to as a strong Allee effect (as opposed to a weak Allee effect, in which population growth is still positive, but the growth rate is reduced

rate at low population densities). In comparison, most experimental work on Allee effects has focused on component Allee effects. Component Allee effects describe a positive relationship between a specific component of individual fitness and population density, for example seed-set in plants (Møeller and Geber 2005), fertilization rates in broadcast spawners (Hobday et al. 2000), or emigration rates in social species (Bonte et al. 2004). This difference in research focus exists because it can be challenging to identify the critical Allee threshold in real populations. This is because when population densities are low in nature, detecting individuals is difficult (Gascoigne et al. 2009). Synthesizing different research approaches, in addition to comparing work on different Allee mechanisms (e.g. mate finding, predation, resource limitation) and taxonomic groups (e.g. plants, vertebrates, invertebrates), can be problematic. However, meta-analysis techniques offer an appropriate method to quantitatively synthesize different study types in ecology and evolution (Koricheva et al. 2013).

This meta-analysis aims to identify whether the measured magnitude of positive density dependence is impacted by Allee effect mechanism or taxonomic group in studies that experimentally manipulated population density with the goal of identifying an Allee effect. Synthesizing these studies presents a significant challenge. For example, as studies on Allee effects are quite varied, formulating a standardized measurement of Allee effect magnitude across study type is not straightforward. The measure of the Allee effect magnitude used here (the positive association between population density and population growth or fitness component) is distinct from the presence of a critical threshold in population growth rate and provides a standardized measure across the largest number of experimental studies. Although a few qualitative reviews on Allee effects have been published (Gascoigne et al. 2009, Kramer et al. 2009), it is our understanding that this is the first meta-analysis on Allee effects and may provide new insights into the ecology of Allee effects across Allee mechanisms and taxonomic groups. This information may help inform ecological management and conservation, as if Allee effects function differently according to Allee mechanism or taxa, different conservation approaches may be needed for different ecological situations or species. Finally, this meta-analysis aims to identify areas of Allee effect research where knowledge is lacking to help guide future research efforts.

Material and methods

Literature searching and data extraction

A meta-analysis was conducted to quantify the magnitude of Allee effects based on experimental manipulations of population density, and we followed PRISMA-EcoEvo guidelines

(preferred reporting items for systematic reviews and meta-analyses in ecology and evolution, O'Dea et al. 2021) to report our synthesis. An initial literature search was conducted using the Web of Science (WOS) Core Collection database (University of South Florida library subscription) on 6 June 2020, using the inclusive keyword string: ('Allee effect' AND 'experiment*'). This search returned 372 articles. A second literature search was conducted on 25 June 2023 in WOS and Scopus using the keyword string ((('population density' OR 'population size') AND ('Allee effect' OR 'positive density dependence' OR 'depensation') AND ('experiment*') AND (ecolog*)). This returned an additional 43 articles from WOS, and 1824 from Scopus. In addition, Pro Quest Open Access Dissertations and Theses was also searched on 25 April 2023 to locate grey literature (relevant but unpublished research), using the following search string: ((('population density') AND ('Allee effect') AND ('positive density dependence') AND ('experiment*') AND (ecolog*)). This search returned 66 dissertation papers (duplicates removed). The search results were downloaded and transformed into a .csv file using the R package 'bibliometrix' (Aria and Cuccurullo 2017). The .csv file was then screened by E. Muir (EM) using the *abstract screener* function of the R package 'metagear' ver. 0.7 (Lajeunesse 2016). This package was used to scan the titles and abstracts of studies to identify studies that appeared to meet the meta-analysis inclusion criteria. A total of 2305 studies were screened, and 162 studies were shortlisted for detailed review. Because the search was focused exclusively on studies considering the presence of positive density dependence, the results cannot speak to the overall prevalence of positive density dependence in nature.

