

# Evolution Transforms Pushed Waves into Pulled Waves

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**ABSTRACT:** Understanding the dynamics of biological invasions is crucial for managing numerous phenomena, from invasive species to tumors. While the Allee effect (where individuals in low-density populations suffer lowered fitness) is known to influence both the ecological and the evolutionary dynamics of an invasion, the possibility that an invader's susceptibility to the Allee effect might itself evolve has received little attention. Since invasion fronts are regions of perpetually low population density, selection should be expected to favor vanguard invaders that are resistant to Allee effects. This may not only cause invasions to accelerate over time but, by mitigating the Allee effects experienced by the vanguard, also make the invasion transition from a pushed wave, propelled by dispersal from behind the invasion front, to a pulled wave, driven instead by the invasion vanguard. To examine this possibility, we construct an individual-based model in which a trait that governs resistance to the Allee effect is allowed to evolve during an invasion. We find that vanguard invaders evolve resistance to the Allee effect, causing invasions to accelerate. This results in invasions transforming from pushed waves to pulled waves, an outcome with consequences for invasion speed, population genetic structure, and other emergent behaviors. These findings underscore the importance of accounting for evolution in invasion forecasts and suggest that evolution has the capacity to fundamentally alter invasion dynamics.

**Keywords:** Allee effect, biological invasion, evolution, pushed/pulled wave, invasion speed.

## Introduction

Biological invasions are ubiquitous. Although typically concerned with invasive organisms, the study of biological invasions applies to a much larger range of phenomena, including species responding to climate change (Thomas et al. 2004), the spread of favorable alleles through a population (Fisher 1937; Barton 1979), the spread of pathogens (Perkins 2011), and the growth of tumors (Orlando

et al. 2013; Gallaher et al. 2019). Managing these diverse phenomena requires reliable projections of, among other things, the speed at which populations are likely to spread (Travis and Dytham 2002; Gallien et al. 2010); to these ends, as well as for broader understanding, a wealth of ecological and mathematical approaches have been developed for modeling spreading populations (Shigesada and Kawasaki 1997; Lewis et al. 2016). However, while these models can be used to forecast the dynamics of real invasions, they are often unreliable in even the simplest of invasive settings (Andow et al. 1990; Williamson 1999; Hastings et al. 2005; Melbourne and Hastings 2009).

Such failures may in part be due to a historically limited appreciation of the importance of evolution in influencing invasion dynamics. A growing body of theory argues that traits governing the dispersal and reproduction of invaders—the two fundamental determinants of an invasion's speed (Fisher 1937; Kolmogorov et al. 1937; Skellam 1951)—should be under strong selective pressures on invasion fronts. These selective pressures involve both standard natural selection, operating to increase reproductive rates on the *r*-selected invasion front (Phillips 2009), and spatial selection, likewise operating to increase dispersal rates through the evolutionary effects of spatial sorting (Shine et al. 2011; Phillips and Perkins 2019). That spatial selection results in increased dispersal ability has been convincingly supported by empirical evaluations in both natural and laboratory settings (Cwynar and MacDonald 1987; Hughes et al. 2007; Urban et al. 2008; Ochocki and Miller 2017; Weiss-Lehman et al. 2017); that natural selection likewise leads to an increase in the reproduction rates of invaders has been far less clear. Frontline invaders in controlled invasions of bean and red flour beetles exhibited a marked increase in dispersal among frontline invaders but no increase in fecundity (Ochocki and Miller 2017; Weiss-Lehman et al. 2017). Conversely, in natural invasions comparisons between core and invasion front populations have often shown the latter to possess a range of traits associated with *r*-selection, albeit with notable exceptions (Bossdorf et al. 2005; Amundsen et al. 2012; Hudson

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et al. 2015). Usually this conspicuous absence is attributed to potential trade-offs between reproductive ability and other traits (Burton et al. 2010); however, actually detecting such trade-offs has proven to be difficult (Chuang and Peterson 2016).

The Allee effect and its impact on selection may be an underappreciated but important mechanism for regulating the evolution of reproduction on invasion fronts. The Allee effect is a phenomenon in which the increasing density of a population positively correlates with the increasing fitness of its members (i.e., positive density dependence; Allee 1938; Stephens et al. 1999). It may be caused by any number of constraints typically faced by individuals exposed to low population densities, such as an inability to find mates, increased vulnerability to predation, and inbreeding (Courchamp et al. 2008; Luque et al. 2016). Fitness may become impaired by the presence of either a weak or a strong Allee effect, with the former lowering it such that population growth is slowed and the latter diminishing it to the extent that a population shrinks when below a critical size, called the Allee threshold (Stephens et al. 1999). Since invasion fronts are by nature regions of low population density, Allee effects may curb the reproduction of frontline invaders for species that are subject to them. Apart from slowing the invasion, this would impose intense selection on traits that contribute to the emergent Allee effect. Thus, it appears plausible that invasion fronts themselves could select for individuals with increased resistance to Allee effects, and, by extension, increased low-density fecundity.

Despite this insight, the evolutionary responses of invaders to Allee effects remain relatively unexplored, as do the impact of such evolution on invasion dynamics. Modelers have long recognized the nonevolutionary importance of Allee effects to invasions, where it has been shown that low-density invasion fronts coupled with Allee effects may considerably slow or even stop the advance of invasions (Lewis and Kareiva 1993; Kot et al. 1996; Keitt et al. 2001; Taylor and Hastings 2005). There has also been ongoing interest in the influence of Allee effects on the successful establishment of invasive species, which has extended to evolutionary considerations (Drake and Lodge 2006; Kanarek and Webb 2010; Kanarek et al. 2015). It has furthermore been appreciated that Allee effects may alter evolutionary trajectories on invasion fronts by both providing selection against long-distance dispersal and, by increasing the degree of mixing across the invasion front, increasing effective population sizes on invasion fronts (Hallatschek and Nelson 2008; Burton et al. 2010). That waves subject to Allee effects exhibit higher rates of mixing also suggests that these higher rates of migration from behind the front may impede evolutionary response to selection in frontal populations (altered migration-selection

balance; Lenormand 2002). There has not, however, been a substantial attempt to examine the possibility that invaders may themselves alter the Allee effect by evolving in response to it or how this might influence overall invasion dynamics.

