Evolution transforms pushed waves into pulled waves

Philip Erm*
philip.erm@unimelb.edu.au

Ben L. Phillips*
phillipsb@unimelb.edu.au

February, 2018

Abstract

Understanding the dynamics of biological invasions is crucial for managing numerous phenomena, from invasive species to tumours. Despite the breadth of application, and substantial theoretical development, invasions have proven difficult to predict. This may partly be due to an underappreciation of the interaction between the Allee effect – where individuals in low-density populations suffer lowered fitness – and evolution during invasions. Since invasion fronts are regions of perpetually low population density, selection should favour vanguard invaders that are resistant to Allee effects. Evolution in response to this pressure could cause invasions to transition from pushed waves, propelled by dispersal from behind the invasion front, to pulled waves, driven 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 evolves during an invasion. We find that vanguard invaders rapidly evolve resistance to the Allee effect, causing invasions to accelerate. This also results in invasions transforming from pushed waves into pulled waves; an outcome with important consequences for the predictability of invasion speed. These findings underscore the importance of accounting for evolution in invasion forecasts, and suggest that it has the capacity to fundamentally alter broader invasion dynamics.

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

*School of BioSciences, The University of Melbourne, Victoria, Australia

Introduction

Biological invasions are ubiquitous. While we might typically think of invasive organisms, the study of biological invasions applies to a much larger range of phenomena, from species responding to climate change [1], to the spread of alleles [2,3], the spread of pathogens [4], and even the growth of tumours [5]. To understand and manage these diverse phenomena, reliable projections of invasion speed are vital [6,7]. To these ends, a wealth of ecological and mathematical approaches have been developed for modelling spreading populations [8,9]. While these models can predict real invasion speeds, they are often unreliable in even the simplest of invasive settings [10–13].

Spread rate is determined by an interaction between dispersal and population growth [2,14], and modelled spread rates are highly sensitive to precisely how these two processes are specified. On the one hand, the shape of dispersal kernels – in particular the shape of the tail of the dispersal distribution – has a profound effect on spread rate [15,16]. On the other, details of population dynamics, such as the presence or absence of Allee effects, also have a major impact on spread rates [9,17,18]. Together, subtle alterations to growth and dispersal result in a wealth of spread dynamics, including wave collapse (extinction), lag-phases, and accelerating spread [8,9].

Allee effects have proved to be particularly important in that they control two major classes of invasion dynamic: pushed and pulled waves [8,19]. Allee effects cause individuals in low-density populations to have lower mean fitness than those in populations at higher densities (*i.e.,* positive density dependence) [20,21]. Since invasion fronts are characteristically regions of low population density, Allee effects may curb the reproduction of front line invaders for species that are subject to them. This acts to slow invasions and can fundamentally change their dynamics: from a 'pulled' wave (in which high growth at low density pulls the invasion front forward) to a 'pushed' wave (in which the movement of the wave is pushed forward by dispersal from high-density populations)[8,17,22]. A pushed dynamic results in slower, or even pinned, invasions [15,17–19,23], and this relationship between the Allee effect and pushed and pulled waves has recently been empirically demonstrated by Gandhi *et al.* [24], who were able to produce both pushed and pulled yeast invasions by subjecting invaders to different strengths of Allee effect.

While spread rate is highly sensitive to dispersal and growth processes (including Allee effects), it is increasingly apparent that these processes themselves rapidly evolve. A growing body of theory argues that life history and dispersal traits 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 [25] – and 'spatial sorting', in which invaders become spatially sorted according to their dispersal abilities, with the best dispersers becoming overrepresented at the leading edge of the invasion front [26,27]. Such theoretical expectations have largely gained empirical support, with the rapid evolution of dispersal now having been observed across a wide array of both natural and experimental systems [28–33]. The rapid evolution of reproductive rates also has empirical support [34], but there have been notable exceptions in which life-history traits relevant to reproductive rate do not appear to have changed on invasion fronts [31,33,35].

Interestingly, although Allee effects not only set up two fundamental classes of invasion, they also serve to undermine many of the evolutionary forces acting on invasion fronts. In the case of spatial sorting, the best dispersers find themselves in a low-density population and so, under Allee effects, suffer reduced fitness, constraining the upward evolution of dispersal [26,36]. And for both spatial sorting and r-selection, the lower growth rate on the leading edge of the invasion should increase the relative genetic contribution of migrants to the leading edge population. Thus, whatever the response to the unique selection pressures on the invasion front, a stronger Allee effect should increase the 'migrant load' in the vanguard, undermining this evolutionary response [37].

Because Allee effects cause lower fitness on invasion fronts, and selection on invasion fronts favours high population growth, we would expect resistance to Allee effects to be favoured there. But this force of selection may need to push against an opposing force of gene flow from high-density parts of the population, where Allee effects are irrelevant [37]. Additionally, selection on invasion fronts needs to be strong enough to counter the strong drift in this region caused by serial founder events [38]. If however there is heritable variation for resistance to Allee effects, and selection can overwhelm migrant load and drift, then there exists a plausible mechanism through which a single invasion can transition from pushed to pulled. Evolution might fundamentally alter the dynamics of the invasion.

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 despite migrant load. We also examine this possibility in the presence and absence of a trade-off between Allee effect resistance, and competitive ability (fitness at high density).

Methods

General description of 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. A1). Both time and space were considered discrete. Generations were non-overlapping, 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 their Allee threshold, and so reproductive output at different densities. In particular simulations, this trait 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 [39]. The model code in its entirety can be accessed at https://github.com/PhilErm/allee-evolution/.

Population dynamics

Reproduction was described by a modified population growth function subject to Allee effects [17,40]. This determined each individual's expected reproductive output W (at location x) as

$$E(W_{ix}) = \exp\left(r\left(1 - \frac{N_x}{K_i}\right)\left(\frac{N_x}{K_i} - \frac{A_i}{K_i}\right)\right). \tag{1}$$

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_i is the individual's carrying capacity (at densities above which $E(W_{ix})$ was lower than 1), and A_i its Allee threshold (at densities below which $E(W_{ix})$ was lower than 1; Fig 1A). In simulations where we implemented a trade-off between fitness at high and low densities, Eq. 1 was additionally modified by

$$K_i = K^* + A_i. \tag{1.1}$$

In this formulation, K^* denotes the carrying capacity at $A_i = 0$. As A_i could take any positive or negative value ($\in \mathbb{R}$), Eq. 1.1 ensured that, as an individual's Allee threshold decreased, so too did its carrying capacity and high-density performance (Fig. 1B).

