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FORUM

Variation in Allee effects: evidence, unknowns, and directions forward

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Abstract Allee effects, positive effects of population size or density on per-capita fitness, are of broad interest in ecology and conservation due to their importance to the persistence of small populations and to range boundary dynamics. A number of recent studies have highlighted the importance of spatiotemporal variation in Allee effects and the resulting impacts on population dynamics. These advances challenge conventional understanding of Allee effects by reframing them as a dynamic factor affecting populations instead of a static condition. First, we synthesize evidence for variation in Allee effects and highlight potential mechanisms. Second, we emphasize the "Allee slope," i.e., the magnitude of the positive effect of density on the per-capita growth rate, as a metric for demographic Allee effects. The more commonly used quantitative metric, the Allee threshold, provides only a partial picture of the underlying forces acting on population growth despite its implications for population extinction. Third, we identify remaining unknowns and strategies for addressing them. Outstanding questions about variation in Allee effects fall broadly under three categories: (1) characterizing patterns of natural variability; (2) understanding mechanisms of variation; and (3) implications for populations, including applications to conservation and management. Future insights are best achieved through robust interactions between theory and empiricism, especially through mechanistic models. Understanding spatiotemporal variation in the demographic processes contributing to the dynamics of small populations is a critical step in the advancement of population ecology.

Keywords Allee threshold · Critical density · Depensation · Extinction · Invasion · Positive density dependence

Introduction

Allee effects have received substantial attention in ecology due to their important role in the dynamics of small or low-density populations, including threatened (Stephens and Sutherland 1999) and invasive species (Wang and Kot 2001; Leung et al. 2004; Johnson et al. 2006), and populations near the edge of a species range (Keitt et al. 2001) or at the nadir of population cycles (Haynes et al. 2009). Originally theorized by W.C. Allee in the context of cooperative behaviors among animals (Allee 1931), the Allee effect occurs when there is a positive effect of population size or density on individual fitness (Stephens and Sutherland 1999; Courchamp et al. 2008). This principle is also referred to as inverse or positive density dependence (Courchamp et al. 1999), depensation (Myers et al. 1995), or undercrowding (Courchamp et al. 1999). The Allee effect has been attributed to a variety of mechanisms resulting in reductions in fitness at low population density including mate or pollen limitation, inbreeding depression, and failure to satiate predators (Gascoigne and Lipcius 2004;

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Kramer et al. 2009; Gascoigne et al. 2009). Although Allee effects have proven difficult to detect empirically (Gregory et al. 2010), they have been observed in species spanning several taxa of plants and animals, and because of this breadth of taxa and the ubiquity of the ecological processes involved, Allee effects are likely widespread (Kramer et al. 2009).

Allee effects are generally described using two classifying terminologies. Component Allee effects describe mechanisms leading to positive effects of population density on any aspect of fitness, while demographic Allee effects occur when one or more component Allee effects translate to a positive relationship between population density and the per-capita rate of population growth (Stephens et al. 1999). These relationships can also be expressed interchangeably in terms of total population size, as opposed to population density, but for simplicity we discuss Allee effects in terms of population density. Component Allee effects may not become demographic Allee effects if relaxation of negative density-dependence at low density compensates for positive fitness effects of increasing density (Hastings et al. 2005). Demographic Allee effects can be further characterized as either weak or strong (Stephens and Sutherland 1999; Courchamp et al. 2008). When strong Allee effects occur, there is a threshold population density, termed the Allee threshold or critical density, representing an unstable equilibrium below which the population growth rate is negative. In deterministic settings the population will go extinct below the Allee threshold without supplementation. Weak Allee effects, by contrast, feature depressed population growth rates at low density, but have no critical threshold.

As the evidence for, and interest in, Allee effects has grown (Kramer et al. 2009), empirical and theoretical studies have grown increasingly nuanced—seeking, for example, to understand interactions between multiple mechanisms underlying Allee effects (Berec et al. 2007; Angulo et al. 2007), impacts of stochasticity (Lee et al. 2011; Potapov and Rajakaruna 2013; Rajakaruna et al. 2013), spatiotemporal variability in Allee effects (Tobin et al. 2007; Robinet et al. 2007; Walter et al. 2015), and interactions between Allee effects and environmental conditions (Gray and Arnott 2011; Kramer et al. 2011). A common theme among these and other recent studies is to investigate the interplay between Allee effects and sources of variability, including demonstrating that many characteristics of Allee effects vary in nature. Here, we use the phrase "variability in Allee effects" to describe variation, in time and/or space, in characteristics of the positive relationship between population density and the growth rate of small populations. Examples of such changes include—but may not be limited to—component Allee effects manifesting as demographic Allee effects in some but not all instances, spatiotemporal variation in the Allee threshold (including thresholds being absent in some populations or years but present in others), and changes in the shape or slope of the population density-growth rate relationship while at low density.