The full texts of the 162 candidate studies were further evaluated by EM to determine whether they met the meta-analysis inclusion criteria and contained relevant data. The inclusion criteria specified studies that experimentally manipulated population density to identify either a component or demographic Allee effect and measured either population growth or change in fitness, independent of whether they found quantitative support for an Allee effect. If a study met these the inclusion criteria but the raw data was inaccessible (e.g. the raw data was not available online and was not extractable from tables or figures), the study was excluded because effect sizes could not be calculated. A total of 62 studies met the meta-analysis inclusion criteria. Experimental outcomes of these studies were obtained from supplementary material, online repositories, or were extracted from the studies either directly (from text, tables etc.) or by reverse engineering figures using Engauge Digitize software (Mitchell et al. 2019). The study outcomes and measurement scales that were extracted varied widely. For example, some studies contrasted population growth/fitness at different density levels (e.g. low, medium, high), while others reported only continuous explanatory variables (e.g. a continuous density gradient).

When isolating the effect of population density, some study designs required additional care to resolve issues of non-independence. For example, in a study that manipulated both population density (meta-analysis criteria) and zinc

concentrations (not relevant to meta-analysis), it was difficult to tease apart the effects of population density and zinc concentration. To address this issue, the study outcomes were separated into subgroups that were analyzed individually. In this case, the data were divided into groups by zinc concentration level before meta-analysis to ensure the calculated effect sizes reflected the impact of population density, not the impact of zinc concentration (Noel et al. 2006). The quality and risk of bias of the studies included in the meta-analysis were not quantitively assessed as quality/bias indicators could not be collected from most studies due to methodological design or incomplete reporting of methods or results. This is a common problem in ecology and evolution as unlike in medical studies, ecological studies are rarely blinded to reduce bias and few studies follow a reporting checklist to ensure the full reporting of results (van Wilgenburg and Elgar 2013, Holman et al. 2015). Instead, each study was individually assessed, and if missing or incomplete information prevented the identification or quantification of density dependence, the study was excluded from the meta-analysis.

Finally, studies were categorized by Allee mechanism, taxa, and Allee effect type. Allee effect type refers to whether the response measured was population growth [demographic Allee effect] or an individual component of fitness [component Allee effect]. To categorize the Allee mechanism, the driver behind the Allee effect was determined. For example, if the reduced population growth at low density was caused by a scarcity of mates, the mechanism was classified at 'mate limitation', or if it was caused an inability to obtain sufficient resources at low population density the mechanism was classified at 'resource limitation'. Supporting information provides detailed definitions of how each Allee mechanism was categorized for this study. Some of these mechanism categories were taken from Courchamp et al. (2008), others were determined based on the study design and findings. Taxa were categorized as broad groups (e.g. plants, vertebrates, microbes), because there were too few studies to investigate narrower taxonomic ranks.

Quantifying Allee effect magnitude

Quantifying Allee effect magnitude was challenging as the studies included in our meta-analysis measured a variety of different response variables. Because of this, the assumption of total-equivalence of scales was not met to allow for a meta-analysis of regression slopes (Becker and Wu 2007). This diversity of measures, units, and models means it is impossible to make generalized and predictive cross-study statements or predict the change in population growth given one unit change in density. Furthermore, some studies of the Allee effect only include two levels (low and high density), while the density ranges of others may be narrow, have few distinct levels, or cover orders of magnitude differences in density. One way to address this non-equivalence of measures and units is to use a common-currency effect size to quantify the magnitude of Allee effects across studies. As wide variety of study outcomes can be converted into Pearson correlation coefficients (r) as effect sizes (Lajeunesse 2013), we opted for

this approach. Here, a higher *r* value indicates a higher correlation between population density and population growth and/or fitness. We interpret a larger positive correlation as an Allee effect of stronger magnitude because it indicates a stronger association between density and fitness. This approach allows the inclusion of the largest range of studies but is not without drawbacks in interpretation.

As each study reported very different methods and results, a variety of methods were needed to extract, calculate, and standardize *r*. First, in studies where *r* was reported, the signs of *r* were adjusted based on study design to ensure positive *r* values indicated positive density dependence (i.e. the Allee effect), and negative *r* values indicated negative density dependence. For example, if a study measured the effect of density on mortality, decreased mortality at high density would be indicative of positive density dependence. By contrast, in a study that looked at the effect of density on seed set, increased seed set at high density would be consistent with positive density dependence. To fix this, we changed the signs of studies that looked at mortality to ensure studies that found positive density dependence had positive effect sizes, and studies that found negative density dependence had negative effect sizes. In studies in that *r* was not directly reported, it was instead calculated from data extracted from bivariate $x-y$ plots using:

$$r = \frac{n\left(\sum xy\right) - \sum x \sum y}{\sqrt{\left[n\sum x^2 - \left(\sum x\right)^2\right]\left[n\sum y^2 - \left(\sum y\right)^2\right]}}, \tag{1}$$

where *x* are density measures, *y* are population growth and/or fitness measures, and n is the total sample size.