To introduce demographic stochasticity and convert the expected number of offspring to an integer value, an individual's realised 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 $x = 0, 1, 2, \ldots$. Individuals dispersed with probability m to neighbouring patches in the landscape. Those that dispersed moved to either $x-1$ or $x+1$ with equal probability. If an individual attempted to move to $x = -1$, they were returned to $x = 0$.

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 $\sigma = \sigma_A$ (50 by default). This established the standing trait variance at the beginning of each invasion. Alternative values of σ_A were also used to explore particular cases (Table 1). 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 pre-mutation A_i, and a standard deviation of σ_{mut}.

Invasion simulations

We used a range of parameterisations 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). All simulations consisted of the same basic scenario. This began with 300 individuals distributed evenly across patches 0, 1, and 2. After the invasions commenced, dispersal and reproduction then took place for 150 generations. We performed 20 replicate invasions for each parameterisation, both with and without the trade-off mediated by Eq. 1.1.

Reference case

The first parameterisation 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 $\bar{A}_x$) and their density N_x. $\bar{A}_x$ over both time and space was also recorded for a single typical realisation of the model.

Sensitivity analysis

We next explored parameter space around this reference case by modelling the impact of changes to r, K^*, p_{mut}, and $\bar{A}_{init}$ on the degree of evolution taking place in the invaders. Each parameter was individually varied across the range of values listed in Table 1, whilst 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 particular trait values). $\bar{A}_{init}$ was specifically chosen to evaluate if differences in migrant load had non-linear effects on evolutionary outcomes. At the end of the simulations, we recorded mean trait values for both the core and vanguard of each invasion ($\bar{A}_{fin}$). The core mean was calculated across individuals that occupied patches 0 to 4, whereas the vanguard mean was calculated across the 5 farthest occupied patches. We also recorded each invasion's speed over time to see how evolution and each parameter affected spreading dynamics more broadly.

The transition from pushed to pulled wave dynamics

Lastly, we undertook a parameterisation that allowed us to observe if invasions transitioned from pushed to pulled wave dynamics over time. So that invasions always started as pushed waves, $\bar{A}_{init}$ was set to 50 and σ_A to 10, subjecting all founding invaders to a strong Allee effect. To ensure that any transition could happen in a computationally tractable time frame, mutation rates were set to $p_{mut} = 0.1$. We then tracked $\bar{A}_{van}$ (the mean $\bar{A}_x$ of the 5 farthest occupied patches) in invasions without a trade-off for 350 generations and in invasions with a trade-off for 200 generations. If each group's mean final $\bar{A}_{van}$ resulted in a monotonically decreasing reproductive output across density when used with with Eq. 1 (and Eq. 1.1 as appropriate), they were considered to have become pulled waves [41]. With our default

parameters, this critical value (hereafter referred to as $\hat{A}$) occurred at $\bar{A}_{van} = -497$ for no-trade-off invasions and $\bar{A}_{van} = -248.5$ for trade-off invasions.

To see if migrant load was capable of slowing the relative time it took for invasions to become pulled, we also performed a similar evaluation using different values for $\bar{A}_{init}$. In this case, replicate invasions were conducted starting with $\bar{A}_{init} = \hat{A}$ (*i.e.,* -497 and -248.5) and for $\bar{A}_{init}$ = -450, -400, -350, ... to $\bar{A}_{init} = 50$. σ_A was set to 0 and values for $\bar{A}_{init} \geq 100$ were not used as these invasions went extinct. For each value of $\bar{A}_{init}$, we recorded the time it took for each replicate invasion's $\bar{A}_{van}$ to reach $\hat{A}$.

Results

Reference case

In the model with no trade-off, $\bar{A}_x$ showed a strong response to selection based on proximity to the invasion front and time since patch colonisation (Fig. 2A). Patches on or close to the front exhibited much lower $\bar{A}_x$ values than patches closer to the invasion origin, indicating increased resistance to the Allee effect there. This difference became even more pronounced in the trade-off model, where core invaders instead evolved heightened vulnerability to the Allee effect to achieve higher fitness at carrying capacity (Fig. 2B). In consequence, individuals from the core possessed larger carrying capacities than organisms on the invasion front (who sacrificed competitive ability for better low-density fecundity).

Changes to $\bar{A}_x$ over time in both the invasion core and vanguard took place at a relatively steady rate (Fig. A2). On the invasion front in the no-trade-off model, $\bar{A}_x$ declined rapidly at first due to selection on standing variation in the founding invaders and their descendants, but then more slowly as standing variation was depleted and novel variation was supplied by mutation (Fig. A2A). In the invasion core, trait values appeared to equilibrate within the first 50 generations, in contrast to the continuing decrease in $\bar{A}_x$ on the invasion front (Fig. A2A). A similar pattern was also observed on the invasion front in the trade-off model. Here, $\bar{A}_x$ also continually decreased over time in the vanguard, but in patches at carrying capacity, $\bar{A}_x$ instead increased steadily over time (Fig. A2B). Neither the trade-off nor the no-trade-off model gave any indication of an equilibrium state emerging on the invasion front, with $\bar{A}_x$ still decreasing when simulations ended.

Sensitivity analysis

These basic results appeared to be robust to variation in parameters (Figs. A3 and A5). Without exception, vanguard individuals always showed a propensity for evolving greater resistance to the Allee effect than core individuals (Figs. A3 and A5). In the no-trade-off model, increases in r accelerated the evolutionary differentiation of the core and vanguard (Fig. A3A). Changes to K^* didn't have an apparent effect on evolution (Fig. A3B), however increases in p_{mut} led to faster evolutionary rates, and so much lower $\bar{A}_{fin}$ values in the

vanguard, as well as to increased variation (Fig. A3C). Even in invasions without mutation, standing variation still enabled differentiation between core and vanguard populations. Again, this differentiation was amplified in the trade-off model, with core and vanguard invaders carrying traits causing strong and weak Allee effects respectively by the end of the invasion (Fig. A5C). Finally, changes to $\bar{A}_{init}$ caused a linear shift in $\bar{A}_{fin}$ by the end of the simulation (Fig. A3D).