In this paper, we first synthesize evidence for variation in Allee effects and propose four main ways that variation in Allee effects can manifest in the density-growth rate relationship. We then introduce the term "Allee slope," to describe the magnitude of the positive effects of population density on the per-capita growth rate, as a quantitative Allee effect metric and justify its use. Finally, we summarize existing knowledge gaps and describe how theoretical and empirical studies can work together to address outstanding questions. The latter topic is important because theory has contributed greatly to current understandings of population dynamics with Allee effects. However, emerging understandings of variation in Allee effects are largely empirically driven and we consequently describe how the interplay between theoretical and empirical studies can benefit knowledge of this important phenomenon.

Variability in Allee effects

Population dynamics vary spatiotemporally due to factors intrinsic to the population as well as environmental heterogeneity and stochasticity, and Allee effects are subject to these same processes. Some studies simply document that variations in component and demographic Allee effects occur (Tobin et al. 2007; Hoffman et al. 2010; Dooley et al. 2013; Bürgi et al. 2014); meanwhile, a small but growing body of literature investigates factors that cause the strength of Allee effects to vary, and the interplay between Allee effects and other sources of variation in population dynamics (Wagenius et al. 2007; Angulo et al. 2007; Gray and Arnott 2011; Walter et al. 2015). Tobin et al. (2007) offered what we believe to be the first empirical evidence of Allee effects varying in both time and space. By assessing the probability of populations replacing themselves in the following year as a function of population density, Tobin et al. (2007) documented spatiotemporal variation in both the Allee threshold and the rate at which increases in population density lead to increases in the population replacement probability. Additionally, spatiotemporally non-uniform invasion patterns were attributed to variation in the Allee threshold (Tobin et al. 2007). The authors did not investigate the causes of this variability, but other investigations corroborate that Allee effects vary in natural populations and shed light on likely causes and their implications (Angulo et al. 2007; Hoffman et al. 2010; Gray and Arnott 2011; Dooley et al. 2013; Budroni et al. 2014; Bürgi et al. 2014; Kaul et al. 2016).

A handful of mechanisms underlying variability in Allee effects have been identified. Environmental conditions can influence component Allee effects, for instance altering predator densities or how rates of mate-finding scale with population density (Kramer et al. 2011; Larsen et al. 2013; Walter et al. 2015). For example, the presence of a predator-driven Allee effect in some—but not all—populations of an endangered island fox contributed to between-island variations in fox population dynamics, leading some toward extinction (Angulo et al. 2007). Just as the impact on growth rate of individual component Allee effects may vary, multiple component Allee effects are theorized to act interactively and have potentially non-additive impacts on the Allee threshold (Berec et al. 2007). Variation in density-independent factors, not traditionally associated with Allee effects, can also contribute to variation in Allee effects (Hoffman et al. 2010; Gray and Arnott 2011; Dooley et al. 2013; Lynch et al. 2014; Walter et al. 2016). For example, density-independent effects of water pH on the birth and death rates of the sexually-reproducing copepod *Epischura lacustris* were shown to alter an Allee threshold, offering a plausible explanation for time-lags and spatial heterogeneity in the recovery of zooplankton communities from lake acidification (Gray and Arnott 2011).

To date, studies revealing mechanisms of variation in Allee effects have predominantly focused on variation in space rather than time. It is perhaps obvious but nonetheless worth stating that factors leading to temporal variations in Allee effects vary temporally themselves. Cycling predator populations that can fluctuate up to an order of magnitude or greater could greatly influence predator satiation Allee effects. Variation in weather is likely a major driver of temporal variation in Allee effects, operating via direct effects on demography or indirectly through interspecific interactions. For example, variation in temperature could directly influence Allee effects through reproductive phenology, and thus mate encounters, in species whose developmental rates are temperature-dependent (Walter et al. 2015). In principle, any species responding to weather-related cues could experience similar effects. Weather variation can affect the outcome of interspecific interactions such as predation (Ovadia and Schmitz 2004), altering indirectly component Allee effects and other aspects of demography.