However, estimating *r* from Allee effect data was not always straightforward. In some cases, the Allee effect presented as a hump-shaped curve, i.e. the per capita population growth rate was low at low density (the Allee effect), it increased as density increased, and then decreased once the population reached carrying capacity (negative density dependence). This is in contrast to other studies in which the data extracted from the candidate studies only encapsulated the first part of this implied growth curve (the data demonstrated positive density dependence at low population densities, but the density ranges were not high enough to also show negative density dependence at high density). Because of this challenge, tests of quadratic significance were performed to determine whether the data from the studies were linear or quadratic before *r* was calculated. This enabled us to use meta-analysis to later assess whether the magnitude of Allee effects were sensitive to these different modeling approaches.

Then, when the data was significantly quadratic, we calculated the quadratic maximum and truncated the data at this point to isolate the initial positive curve (positive density dependence) and exclude negative density dependence. We then analyzed this data and estimated *r* using the same linear method described in Eq. 1. Finally, for studies that reported only pairwise comparisons of two densities (e.g. studies that compared population growth or fitness at high versus low densities), a Hedges' *d* effect size quantifying the standardized difference between each density was calculated (Eq. 3 in Hedges 1981). This effect size uses the means ($\bar{X}$), standard deviation (*s*), and sample sizes (*n*) of two densities (*A* and *B*) as follows:

$$\text{Hedges}'d = \left(\bar{X}_A - \bar{X}_B\right) \Big/ \sqrt{\left[\left(n_A - 1\right)s_A^2 + \left(n_B - 1\right)s_B^2\right] / \left(n_A + n_B - 2\right)}, \tag{2}$$

and then Hedges' *d* was converted to *r* following Lajeunesse (2013) with

$$r = \frac{d}{\sqrt{d+4}} \tag{3}$$

A total of 155 correlation coefficients were extracted from the 62 studies selected for inclusion in our meta-analysis – 106 of these effect sizes were linear, 18 were quadratic, and 31 effect sizes were obtained from pairwise comparison data using Hedges' *d*. Data is archived at Data Dryad (Muir et al. 2024).

Mixed-effects meta-analysis

Prior to meta-analysis, all Pearson correlation coefficients (*r*) were transformed into Fisher's *Z* effect sizes (Eq. 2 of Olkin and Pratt 1956) with:

$$\text{Fisher's } Z = 0.5\left(\ln\left[1+r\right] - \ln\left[1-r\right]\right) \tag{4}$$

that has a variance of var(Z) = $1/(n-3)$ used as weights in the mixed-effects meta-analysis model. This transformation both normalizes the effect sizes and stabilizes variances (Olkin and Pratt 1956), which is necessary to satisfy the statistical assumptions of meta-analysis (Koricheva et al. 2013). Finally, *k* designates the number of effect sizes or the sample size of meta-analyses.

These Fisher's *Z* effect sizes (that quantify the magnitude of Allee effects across studies) were then analyzed using meta-analysis in R (ver. 4.2.2, www.r-project.org). Our first goal was to test for sources of bias among our effect sizes. Publication bias was assessed using Egger's test (Egger et al. 1997) assuming a fixed-effect meta-analysis (i.e. weighted analysis without random factors) based on the *regtest* function of the R package 'metafor' ver. 3.8 (Viechtbauer 2010). Second, we tested for methodological bias due to the diversity of statistical methods used to quantify Allee effects via either linear, quadratic, or pairwise-contrast models (quantifying Allee effect magnitude). Here, bias was tested using a mixed-effects meta-analysis with statistical method as a fixed effect moderator, and two random effects that accounted for between-study variability (as assumed in all random-effects meta-analyses, τ^2) and the over-representation of multiple

effect sizes per study (γ^2). 'Moderator' is a standard term used in meta-analysis to describe fixed-effect variables in mixed-effect models. They are groupings that test whether variation among effect sizes is associated with differences in study methods, practices, or biological groups. This model was run using the *rma.mv* function of 'metafor', applying the restricted maximum likelihood method (REML) approach to estimate random effects. If methodological bias was detected via omnibus Q_{df}^B tests (df = degrees of freedom as the number of groups minus one, B = between-group differences within moderators; Hedges 1981, Hedges and Olkin 1985), we augmented our final mixed-effects meta-analyses aimed to test conceptual differences among studies (following paragraph) with a third random effects component (ρ^2) accounting for these differences in methodology among linear, quadratic, and contrast-based outcomes of Allee effects. Code is available with the archived data at Dryad (Muir et al. 2024).