Invasion speeds changed substantially with all parameters, although invasion acceleration rates appeared to be less sensitive (Fig. A4). In the no-trade-off model, increases in r led to an increase in speed, whereas the opposite occurred for K^* (Fig. A4A and B). As would be expected if mutation was supplying variance, higher mutation rates resulted in more obviously accelerating invasions, with those using $p_{mut} = 0.1$ increasing in speed rapidly and eventually reaching a steady velocity (Fig. A4C). Decreases in A_{init} gave rise to invasions that moved faster, but whose rate of acceleration nonetheless remained similar to each other (Fig. A4D). Similar patterns were also seen for invasions using the trade-off model, however these were able to achieve relatively higher speeds and rates of acceleration compared to invasions without a trade-off (Fig. A6).

The transition from pushed to pulled wave dynamics

Invasions under both growth models transformed from pushed to pulled waves (Fig. 3). After invasions commenced, $\bar{A}_{van}$ quickly decreased below 0 (the transition point from a strong Allee effect to a weak Allee effect) and kept decreasing (Fig. 3A). Unlike the reference case, this decrease appeared to equilibrate in the trade-off model. However, in the no-trade-off model, $\bar{A}_{van}$ declined even up to the end of the simulation. As $\bar{A}_{van} \leq \hat{A}$ in both cases (indicating that Eq. 1 was monotonically decreasing; Fig. 3B), invasions had transformed from pushed to pulled waves.

In the subset of parameter space we explored, $\hat{A}$ was always reached, but the time taken to do so increased with $\bar{A}_{init}$ (Fig. 4). This increase was a non-linear concave downward slope for both the trade-off and no-trade-off model (Fig. 4), contrary to our expectations concerning the effects of migrant load, which was expected to manifest as time increasing super-linearly with $\bar{A}_{init}$.

Discussion

Due to 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 [42]. In spreading populations, Allee effects result in a slower and particular spread dynamic: pushed invasions [8]. Recently, it has also become apparent that Allee effects can undermine evolutionary processes on the invasion front by reducing fitness there and increasing gene flow between core and frontal populations [26,36,43]. In this way Allee effects

may apply a handbrake to invasions; not only through fundamental demography, but by slowing the evolutionary processes that cause invasions to accelerate.

Here, we consider the possibility that Allee effects themselves might evolve. 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 may transition from pushed to pulled dynamics as Allee effects weaken, and accelerate despite the influence of migrant load.

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 caused ongoing and intense selection for individuals that could reproduce successfully there. Evolution of resistance to Allee effects proved robust to varying initial conditions, parameters, and the presence of a trade-off between fitness at high and low density (Figs. A3 and A5). In some sense, such an outcome is unsurprising. On low-density invasion fronts, invaders with superior low-density fecundity should outcompete rivals. However evolution of resistance to Allee effects is not a foregone conclusion; Allee effects should also cause an increase in maladaptive gene flow from the invasion core, an effect that has been observed to impede the evolution of traits on the invasion front in other models [26,36,43]. Additionally, trait evolution on invasion fronts needs to overcome the often strong drift associated with serial founder events [38]. The evolutionary shifts we observed in resistance to Allee effects appear to have occurred in our model despite these opposing forces.

Our findings support existing theory about the evolution of life-histories within invasions. The principles of r- and K-selection, although antiquated in a number of non-trivial aspects, act as useful conceptual tools in this instance [44,45]. 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 [44]. It follows that individuals in the vanguard should evolve traits that enable them to reproduce rapidly at low density, whereas those living in the invasion core should instead evolve traits that enhance competitiveness at high density. In our model, the gradient in $\bar{A}_x$ 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 [31,33,44,46], but it is entirely possible that these ambiguous results arise from the complex relationship between measurable traits, and actual population growth rates [45]. Allee effects introduce additional complexity. For example, in a hypothetical common garden we might find no difference in seed production, say, 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 stigmata; a low-density adaptation that, on the invasion front, would see the vanguard individuals exhibit much higher reproductive rates than individuals

from the core. Thus, we need to be very careful about the environment in which we measure reproductive traits, and 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 colonised ranges may have evolved to offset Allee effects. 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 unfertilised within invading populations [47,48]. In terms of behaviour, European starlings from recently established colonies have been shown to be more attuned to social signals from conspecifics [49], and cane toads from the invasion front in northern Australia appear to exhibit increased sociality [50]. In both cases, these behaviours enhance each species' capacity to aggregate despite low population densities. More broadly, it has been noted that selfing in plants is particularly prominent in marginal populations [51], and it has long been argued that biogeographical biases in the global distribution of parthenogenetic species may in fact reflect their inherent superiority as colonisers [52]. 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 findings.

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). Were this to occur in a real invasion, it would have far-reaching and profound impacts on the population's structure and dynamics. Because an absence of Allee effects allows populations to grow from small sizes, demographic stochasticity on the invasion front becomes a more powerful force as Allee effects diminish. This stochasticity not only results in intrinsically more variable invasion speeds [13,23], but also has several evolutionary consequences. The increased demographic stochasticity and success of small founder populations mean that pulled invasions experience substantial genetic drift – a force that should be strongly mitigated in pushed invasions [38]. In pulled invasions, this powerful drift can cause 'gene surfing', where deleterious alleles persist in the vanguard and are spread over wide geographical areas [53,54], ultimately contributing to populations suffering from high levels of 'expansion load' [55]. This expansion load can also affect the very traits responsible for spread rate – dispersal and reproduction – such that evolutionary stochasticity makes a very large contribution to making invasion speeds unpredictable [31,33,43]. All of these effects are mitigated on pushed invasion fronts. Here the requirement for large founding populations maintains relatively high levels of genetic diversity [53]. If invasions become more pulled with time, then all of the stochastic outcomes attendant on pulled waves will increasingly manifest as invasions progress.

The evolution of higher reproduction rates as Allee effects diminish would also facilitate the evolution of increased dispersal ability [56]. As Allee effects weaken, highly dispersive individuals accumulating on the invasion front through spatial sorting also accrue a fitness benefit, with spatial sorting and natural selection conspiring to drive increasing dispersal rates. Again, as invasions transition from pushed to pulled, we should see evolutionary processes accelerate.

