ECOLOGY LETTERS

Ecology Letters, (2011) **14**: 615–624 doi: 10.1111/j.1461-0248.2011.01614.x

REVIEW AND SYNTHESIS

Exploiting Allee effects for managing biological invasions

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Abstract

Biological invasions are a global and increasing threat to the function and diversity of ecosystems. Allee effects (positive density dependence) have been shown to play an important role in the establishment and spread of non-native species. Although Allee effects can be considered a bane in conservation efforts, they can be a benefit in attempts to manage non-native species. Many biological invaders are subject to some form of an Allee effect, whether due to a need to locate mates, cooperatively feed or reproduce or avoid becoming a meal, yet attempts to highlight the specific exploitation of Allee effects in biological invasions are surprisingly unprecedented. In this review, we highlight current strategies that effectively exploit an Allee effect, and propose novel means by which Allee effects can be manipulated to the detriment of biological invaders. We also illustrate how the concept of Allee effects can be integral in risk assessments and in the prioritization of resources allocated to manage non-native species, as some species beset by strong Allee effects could be less successful as invaders. We describe how tactics that strengthen an existing Allee effect or create new ones could be used to manage biological invasions more effectively.

Keywords

Allee dynamics, biological invasions, component Allee effect, demographic Allee effect, invasion ecology, invasive species management, non-native species.

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INTRODUCTION

While considerable ecological intellectual investment was spent on negative density dependence, that is, that overcrowding was a primary force in the dynamics of populations (e.g. Nicholson & Bailey 1935), Allee concentrated on 'undercrowding' dynamics (Allee 1938; Allee *et al*. 1949). He and his colleagues observed that in many species, low-density populations, though perhaps free from intraspecific competition, were not always destined for positive population growth. They argued that some species depended upon cooperative or gregarious behaviours when foraging, evading natural enemies, raising their young, conditioning their environment or locating and selecting mates. Although Allee's work dates back to the 1930s and 1940s, the critical importance of his work was not realized until much later, first within the conservation biology community that likewise observed that certain processes could result in declining per capita population growth rate with decreases in population density. Thus, there could be a minimum population density threshold below which rare and endangered species are driven towards extinction (Courchamp *et al*. 2008).

Invasion biologists also now realize the importance of Allee effects, albeit from the opposite perspective of conservation biologists (Taylor & Hastings 2005). Whereas conservation biologists may attempt to minimize Allee effects so that extinction is less likely, invasion biologists should consider Allee effects as a benefit in limiting establishment success or the spread of an invading species. Allee effects may also be of critical importance to understanding life-history traits associated with species that are successful invaders. For example, in sexually reproducing species, mate-finding failure can often be a cause of an Allee effect in low-density populations, while in gregarious species, behaviours such as cooperative feeding, defence and breeding can be challenged in sparse populations (Kramer *et al*. 2009). Regardless of the mechanism or mechanisms behind an Allee effect, its existence provides a potential Achilles' heel that could be exploited and enhanced, or even created, in the management of non-native species.

In this review, we first briefly review Allee effects and the role they play in biological invasions to set the stage for how they could be exploited to manage invasions. We then consider current and potential strategies that exploit or could exploit an Allee effect, which can be used in eradication or containment programs. We also highlight conceptual approaches for exploiting an Allee effect, which can be used in efforts to manage the arrival, establishment and spread of invasive pests, and in doing so develop context-based recommendations geared at managing a non-native species with the concept of Allee effects in mind. To supplement our references to the primary literature in this review, we present additional references in Appendix S1.

THE ALLEE EFFECT

The Allee effect refers to a positive relationship between individual fitness and population size or density. (We will speak mostly of density, even though we recognize that some Allee effects operate on population size). There are many references that describe and define the Allee effect (e.g. Stephens *et al*. 1999; Taylor & Hastings 2005; Berec *et al*. 2007; Courchamp *et al*. 2008; Appendix S1). Our objective here is not to duplicate these efforts; however, to facilitate an understanding of Allee effect manipulation to the detriment of unwanted invaders, we will describe succinctly component and demographic Allee effects.

Component Allee effects arise when a decrease in one or more fitness components result from a decrease in population density, such as when individuals fail to locate mates in sparse populations or when there are too few individuals in a population to saturate natural enemies. When component Allee effects, whether caused by one or several interacting mechanisms, lead to a decline in per capita population growth rates as population density decreases, then this is known as a demographic Allee effect. Component Allee effects may not necessarily result in a demographic Allee effect. For example, advantages of being in a low-density population, such as reduced intraspecific competition, could compensate sufficiently for the reduction in a component of individual fitness (Fig. 1, Courchamp *et al.* 2008). Nevertheless, both are critical in our discussion because it is component Allee effects that are or could be exploited, and component Allee effects must be sufficiently exploited to result in a demographic Allee effect so that populations decline.

There are numerous causes for an Allee effect in low-density populations; these include inbreeding depression, reduced foraging efficiency and the failure to attract or locate mates, saturate or repel natural enemies or overcome host defence mechanisms (Courchamp *et al.* 2008). Any or a combination of these mechanisms can reduce per capita population growth rates. Because many non-native populations that are introduced initially consist of a small number of individuals, they are often subject to Allee dynamics. New invaders can also be influenced by the degree of invasibility in the habitat in which they arrive (Lonsdale 1999), and although invasibility is a separate factor, it can interact with and sometimes enhance an Allee effect.

THE ROLE OF ALLEE EFFECTS IN BIOLOGICAL INVASIONS

Biological invasions are a global problem that is largely a consequence of ever-increasing trade and travel (Lockwood *et al.* 2007). In particular, global trade has dramatically increased in recent years. The world's busiest maritime ports each handle more than 500,000 tonnes of cargo each day, and products are shipped continuously around the world, occasionally with unwanted hitchhikers such as insects and pathogens within solid wood packaging materials or on imported plants, and aquatic species that are transported in ship hulls and ballast water (Hulme *et al.* 2008). Moreover, new species can be carried to new destinations through seemingly innocuous articles such as personal airline baggage (Liebhold *et al.* 2006). In general, there are four stages of the biological invasion process: (1) arrival, (2) establishment, (3) spread and (4) impacts to environments and economies (Lockwood *et al.* 2007), and Allee effects can be particularly important during establishment and spread (Taylor & Hastings 2005; Liebhold & Tobin 2008).