Our second goal with meta-analysis was to apply the same mixed-effect model to test the conceptual moderators (Allee mechanism, taxonomic group, Allee effect type). These moderators of groups of effect sizes were pooled according to the Allee mechanisms, taxonomic groups and Allee effect types reported in the studies. The Allee mechanisms described in the studies fell into nine categories (mate limitation, resource limitation, pollen limitation, group living, interspecific competition, fear, predation, parasitism and genetic; see the Supporting information), and the study organisms were grouped into five broad taxa (plants, terrestrial invertebrates, aquatic invertebrates, vertebrates, and microbes). To infer non-zero (significant) effects within the pooled group, 95% confidence intervals not overlapping with zero indicated significant effects, and Q_{df}^B tests were used to infer differences between pooled groups. Our goal with this meta-analysis was to generalize across studies to test potential variation due to Allee mechanism or taxa, but interpretation of these conceptual tests may be complicated by the strong methodological effects of how Allee effect were modelled within studies (e.g. linear, quadratic, pairwise contrasts). To address this issue, we also report all conceptual tests parsed by methodological effects in the Supporting information to better assess the impact of mechanism and taxa on Allee effects.

Results

Study composition and bias

A total of 155 effect sizes were included in the meta-analysis from 62 different experimental studies (full screening process outlined in the PRISMA plot in Fig. 1). These studies encompassed a range of Allee mechanisms and taxa. However, the literature was imbalanced with some groups being studied at a much higher frequency than others. Mate limitation and pollen limitation were the most common Allee mechanisms reported in the studies ($k = 46$ effect sizes calculated for mate limitation studies, $k = 40$ effect sizes calculated for pollen limitation studies), with interspecific competition, fear and
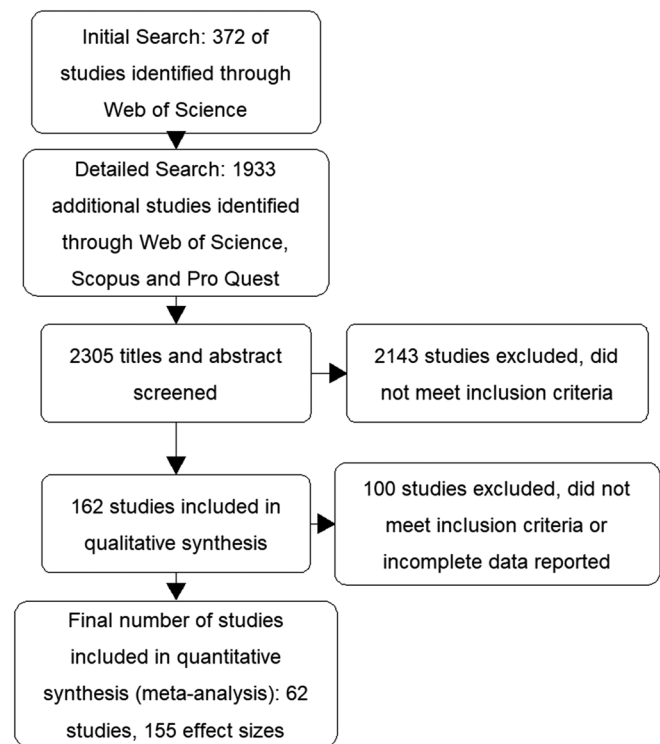

Figure 1. PRISMA plot summarizing the literature searching and screening process of our meta-analysis of Allee effects across 62 studies.

parasitism being the least common ($k = 3$ effect sizes calculated for competition and fear studies, $k = 2$ effect sizes calculated for parasitism studies). Terrestrial invertebrates were the most common taxa studied in experimental Allee effect studies, with studies on this group contributing a total of 52 effects sizes to the meta-analysis. The other taxonomic groups were less common in our literature search ($k = 44$ for plants, $k = 35$ for aquatic invertebrates, $k = 20$ for vertebrates, and $k = 3$ for microbes).