In previous empirical studies and theoretical models, we find four characteristic types of variability in Allee effects (Fig. 1). A description of selected theoretical models and the types of variability each model can produce is provided in Table 1. First, the shape of the density-growth rate relationship may remain constant as the growth rate changes equally across all densities, changing the Allee threshold (Fig. 1a; see also Fig. 4b-c in Tobin et al. 2007). Variations in density-independent factors, such as weather or habitat quality, likely underlie this pattern. Second, the Allee threshold may act as a pivot point for the density-growth rate relationship, and the slope of the density-growth rate relationship changes over time or space (Fig. 1b). Third, changes to the slope of the density-growth rate relationship may result in a divergence of growth rate with increasing density and a change in the Allee threshold (Fig. 1c; see also Fig. 3 in Walter et al. 2015). This pattern was produced by varying a component Allee effect in a mechanistic model, albeit one that ignored negative density dependence at high density (Walter et al. 2015). Finally, the Allee threshold and the density-growth rate relationship may be altered at low density, with per-capita growth rates at higher population densities affected little or not at all (Fig. 1d; see also Fig. 1 in Berec et al. 2007; Fig. 2d–f in; Dooley et al. 2013; Fig. 3 in; Hoffman et al. 2010; Fig. 5a in; Tobin et al. 2007).

The pattern illustrated in Fig. 1d, in which variation is greatest at the lowest population density, may best characterize variation in the magnitude of component Allee effect(s). This pattern can be seen in the temporal variation in population replacement below the Allee threshold found in gypsy moth populations in Wisconsin (Fig. 5a in Tobin et al. 2007). Allee effects in gypsy moth are driven, at least partially, by the failure to locate mates at low densities (Contarini et al. 2009). Mechanistic models show that environmental factors can alter rates of mate encounters, and ultimately cause fluctuations in low density population growth rates (Walter et al. 2015, 2016). This does not preclude the possible roles of other mechanisms, environmental or otherwise, interacting to generate variation in low-density population patterns and Allee effects.

In Fig. 1 we largely disregarded dynamics at higher population densities, at which negative density dependence ostensibly drives down the growth rate toward a carrying capacity. This omission in part reflects our inherent focus on small populations. However, for populations subject to Allee effects the impacts of negative density-dependence may be important but are poorly understood. The failure of some component Allee effects to become demographic Allee effects is attributed to relaxed competition at low density (Hastings et al. 2005), and variability in negative density-dependence has been implicated in spatiotemporal patterns in the dynamics of populations also subject to Allee effects (Dooley et al. 2013). Logically, if effects of negative density dependence are strong enough at low densities, then variation in these effects could lead to variation in demographic Allee effects, even if the underlying component Allee effect is unchanged. This pattern may be qualitatively similar to the diverging density-growth rate relationship reflected in Fig. 1c. We are not aware of studies on the interplay between negative density dependence and Allee effects, again likely due to the focus of research on Allee effects on small populations.