Any evolution concerning Allee effects would have the potential to reshape the fundamental structure of an invasion. Allee effects are particularly important in that they control the two major classes of invasion: pushed waves and pulled waves (van Saarloos 2003; Barton and Turelli 2011; Lewis et al. 2016). Pushed invasion waves are primarily driven by individuals from behind the invasion front and are typical of populations subject to a strong Allee effect, where growth is highest at intermediate densities (Lewis et al. 2016). Pulled invasion waves, on the other hand, are driven by individuals on the leading edges of invasions, where growth can be high if a population is instead subject to a weak or even no Allee effect (Lewis et al. 2016). This relationship between the Allee effect and pushed and pulled waves has been empirically demonstrated by Gandhi et al. (2016), who were able to produce both pushed and pulled yeast invasions by subjecting invaders to different strengths of Allee effect. As Allee effects may be expected to exercise selection on the low-density fecundity of frontline invaders, there exists a plausible mechanism through which a single invasion wave could itself transition between wave classes. If frontline invaders evolve higher low-density fecundity in response to an Allee effect, then what began as a pushed wave could potentially transform into a pulled wave, fundamentally altering the dynamics of an invasion as it progresses.

To examine these possibilities, we develop a simulation model of an invasion with heritable variation in individual resistance to an Allee effect. We observe whether invasions can exert selection on a trait that governs the strength of the Allee effect and whether the resultant evolutionary response is sufficient to have an invasion transition from a pushed to pulled wave.

## Methods

### *General Description of the Model*

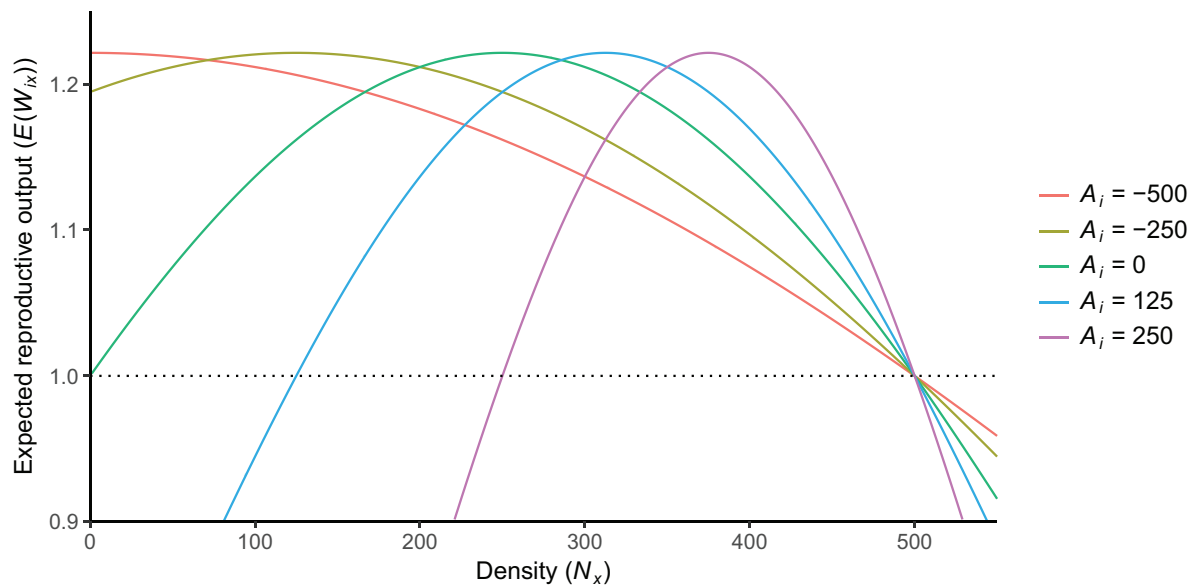
We developed an individual-based model in which invaders were tracked as they dispersed and reproduced across a one-dimensional landscape of patches (fig. S1; figs. S1–S6 are available online). Both time and space were considered discrete. Generations were nonoverlapping, with each cohort of invaders dying after one opportunity at reproduction and dispersal. All invaders in the founding generation were randomly assigned a value for a trait ( $A$ ) that determined reproductive output at different densities. Although not strictly defining the Allee threshold (which,

like the Allee effect, is a population-level phenomenon; Stephens et al. 1999), it operated analogously to it, defining the local population size below which an individual could not be expected to reliably replace itself. It also governed a fitness trade-off across high and low densities, such that individuals adapted to low densities were disadvantaged at high densities and vice versa. All individuals reproduced clonally, with offspring receiving their parent's  $A$  trait. The trait was, however, allowed to mutate in randomly selected offspring. All simulations were performed using R version 3.5.0 (R Core Team 2018). The model code in its entirety can be accessed at <https://github.com/PhilErm/allee-evolution>, and our simulation outputs are in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.zpc866t52>; Erm and Phillips 2019).

### Population Dynamics

Rather than specify a particular mechanism that causes an Allee effect to emerge (i.e., a component Allee effect), we modeled a phenomenological growth function describing an Allee effect and allowed individual variation in the Allee threshold of the function. This was a modified version of a growth function subject to Allee effects first used by Haond et al. (2018). The function determined each individual's expected reproductive output  $W$  (at location  $x$ ) as

$$E(W_{ix}) = \exp\left(4r \frac{K}{(K - A_i)^2} (1 - N_x/K)(N_x - A_i)\right). \quad (1)$$



**Figure 1:** Sensitivity analysis of equation (1), a growth function with an Allee effect and reproductive trade-off across densities.  $A_i$  determines the critical density below which an individual will not reliably replace itself (here seen for values of  $E(W_{ix})$  below the dotted line), analogous to the Allee threshold.

Here,  $E(W_{ix})$  is individual  $i$ 's expected number of offspring at a particular location  $x$ ,  $r$  is the density independent reproductive rate,  $N_x$  is the number of individuals at location  $x$ ,  $K$  is patch carrying capacity (at densities above which  $E(W_{ix})$  was lower than 1), and  $A_i$  is the threshold below which an individual's  $E(W_{ix})$  was lower than 1 (fig. 1). As  $A_i$  could take any positive or negative value ( $\in \mathbb{R}$ ), equation (1) ensured that as an individual's  $A_i$  decreased, so too did its high-density performance (fig. 1).

To introduce demographic stochasticity and convert the expected number of offspring to an integer value, an individual's realized reproductive output  $W_{ix}$  was drawn from a Poisson distribution with  $\lambda = E(W_{ix})$ .

### Spatial Dynamics

The invasion space was bounded at  $x = 0$ , with patches taking values of  $x = 0, 1, 2, \dots$ . Individuals dispersed with probability  $m$  either forward or backward for a maximum of  $dist$  patches. If an individual attempted to move to  $x < 0$ , they were returned to  $x = 0$ . For parameterizations where  $dist > 1$ , the probability of dispersing to any given patch within the maximum dispersal distance was equal.

### Trait Variation and Inheritance

All founding individuals for each invasion were assigned a value for  $A_i$  drawn from a Gaussian distribution with  $\mu = \bar{A}_{init}$  and  $\sigma = \sigma_A$ . This established the standing trait

variance at the beginning of each invasion. Except where mutation occurred,  $A_i$  was passed with perfect inheritance to any offspring produced.