We could not detect publication bias among our effect sizes (Egger's test: $z = 1.56$, $p = 0.1195$, $k = 155$, assuming a fixed-effect meta-analysis), although we recognize that assumptions of this test were violated due to many studies having low sample sizes (n < 15; Ioannidis and Trikalinos 2007). We also aimed to assess whether our meta-analysis could be biased by methodological approaches used to quantify Allee effects (e.g. via linear regression, linear regression with truncated quadratic data, or Hedges' *d* pairwise contrasts), and we were able to detect a significant difference among these three quantitative approaches ($Q^B = 14.91$, df = 2, p < 0.001, k = 155) with a mixed-effect meta-analysis. The pooled effect among each method ranked from large to small magnitudes of Allee effects were: quadratic regression (pooled Fisher's $Z = 1.23$, 95% CI = [0.834, 1.63], $k = 18$); linear regression (pooled Fisher's $Z = 0.557$, 95% CI = [0.379, 0.735], $k = 106$); and Hedges' *d* pairwise contrast (pooled Fisher's $Z = 0.188$, 95% CI = [–0.174, 0.550], $k = 31$). Given these differences among methodological approaches, the following
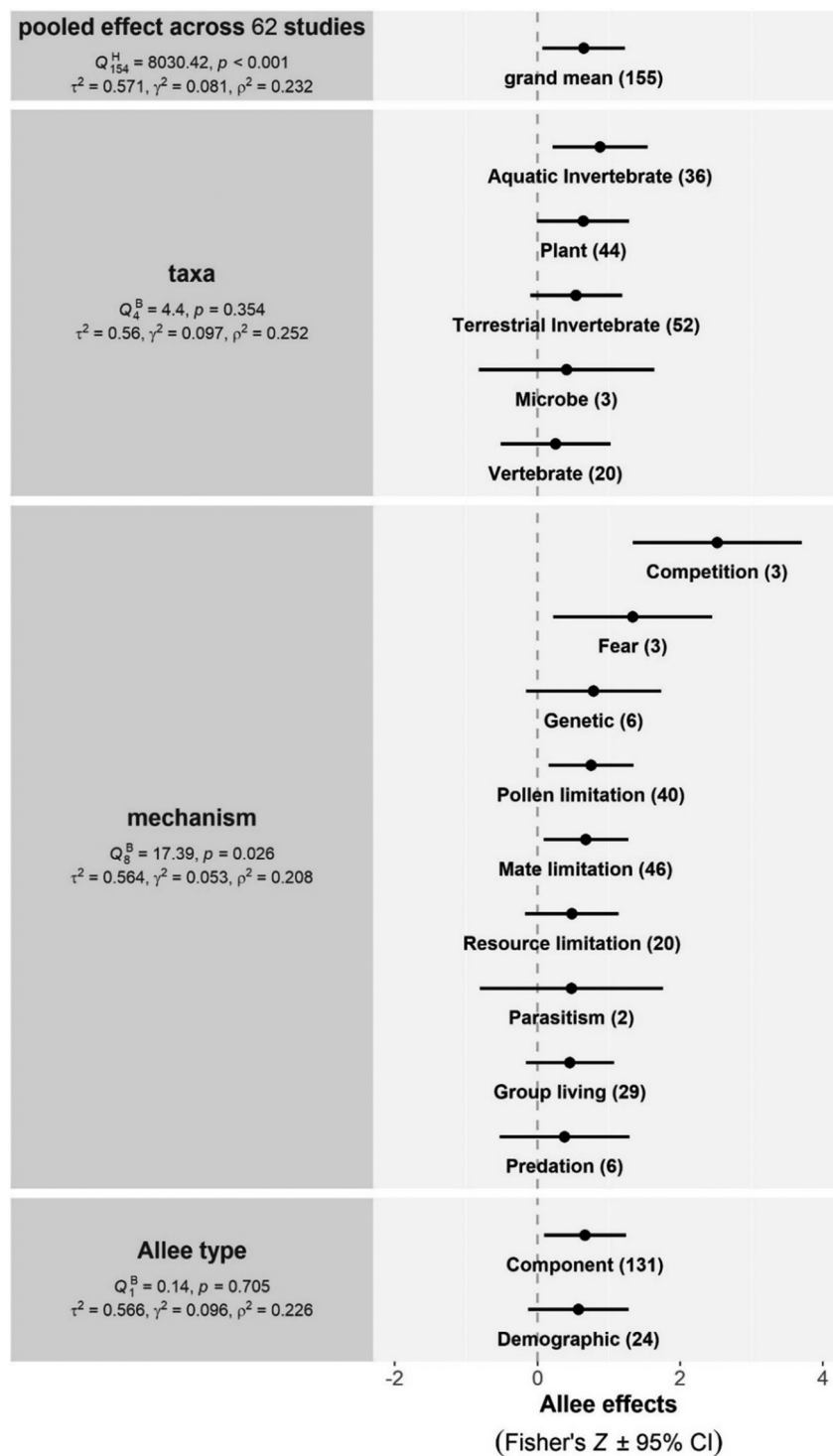
Figure 2. Forest plot of pooled effect sizes (Fisher's Z ± 95% CI) using mixed-effects meta-analysis. The black points indicate the mean magnitude of pooled density dependence – zero indicates no density dependence, positive values indicate positive density dependence with increasing magnitude, and negative values indicate negative density dependence with increasing magnitude. Allee effects caused by inter-specific competition, fear, pollen limitation and mate limitation are shown to be positive with confidence intervals that do not overlap zero, indicating that these mechanisms significantly impacted the magnitude of Allee effects in these studies. Numbers in parentheses indicate the number of effect sizes pooled (k), Q_{k-1}^H is the fixed-effect meta-analysis test for assessing whether heterogeneity exists among all effect sizes, Q_{df}^B is the omnibus test for group differences, τ^2 is the between-study variance of the random-effect meta-analysis, γ^2 is the variance due to the over-representation of multiple effect sizes per study, and ρ^2 is the random-effect component of the model that accounts for differences in methodology used among studies to quantify linear, quadratic, and contrast-based outcomes of Allee effects.