Accounting for the possibility that invasions may transition from being pushed waves to pulled waves would considerably complicate attempts to predict invasion speed, especially given that the equations conventionally used to model the velocities of pushed and pulled waves are different from one another [8]. Furthermore, since pushed and pulled waves each favour the deployment of different control techniques [24], the most effective strategy for managing a particular invasion may also change as the invaders evolve. Since many control techniques exploit the Allee effect, accounting for the resultant selection these impose may be prudent [57]. If control techniques strengthen selection for individuals that are resistant to Allee effects, then they may inadvertently contribute to a less controllable and less predictable invasion.

Migrant load

The increased gene flow from high-density-adapted core individuals did not appear to reduce evolutionary rates, and was unable to suppress the evolution of increased Allee resistance on the invasion front (Fig. 4). This suggests that selection for low-density fecundity can occur even in strongly pushed invasions. Our result may be sensitive to the model's assumptions, however, rather than representing a general principle. The choice to treat all invaders as asexual, in particular, means migrant load would have affected the vanguard's average trait value without (through recombination and random mating) necessarily causing individuals and their offspring to become maladapted. That is, Allee resistant individuals would pass their resistant trait onto their offspring undiluted. Certainly, asexual populations appear more robust to migrant load than sexual populations [58]. It will be important, therefore, to extend the modelling presented here to examine sexual populations.

Conclusion

Our model represents a first step in describing the possibility that Allee effects may evolve on invasion fronts. Although our simulation results support the hypothesis that invasion fronts ought to select for individuals that are resistant to Allee effects, further theoretical and empirical work is required. In particular, models that incorporate recombination may see slower or stalled evolution depending on initial Allee effects. Experimental invasions and observational studies of real invasions may also help determine if transitions from pushed to pulled waves can happen on ecologically relevant timescales. Irrespective, future empirical efforts should pay careful attention to the context in which reproductive rate is assessed. If our findings hold in reality, rapid evolution can act to release the handbrake applied by Allee effects, with faster invasions and more dispersive invaders the result.

Data accessibility

The model code can be accessed at https://github.com/PhilErm/allee-evolution/.

Authors' contributions

P.E. and B.L.P. conceived the original idea. P.E. designed and programmed the simulation model. P.E. and B.L.P. wrote the manuscript.

Competing interests

We declare we have no competing interests.

Funding

This research was funded by the Australian Research Council (DP160101730).

Acknowledgements

We thank Mike Kearney, Luke Holman, and Katrina-Lee Ware for their critique and discussion of these ideas.

References

1. Thomas CD *et al.* 2004 Extinction risk from climate change. *Nature*, 145. (doi:10.1038/nature02121)

2. Fisher RA. 1937 The wave of advance of advantageous genes. *Annals of Eugenics* **7**, 355–369. (doi:10.1111/j.1469-1809.1937.tb02153.x)

3. Barton NH. 1979 The dynamics of hybrid zones. *Heredity* **43**, 341–359. (doi:10.1038/hdy.1979.87)

4. Perkins TA. 2011 Evolutionarily labile species interactions and spatial spread of invasive species. *The American Naturalist* **179**, E37–E54. (doi:10.1086/663682)

5. Orlando PA, Gatenby RA, Brown JS. 2013 Tumor evolution in space: The effects of competition colonization tradeoffs on tumor invasion dynamics. *Frontiers in oncology* **3**. (doi:10.3389/fonc.2013.00045)

6. Gallien L, Münkemüller T, Albert CH, Boulangeat I, Thuiller W. 2010 Predicting potential distributions of invasive species: Where to go from here?: Predicting potential

distributions of invasive species. *Diversity and Distributions* **16**, 331–342. (doi:10.1111/j.1472-4642.2010.00652.x)

7. Travis JMJ, Park KJ. 2004 Spatial structure and the control of invasive alien species. *Animal Conservation* **7**, 321–330. (doi:10.1017/S1367943004001507)

8. Lewis MA, Petrovskii SV, Potts JR. 2016 *The mathematics behind biological invasions.* Switzerland: Springer.

9. Shigesada N, Kawasaki K. 1997 *Biological invasions: Theory and practice.* UK: Oxford University Press.

10. Andow D, Kareiva P, Levin SA, Okubo. A. 1990 Spread of invading organisms. *Landscape Ecology* **4**, 177–188. (doi:10.1007/BF00132860)

11. Williamson M. 1999 Invasions. *Ecography* **22**, 5–12. (doi:10.1111/j.1600-0587.1999.tb00449.x)

12. Hastings A *et al.* 2005 The spatial spread of invasions: New developments in theory and evidence. *Ecology Letters* **8**, 91–101. (doi:10.1111/j.1461-0248.2004.00687.x)

13. Melbourne BA, Hastings A. 2009 Highly variable spread rates in replicated biological invasions: Fundamental limits to predictability. *Science* **325**, 1536–1539. (doi:10.1126/science.1176138)

14. Skellam JG. 1951 Random dispersal in theoretical populations. *Biometrika* **38**, 196–218. (doi:10.2307/2332328)

15. Kot M, Lewis MA, van den Driessche P. 1996 Dispersal data and the spread of invading organisms. *Ecology* **77**, 2027–2042. (doi:10.2307/2265698)

16. Clark JS, Lewis M, Horvath L. 2001 Invasion by extremes: Population spread with variation in dispersal and reproduction. *The American Naturalist* **157**, 537–554. (doi:10.1086/319934)

17. Lewis MA, Kareiva P. 1993 Allee dynamics and the spread of invading organisms. *Theoretical Population Biology* **43**, 141–158. (doi:10.1006/tpbi.1993.1007)

18. Keitt TH, Lewis MA, Holt RD. 2001 Allee effects, invasion pinning, and species' borders. *The American Naturalist* **157**, 203–216. (doi:10.1086/318633)

19. Barton NH, Turelli M. 2011 Spatial waves of advance with bistable dynamics: Cytoplasmic and genetic analogues of Allee effects. *The American Naturalist* **178**, E48–E75. (doi:10.1086/661246)