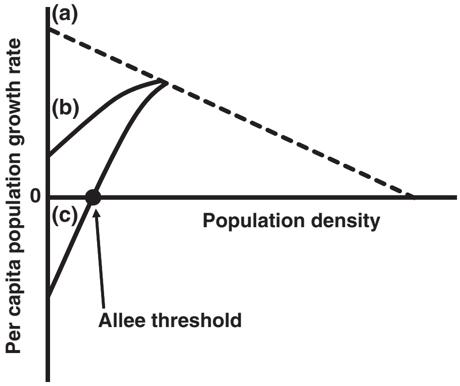

Figure 1 Representation of the change in the per capita population growth rate over increasing population density. (a) Classic negative density dependence. (b) Weak Allee effect in which the population growth rate declines at low densities but remains positive. (c) Strong Allee effect in which the population growth rate is negative at low densities. The Allee threshold is thus the minimum population size to ensure persistence (modified from Taylor & Hastings 2005).

After its arrival to a new habitat, a species will either establish or go extinct. Fortunately, most arriving populations seem to fail to establish, perhaps because they arrive in a new habitat in low numbers that are subject to Allee dynamics and stochasticity (Williamson & Fitter 1996; Liebhold & Bascompte 2003; Simberloff & Gibbons 2004; Lockwood *et al.* 2005; Drake & Lodge 2006). Although it is challenging to quantify the number of invasions that fail, previous studies have highlighted that successful introductions are more consistently observed following releases, and often multiple releases, of larger numbers of individuals (Stiling 1990; Hopper & Roush 1993; Leung *et al.* 2004; Lockwood *et al.* 2005; Simberloff 2009).

The process of new species establishment is not only important following initial arrival, but it is also linked to the rate of spread following successful establishment because of the importance of stratified dispersal in biological invasions. In nearly all successful biological invasions, spread includes the coupling of localized dispersal with population growth (Skellam 1951), often resulting in an asymptotically linear increase in the distributional range radius through time (Shigesada & Kawasaki 1997). This reaction-diffusion process is perhaps best exemplified by the classic analysis of the spread of the muskrat, *Ondatra zibethicus* (L.), in Europe (Elton 1958). However, more often than not invaders spread through stratified dispersal in which disjunct population 'jumps,' through which new colonies arrive and establish ahead of the expanding population front, are coupled with local population growth and diffusive spread (Shigesada & Kawasaki 1997). In many biological invasions, these jumps are facilitated by the anthropogenic, atmospheric and hydrological movement of life stages (Lockwood *et al.* 2007).

Regardless of the mechanism of dispersal as well as the relative contribution of short- and long-range dispersal, Allee effects can have a profound influence on spread. The dispersal of individuals from a source population to a new area is conceptually akin to the arrival stage after which a new population may or may not successfully establish. In some cases, new founder populations that arise from long-range dispersal are comprised of few individuals over a limited spatial extent, such as when life stages are transported anthropogenically (Lewis & Kareiva 1993; Memmott *et al.* 2005; Liebhold & Tobin 2006). As these new populations furthermore arise in areas that are devoid of conspecifics, it is not surprising that the spread of invasive species has been shown to be influenced by Allee dynamics (Lewis & Kareiva 1993; Hastings *et al.* 2005), resulting in initial transient periods within which populations nearly do not expand, slower rates of spatial spread and invasion pinning (Keitt *et al.* 2001; Taylor *et al.* 2004; Tobin *et al.* 2007).

MANAGEMENT STRATEGIES THAT EXPLOIT AN ALLEE EFFECT

Because of the importance of Allee dynamics in the invasion dynamics of non-native species across several taxa (Taylor & Hastings 2005; Kramer *et al.* 2009), efforts to reduce the density of populations below an Allee threshold (Fig. 1) can be an effective strategy in efforts to manage invasive pests. In particular, culling, regardless of the technique used (e.g. pesticides, mass trapping of individuals and shooting and trapping individuals), is a commonly used tactic in efforts to manage population densities of native and non-native pest species alike. However, efforts to manipulate Allee dynamics or create an Allee effect within the context of biological invasions are less documented, as are attempts to capitalize on diverse mechanisms of Allee effects across taxa in efforts to develop context-based strategies. The primary mechanisms behind an Allee effect can vary among taxa (Table 1), suggesting corresponding differences in approaches to exploit Allee effects in the management of biological invaders. In our attempt to synthesize current knowledge into a framework for exploiting Allee dynamics in non-native species management, we now address current and potential strategies that exploit or could exploit an Allee effect.

Culling

Because Allee effects act upon low-density populations, the removal of individuals from a population could result in a density that is below an Allee threshold (Fig. 1, Taylor & Hastings 2005). Thus, culling strategies can be potentially used to exploit Allee dynamics across a diversity of taxa (Table 1). Conceptually, culling tactics can be broadly classified into one of three categories: (1) strategies that decrease the population density below an Allee threshold but neither modify an existing Allee effect nor create a new one, (2) strategies that modify an existing Allee effect but do not create a new one and (3) strategies that create a new Allee effect. Moreover, a management tactic could be classified in any of these categories depending on its specific use. For example, culling continuously over time, such as through repeated pesticide applications, would modify the current population density but also could affect the overall population dynamics, resulting in an increase in the Allee threshold (see Appendix S2).

A method used to manage many biological invasions is the application of pesticides. In most of these cases, the demographic Allee effect is not affected but by culling a large enough fraction of the population, the surviving population could fall below an Allee threshold and proceed towards extinction without further intervention (Fig. 2b, Liebhold & Bascompte 2003; Liebhold & Tobin 2008). Culling methods often depend on the taxa being targeted, and include the removal of host material that is suspected to be infested with an invasive species (i.e. plant pests, Poland & McCullough 2006), cleansing of vehicles on which invasive species can be transported (i.e. aquatic pests on ships, Lewis *et al.* 2009), manual removal of individuals (Johnson *et al.* 1990), herbicidal applications against subpopulations of plants (Taylor & Hastings 2004), shooting (Frederiksen *et al.* 2001), trapping (Chu *et al.* 2003) and aerial poisoning and baiting (Howald *et al.* 2007). The efficiency of culling can be reduced when negative density-dependent effects compensate for a decrease in population density. For example, in the great cormorant, *Phalacrocorax carbo sinensis* L., the effect of culling at the 1998–1999 level (i.e. 17 000 birds shot) was limited, while increasing the annual number of culled individuals to 30 000 still had a limited effect; however, shooting 50 000 birds per year led to extinction within 20–40 years (Frederiksen *et al.* 2001).

Although a sustained removal of a fixed fraction of the population per unit time (culling based on constant effort) increases mortality rate in a density-independent manner and thus would not lead to a component Allee effect, it could still enhance an existing one (Boukal & Berec 2009). Culling tactics can also produce a component Allee effect that otherwise would not exist, and if such a component Allee effect can be exploited to produce a strong demographic Allee effect, then sufficiently small populations will decline towards extinction. An example is culling based on constant yield. If a constant number of individuals is removed per unit time, then the per capita survival probability declines as population density declines; hence, giving rise to a component Allee effect (Courchamp *et al.* 2008; Boukal & Berec 2009). This is because at low densities, a constant number of individuals removed would represent a proportionally larger fraction of the population than at higher densities.