In simulations with mutation, newborn offspring were randomly selected with probability  $p_{mut}$  and assigned a new  $A_i$  value. Their new mutated value was randomly drawn from a Gaussian distribution with a mean set to their premutation  $A_i$  and a standard deviation of  $\sigma_{mut}$ .

*Invasion Simulations*

We used a range of parameterizations to investigate the interaction between evolution and Allee effects as well as to explore the transition of invasions from pushed to pulled waves (table 1). Most simulations consisted of the same basic scenario: 300 individuals were distributed evenly across patches 0, 1, and 2 and then underwent 250 generations of dispersal and reproduction. Twenty such replicate invasions were generally conducted for each parameterization.

*Reference Case.* The first parameterization served as a reference case to provide a general impression of how  $A_i$  changed over the breadth and duration of the simulated invasions. At the end of each replicate invasion, we recorded the mean  $A_i$  value of invaders in each patch (hereafter called  $A_x$ ) and their density  $N_x$ . We also recorded  $\bar{A}_x$  over both time and space for a single typical realization of the model.

*Sensitivity Analysis.* We next explored the parameter space around this reference case by modeling the impact of changes to  $r$ ,  $K$ ,  $p_{mut}$ ,  $\bar{A}_{init}$ ,  $m$ , and  $dist$  on the degree of evolution taking place in the invaders. Each parameter was individually varied across the range of values listed

in table 1, while the other parameters were fixed at their reference case values (except for the exploration of  $\bar{A}_{init}$ , which used  $\sigma_A = 0$  to ensure that the initial invaders possessed exact trait values). At the end of the simulations, we recorded mean trait values for both the core and the vanguard of each invasion ( $\bar{A}_{fin}$ ). The core mean was calculated across individuals that occupied patches 0–4, whereas the vanguard mean was calculated across the five farthest occupied patches. We also recorded each invasion’s speed over time (i.e., the number of the farthest occupied patch each generation) to see how evolution and each parameter affected spread dynamics more broadly.

*The Transition from Pushed to Pulled Waves.* To determine whether evolution in the vanguard was capable of causing invasion waves to transition from pushed to pulled, we undertook a parameterization in which all replicate invasion waves started as pushed. We achieved this by setting  $\bar{A}_{init}$  to 250 and  $\sigma_A$  to 10, subjecting all founding invaders to a strong Allee effect. This necessitated increasing the starting population size in each initially occupied patch to 500 (up from the default of 100) to ensure that the populations remained above their Allee thresholds and so prevent extinction in the first few generations. We also increased  $\sigma_{mut}$  to 100 to ensure that any evolution would happen in a tractable time frame. We then tracked  $\bar{A}_{van}$  (the mean  $\bar{A}_x$  of the five farthest occupied patches) in invasions for 500 generations. If the mean final value for  $\bar{A}_{van}$  resulted in a monotonically decreasing reproductive output across density for equation (1), then the invasions were considered to have become pulled waves (Kolmogorov et al. 1937; Gandhi et al. 2016; Lewis et al. 2016). For our parameterization, this critical value (hereafter referred to as  $\hat{A}$ ) occurred at  $\bar{A}_{van} = -497$ . Furthermore, neutral traits were tracked in the vanguard according to the protocol described below.

**Table 1:** Invasion simulation parameterizations

Parameter	Description	Reference case	Sensitivity analysis	Pushed to pulled	Mixing analysis
$r$	Density independent reproduction rate	.2	.1, .2, .3	.2	.2
$K$	Carrying capacity	500	250, 500, 750	500	500
$\bar{A}_{init}$	Mean value of Allee trait for initial invaders	0	-50, -25, 0, 25, 50	250	250/-497
$\sigma_A$	Standard deviation of Allee trait for initial invaders	20	20 (0 for exploration of $\bar{A}_{init}$ )	10	0
$p_{mut}$	Allee trait mutation probability	.1	0, .001, .01, .1	.1	0
$\sigma_{mut}$	Standard deviation of Allee trait mutation	20	20	100	0
$m$	Dispersal probability	.5	.25, .5, .75	.5	.5
$dist$	Maximum dispersal distance	1	1, 2, 3	1	1

Note: For the sensitivity analysis, parameters were fixed at reference case values as one parameter was explored across the ranges indicated. For the mixing analysis, invasions in which  $A_i$  (a trait determining reproductive output at different densities) evolution was possible used the pushed to pulled parameters.

*Mixing Analysis.* Finally, to explore the genetic effects of the transition and to confirm that the waves had transformed from pushed to pulled in practice, we compared the genetic mixing of neutral traits in the transitioning invasions above with two sets of invasions where all invaders possessed either  $A_i = 250$  (a strong Allee effect) or  $A_i = -497$  (no Allee effect) and in which no mutation of  $A_i$  was allowed to occur. For pushed invasion waves in general, genetic diversity stays high on the wave front, as many individuals contribute to the colonization process, whereas for pulled invasion waves, genetic diversity is rapidly eroded due to repeated instances of the founder effect (Roques et al. 2012). Waves transitioning from pushed to pulled through evolution should therefore be expected to lose neutral trait diversity faster than equivalent waves that stay pushed but more slowly than equivalent waves that stay pulled. To see whether these processes were occurring in our own waves, we assigned all initial invaders a perfectly heritable neutral trait determined by the patch that they started in. Individuals starting in patch 0 were assigned trait 0, individuals starting in patch 1 were assigned trait 1, and so on. To allow for a greater number of traits than would exist for our default number of three starting patches, initial invaders were instead spread over five patches, with 500 individuals per occupied patch. These invasions were run for 500 generations.

We measured mean neutral trait diversity over time in the vanguard ( $\bar{D}_{van}$ ; mean diversity in the five farthest occupied patches) using Simpson’s (1949) diversity index:

$$D = 1 - \frac{\sum_{i=1}^R n_i(n_i - 1)}{N(N - 1)},$$

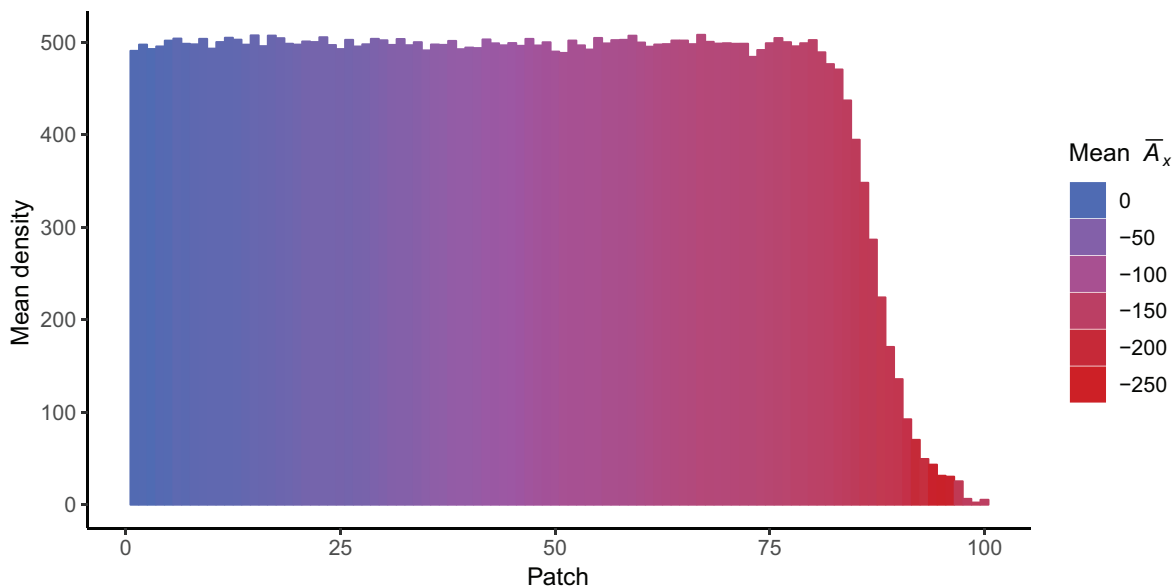
where  $D$  is the degree of diversity (1 is infinite diversity, 0 is no diversity),  $R$  is the number of unique traits in the population,  $n_i$  is the number of individuals with trait  $i$ , and  $N$  is the number of individuals in total. For the invasions in which mutations of  $A_i$  could not occur, we also recorded the number of individuals carrying each trait in each patch across the whole invasion extent for a single typical realization of each kind of wave. Since invasions with a strong Allee effect moved much more slowly than those with no Allee effect, we performed an additional three simulations of invasions with  $A_{init} = 250$  that ran for 5,000 generations. This meant that they covered the same approximate number of patches as the invasions with no Allee effect that had run for 500 generations.

### Results

#### Reference Case

Values of  $\bar{A}_x$  showed a strong response to selection based on proximity to the invasion front and time since patch colonization (fig. 2). Patches on or close to the front exhibited much lower  $\bar{A}_x$  values than patches closer to the invasion origin, indicating that increased resistance to the Allee effect had evolved there.

Changes to  $\bar{A}_x$  over time in the invasion vanguard took place at a relatively steady rate, whereas it was comparatively



**Figure 2:** Mean  $\bar{A}_x$  (the mean value of  $A_i$ , a trait determining reproductive output at different densities, for all individuals located in the same patch at a particular location  $x$ ) and mean density for invasions ( $n = 20$ ) after 250 generations under default parameters. More recently colonized patches exhibit greater low-density fecundity, as shown by their lower mean values of  $\bar{A}_x$ .

inelastic in the invasion core (fig. S2A). The invasion front in particular was also characterized by highly stochastic deviations in  $\bar{A}_x$  driven by instances when the front patch was occupied by just one or a few individuals. There was, however, no indication of evolution slowing down on the invasion front by generation 250, with  $\bar{A}_x$  still decreasing when simulations ended. Invasions exhibited standard wave profiles over time (fig. S2B), and, once reaching carrying capacity, patch population densities fluctuated by approximately  $\pm 50$  individuals around  $K$ .

### Sensitivity Analysis

These basic results appeared to be robust to variation in parameters. Without exception, vanguard individuals always showed a propensity for evolving greater resistance to the Allee effect than did core individuals (fig. S3). Increases in  $r$  and  $K$  accelerated the evolutionary differentiation of the core and vanguard (fig. S3A, S3B). Increases in  $p_{\text{mut}}$  also did so in a more dramatic fashion, with higher mutation rates resulting in much lower  $\bar{A}_{\text{fin}}$  values in the vanguard as well as increased variation in simulation outcomes (fig. S3C). Even in invasions without mutation, standing variation still enabled differentiation between core and vanguard populations. Changes to  $\bar{A}_{\text{init}}$  caused an approximately linear shift in  $\bar{A}_{\text{fin}}$  by the end of the simulations (fig. S3D), whereas changes to  $m$  and  $\text{dist}$  caused virtually no change at all (fig. S3E, S3F).

Invasion speeds changed with all parameters (fig. S4). Increases in  $r$  led to an increase in speed (fig. S4A), whereas the opposite occurred for  $K$  (fig. S4B). As would be expected if mutation was supplying variance, a high mutation rate resulted in faster and more obviously accelerating invasions, with those using  $p_{\text{mut}} = 0.1$  increasing in speed steadily (fig. S4C). Decreases in  $\bar{A}_{\text{init}}$  gave rise to invasions that moved faster but whose ultimate spreading rates nonetheless remained similar to other  $\bar{A}_{\text{init}}$  values (fig. S4D). Increasing  $m$  and  $\text{dist}$  sped up invasions accordingly (fig. S4E, S4F).

### The Transition from Pushed to Pulled Wave Dynamics

Invasions readily transformed from pushed to pulled waves over time (fig. 3). After invasions commenced,  $\bar{A}_{\text{van}}$  quickly decreased below zero (the transition point between a strong Allee effect and a weak Allee effect on the invasion front) and kept decreasing (fig. 3A). This decrease eventually subsided, with  $\bar{A}_{\text{van}}$  stabilizing around a quasi-equilibrium value of  $-497$  (i.e.,  $\hat{A}$ ) by the end of the simulations. As  $\bar{A}_{\text{van}} \leq \hat{A}$  after 500 generations (indicating that eq. [1] was monotonically decreasing in the vanguard; fig. 3B), invasions had transformed from pushed waves, subject to strong Allee effects, to pulled waves, subject to no Allee effects at all.

This was reflected in both the wave front profiles and the regions of highest population growth (fig. S5). After 20 generations, when an Allee effect was still present in the vanguard and waves were still pushed (fig. 3A), population growth was highest at intermediate densities on the wave front (fig. S5A), whereas after 220 generations, when the Allee effect had disappeared in the vanguard and waves were pulled (fig. 3A), population growth was instead highest at low densities (fig. S5B). Reflecting their pushed nature, wave fronts at generation 20 were also much steeper (spanning approximately eight patches) than wave fronts at generation 220 (spanning approximately 17 patches).