20. Allee WC. 1958 *The Social Life of Animals.* New York: W. W. Norton and Co.

21. Stephens PA, Sutherland WJ, Freckleton RP. 1999 What is the Allee effect? *Oikos* **87**, 185–190. (doi:10.2307/3547011)

22. van Saarloos W. 2003 Front propagation into unstable states. *Physics Reports* **386**,

29–222. (doi:10.1016/j.physrep.2003.08.001)

23. Taylor CM, Hastings A. 2005 Allee effects in biological invasions. *Ecology Letters* **8**, 895–908. (doi:10.1111/j.1461-0248.2005.00787.x)

24. Gandhi SR, Yurtsev EA, Korolev KS, Gore J. 2016 Range expansions transition from pulled to pushed waves as growth becomes more cooperative in an experimental microbial population. *Proceedings of the National Academy of Sciences of the United States of America* (doi:10.1073/pnas.1521056113)

25. Phillips BL. 2009 The evolution of growth rates on an expanding range edge. *Biology Letters* **5**, 802–804. (doi:10.1098/rsbl.2009.0367)

26. Travis JM, Dytham C. 2002 Dispersal evolution during invasions. *Evolutionary Ecology Research* **4**, 1119–1129.

27. Shine R, Brown GP, Phillips BL. 2011 An evolutionary process that assembles phenotypes through space rather than through time. *Proceedings of the National Academy of Sciences* **108**, 5708–5711. (doi:10.1073/pnas.1018989108)

28. Cwynar LC, MacDonald GM. 1987 Geographical Variation of Lodgepole Pine in Relation to Population History. *The American Naturalist* **129**, 463–469. (doi:10.1086/284651)

29. Fronhofer EA, Altermatt F. 2015 Eco-evolutionary feedbacks during experimental range expansions. *Nature Communications* **6**. (doi:10.1038/ncomms7844)

30. Hughes CL, Dytham C, Hill JK. 2007 Modelling and analysing evolution of dispersal in populations at expanding range boundaries. *Ecological Entomology* **32**, 437–445. (doi:10.1111/j.1365-2311.2007.00890.x)

31. Ochocki BM, Miller TE. 2017 Rapid evolution of dispersal ability makes biological invasions faster and more variable. *Nature Communications* **8**. (doi:10.1038/ncomms14315)

32. Phillips BL, Brown GP, Webb JK, Shine R. 2006 Invasion and the evolution of speed in toads. *Nature* **439**, 803. (doi:10.1038/439803a)

33. Weiss-Lehman C, Hufbauer RA, Melbourne BA. 2017 Rapid trait evolution drives increased speed and variance in experimental range expansions. *Nature Communications* **8**. (doi:10.1038/ncomms14303)

34. Amundsen P-A, Salonen E, Niva T, Gjelland KØ, Præbel K, Sandlund OT, Knudsen R, Bøhn T. 2012 Invader population speeds up life history during colonization. *Biological Invasions* **14**, 1501–1513. (doi:10.1007/s10530-012-0175-3)

35. Hudson CM, Phillips BL, Brown GP, Shine R. 2015 Virgins in the vanguard: Low reproductive frequency in invasion-front cane toads. *Biological Journal of the Linnean Society* **116**, 743–747. (doi:10.1111/bij.12618)

36. Burton OJ, Phillips BL, Travis JM. 2010 Trade-offs and the evolution of life-histories during range expansion. *Ecology Letters* **13**, 1210–1220. (doi:10.1111/j.1461-0248.2010.01505.x)

37. Lenormand T. 2002 Gene flow and the limits to natural selection. *Trends in Ecology &*

Evolution **17**, 183–189. (doi:10.1016/S0169-5347(02)02497-7)

38. Slatkin M, Excoffier L. 2012 Serial founder effects during range expansion: A spatial analog of genetic drift. *Genetics* **191**, 171–181. (doi:10.1534/genetics.112.139022)

39. R Core Team. 2016 *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

40. Courchamp C, Berec L, Gascoige J. 2008 *Allee effects in ecology and conservation.* Oxford: Oxford University Press.

41. Kolmogorov AN, Petrovsky IG, Piskunov NS. 1937 Etude de l'équation de la diffusion avec croissance de la quantité de matiere et son applicationa un probleme biologique. *Moscow University Mathematics Bulletin* **1**, 129.

42. Boukal D, Berec L. 2002 Single-species models of the Allee effect: Extinction boundaries, sex ratios and mate encounters. *Journal of Theoretical Biology* **218**, 375–394. (doi:10.1006/jtbi.2002.3084)

43. Phillips BL. 2015 Evolutionary processes make invasion speed difficult to predict. *Biological Invasions* **17**, 1949–1960. (doi:10.1007/s10530-015-0849-8)

44. Phillips BL, Brown GP, Shine R. 2010 Life-history evolution in range-shifting populations. *Ecology* **91**, 1617–1627. (doi:10.1890/09-0910.1)

45. Reznick D, Bryant MJ, Bashey F. 2002 R-and K-selection revisited: The role of population regulation in life-history evolution. *Ecology* **83**, 1509–1520. (doi:10.1890/0012-9658(2002)083[1509:RAKSRT]2.0.CO;2)

46. Chuang A, Peterson CR. 2016 Expanding population edges: Theories, traits, and trade-offs. *Global Change Biology* **22**, 494–512. (doi:10.1111/gcb.13107)

47. Hung ACF, Day WH, Hedlund RC. 1988 Genetic variability in arrhenotokous and thelytokous forms ofMesochorus nigripes [Hym.: Ichneumonidae]. *Entomophaga* **33**, 7–15. (doi:10.1007/BF02372308)

48. Hopper KR, Roush R. 1993 Mate finding, dispersal, number released, and the success of biological control introductions. *Ecological Entomology* **18**, 321–331. (doi:10.1111/j.1365-2311.1993.tb01108.x)

49. Rodriguez A, Hausberger M, Clergeau P. 2010 Flexibility in European starlings' use of social information: Experiments with decoys in different populations. *Animal Behaviour* **80**, 965–973. (doi:10.1016/j.anbehav.2010.08.010)

50. Gruber J, Whiting MJ, Brown G, Shine R. 2017 The loneliness of the long-distance toad: Invasion history and social attraction in cane toads (Rhinella marina). *Biology Letters* **13**, 20170445. (doi:10.1098/rsbl.2017.0445)