Disruption of successful mating

Many species reproduce sexually. Successfully locating mates in space within the reproductive period generally declines with decreasing density, which can result in deaths exceeding births and hence, population extinction (Boukal & Berec 2009; Gascoigne *et al.* 2009; Tobin *et al.* 2009). The failure to locate viable mates can also be compounded in nascent invading populations establishing outside of their native range because within such isolated colonies, population loss due to emigration may not be compensated by immigration (Berec *et al.* 2001; Robinet *et al.* 2008). Seasonal asynchrony in development between males and females can further challenge

Table 1 Summary of the primary mechanisms documented to contribute to an Allee effect across taxa (c.f. Berec *et al.* 2007; Courchamp *et al.* 2008; Kramer *et al.* 2009) and possible management tactics that could exploit Allee effects

Taxon	Primary mechanism(s)	Ways to exploit an Allee effect
Birds	Cooperative defence, cooperative breeding, cooperative feeding	Culling
Fish	Predator satiation, cooperative defence	Culling, predator augmentation
Invertebrates – aquatic	Mate-limitation, predator satiation	Culling, disruption of mating, predator augmentation
Invertebrates – terrestrial	Mate-limitation, cooperative feeding, predator satiation	Culling, disruption of mating, increase host vigour, predator augmentation
Mammals	Cooperative defence, cooperative breeding, cooperative feeding, predator satiation	Culling, mating disruption through sterilization, predator augmentation
Plants	Pollination failure, inbreeding	Culling
Reptiles/amphibians	Mate-limitation	Culling, disruption of mating

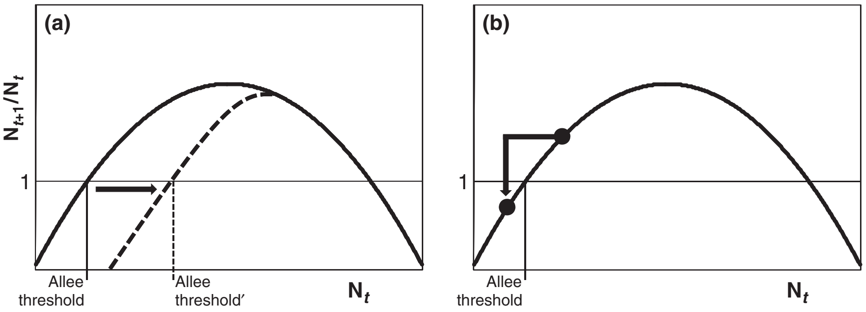

Figure 2 Exploiting an Allee effect in population management. The change in population density, N_{t+1}/N_t is plotted as a function of density at the beginning of the generation, N_t. (a) Strategies such as mating disruption, which do not directly affect population density, can strengthen an existing Allee effect due to mate-finding failure; thus, a higher density N_t is required to surpass the modified Allee threshold′. (b) Removing individuals from a population may not affect the Allee threshold as in (a), but it could still lead to population decline even if not all individuals are killed. Some tactics, such as mass trapping, or a combination of tactics, could effectively accomplish both (a) and (b) (modified from Liebhold & Tobin 2008).

successful mate-location in sparse populations (Calabrese & Fagan 2004; Robinet *et al.* 2007). It is thus not surprising that some of the more effective management strategies that essentially exploit an Allee effect are those that disrupt the mating process (Yamanaka & Liebhold 2009).

Techniques that disrupt successful mating are probably best known in insect population control (Cardé & Minks 1995; El-Sayed *et al.* 2006; Yamanaka 2007), but are not exclusive to insect populations (Ziv *et al.* 1981; Li *et al.* 2007). One common approach is to deploy synthetically produced pheromones that chemically interfere with the male's ability to locate females. The precise mechanism of reduced mating remains unknown for most species, but it is suspected that continual exposure to high levels of pheromones effectively shuts down male searching behaviour due to adaptation, or that males are simply unable to pinpoint the location of a calling female (Yamanaka 2007). Another management tactic that decreases the rate of successful mating is the sterile male release technique (Krafsur 1998; Boukal & Berec 2009), or the sterilization of one sex, such as in mammal or bird species (Dell'Omo & Palmery 2002; Deredec *et al.* 2008). Unlike the use of pheromone applications to reduce the ability of males to locate females, releases of sterile males or sterilizing individuals in the population depend upon mate-finding with the goal of reproductive failure.

Because mate-finding failure can already be a source of a component Allee effect even in the absence of management (Gascoigne *et al.* 2009; Tobin *et al.* 2009), the use of tactics that disrupt mating success can strengthen this effect. Since mating disruption tactics do not kill individuals, the result is that a higher density of individuals in a population would be needed to ensure population persistence. From an applied management perspective, populations that otherwise would exceed an Allee threshold or be subject to a weak Allee effect in the absence of these tactics could then fall below the threshold or be subject to a strong Allee effect when these tactics are applied (Fig. 2a). The sterile male release technique can also create a mate-finding Allee effect if none is present in its absence (Boukal & Berec 2009). Furthermore, the use of culling tactics could be used to strengthen an existing Allee effect due to mate-location failure, such as the use of sex pheromone-baited traps that are deployed en mass (i.e. mass trapping) to reduce the male population (Borden 1989; Yamanaka 2007). In such a case, the decrease in male density can also be complemented with the chemical inhibition of those remaining males from locating females.

Augmentation of natural enemy populations

Virtually every type of organism is subject to predation. However, interactions between predators and prey are varied and Allee effects in prey due to predation may arise in certain circumstances. First, it is necessary to distinguish between the numerical response (predator population growth that tracks prey abundance) and the functional response (behavioural changes in individual predator feeding rates in response to prey abundance) of predators to prey density. The magnitude of the numerical response, if any, varies considerably among pairs of predator and prey species; however, numerical responses generally do not produce positive density dependence in prey growth (Varley *et al.* 1973) that is characteristic of an Allee effect. In contrast, there is good evidence that Type II functional responses are capable of producing an Allee effect in a variety of biological systems (Gascoigne & Lipcius 2004), including those involving terrestrial insects (Bjørnstad *et al.* 2010), aquatic species (Kramer & Drake 2010) and mammals (McLellan *et al.* 2010).