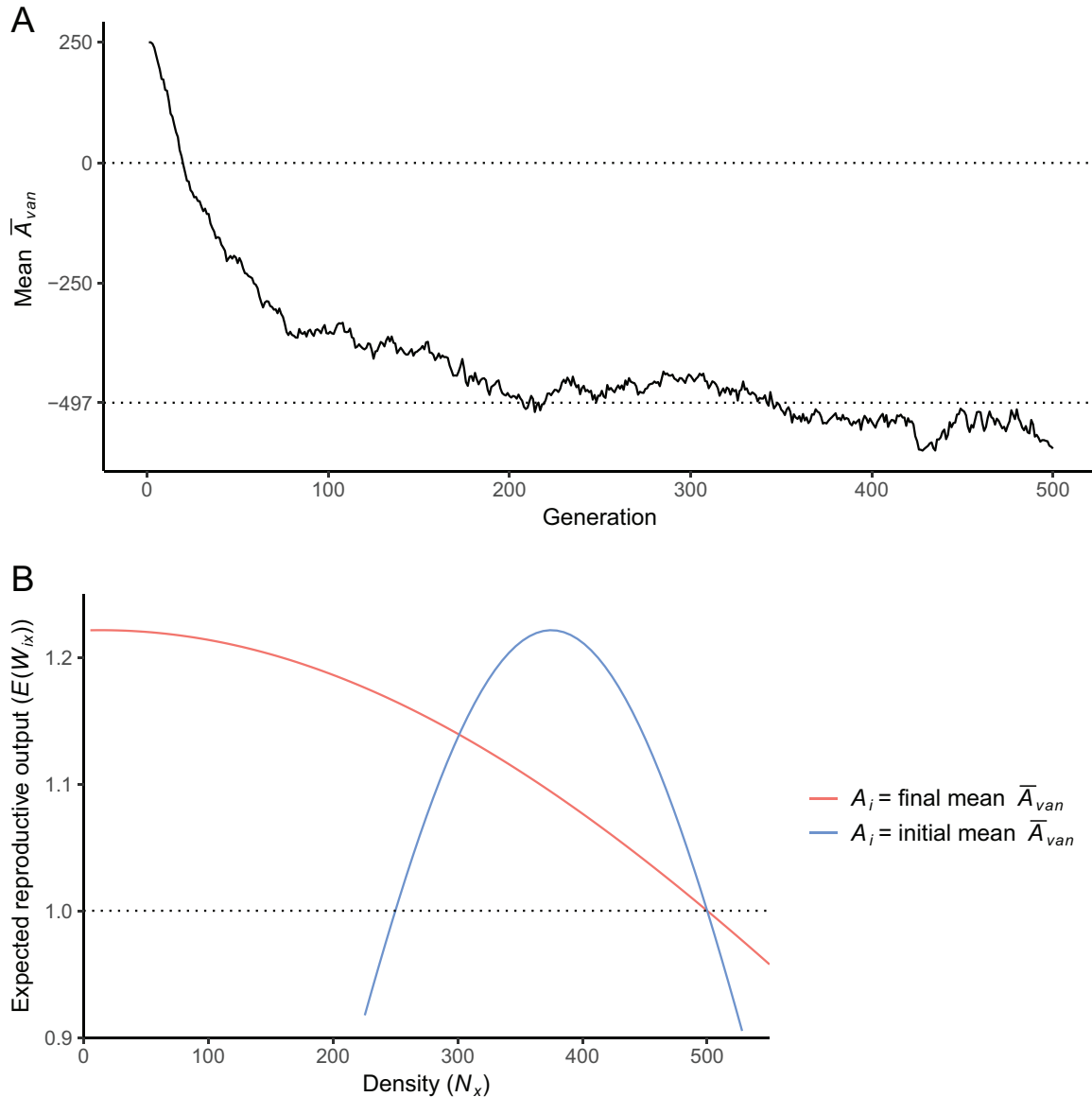
### Mixing Analysis

Pulled waves ( $\bar{A}_{\text{init}} = -497$ ;  $A_i$  evolution not possible) rapidly lost vanguard diversity, whereas pushed waves ( $\bar{A}_{\text{init}} = 250$ ;  $A_i$  evolution not possible) maintained close to maximum diversity (fig. 4A). By the final generation diversity was still very high ( $\bar{D}_{\text{van}} = 0.725$ ) in the pushed waves, indicating that they had maintained a high degree of mixing in the vanguard (fig. 4B). Conversely, all unevolving pulled wave replicates instead eventually possessed no diversity at all in the vanguard by generation 500 (fig. 4A). For these waves, one trait eventually dominated the front despite conferring no fitness advantage whatsoever (fig. 4C). Although losing diversity more slowly, waves transitioning from pushed to pulled ( $\bar{A}_{\text{init}} = 250$ ;  $A_i$  evolution possible) reached low diversity levels by generation 500 (fig. 4A), comparable to the final state of waves that were pulled from the outset.

Pushed waves run for 5,000 generations (so as to spread a similar distance to pulled waves) did exhibit a steady decrease in  $\bar{D}_{\text{van}}$  throughout the simulations (fig. S6A), but this loss did not occur notably faster than the loss of diversity in the core of the range, and even by generation 5,000 some diversity was still maintained in the vanguard (fig. S6).

### Discussion

Because of their importance in dictating the low-density growth rates of stationary and spreading populations, Allee effects have been of long-standing interest to both theoretical and applied ecologists (Boukal and Berec 2002). Here, we consider the possibility that sensitivity to the Allee effect may itself be under selection and evolve in invasions. By permitting invaders to mount an evolutionary response to Allee effects, we show that invasive populations can become resistant to them. As a consequence, invasion waves transition from pushed dynamics to pulled dynamics as Allee effects weaken, with implications for both wave speed and genetic structure.