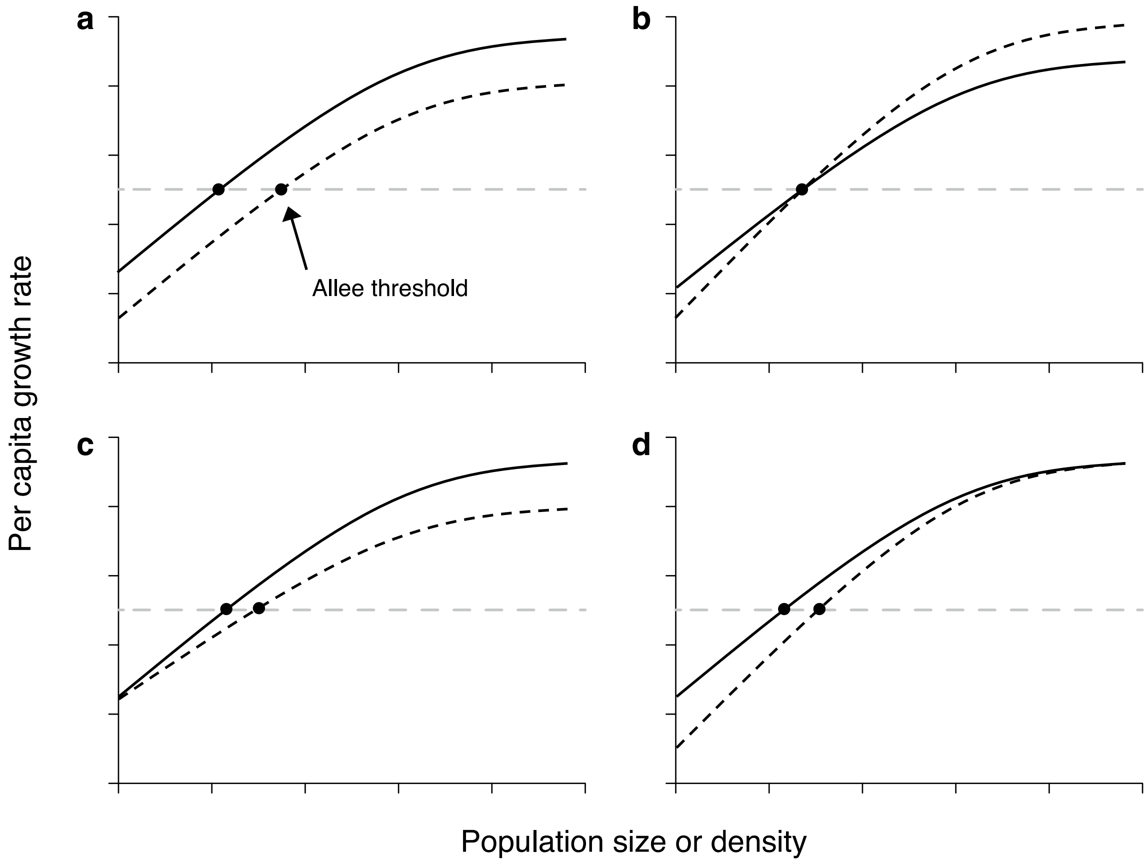

Fig. 1 Illustration of ways in which the Allee effect may vary: **a** the Allee threshold (critical density) changes while the slope remains the same across all densities; **b** the slope changes while the Allee threshold remains the same; **c** the Allee threshold changes as a result of changing the slope; **d** the threshold and the density-growth rate relationship change at low density, while per-capita growth rates at higher population densities affected little or not at all. *Solid* and *dashed black lines* are alternative realizations of the density-growth rate relationship illustrating an idealized pattern of variation in the Allee effect. The *dashed grey line* corresponds to the replacement population growth rate; Allee thresholds (*black circles*) occur where the density-growth rate curve crosses the replacement population growth rate. For similar patterns in published studies of empirical data or mechanistic models, see: **a** Fig. 4b–c in Tobin et al. 2007; c Fig. 3 in Walter et al. 2015; d Fig. 1 in Berec et al. 2007; Fig. 2d–f in Dooley et al. 2013; Fig. 5a in Tobin et al. 2007

Table 1 Five phenomenological theoretical population models with Allee effects (reviewed in Courchamp et al. 2008) capable of producing patterns of variation in low-density population dynamics similar to those in Fig. 1

	Per capita growth rate $g(N)$	Vary	Pattern	References
1	$r\left(1-\frac{N}{K}\right)\left(\frac{N}{K}-\frac{A}{K}\right)$	A r	Figure 1d Figure 1b	Lewis and Kareiva (1993), Amarasekare (1998a, b), Keitt et al. (2001) and Morozov et al. (2004)
2	$r\left(1-\frac{N}{K}\right)\left(\frac{N}{A}-1\right)$	A r	Figure 1c Figure 1b	Gruntfest et al. (1997) and Courchamp et al. (1999)
3	$b+(a-N)(1+cN)N$	a b	Figure 1c Figure 1a	Takeuchi (1996)
4	$\frac{pN}{a+N^2}$	a p	Figure 1d Figure 1a	Hoppensteadt (1982)
5	$N^{\gamma}+r\left(1-\frac{N}{K}\right)$	γ or r	Figure 1c	Aviles (1999)

We indicate what pattern of variation is produced by independently varying different model parameters

While the available evidence cannot resolve which of the above patterns are most common, Fig. 1b seems least likely. We were unable to find empirical examples of per-capita growth rates having a pivot-point at the Allee threshold, but include it because multiple theoretical models have this structure, including model Eqs. 1 and 2 (Table 1). Given evidence that the Allee threshold is an outcome of multiple density-dependent and density-independent factors (Gray and Arnott 2011; Kramer et al. 2011; Dooley et al. 2013; Kaul et al. 2016), it appears that such an outcome could result only when there are tradeoffs between component Allee effects and other processes, and there is no *a priori* reason to believe that this pivot point would be located at the Allee threshold.