The strategy of introducing a new generalist predator or increasing the density of an existing predator population could produce or increase the strength of the component Allee effect arising from a Type II functional response respectively (Fig. 3, Gascoigne & Lipcius 2004). As such, augmentation of generalist predator abundance could be a tactic applicable against invasive species. The potential for predators to drive populations to extinction has been raised from the context of conservation of rare species (Courchamp *et al.* 2008), but

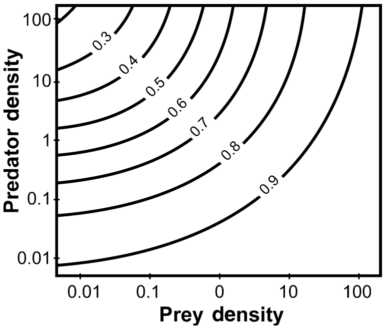

Figure 3 Survival probability (as denoted by contours) of prey as a function of prey and predator density when assuming a Type II functional response (modified from Gascoigne & Lipcius 2004). Note that any augmentation of predator abundance will increase the strength of the component Allee effect caused by predation.

the potential for augmenting natural enemy populations to promote extinction of invading populations has received only modest attention. Theory suggests that releasing specialist natural enemies shortly after a successful species invasion can slow down or prevent further spread, or even reverse its spread and potentially lead to extinction (Fagan *et al.* 2005; Hilker *et al.* 2005). A key to reversing the spread is the presence of an Allee threshold in the invading species. Models of the interaction between the invasive Pacific lupine, *Lupinus lepidus* Douglas and its herbivorous insect natural enemies (*Filatima* sp. and *Staudingeria albipenella* (Hulst)), on Mount St. Helens showed that the chance of reversing the invasion decreased when the temporal lag between plant and herbivore arrivals increased (Fagan *et al.* 2005). For the control agent to be successful, high natural enemy dispersal rates relative to that of its prey are thus required.

One of the few empirical examples where the release of natural enemies has lead to the widespread extinction of a non-native species was the release of the generalist insect parasitoid *Compsilura concinnata* (Meigen), which has been implicated as causing the dramatic population collapse and range retraction of the brown-tail moth, *Euproctis chrysorrhoea* (L.), in eastern North America (Elkinton *et al.* 2006). Introduced outside of Boston, Massachusetts in 1897, *E. chrysorrhoea* quickly spread into most of New England by 1914, but subsequently began to collapse to its present range, which is restricted to isolated patches along the most northern tip of Cape Cod, Massachusetts (Elkinton *et al.* 2006). Although *C. concinnata* is justifiably considered as a biological control failure due to its pronounced inimical non-target effects (Simberloff & Stiling 1996; Strong & Pemberton 2000), it does provide evidence that natural enemies can induce extinction and reduce the range of an invading species.

Another example of how predator populations might potentially be manipulated is provided by the gypsy moth, *Lymantria dispar* (L.). This species is native to most of temperate Eurasia but has been expanding its range in eastern North America. It is occasionally accidentally introduced to western North America where surveys are annually conducted to find newly arrived populations that are subsequently eradicated, mostly through aerial application of microbial pesticides (Hajek & Tobin 2010). Predation by generalist predators, mostly mice in the genus *Peromyscus*, is regarded as the largest source of mortality in low-density gypsy moth populations established in North America (Elkinton *et al.* 1996). Mortality caused by predators is related both to *Peromyscus* density and to *L. dispar* density through a Type II functional response (Elkinton *et al.* 1996), thus contributing to a demographic Allee effect (Bjørnstad *et al.* 2010). Furthermore, it has been shown that predator populations can be augmented through winter feeding and that this produces greater levels of mortality in *L. dispar* populations (Elkinton *et al.* 2004). Though predator augmentation experiments have only been conducted in areas where *L. dispar* is widely established, it may be practical to utilize augmentation of predator populations through winter feeding as a tool for eradicating new *L. dispar* colonies. Generalist predators, such as *Peromyscus* spp., are known to significantly affect a variety of forest-dwelling insect herbivore species so this method could have applications for numerous species.

Chemical enhancement of host plant defence

One of the most important groups of biological invaders are invertebrate herbivores, in part due to the frequency of the movement of plants and plant products along global trade pathways and their potential impacts on agriculture (Lockwood *et al.* 2007; Hulme *et al.* 2008). Fortunately, plants are capable of deploying a variety of chemical defences against attacking herbivores (Gatehouse 2002), although these defences are sometimes insufficient especially against herbivores with which plants have not previously evolved (Eyles *et al.* 2007). An example can be seen in comparisons between the insect borers *Agrilus anxius* Gory and *A. planipennis* Fairmaire. The former species is native to North America and caused significant mortality to non-native birch species planted in North America, while native birch species were rarely killed (Nielsen 1989). The latter species, *A. planipennis*, is native to Asia to which its native ash species are resistant, while non-native ash species are extremely susceptible (Poland & McCullough 2006).

Plant defensive compounds, upon ingestion, can reduce growth, inhibit digestion or induce mortality in foliage- and phloem-feeding insects (Christiansen *et al.* 1987; Karban & Myers 1989; Gatehouse 2002). In some cases, plant defences can be overcome when herbivores exist in such high numbers that plants are not able to produce defensive compounds in sufficient quantities. Consequently, many individuals of a new invader may be required to successfully colonize a host plant. For example, in the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, at least 40 attacks per m^2 on an individual tree were required to overcome the effect of tree defensive compounds on their brood (Raffa & Berryman 1983). This mass colonization behaviour through the use of aggregation pheromones is typical among tree-killing bark beetles, and efforts to disrupt aggregation through semiochemical treatments could maintain a population at densities below the threshold required for successful colonization (Borden 1989). Also, efforts to limit plant or stand stress that often serve as a precursor to attacks by bark beetles and other insects (Christiansen *et al.* 1987), or chemically or genetically boost plant defensive compounds (Dudareva & Pichersky 2008), could induce or strengthen a component Allee effect due to a failure to overcome host plant defences (Nelson & Lewis 2008).

Plant-induced defensive volatiles can also be detected by herbivore natural enemies, such as parasitoids, that can use these compounds to locate hosts (Rasmann *et al.* 2005). These tritrophic interactions among host plants, herbivores and natural enemies could have profound implications in the management of non-native invasive species (Turlings & Ton 2006). For example, the chemical induction of plant defensive compounds could potentially result in two component Allee effects. First, there is an Allee effect caused by a failure to overcome enhanced host defence (Nelson & Lewis 2008). Second, because natural enemies respond positively to host plant defensive compounds, there could be an Allee effect due to the failure to satiate a greater abundance of natural enemies (Degenhardt *et al.* 2003). Although these component Allee effects may not individually translate into a strong demographic Allee effect on their own, the concurrent combination of both could increase the probability of a strong demographic Allee effect (Berec *et al.* 2007). These tactics could also be enhanced through the use of semiochemicals applied under 'push-pull' strategies (Agelopoulos *et al.* 1999; Cook *et al.* 2007), whereby the invader is drawn to a specific area, in this case an area of plant hosts that have been induced to produce defensive compounds. Although we recognize that wide-spread implementation of this approach may be not economically feasible, smaller-scale operations that specifically target a newly arriving population could be an economically feasible strategy against non-native insect pests. At the very least, the manipulation of host plant chemistry in an effort to induce an Allee effect presents an intriguing and novel concept in invasive species management.