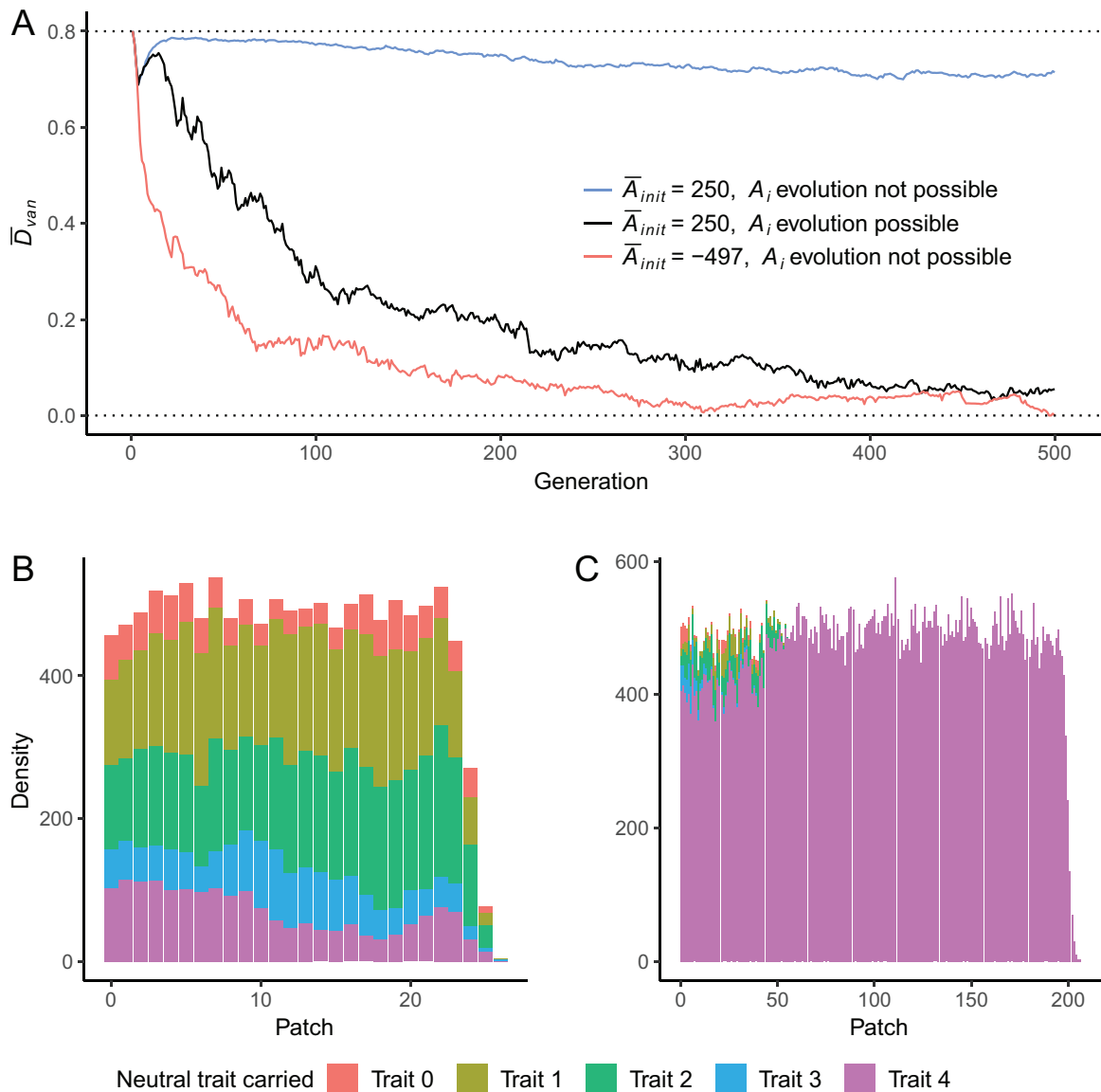


**Figure 3:** A, Evolution of  $\bar{A}_{van}$  (the mean value of  $A_i$ , a trait determining reproductive output at different densities, for all individuals located in the five farthest occupied patches) over time for  $n = 20$  invasions. The founding invaders are subject to a strong Allee effect, meaning that invasions start as pushed waves. The dotted line at mean  $\bar{A}_{van} = 0$  shows the point at which a transition between a strong (above the line) and a weak (below the line) Allee effect occurs. The dotted line at mean  $\bar{A}_{van} = 497$  shows the point below which no Allee effect occurs. B, Comparison of the expected reproductive output of vanguard invaders at both the beginning and the end of the invasions in A. Despite the initial invaders experiencing a strong Allee effect (blue line), by the final generation vanguard invaders have evolved to experience no Allee effect at all (red line). Because of the final generation's monotonically decreasing reproductive output, pulled invasion waves are theoretically expected to result.

#### *Evolved Resistance to the Allee Effect*

In our model, resistance to the Allee effect manifested most strongly on the invasion front, where persistently low population densities appeared to cause ongoing and intense selection for individuals that could reproduce successfully there. Evolution of resistance to Allee effects

proved robust to varying initial conditions and key parameters (fig. S3). This was in contrast to the invasion core, where resistance remained largely static (figs. 2, S3). In these patches, high population densities would have instead ensured that individuals with higher  $A_i$  values—and so high-density fitness—had a competitive advantage. There was, however, still a slight downward shift in mean



**Figure 4:** A,  $\bar{D}_{van}$  (mean neutral trait diversity in vanguard patches as measured by Simpson's diversity index) over time for  $n = 20$  invasions. We compare nonevolving pushed and pulled waves against a wave that evolves from pushed to pulled. Nonevolving scenarios are  $\bar{A}_{init}$  (the mean value of  $A_i$ , a trait determining reproductive output at different densities, for all founding individuals in the invasion) = 250 (a pushed wave with a strong Allee effect) and  $\bar{A}_{init} = -497$  (a pulled wave with no Allee effect).  $A_i$  was allowed to evolve in an additional set of invasions that started at  $\bar{A}_{init} = 250$ . Neutral trait diversity was maintained in the pushed waves, where a strong Allee effect operated (blue line), but was rapidly lost in the pulled waves, where no Allee effect operated (red line) as well as in the waves that started as pushed but became pulled with the evolution of  $A_i$  in the vanguard (black line; fig. 3). B, C, Structure of neutral trait mixing in the final generation of typical invasion simulations under  $\bar{A}_{init} = 250$  (B; with no  $A_i$  evolution) and  $\bar{A}_{init} = -497$  (C; with no  $A_i$  evolution). In B a mix of neutral traits was maintained on the invasion front, whereas in C, despite conferring no fitness advantage, one trait came to dominate.

$\bar{A}_x$  there; this was likely to have been caused by the particular behavior of equation (1) at densities above  $K$  (fig. 1), since individuals with lower  $A_i$  values would have momentarily enjoyed increased competitiveness when patch densities oscillated above carrying capacity. This behavior is doubtless unrealistic—individuals adapted to high den-

sities should rightfully be better high-density performers both above and below  $K$ —and represents a weakness in our growth function that is shared by other popular Allee effect growth functions in which the Allee threshold is moveable (e.g., Lewis and Kareiva 1993). Without this model peculiarity, which is likely to have led to unrealistic



and counterintuitive evolutionary dynamics in patches around  $K$ , we might expect that resistance to the Allee effect would decrease in the core and spread throughout patches around carrying capacity, as opposed to remaining mostly static.

Our findings nonetheless support existing theory about the evolution of life histories within invasions. The principles of  $r$ - and  $K$ -selection (MacArthur and Wilson 2001), although antiquated in a number of nontrivial aspects (Reznick et al. 2002; Mallet 2012), act as useful conceptual tools in this instance (Phillips et al. 2010). Since the leading edges of invasions are regions of low population densities and the long-occupied inner cores of invasions are regions of high population densities, there ought to be a continuum of  $r$ - to  $K$ -selective environments from the outer fringes of an invasion back to its point of origin (Phillips et al. 2010). It follows that individuals in the vanguard should possess traits that enable them to reproduce rapidly at low density, whereas those living in the invasion core should instead possess traits that enhance competitiveness at high density. In our model, the gradient in  $A_x$  observed across invasions is strongly concordant with these theoretical expectations (fig. 2).