Quantifying variation in Allee effects

From our above synthesis of recent literature, we assert that understanding variability in Allee effects and interactions between Allee effects and other spatiotemporally varying population processes has emerged as a vital new direction in population ecology. However, efforts to understand variation in Allee effects may fall short unless description and quantification of Allee effects are improved. The current terminology has limited utility for describing complex variation in Allee effects and its impact on population dynamics. For example, distinguishing strong versus weak Allee effects poorly describes empirical observations that an Allee threshold may be absent in some years or locations, and present but occurring at varying densities in other years or at other places (Tobin et al. 2007; Dooley et al. 2013). The dichotomy between component and demographic Allee effects is useful, but is nevertheless complicated in a context of varying Allee effects.

The most common quantitative metric of Allee effects, the Allee threshold, is similarly limited in two main ways. First, it provides no description of weak Allee effects (i.e., those in which the growth rate is depressed at low density, but there is no critical threshold), which may still affect aspects of population dynamics such as rates of range expansion (Wang and Kot 2001) and could become strong Allee effects under varying environmental conditions. Second, and perhaps more importantly, the Allee threshold is sensitive not only to the magnitude of component Allee effects underlying positive density-dependence, but also factors that do not influence causes of Allee effects (Gray and Arnott 2011; Walter et al. 2016). Hence, despite the Allee threshold's substantial implications for population persistence, it provides little insight into underlying mechanisms, and is a limited indicator of the magnitude of positive density dependence.

It is in this context that we propose the "Allee slope" be adopted as a quantitative metric of Allee effects that can be used to describe multiple types of spatiotemporal variability. By the "Allee slope," we refer to the magnitude of the positive relationship between population size and the per-capita growth rate while at low density[1]. The importance of this relationship is already recognized, since a positive relationship between population density and the per-capita growth rate is the defining characteristic of demographic Allee effects. Moreover, at least two prior studies discuss parameters in different terminology that essentially describe the Allee slope (Stephens and Sutherland 1999; Morris 2002). Allee slopes are more closely linked to the underlying mechanisms leading to variation in Allee effects and provide a continuous variable capable of describing spatiotemporal variation in far greater detail than the present dichotomies. This slope represents the rate at which increases (or decreases) in the population size or density translate into increases (or decreases) in the population growth rate.

Allee slopes have implications for population dynamics and persistence. One can imagine that a population with a strong Allee effect and a shallow Allee-effect slope would decline slowly below the Allee threshold, making it relatively less sensitive to stochastic extinction and offering the potential for intervention before extinction. That population also may have a low maximum per-capita rate of population growth or achieve it only at relatively high densities, making the population slow to rebound from low density. On the other hand, populations with steep Allee slopes might have the potential to rebound quickly from a population crash, but population losses would have large costs in terms of reductions in the population growth rate, and risk of stochastic extinction would be relatively high. From an applied perspective, these distinctions could inform the choice to focus on managing factors related to population growth (e.g., mating success) versus population supplementation (e.g., dispersal).

Empirical studies show that the slopes of Allee effects vary, and suggest that variability is at least somewhat independent of changes in the Allee threshold (Tobin et al. 2007; Hoffman et al. 2010; Dooley et al. 2013). In two studies employing mechanistic models, combining multiple component Allee effects (Berec et al. 2007) or altering rates of mate finding (Walter et al. 2015) affected the Allee slope and Allee threshold together. A subsequent study found variation in the Allee threshold to be driven primarily by increases in density-independent mortality, with little influence of variability in a

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[1] In many models and empirical populations, the relationship between density and growth rate is nonlinear. This concept can be extended as the first derivative of the density-growth rate relationship at the Allee threshold, or perhaps averaged around the Allee threshold or over a range of low population densities.

component Allee effect (Walter et al. 2016). Hence, the Allee threshold and slope may be affected differently by variation in mechanisms underlying Allee effects versus factors not producing Allee effects such as density-independent birth and death rates. As such, the slope of the Allee effect may provide different and complimentary information to the Allee threshold, although further research is required to elucidate the connections between these two factors and evaluate how different aspects of population dynamics affect each.