Exploiting Allee effects across space

The management of non-native populations is typically more practical when the target population is distributed across a smaller spatial extent (Liebhold & Bascompte 2003; Simberloff 2003; Liebhold & Tobin 2006). In parallel, conservation biologists recognize the importance of not only the spatial extent of rare and endangered species but also fragmentation due to habitat loss (Fahrig 1997; Courchamp *et al.* 2008). Although habitat loss is not a cause of an Allee effect, it can reduce population size such that the population could then become susceptible to an Allee effect (Amarasekare 1998; Keitt *et al.* 2001; Courchamp *et al.* 2008). Allee (1938), when addressing the notion of a minimum viable population size, noted that the minimum number of elephants within a herd in South Africa could vary from 25 to over 300 depending on the range on which the herd resided. He also noted that early efforts to control tsetse fly, *Glossina* spp., populations in Africa were successful when habitat-rich areas were targeted for management, and that there was no need 'to catch the very last flies' when the population fell below the minimum viable size; rather, the remaining flies 'disappeared spontaneously from the area' (Allee 1938).

The loss of habitat and fragmentation, which are a detriment to rare and endangered species, are complementary in attempts to eliminate unwanted species from an area. Consequently, selective and spatially limited habitat modifications could be used to exploit an existing Allee effect if done on a limited time scale but one of sufficient duration to achieve eradication, such as in the case of terrestrial (Suckling & Brockerhoff 2010) or aquatic animals (Hopkins *et al.* 2011). A population or metapopulation of non-native species could be spatially managed through site-specific control tactics so that large populations are fragmented, or that certain smaller patches across a metapopulation connected through dispersal are targeted. The result could be sufficient fragmentation that eliminates recolonization through patch-to-patch dispersal, and smaller population densities in each fragmented patch, which could then be subjected to an Allee effect or to tactics that exploit an Allee effect (Fig. 4). Prior work has highlighted that invading species with an Allee effect must often exceed a spatial threshold, in addition to a density threshold, to persist and establish (Lewis & Kareiva 1993; Vercken *et al.* 2011); thus, sufficiently small and distant patches could lead to extinction of the population. Also, habitats could be manipulated to conserve natural enemy populations and thus potentially enhance biological control of invasive species (Jonsson *et al.* 2010). Such tactics could be complementary to those that strengthen or create an Allee effect, including the use of habitat manipulation against the non-native species itself.

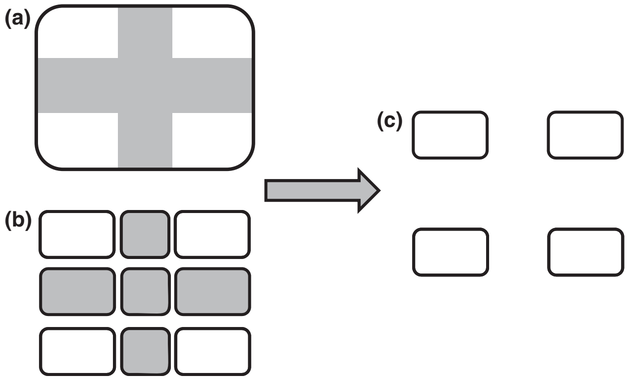

Figure 4 Site-specific control tactics (denoted by shaded areas) can be used against an invasive species population that is widely distributed across space (a), or against a selected number of patches within a metapopulation (b) as a means to fragment the remaining population (c) that in turn can be subjected to Allee effects or additional control tactics that can exploit one or several Allee effects.

Because of the important role of stratified dispersal in biological invasions, exploiting an Allee effect in spread management has an inherent spatial component. Propagules that arrive ahead of the leading edge of an invading species have many characteristics that often are subject to Allee dynamics. These new founder populations typically exist at low densities, are distributed over a small spatial scale, and are far enough away from the leading edge such that they are no longer connected with the established area through dispersal. Past research on the *L. dispar* invasion of North America has revealed that most newly arrived colonies go extinct without any management intervention (Liebhold & Bascompte 2003). Because Allee effects can play an important role in new colony establishment, thereby affecting the speed of invasion (Taylor *et al.* 2004; Tobin *et al.* 2007), they can in turn be exploited to improve management strategies (Taylor & Hastings 2004; Liebhold & Tobin 2010). In particular, propagules that arrive ahead of the expanding front could be strategically fragmented through control tactics or selectively targeted based upon their density and spatial extent so that only fragmented colonies remain (Fig. 4).

RISK ASSESSMENTS

As the world continues to become increasingly interconnected, biological invaders will continue to arrive to new habitats on an unprecedented scale. Although advances have been made to exclude organisms through regulatory activities, it will never be possible to exclude all species through the inspection of shipping vessels, cargo and other transport vectors as a means to limit unwanted introductions. Thus, optimizing quarantine and inspection programs that target habitats and species most likely to be invaded or invasive, respectively, is critical to minimize the number of noxious invaders that establish given financial and logistical constraints. For example, some species could be beset by such a strong Allee effect that their establishment in a new area is unlikely. However, identifying which species are more invasive than others is not an easy task. The difficulties in predicting which species can successfully establish in new areas and when founding populations are small could reflect a greater attention to high-density dynamics and the eruptive potential of outbreaking species instead of constraints they face at low densities. Past work has highlighted the importance of an invader's life-history traits during all phases of the invasion process (Kolar & Lodge 2001) and the importance of the genetic architecture of a founding population in driving establishment success (Lee 2002).

In conservation management efforts, species are sometimes reintroduced to restore them to habitats from which they were previously displaced. Such efforts are conceptually equivalent to the arrival and subsequent establishment of biological invaders. To maximize establishment success in conservation management, a reintroduction strategy could be to maximize the number of releases (e.g. increase propagule number), maximize the number of individuals released (e.g. increase propagule size) and to distribute reintroductions in space and time to minimize the risk of establishment failure (e.g. reduce the risk of extinction due to inimical stochastic events) (Leung *et al.* 2004; Courchamp *et al.* 2008). Propagule size, in particular, tends to be an important factor in determining establishment success (Hopper & Roush 1993; Leung *et al.* 2004; Lockwood *et al.* 2005; Simberloff 2009). The natural history details of both the intended host target and the released enemy also play a role in establishment success (Stiling 1990). Thus, in the case of biological invasions, applying inverse strategies could minimize establishment success.