This suggests that evolutionary responses to the Allee effect provide yet another life-history axis along which vanguard populations may evolve. The empirical evidence for shifts in reproductive rates in vanguard populations has been mixed (Phillips et al. 2010; Chuang and Peterson 2016; Ochocki and Miller 2017; Weiss-Lehman et al. 2017), but it is entirely possible that these ambiguous results arise from reproduction-dispersal trade-offs (Burton et al. 2010; Phillips and Perkins 2019) or the complex relationship between measurable traits and actual population growth rates (Reznick et al. 2002). Allee effects introduce additional complexity. In a hypothetical common garden, we might find no difference in seed production, for example, between core and vanguard populations. We might take this as evidence for no shift in reproductive rate. However, it is possible that individuals in the vanguard have more attractive flowers and larger stigma, a low-density adaptation that, on the invasion front, would see the vanguard individuals exhibit much higher reproductive rates than individuals from the core. We thus need to be very careful about the environment in which we measure reproductive traits and to be aware that it may be very easy to miss a key trait altogether.

Certainly, direct evidence from invasions themselves appears to support the notion that individuals from recently colonized ranges may have undergone evolution to minimize the deleterious effects of low population densities. Some organisms that ordinarily exhibit sexual reproduction, such as the parasitic wasp *Mesochorus nigripes*, have instead been found to produce eggs that can hatch

even when unfertilized within invading populations (Hung et al. 1988; Hopper and Roush 1993). It has also been noted that selfing in plants is particularly prominent in marginal populations (Pannell 2015), and it has likewise long been argued that biogeographical biases in the global distribution of parthenogenetic species may in fact reflect their inherent superiority as colonizers (Kearney 2005). Given the relatively straightforward nature of our model's predictions, further comparisons between core and vanguard populations in nature may prove useful in evaluating its finding that invasion fronts ought to select for organisms adapted to low population densities.

### Wave Type Transitions

In the vanguard, the evolution of resistance to the Allee effect was able to progress to such an extent that invasions transitioned from pushed to pulled waves (fig. 3), a result supported by the mixing analysis in which these same waves lost neutral trait diversity less quickly than waves starting as pulled but much more quickly than waves starting and staying as pushed (fig. 4). Wave fronts also became less steep over time (fig. S5), in accordance with theoretical and empirical expectations for pushed and pulled waves (Gandhi et al. 2016; Lewis et al. 2016). Were the transition from a pushed to a pulled wave to occur in a real invasion, it would have a number of impacts on a population's structure and dynamics. Any periodic fluctuations in invasion speed caused by density-dependent processes acting in concert with the Allee effect would cease to occur (Sullivan et al. 2017). However, because an absence of Allee effects allows populations to grow from small sizes, demographic stochasticity on the invasion front would become a more powerful force as the Allee effect diminishes. This stochasticity not only results in intrinsically more variable invasion speeds (Taylor and Hastings 2005; Melbourne and Hastings 2009) but also has several evolutionary consequences. The serial foundering and success of small founder populations mean that pulled invasions experience high levels of spatial genetic drift (Slatkin and Excoffier 2012). In pulled invasions, spatial and temporal drift can cause gene surfing, where deleterious alleles fix in the vanguard and are spread over wide geographical areas (Hallatschek and Nelson 2008; Graciá et al. 2013), ultimately contributing to populations suffering from high levels of expansion load (Peischl et al. 2015). This expansion load can also affect the very traits responsible for spread rate—dispersal and reproduction—such that evolutionary stochasticity contributes to making invasion speeds very unpredictable (Phillips 2015; Ochocki and Miller 2017; Weiss-Lehman et al. 2017). All of these effects are mitigated on pushed invasion fronts. Here, the requirement for large founding populations maintains relatively high levels of genetic diversity (Hallatschek

and Nelson 2008; Roques et al. 2012), an expectation reflected in figure 4. If invasions become more pulled with time, then all of the stochastic outcomes attendant on pulled waves will increasingly manifest as invasions progress.

Despite the above, in our simulations even pushed waves saw a gradual loss of diversity in both the vanguard and the entire breadth of the population if simulated for 5,000 generations (fig. S6). In the present instance this is unsurprising. Although pushed waves driven by strong Allee effects may be expected to maintain diversity indefinitely in an idealized scenario free of genetic drift (Roques et al. 2012), in instances like our own, in which we have finite population sizes (thereby permitting some genetic drift to manifest) and no mutation, diversity will decrease over time regardless of circumstances (Hallatschek and Nelson 2008). Thus, even a pushed wave will experience a loss in diversity, although the difference in diversity loss between pulled and pushed waves that have covered approximately the same distance (i.e., figs. 4C, S6B, with the latter requiring an extra 4,500 generations to do so) is striking.

In reality, the amount of time it would take for an invasion wave to switch from pushed to pulled would be difficult to predict. For the transition to occur, traits governing component Allee effects must evolve such that a demographic Allee effect is no longer present or present in only a very weak form. In a solitary organism where a demographic Allee effect manifests due to obligate sexual reproduction alone, it is plausible that the transition could happen quickly; switches to parthenogenic reproduction from sexual reproduction can occur virtually instantaneously, whether by mutation or hybridization (Simon et al. 2003). Such a pathway would presumably be closed to mammals and birds, however, among which no parthenogenic species have been observed (Avisé et al. 1992). In general, much would depend on the evolutionary lability of traits governing component Allee effects, their standing variance, and any trade-offs associated with adopting more solitary modes of living.

The evolution of higher reproduction rates as Allee effects diminish should also facilitate the evolution of increased dispersal ability (Travis and Dytham 2002; Perkins et al. 2013). As Allee effects weaken, highly dispersive individuals accumulating on the invasion front through spatial sorting also accrue a fitness benefit, with spatial selection and natural selection conspiring to drive increasing dispersal rates (Perkins et al. 2013). Again, as invasions transition from pushed to pulled, we should see evolutionary processes accelerate, although models incorporating both the evolution of dispersal and Allee effects would be necessary to evaluate such speculation.

Accounting for the possibility that evolution may drive invasions to transition from being pushed to pulled would

considerably complicate attempts to predict invasion speed. This complexity is reflected in the fact that the equations conventionally used to model the velocities of pushed and pulled waves are different from one another (Lewis et al. 2016). Furthermore, since pushed and pulled waves each favor the deployment of different control techniques (Gandhi et al. 2016), the most effective strategy for managing a particular invasion may also change as the invaders evolve. Since many control techniques exploit the Allee effect (Tobin et al. 2011), accounting for the resultant selection these impose may be prudent. If control techniques impose additional selection on invasion fronts for individuals that are resistant to Allee effects, then they may inadvertently contribute to the emergence of a less controllable and less predictable invasion.