51. Pannell JR. 2015 Evolution of the mating system in colonizing plants. *Molecular Ecology* **24**, 2018–2037. (doi:10.1111/mec.13087)

52. Kearney M. 2005 Hybridization, glaciation and geographical parthenogenesis. *Trends in*

Ecology & Evolution **20**, 495–502. (doi:10.1016/j.tree.2005.06.005)

53. Hallatschek O, Nelson DR. 2008 Gene surfing in expanding populations. *Theoretical Population Biology* **73**, 158–170. (doi:10.1016/j.tpb.2007.08.008)

54. Graciá E, Botella F, Anadón JD, Edelaar P, Harris DJ, Giménez A. 2013 Surfing in tortoises? Empirical signs of genetic structuring owing to range expansion. *Biology Letters* **9**. (doi:10.1098/rsbl.2012.1091)

55. Peischl S, Kirkpatrick M, Excoffier L. 2015 Expansion load and the evolutionary dynamics of a species range. *The American Naturalist* **185**, E81–93. (doi:10.1086/680220)

56. Perkins TA, Phillips BL, Baskett ML, Hastings A. 2013 Evolution of dispersal and life history interact to drive accelerating spread of an invasive species. *Ecology Letters* **16**, 1079–1087. (doi:10.1111/ele.12136)

57. Tobin PC, Berec L, Liebhold AM. 2011 Exploiting Allee effects for managing biological invasions. *Ecology Letters* **14**, 615–624. (doi:10.1111/j.1461-0248.2011.01614.x)

58. Peck JR, Yearsley JM, Waxman D. 1998 Explaining the geographic distributions of sexual and asexual populations. *Nature* **391**, 889–892. (doi:10.1038/36099)

Tables

Table 1: Invasion simulation parameterisations. For the sensitivity analysis, parameters were fixed at reference case values as one parameter was explored across the ranges indicated.

Parameter	Description	Reference case	Sensitivity analysis	Pushed to pulled	Time to pulled
r	Density independent reproduction rate	1	0.5, 1, 1.5	1	1
K^*	Carrying capacity (at $A_i = 0$ for simulations with trade-off)	500	250, 500, 750	500	500
$\bar{A}_{init}$	Mean value of Allee trait for initial invaders	0	-50, -25, 0, 25, 50	50	-497 – 50
σ_A	Standard deviation of Allee trait for initial invaders	50	50	10	0
p_{mut}	Allee trait mutation probability	0.01	0, 0.001, 0.01, 0.1	0.1	0.1
σ_{mut}	Standard deviation of Allee trait mutation	20	20	20	20
m	Dispersal probability	0.5	0.5	0.5	0.5

Figures

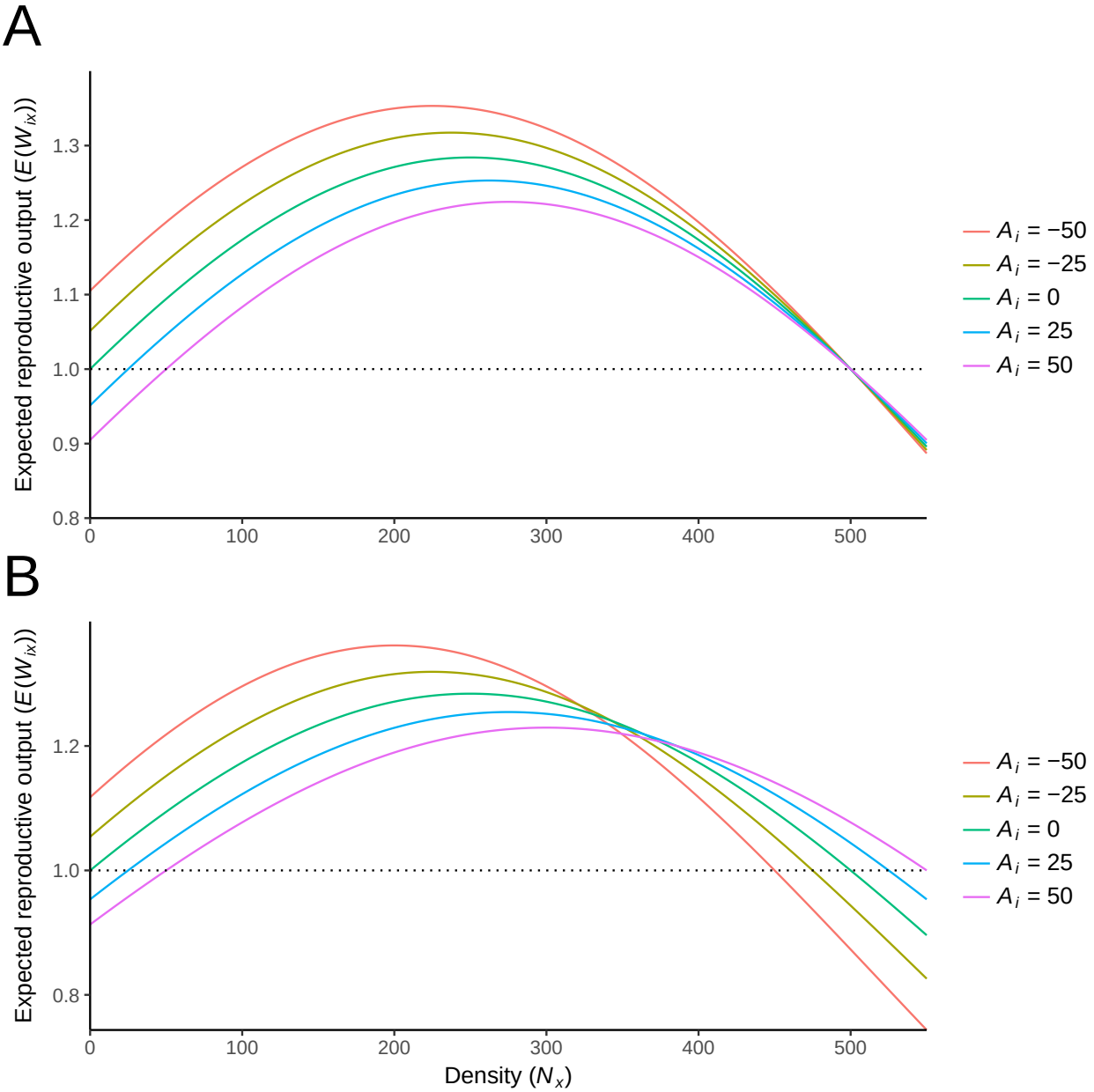

Figure 1: (**A**): Sensitivity analysis of Eq. 1, a growth function subject to the Allee effect. (**B**): Sensitivity analysis of Eq. 1, but with a reproductive trade-off across densities mediated by Eq. 1.1. In both cases, A_i determines the Allee threshold, or the critical density below which a population begins to shrink (here seen for values of $E(W_{ix})$ below the dotted line).