Due to variation in life histories among invaders, some species could require a considerably larger founder population size to overcome an Allee effect and establish upon arrival, while in others, the founder population size may not need to be large. The invasion of Europe by *O. zibethicus* is thought to have started with only five individuals, and the European starling, *Sturnus vulgaris* L., established in North America from only a 'few pairs' (Elton 1958). The founding *L. dispar* population in North America is reported to have consisted of only a few egg masses (Tobin *et al.* 2009). In contrast, the European spruce bark beetle, *Ips typographus* L., one of Europe's most economically important forest pests, is continuously and consistently intercepted by US and New Zealand ports outside of its native European range. Yet, it has never established in either (Brockerhoff *et al.* 2006), even though it has been argued that phytophagous species from Europe, in general, may be more adapted for invasion success because of selection for plasticity during the Pleistocene and Holocene that was marked by spatially disjunct metapopulations subject to unstable conditions (Mattson *et al.* 2007). Perhaps one needs not look any further than the role that Allee effects play in limiting its establishment success. Many species of bark beetles, including *I. typographus*, rely on mass attack mechanisms facilitated by aggregation pheromones to overwhelm host tree defence responses (Raffa & Berryman 1983; Christiansen *et al.* 1987). Although aggregation pheromones represent an adaptive strategy in native ranges by which conspecifics can mount sufficient numbers to overcome host resistance, they would not necessarily be productive in an introduced area devoid of conspecifics. Consequently, depending on details of natural history, the number of individuals in the founding population (i.e. population size) may need to be high for establishment to be successful, even when the frequency of introductions (i.e. propagule number) occurs at a high rate.

MULTIPLE ALLEE EFFECTS AND THEIR SYNERGISTIC INTERACTION

The incorporation of multiple strategies that induce, enhance or create an Allee effect can be an important consideration in the design of an appropriate management response. Mechanisms responsible for positive density dependence in individual fitness have long been considered in isolation. Recently, the concept that multiple Allee effects could interact in a non-additive fashion has attracted increased attention, and species that possess two or more component Allee effects are not uncommon (Berec *et al.* 2007). Small pack sizes of the African wild dog, *Lycaon pictus* (Temminck), for example, can suffer from many concurrent causes of an Allee effect, including reduced foraging efficiency, increased kleptoparasitism of carcasses, reduced cooperative breeding, reduced gene flow and reduced protection of young (Courchamp *et al.* 2000). In plants, reduced seed set in sparse populations, owing to the failure to attract pollinators (Anstett *et al.* 1997), could also be coupled with disproportionate predation on the resulting seeds, owing to the failure to satiate seed predators. Small overwintering groups of the Alpine marmot, *Marmota marmota* L., have difficulties in finding mates and decreased survival due to less efficient social thermoregulation (Stephens *et al.* 2002), as do small overwintering populations of the Monarch butterfly, *Danaus plexippus* L. (Wells *et al.* 1990).

The interactions of two or more component Allee effects can have profound ramifications in the dynamics of populations (Oostermeijer 2000; Berec *et al.* 2007). Two component Allee effects that each give rise to a strong demographic Allee effect on their own may interact such that the resulting Allee threshold will be larger than the sum of each Allee threshold; such multiple Allee effects have been termed superadditive (Berec *et al.* 2007). Special cases of synergy also occur when a weak Allee effect and a strong Allee effect combine to significantly enhance an Allee threshold, or when two weak Allee effects combine to give rise to a strong one. These special cases imply that even weak Allee effects, which separately may be considered inconsequential, could induce a strong Allee effect when combined.

The synergy among Allee effects and superadditive Allee effects, in particular, can thus have immense practical importance in invasive species management. This importance becomes even greater given that some component Allee effects can be generated artificially through pest control techniques such as mass trapping, release of natural enemies and release of sterile conspecifics (Boukal & Berec 2009; Yamanaka & Liebhold 2009). The more individual component Allee effects that a species faces, the stronger the resulting demographic Allee effect, the higher the corresponding Allee threshold, and in eradication programs, the more feasible it could be to reduce pest populations below this threshold towards extinction (Liebhold & Bascompte 2003; Liebhold & Tobin 2008; Boukal & Berec 2009). Even if eradication is not the goal, the presence of multiple Allee effects can still be a benefit in achieving the desired management goals, and less management effort could be needed for a desired outcome (i.e. reduction in rates of spread, Taylor *et al.* 2004) providing that the optimal combinations of Allee effects can be exploited. Moreover, even individual weak Allee effects need not be discounted if they can be manipulated synergistically.

CONCLUSION

All biological invaders, upon their arrival to a new area, must successfully establish or go extinct. Many are likely subject to some form of an Allee effect, whether due to a need to locate suitable mates, cooperatively feed or reproduce, or avoid becoming a meal for another species. The strength of this effect can vary tremendously among species, and some species are beset by such a strong Allee effect that their potential for invasion is limited. Although there are numerous documented invasion pathways by which non-native species can be transported around the world (Liebhold *et al.* 2006; Lockwood *et al.* 2007; Hulme *et al.* 2008), only a minority of arriving species are believed to become established in new environments (Williamson & Fitter 1996; Simberloff & Gibbons 2004; Brockerhoff *et al.* 2006). It would be naïve to believe that the lack of successful establishment, and the economic and environmental harm that can follow successful establishment, is simply due to sheer luck. As is evident from prior analyses of the role of propagule pressure in the invasion process (Stiling 1990; Hopper & Roush 1993; Leung *et al.* 2004; Lockwood *et al.* 2005; Drake & Lodge 2006; Simberloff 2009), the number of individuals in a founding population is a critical element in driving establishment success because populations initiated at higher densities are typically not limited by Allee dynamics.

There are many biotic and abiotic factors, such as the presence of suitable hosts and a compatible climate that are important during the arrival, establishment and spread stages of biological invasions (Lockwood *et al.* 2007). Programs to manage invasions, whose goals range from eradication to containment, typically target populations that are established but still exist at low densities. At these densities, Allee effects can play a dominant role in the dynamics of invader populations and hence they can be potentially exploited for management. A primary consideration in exploiting Allee dynamics in management programs against an unwanted invader is determining if the targeted species is affected by Allee dynamics, and if so, identifying the primary mechanisms that contribute to Allee effect and evaluating the availability and feasibility of a management strategy that exploits these mechanism (Table 1). Fortunately, there is modest guidance from the literature. In *L. dispar*, a strong Allee effect due to mate-finding failure has been exploited in both eradication and spread containment, often through the use of mating disruption tactics (Liebhold & Bascompte 2003; Tobin *et al.* 2009). Management of the non-native plant *Spartina alterniflora* Loisel is thought to be optimized by the culling of plant subpopulations, effectively exploiting an Allee effect due to pollination failure (Taylor & Hastings 2004; Taylor *et al.* 2004). The use of culling and habitat fragmentation through dredging techniques was used against the brown mussel, *Perna perna* (L.), and effectively reduced populations below a minimum density required for survival and reproduction (Hopkins *et al.* 2011). A modelling approach has suggested that culling sufficient numbers of *P. carbo sinensis* could led to extinction by effectively exploiting cooperative breeding behaviour (Frederiksen *et al.* 2001). Because species across taxa are influenced by different mechanisms generating component Allee effects, corresponding management approaches can vary (Table 1). Despite the logistic differences in the types of strategies that might be implemented, all of these methods function to exploit Allee dynamics in populations being targeted.