Directions forward

Many important questions remain and are ripe for investigation. For example, how common are the different types of variability in Allee effects that we propose (Fig. 1)? Relatedly, are there typical spatiotemporal patterns of variation in Allee effects, and what are the implications for populations (Walter et al. 2017)? Do different population dynamic factors affect the density-growth rate relationship in predictable ways? Moreover, Allee effects can have substantial bearing on population extinctions, the establishment of non-native species, and range expansion, all of which may involve management applications. Some implications for management are intuitive; for example, unaccounted-for variations in strong Allee effects could adversely impact the efficacy of management efforts. However, a more complete understanding of how and why Allee effects vary is likely to suggest ways to exploit this aspect of a species' ecology to achieve desirable management outcomes, particularly when the goal is to drive a pest species to extinction (Tobin et al. 2011).

Given the importance of variation in Allee effects and gaps in detailed knowledge of the causes and consequences of this phenomenon, it is clear that further study is needed. In addition to evaluation of the Allee slope, what sorts of studies will advance the field? Empirical studies have drawn our attention to this phenomenon, but in part because Allee dynamics are notoriously difficult to study in natural populations we envision a substantial role for theory, and robust interplay between theory and empiricism. Theory can form the basis for understanding interactions between component Allee effects and other population processes, and also predict how variation in Allee effects influences key outcomes such as population establishment, persistence versus extinction, and range boundary dynamics (Walter et al. 2017).

Questions raised above and throughout this paper mainly fall into three categories: (1) characterizing the range of patterns of variation in Allee effects in natural populations; (2) elucidating mechanisms of variation; and (3) determining consequences and applications. The first of these categories is clearly a space where empiricism predominates. More populations need to be studied and the findings synthesized to understand in detail what types of variation occur naturally (e.g., Fig. 1), and the spatial and temporal structures of variations (e.g., is spatial variation patchy or clinal? Do temporal variations have serial autocorrelation?). This can occur through both new studies and re-analysis of existing datasets, as earlier studies may have overlooked the possibility of variation in Allee effects. Note also that current evidence for variation in Allee effects comes largely from invertebrates, and one goal of future work should be to broaden these investigations to other taxa.

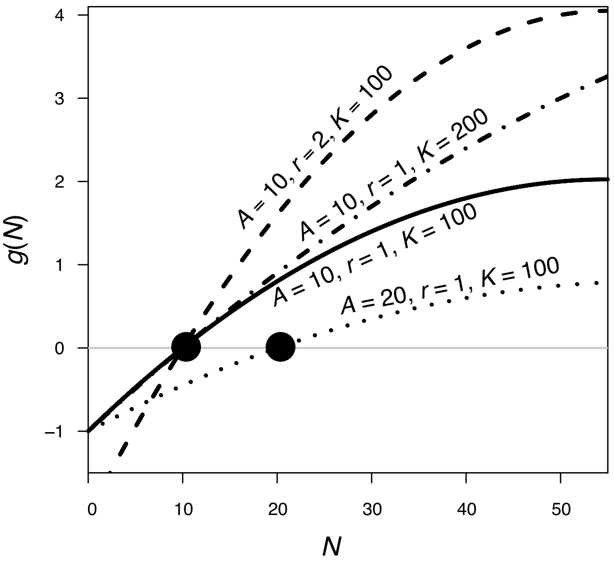

Fig. 2 An example, using Eq. 2 from Table 1, illustrating effects of the Allee threshold parameter (*A*), intrinsic rate of population growth (*r*), and carrying capacity (*K*) on the density-growth rate relationship. The *grey line* indicates the replacement population growth rate, and *black points* indicate Allee thresholds