#### *Key Assumptions and Limitations*

There are several key assumptions and limitations of our approach that should be borne in mind when interpreting our findings. First, we have examined only a simple genetic system with asexual (haploid) reproduction and complete inheritance. For invaders that reproduce sexually, recombination may cause the gene flow from the invasion core to place a stronger brake on adaptation to the invasion front (i.e., to shift the migration-selection balance; Lenormand 2002). Evolution of traits on the invasion front has been slowed by Allee effects in other models that both lack (e.g., Travis and Dytham 2002; Burton et al. 2010) and incorporate (e.g., Lenormand 2002; Phillips 2015) recombination, however. While it may be profitable to compare sexual and asexual cases directly then, it seems unlikely that recombination would qualitatively alter our findings. Nonetheless, diploidy, recombination, and polygenic inheritance would all significantly increase the complexity of the modeled system, and so it remains important to extend the modeling presented here to examine sexual populations carrying a quantitative trait under different assumptions around expression patterns and genetic architecture. Such an analysis may additionally shed light on the speed with which a pushed to pulled transition could realistically take place.

Our model also treats the Allee effect phenomenologically: we do not specify a particular mechanism (a component Allee effect) through which the population-level effect manifests. Such an approach is a useful place to start (many classic models examine individual variation around population-level parameters such as  $r$  and  $K$ ) but is a level of abstraction away from traits that are directly measurable in individuals. This also extends to the growth trade-off structure employed in our model, in which it is assumed (with the aforementioned exception of dynamics above carrying capacity) that being adapted for high reproductive

output at low densities maladapted one for high densities and vice versa. Such a trade-off, suggested by Courchamp et al. (2008) to be a reasonable criterion for showing that a trait has likely been selected for to mitigate Allee effects, seems a fair baseline assumption given that populations that usually maintain high densities (and so lack exposure to Allee effects) should not be expected to experience selection for traits that boost fitness at low densities (Courchamp et al. 2008), nor should, in our view, populations that experience perpetually low population densities be expected to experience selection for traits that boost fitness at high densities. It also carries some empirical support; for example, in the urchins *Strongylocentrotus purpuratus*, *S. franciscanus*, and *S. droebachiensis*, density-dependent selection has appeared to favor gamete traits that boost fitness at each species' typical population density at the cost of reducing their fitness at others (Levitan 2002). Still, since Allee effects can emerge from a wide range of proximate mechanisms from mate searching to cooperation (Stephens et al. 1999), particular trade-off structures are likely to take many forms; it could well be that many adaptations to mitigate Allee effects inadvertently boost fitness across all population densities (Courchamp et al. 2008). Given this likely variation in the fundamentals of the system, it remains quite possible that our results will qualitatively differ between contrasting proximate mechanisms. Moreover, given that the traits that influence reproductive output may themselves possess trade-offs with other traits that are under selection during invasions, such as dispersal ability (Travis and Dytham 2002; Burton et al. 2010; Chuang and Peterson 2016), it is likely that there will be many exceptions to the scenario we have modeled; particular cases should therefore be examined and classified in terms of trade-off structures to consider the likely resultant evolutionary trajectory on invasion fronts.

### Conclusion

Our theoretical model represents a first proof of concept in describing the higher-order effects of the evolution of resistance to Allee effects on invasion fronts. Although our results support the hypothesis that invasion fronts ought to select for individuals that are resistant to Allee effects and that this may cause invasions to transform from pushed to pulled waves, further theoretical and empirical work is required. Experimental invasions and observational studies of real invasions may in this instance be particularly fruitful, since the evolution of Allee effects on invasion fronts has not been empirically assessed. Such work could also test whether transitions from pushed to pulled waves can happen, as we predict here, and whether they may occur on ecologically relevant timescales. If our findings hold in reality, evolution can act to release the

handbrake applied by Allee effects on invasions, with faster and more stochastic range expansions the result.

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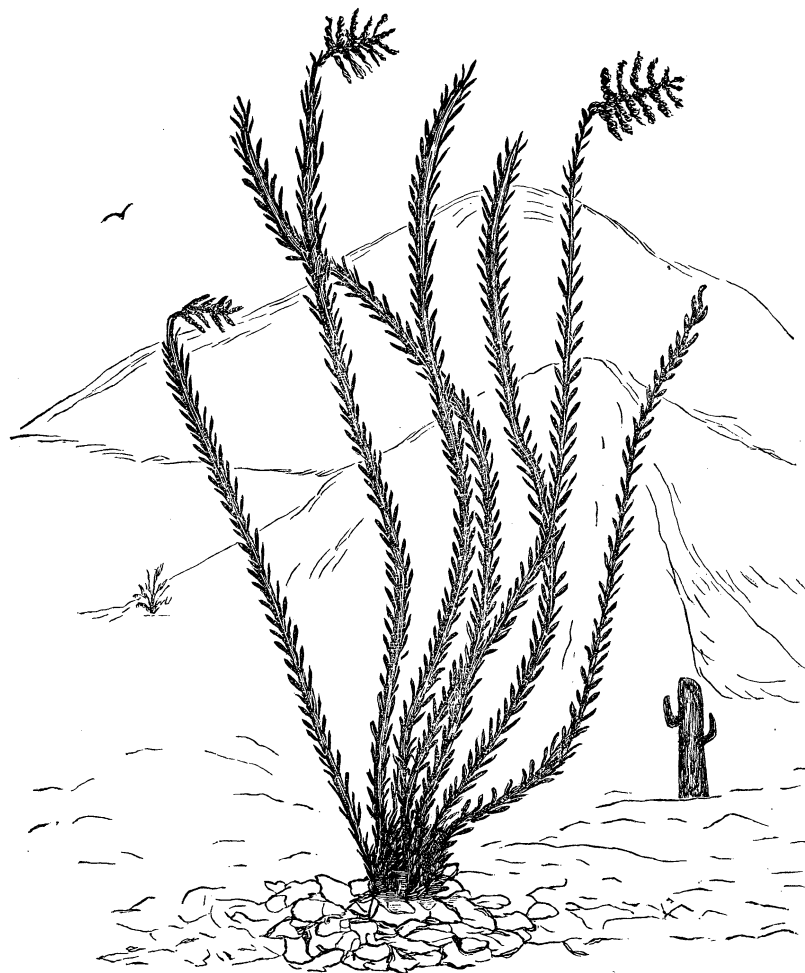
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“Still another very common and at the same time a very curious plant is the *Fouquieria splendens*, one of the Tamariscineæ, and known to the Mexicans as ‘ochotilla.’ . . . The branches are long and whip-like, armed with innumerable sharp, curved thorns an inch or more long.” From “Botanical Notes from Tucson” by Jos. F. James (*The American Naturalist*, 1881, 15:978–987).