Although Allee and his colleagues first proposed the idea of positive density dependence several decades ago (Allee 1938), the role of Allee effects in conservation and invasion ecology have only been more recently considered (Taylor & Hastings 2005; Berec *et al.* 2007; Lockwood *et al.* 2007; Courchamp *et al.* 2008). Even less prevalent is the consideration of Allee effects and specifically, their possible exploitation, in the management of non-native species. This is especially surprising since many management tactics used in eradication efforts against non-native species already effectively exploit, perhaps unknowingly to personnel in charge of eradication efforts, an Allee effect. Contrary to the notion that control tactics must kill 100% of the non-native population to achieve eradication success (Dahlsten *et al.* 1989), populations subject to Allee dynamics that are reduced to a density below an Allee threshold could proceed towards extinction on their own. This has non-trivial ramifications because the costs associated with killing all or nearly all individuals is disproportionally greater than killing the portion of the population above an Allee threshold. Indeed, conservation biologists recognize the importance of Allee thresholds, which is why strategies are developed to manage rare and endangered species *before* populations become so low that extinction is inevitable. The converse principle is to our benefit and thus could be exploited, especially if the gap between the theory of Allee effects in biological invasions and the implementation of management programs against a biological invader can be bridged.

ACKNOWLEDGEMENTS

We thank Franck Courchamp (University of Paris South), Andrew Kramer (University of Georgia) and Kenneth Raffa (University of Wisconsin) for helpful comments and suggestions on an earlier draft of this manuscript. We also appreciate the comments from three anonymous referees. Part of this work was conducted in conjunction with the 'Applying population ecology to strategies for eradicating invasive forest insects' Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #EF-0553768), the University of California, Santa Barbara, the State of California and the U.S. Forest Service Eastern Forest Environmental Threat Assessment Center, Asheville, North Carolina. Ludek Berec also acknowledges funding from the Institute of Entomology, Biology Centre ASCR (Z50070508).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional references relevant to this review.

Appendix S2 How different ways of culling interact with an Allee effect.

Editor, Andrew Sih
Manuscript received 20 October 2010
First decision made 25 November 2010
Manuscript accepted 3 March 2011

Appendix S1: Additional References

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Appendix S2: How different ways of culling interact with an Allee effect

Consider the following simple population model,

$$N_{t+1} = \lambda N_t \frac{N_t}{N_t + \theta}, \qquad (1)$$

which involves a mate-finding Allee effect and for simplicity does not involve any negative density dependence. In short, population density N_{t+1} at time t+1 equals the per capita fecundity λ times the population density N_t at time t times the fraction $N_t/(N_t + \theta)$ of individuals that succeed in finding mates and reproduce; θ is the Allee effect strength. Setting $N_{t+1} = N_t = A$, the Allee threshold is

$$A = \frac{\theta}{\lambda - 1} \ . \qquad (2)$$

Thus, populations with densities above A thrive, while those below A are doomed to extinction.

We now consider different types of culling, using the application of pesticides as an illustrative example. When assuming that a fraction p ($0 < p < 1$) of individuals die from the pesticide application, we consider the minimum value of p that would be needed to eradicate a population under different conditions. Since the use of a pesticide prior to reproduction is more efficient than targeting a population after reproduction is complete, we consider only the former.

1. ***Applying a pesticide one time***

Technically, this is the simplest approach. Let the current population have density *N* and subject it to one pesticide application. To eradicate the population, we require its next season's density to fall below the Allee threshold,

$$\lambda(1-p)N\frac{(1-p)N}{(1-p)N+\theta} < A \ , \qquad (3)$$

which results in

$$p > p_1 = 1-\frac{A+\sqrt{A^2+4A\lambda\theta}}{2\lambda N} \ , \qquad (4)$$

which is the minimum fraction to be killed. Thus, one application of a pesticide does not affect the strength of an existing Allee effect – the Allee threshold equals A – but simply pushes the current population density below the Allee threshold (Liebhold & Bascompte 2003; Liebhold & Tobin 2008).

2. ***Applying a pesticide every year***

The use of a pesticide every year requires a change in the model (Eq. 1) as the application now becomes a regular part of the species' life cycle according to:

$$N_{t+1} = \lambda(1-p)N_t \frac{(1-p)N_t}{(1-p)N_t + \theta} \ . \tag{5}$$

The Allee threshold, A_p, corresponding to the model (Eq. 5) is thus

$$A_p = \frac{\theta}{(1-p)[(1-p)\lambda - 1]} \ . \tag{6}$$

To eradicate the population, we again require that the population density in the next time step falls below the Allee threshold:

$$\lambda(1-p)N \frac{(1-p)N}{(1-p)N + \theta} < A_p \ . \tag{7}$$

Solving the equation (7) for *p*, the minimum fraction to be killed p_2 is a solution of the fourth-order equation in (1-*p*),

$$\lambda^2 N^2 (1-p)^4 - \lambda N^2 (1-p)^3 - N\theta(1-p) - \theta^2 = 0, \tag{8}$$

satisfying $0 < p < 1$. Thus, applying a pesticide regularly and in every year, we affect both the Allee effect strength and push the current population density below the Allee threshold. Because of this, we expect $p_2 > p_1$.

3. ***Applying a pesticide every year with increasing efficiency as population density declines***

In the absence of an Allee effect (i.e., with $\theta = 0$ in the model in Eq. 5), maintaining the control efficiency *p* fixed over time cannot create an Allee effect. However, if we allow *p* to be flexible such that it increases as population density *N* declines, an Allee effect could emerge. For example, if

$$p(N) = \frac{1}{1 + cN} \ , \tag{9}$$

then for a positive constant *c*, inserting (Eq. 9) into (Eq. 5) with $\theta = 0$ gives

$$N_{t+1} = \lambda N_t \frac{N_t}{N_t + 1/c} \ , \tag{10}$$

which is a population model with an Allee effect that gives rise to an Allee threshold $1/[c(\lambda-1)]$; this is equivalent to replacing θ by $1/c$ in the model (Eq. 1). To some extent, this is analogous to constant yield control (reducing population density by the same amount at each time step), since this also becomes more difficult and requires more effort as population density declines. Indeed, if we model constant yield control as $N_{t+1} = \lambda N_t - E$, the Allee threshold becomes $E/(\lambda - 1)$.