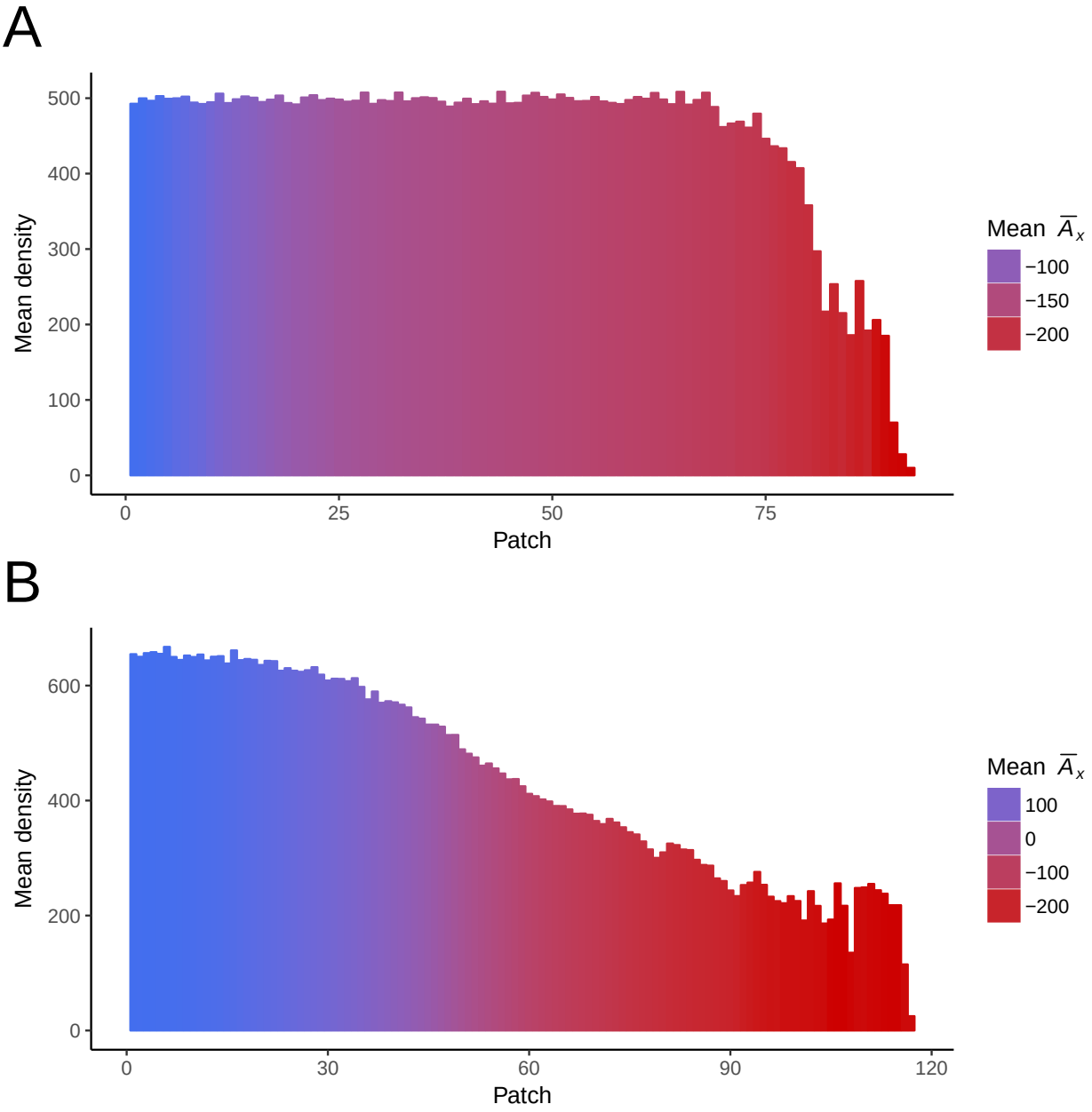

Figure 2: (**A**): Mean $\bar{A}_x$ (the mean value of A_i, an Allee threshold governing trait, for all individuals located in the same patch) and mean density for invasions (n = 20) after 150 generations. More recently colonised patches exhibit greater levels of resistance to the Allee effect, as shown by lower mean values of $\bar{A}_x$. (**B**): Invasions with a reproductive trade-off. As the trade-off influences carrying capacity, core and frontier patches support differing numbers of invaders.