Understanding mechanisms of variation—both fluctuations in the magnitude of component Allee effects and impacts of other population processes on Allee effects—is one area where theory should be especially profitable, but the choice of model is critical. Many commonly used theoretical models of Allee effects are phenomenological in the sense that they do not specify an underlying mechanism [an incomplete list from Courchamp et al. (2008) is provided in Table 1]. Generally, these models directly control the strength of the Allee effect using a prescribed model parameter, determining the shape of the density-growth rate relationship through an *a priori* choice of equation (e.g., Keitt et al. 2001; Wang et al. 2002; Johnson et al. 2006). As an example, the parameter *A* in Table 1 Eqs. 1, 2 sets the Allee threshold, and the Allee slope is jointly determined by *A* and other specified parameters (Fig. 2). For some questions, the greater generality that can be achieved by remaining agnostic to the underlying biology serves an important purpose. However, in the context of understanding causes of variation, mechanistic models, in which Allee effects emerge from the dynamics of the model rather than being prescribed, are preferable. Indeed, much of our existing understanding of mechanisms of variation in Allee effects comes from mechanistic models, and there are several mechanistic models producing Allee effects in the literature. These span a continuum from highly system-specific to relatively more general (a non-exhaustive list includes: Berec et al. 2007; Robinet et al. 2008; Fagan et al. 2010; Kramer and Drake 2010; Shaw and Kokko 2014; Ribeiro 2015). Existing models can be studied to explicitly address how variability in component Allee effects and other demographic factors influence the density-growth rate relationship, or form the basis for development of new models. Controlled experiments, for example using artificial laboratory populations (Kramer and Drake 2010; Kaul et al. 2016), can develop further insights and help bridge the gap between theory and the dynamics of wild populations.

Lastly, variations in Allee effects have implications for conservation and management that should be further explored. Here too, we envision robust interplay between empiricism and theory, including a role for phenomenological theoretical models. Questions like "how does changing the Allee slope affect rates of population extinction" need not consider mechanisms of variation, and in fact the generality of a simple phenomenological model may be advantageous. On the other hand, applications to specific systems may require more realistic, data-driven approaches and thus empirical data will be critical to defining problems for study and parameterizing models. Direct empirical tests of manipulations inspired by theoretical investigations are possible for pests and exotic invaders, but should be approached cautiously for populations of conservation concern since the costs of failure may be great and strength of inference may be limited by small samples.

One challenge to those seeking to study variation in Allee effects empirically is the difficulty of detecting Allee effects. A wide variety of statistical approaches appear in the literature, and it is not clear which approach or approaches are best, and under what conditions. Most empirical studies showing variation in Allee effects applied flexible and simple approaches, such as non-parametric smoothing (Tobin et al. 2007), linear (Hoffman et al. 2010), and quadratic models (Dooley et al. 2013). In contrast, a study of over 1100 natural populations spanning many taxa found sparse evidence for demographic Allee effects by assessing the support for phenomenological theoretical population models representing a random walk, exponential growth with and without an Allee effect, and logistic growth with and without an Allee effect (Gregory et al. 2010). This pattern raises the possibility that common phenomenological theoretical population models perform poorly at describing how growth rates change with population densities in real populations experiencing Allee effects, and at detecting Allee thresholds. We clarify that we see a distinction between phenomenological theoretical models and fitting statistical models, which can also be considered phenomenological in the sense that they do not specify an underlying mechanism, but are generally less prescriptive of the form of the density-growth rate relationship.

Whether common phenomenological theoretical models truly are poor descriptors of real-world density-growth rate relationships, of course, should be rigorously evaluated with the goal of identifying the models and statistical techniques that best reflect biological reality and offer the most optimal balance between errors of omission and commission. Beyond the aforementioned approaches, recently developed Bayesian techniques are promising (Sugeno and Munch 2013; Stenglein and Van Deelen 2016). The growing accessibility of Bayesian and likelihood-based approaches may be particularly helpful to this area of research by better accounting for error and uncertainty, and by enabling the fitting of more process-based models.

Conclusions

Ecologists have begun to document variations in Allee effects and the dynamics of populations subject to them, to investigate mechanisms underlying these variations, and to evaluate their implications for important population processes including extinction and range expansion. This represents a significant advance, building from the classical Allee effect concept, which largely assumed deterministic, spatiotemporally homogenous systems. For broad questions like "what causes variability in Allee effects?" and "how do varying Allee effects affect important outcomes like extinction and range dynamics?" the answers are partial at best, and many significant questions are currently unaddressed. Combining mechanistic models with controlled experiments and empirical data on real-world populations will be key to moving forward. One hindrance to moving forward is overemphasis on the Allee threshold, because it provides limited insight into the forces regulating a population. Alternatively, we suggest investigating the slopes of Allee effects because they are more closely linked to underlying mechanisms that lead to demographic Allee effects. Broadening knowledge of how multiple demographic processes interactively contribute to the dynamics of small populations is a critical step in the advancement of population ecology, with applications to contemporary issues including the conservation of declining species, the establishment and spread of non-native invaders, and range shifts resulting from environmental change.

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