mixed-effect models will include a third random-effects component that controls for heterogeneity associated with these statistical practices (see ρ^2 described in Material and methods), unless otherwise stated.

Overall meta-analysis of Allee effects and sources of variability among studies

The average magnitude of Allee effects across all 62 studies did not overlap zero (pooled Fisher's $Z = 0.59$, 95% CI = [0.426, 0.754], $k = 155$; Fig. 2), indicating an overall significant positive correlation between population density and either population growth or fitness (i.e. positive density dependence). Further, the magnitude of the Allee effects differed among the nine types of Allee mechanisms ($Q^B = 16.43$, df = 8, p = 0.037, $k = 155$; Fig. 2), with interspecific competition having the strongest Allee effects, followed by fear, pollen limitation, and mate limitation. There were no detectable Allee effects among resource limitation, group living, predation, parasitism or genetic Allee mechanisms, as there was no significant correlation between population density and population growth or fitness for these groups.

Taxonomic group was less useful at explaining variation in Allee effect magnitude with no statistical difference among all groups (Q^B = 4.4, df = 4, p = 0.252, k = 155; Fig. 2). However, the results suggest that Allee effects may present more strongly in aquatic invertebrates and plants because the effects sizes for these three groups were significantly non-zero, while the effect sizes for the three other taxa all overlapped zero. The τ^2 values calculated for both the mechanism and taxa models were similar, indicating low heterogeneity and between-study variance. When grouped by Allee effect type (i.e. demographic or component Allee effects), the results also showed no significant effect between the two types ($Q^B = 0.14$, df = 1, p = 0.705, $k = 155$; Fig. 2), however the pooled effect size for component Allee effects was significantly non-zero.

When the results were parsed more minutely by including methodological effects as moderators, results were congruent to those of the overall mixed effects model (Supporting information). However, it is clear that studies requiring conversion of effect sizes to Hedges' d exhibited smaller effect sizes on average.