Combining the model (Eq. 5) with $\theta > 0$ and with density-dependent control effort (Eq. 9), a double Allee effect occurs and the population model is

$$N_{t+1} = \lambda N_t \frac{N_t}{N_t + 1/c} \frac{N_t}{N_t + \theta(1 + 1/cN_t)} \quad . \tag{11}$$

Comparison and discussion

We will now apply the above-derived theory to the gypsy moth, *Lymantria dispar* (L.), a non-native species in North America for which there is abundant data on its population dynamics, demographics, management, and the role of Allee effects in its dynamics (e.g., Elkinton & Liebhold 1990; Liebhold *et al.* 1992; Tobin & Blackburn 2007; Tobin *et al.* 2009). For this species, the parameters λ and θ can roughly be estimated as 15 and 105, respectively (Robinet *et al.* 2008). As expected, applying a pesticide each year decreases the minimum control efficiency required to eradicate a population relative to a single application (Fig. A1). Interestingly, at high enough population densities, the minimum control effort required when using only a single application is so high that it can be virtually impossible to achieve, which suggests that when considering these two options, the yearly application of pesticides is the only viable approach for eradicating high density populations.

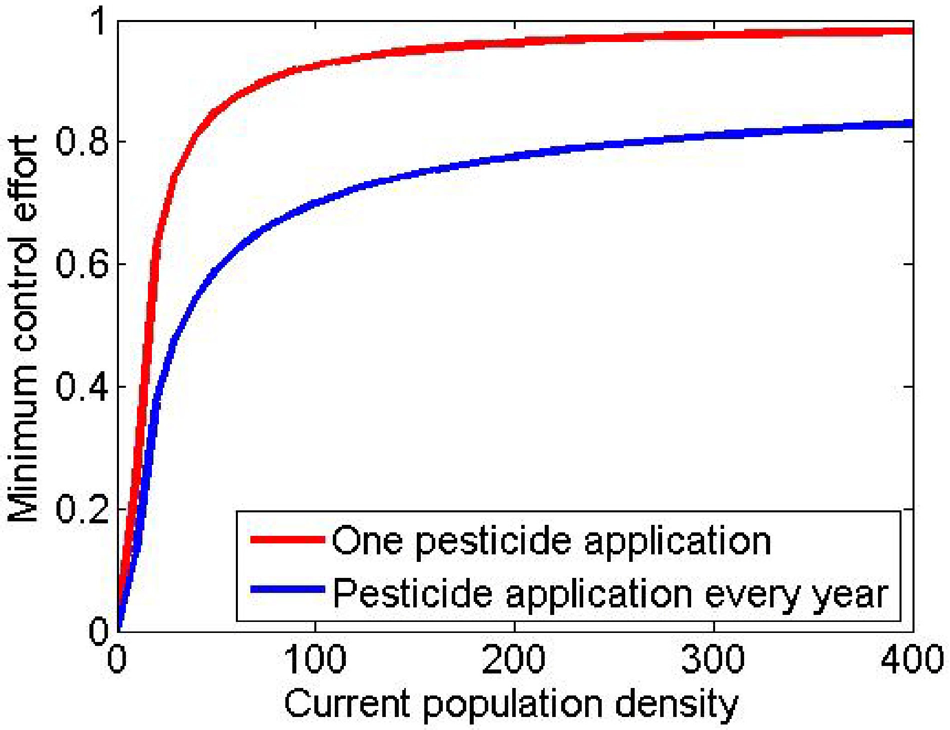

Figure A1. Minimum control efficiency required to eradicate the pest population under two pesticide application options based upon the density of the target population.

A double Allee effect – a mate-finding Allee effect and the Allee effect due to density-dependent control effort – is always superadditive, meaning that the Allee threshold due to the double Allee effect exceeds the sum of Allee thresholds due to single Allee effects (Fig. A2, Berec *et al.* 2007). This synergistic effect of the interaction of the two component Allee effects increases as c declines; that is, the lower is the decline of the density-dependent control effort $p(N)$ in (9) with increasing N.

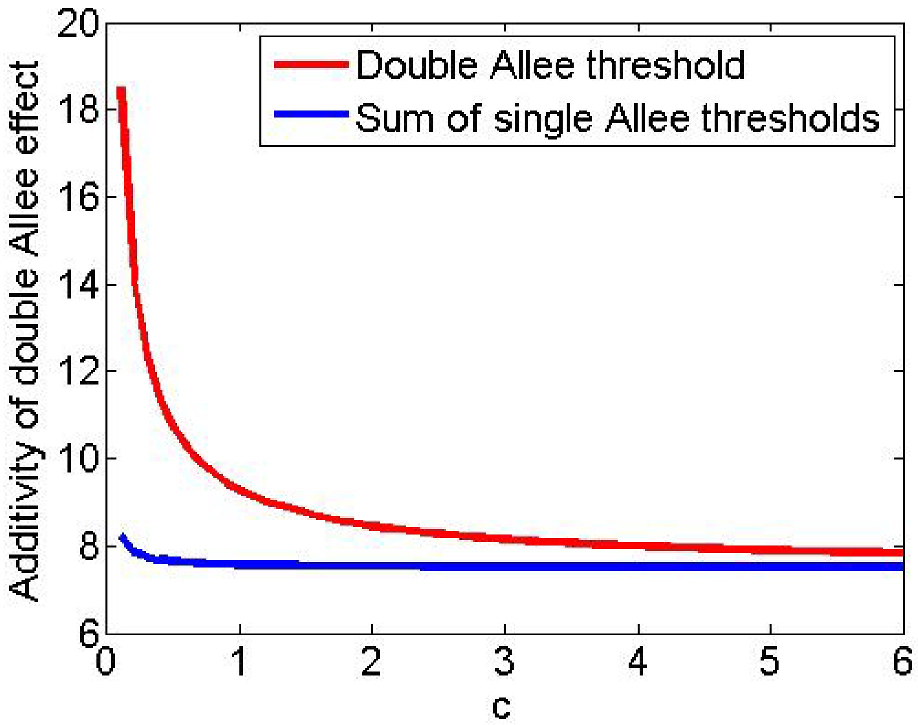

Figure A2. Additivity of the double Allee effect as it depends on the parameter *c*.

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