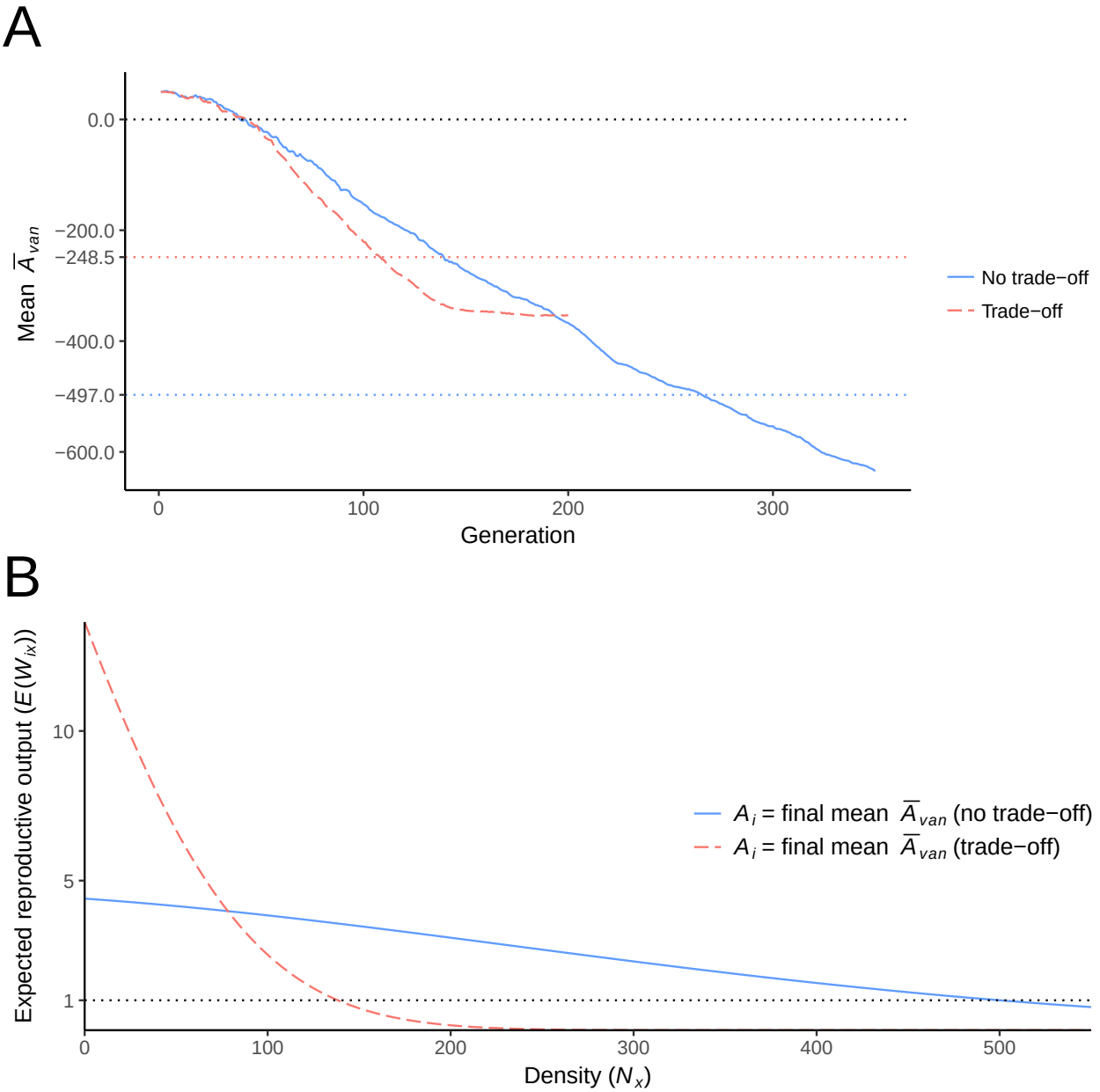

Figure 3: (**A**): The evolution of $\bar{A}_{van}$ ($\bar{A}$ of the vanguard invaders) over time for n = 20 invasions with (red line) and without (blue line) a reproductive trade-off. The founding invaders are subject to a strong Allee effect, meaning that invasions start as pushed waves. As the vanguard becomes more resistant to Allee effects, increasing levels of low-density fecundity make the invasions instead transition into pulled waves. (**B**): The expected reproductive output of vanguard invaders across differing population densities after 200 generations (trade-off) and 375 generations (no trade-off). Vanguard invaders have become highly adapted to low densities, and experience no Allee effects. Because their growth functions are monotonically decreasing, pulled invasion waves will result.

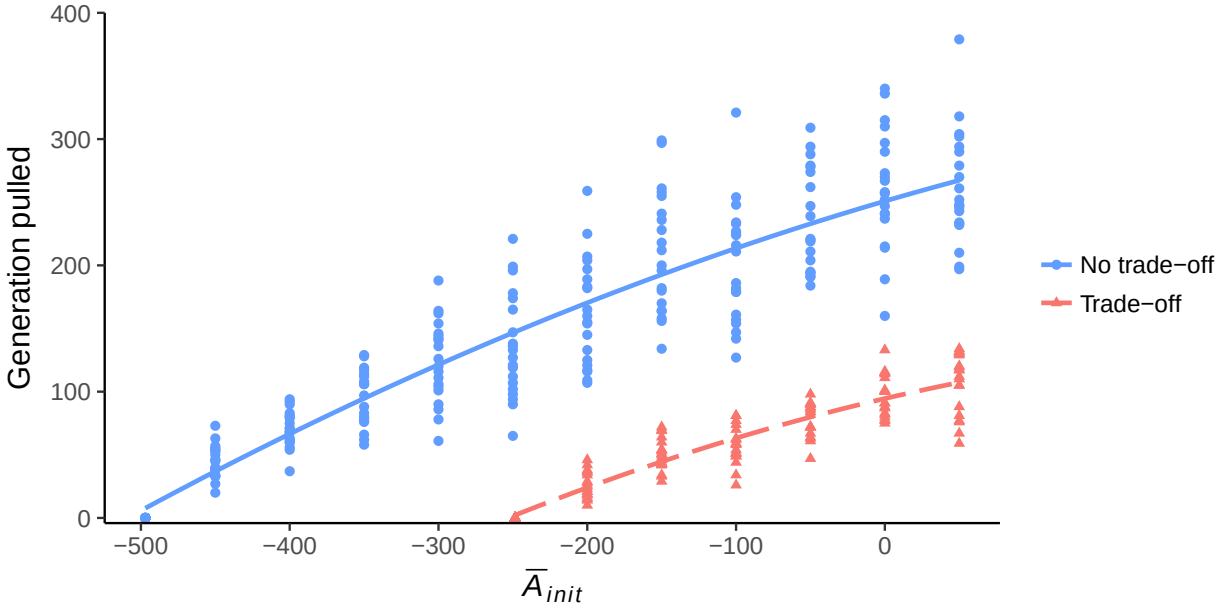

Figure 4: The time it took for invasions starting with different $\bar{A}_{init}$ values to become pulled, both with (red line) and without (blue line) a reproductive trade-off. Fitted lines are of the form $y = x^2$, and points represent individual replicates. Migrant load associated with larger $\bar{A}_{init}$ neither super-linearly increased the time taken until invasions became pulled, nor prevented them from becoming pulled altogether.