Discussion

To our knowledge, this meta-analysis provides the first quantitative synthesis of experimental research on Allee effects, and is the first to test how Allee mechanism, taxonomic group, and Allee effect type impact the magnitude of density dependence in experimental systems. Our synthesis demonstrates that the magnitude of Allee effects may be more dependent on Allee mechanism than taxa or Allee effect type, and that Allee effects may function differently depending on the underlying Allee mechanism. Furthermore, the results illustrate that some Allee mechanisms may tend to result in larger Allee effects than other mechanisms, providing potentially important information for conservation managers. The

lack of evidence that Allee effect magnitude was impacted by taxonomic group or Allee effect type suggests that demographic and component Allee effects may present similarly across a broad range of taxa.

A total of nine Allee mechanisms were included in this meta-analysis. Allee mechanism refers to the process that results in positive density dependence within a population, for example, limited mates within a sparse population may inhibit successful reproduction, thus causing a mate-finding Allee effect (Contarini et al. 2009, Régnière et al. 2013). The results of this study showed positive density dependence (positive mean values, confidence intervals did not overlap zero) for several mechanisms reported across these experiments, but not for others (confidence intervals overlapped zero; Fig. 2). However, mechanism groups overlapping zero could have had smaller correlation coefficients and higher variance, perhaps due to lower sample size, or the groups may have included studies that lacked positive density dependence that pulled down the average effect size (Halliday and Blouin-Demers 2016). The results showed that mate limitation and pollen limitation (which can be considered a form of mate limitation) were the two most studied mechanisms; however, it is uncertain if this reflects the prevalence of certain mechanisms in nature or is instead biased by research interest. The other mechanisms were less well-studied, however these studies also successfully identified Allee effects in the study populations. For example the magnitude of Allee effects caused by interspecific competition and fear caused were significantly non-zero. However, as these were the two of the least studied Allee mechanisms, additional confirmation should be sought for these results.

These results suggest that to better understand the potentially differing impacts of various Allee mechanisms, experimental research must focus on a wider range of Allee mechanisms. Likewise, theoretical studies on Allee effects often focus on the dynamics of demographic Allee effects in phenomenological models, however this research does not correspond well to specific mechanisms or to the much lower number of empirical studies on demographic Allee effects. It would be an interesting next step use a systematic review of theoretical studies to see if model results provide support or context for the order of Allee effect magnitudes found here, for example, is mate limitation theoretically predicted to produce Allee effects of greater magnitude than Allee effects driven by predation in models?

Although the meta-analysis found no significant difference across taxa (Fig. 2), these results still offer insight into how Allee effects may function in different taxonomic groups. Of particular interest, the confidence intervals for studies on plants and aquatic invertebrates did not overlap zero. This effect could suggest that plants and invertebrates are more susceptible to Allee effects than other groups; however, these results may also be vulnerable to small sample size in some studies. Similar to the research imbalance in the Allee mechanism studies discussed above, it appears the Allee effect research has also disproportionately focused on certain taxonomic groups. Plants and invertebrates were the most studied taxa, likely because they are the easiest groups to work with.

The other three groups included in this meta-analysis all had effect size confidence intervals that overlapped zero (Fig. 2); however, differences in study design prevalence may matter here if categorical studies that required Hedges'*d* conversion are skewing the results. The taxonomic groups studied in this meta-analysis were also very broad at the Kingdom and Phylum level. A vast range of physiological and behavioral adaptations are seen within each Kingdom and Phylum, and because of this, it is likely that an equally vast range of ecological responses to low population density are seen amongst different species. Although it is helpful to get a broad insight in how Allee effects may present and function in different taxonomic groups, meta-analysis at the more precise species-level would provide a better understanding. However, more work is needed to make synthesis at this level meaningful.

In addition to the problem of small sample size, another potential issue is publication bias. Although the results of the Egger's test showed no evidence of bias, the assumptions of the test were violated meaning bias cannot be discounted. Allee effects are difficult to study by nature, as reflected in the imbalance in research on certain Allee mechanisms and taxonomic groups. This means that the studies included in this meta-analysis may not illustrate the full picture. For example, Allee effects could be equally as likely to result from the understudied Allee mechanisms as the more commonly studied mechanisms, and they may be just as prevalent in vertebrates as they appear to be in invertebrates and plants. Furthermore, negative density dependence is also common in nature. Studies that aimed to identify positive density dependence, but instead found negative density dependence, may not have been published or they may have been reframed in a way that prevented them from showing up in the literature searching procedure conducted in this meta-analysis (e.g. not referring to the term 'Allee effect'). This is a common problem highlighting the need for better reporting and research transparency in ecology and evolution. However, it does not directly interfere with our goal to see how the magnitude of experimentally tested Allee effects varied across different mechanisms and taxa, which is distinct from looking at the prevalence of negative and positive density dependence in experimental populations as a whole. Instead, this study reveals patterns in the magnitude of the Allee effects when looked for, similar to how a meta-analysis of non-consumptive effects does not indicate the prevalence of these effects across all predator–prey interactions (Preisser et al. 2009). As such, the effect sizes included in this meta-analysis cannot be considered representative of all members of a specific taxon or for all cases of a specific Allee mechanism.

As is common in ecology and evolution, study design and outcomes were diverse. The variety of study types and methodologies used in the studies included in this meta-analysis meant multiple methods were needed to calculate effect sizes. Although converting these different effect sizes to correlation coefficients (and then to Fisher's Z) enabled between study comparisons, it also had drawbacks. First, when the different methods used to calculate Fisher's Z were compared, the difference was significant. This could suggest that the different methods used to calculate effect size are not fully compatible, or that the different research methods used may over or underestimate the magnitude of Allee effects. However, tests of between and within study heterogeneity indicated low variance, meaning these differences should not significantly impact the results reported here. Second, correlation coefficients depend on variance amongst replicates, meaning a low (high) correlation coefficient could result from a high (low) degree of variance between replicates, even if the increase in fitness with density is apparently large (small). A meta-analysis of regression slopes would be an ideal approach to quantifying Allee effect magnitude, but combining regression slopes assumes similar X and Y variables with similar reliability of measurement of those variables (Becker and Wu 2007), which is not the case for the Allee effect studies included in this meta-analysis. We chose to assess the broadest set of literature with an inclusive measure of a unitless effect size and believe that correlation coefficients offer an effective tool to capture a key aspect of the strength of support for positive density dependence, namely is there a reliable increase in fitness with population density.

This meta-analysis offers the first quantitative insight into the type, prevalence, and magnitude of Allee effects reported in experimental studies in ecology and evolution. These results may inform conservation as understanding which populations may be particularly vulnerable to Allee effects (either from mechanism, taxa, or Allee type) can help direct management efforts. However, although this meta-analysis provides valuable information, small sample sizes and research imbalance somewhat limit the applications of this work. Currently, there is a greater number of theoretical studies on Allee effects being published than experimental studies on Allee effects (Supporting information), and although this theoretical work is valuable, experimental research on the under-studied Allee effect mechanisms and taxonomic groups is crucial in order to fill the identified knowledge gaps and strengthen the conclusions tentatively made here. Moreover, there is evidence that some species may be subject to multiple Allee effects driven by different mechanisms, creating possible interactions that could be of research interest (Berec et al. 2007, Pavlová et al. 2010). Finally, we think that the challenge of synthesizing effect sizes across studies on diverse species may be reduced if future studies consider a sufficient number of densities and measure population growth rate or other consistent response variables whenever possible. There may be potential to standardize densities if authors can situate experimental densities within benchmarks, such as lowest observed densities, carrying capacity, or the inflection point from positive to negative density dependence.

Incorporating theoretical Allee effect research into future research synthesis could strengthen this work as theoretical methods offer an invaluable tool for understanding the difficult-to-study Allee effect in ecology. Likewise, determining whether experimental and theoretical methods generate consistent results would provide useful information for future syntheses. The results presented here suggest the Allee effect mechanism may impact the magnitude of the Allee effect,

illustrating the importance of research synthesis in understanding this important ecological phenomenon.

Author contributions

Eva J. Muir: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Methodology (equal); Visualization (supporting); Writing – original draft (lead); Writing – review and editing (equal). **Marc J. Lajeunesse:** Formal analysis (equal); Methodology (equal); Supervision (supporting); Visualization (lead); Writing – review and editing (equal). **Andrew M. Kramer:** Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Methodology (equal); Supervision (lead); Visualization (supporting); Writing – review and editing (equal);.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2ngf1vhvj (Muir et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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