**Trends in Ecology & Evolution**

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Opinion

# How Evolution Modifies the Variability of Range Expansion

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**Eco-evolutionary theory suggests that rapid evolution can accelerate range expansion speed. In addition to average speed, recent experimental studies reveal that evolution can also influence the amount of variability across replicates of spreading populations, but in contrasting ways. Here we develop a predictive framework, drawing on ideas from population genetics and spread theory, to understand when, why, and in what direction evolution will modify the variability of range expansion. Our framework revolves around the balance of variance-generating (drift) and variance-reducing (selective) evolutionary processes, and factors that may tip this balance, including population size at the leading edge and mating system. We suggest hypotheses to clarify contrasting experimental results and highlight a way forward for studying eco-evolutionary dynamics of range expansion.**

## Many Populations Are Spreading, and Also Evolving

Understanding the expansion of populations across a landscape is essential for predicting the speeds at which introduced species invade their new ranges and native species invade habitats that are made newly suitable by climate change [1–3]. Two underlying processes collectively drive **expansion speed** (see Glossary), dispersal and reproduction at the expanding edge [2,4,5]. Eco-evolutionary theory makes the prediction that evolutionary processes at the expanding edge (**spatial sorting** leading to increased dispersal and natural selection on life-history traits leading to increased fitness) can increase the spread velocity [2,5–8]. With the exception of a few observational field studies, which are necessarily retrospective [9–12], this theory went untested until very recently, with a surge of experimental studies in laboratory-based model systems in the last few years [13–18]. These recent experimental studies are a key advance because they impose manipulations of evolutionary processes on replicated expanding populations and thus test the repeatability of and evolutionary effects on these trajectories.

Recent eco-evolutionary experiments on expanding populations have generated two key results. First, they all support the prediction that rapid evolution can accelerate the speed of population expansion [13–18] (Figure 1). Specifically, in all of these studies, experimental populations moved faster, on average, where evolution was operating than where it was suppressed. Second, evolutionary processes also modified the amount of replicate-to-replicate variability in expansion speed, which we call **expansion variability**. Surprisingly, despite a consistently positive effect on mean velocity across studies, evolutionary effects on expansion variability were themselves variable in direction and magnitude; depending on the system, evolution increased, decreased, or had no effect on variability (Figure 1). Variability is a key measure of spread dynamics because it affects how precisely we can predict the trajectories of expanding populations [19], something ecologists are increasingly called upon to do. A recent call for evolutionary biologists to explore and quantify the predictability of evolution highlights the importance of studying predictability as well as the difficulties [20,21]. Resolving when,

### Highlights

Outcomes of range expansions are variable; evolution can increase or decrease that variation.

Expansion outcomes reflect a balance of variance-generating and variance-reducing evolutionary processes.

Mating system and edge population size may determine whether evolution increases or decreases variance.

These ideas can be tested with mathematical modeling, additional experiments, and data from natural range expansions.

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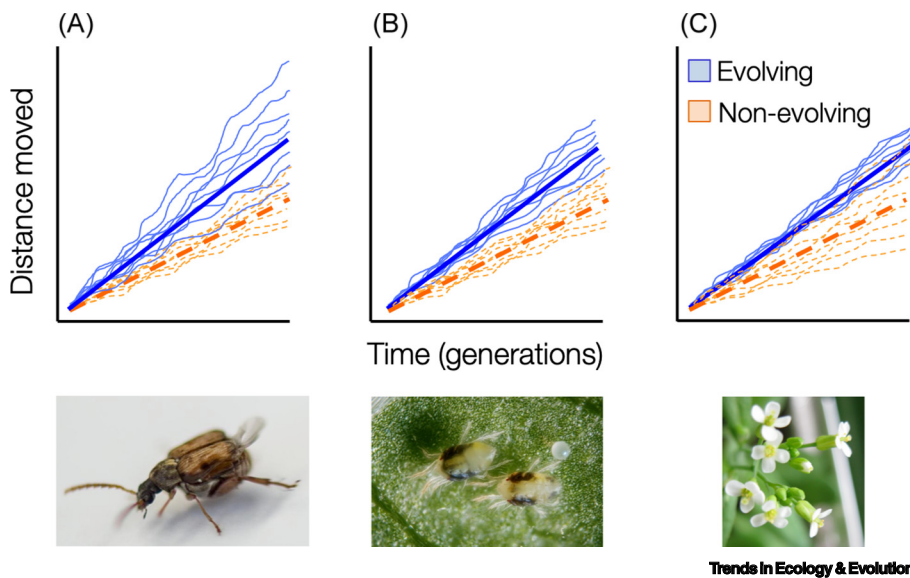
Figure 1. Evolutionary Effects on Variability in Speed among Replicates. Evolution can lead to the trajectories of replicate expanding populations being (A) more variable than the comparable non-evolving populations, as observed in bean beetles, *Callosobruchus maculatus* [14] and flour beetles, *Tribolium castaneum*, in a benign environment, [15]; (B) similarly variable, as observed in spider mites, *Tetranychus urticae* [17] and flour beetles in a challenging environment [18]; or (C) less variable, as observed in thale cress, *Arabidopsis thaliana* [13]. Figures demonstrate the qualitative patterns rather than reproducing results from each experiment, with thin lines representing individual replicates and thick lines the mean across replicates. Photo credits: (A) Jeff Fitlow, Rice University; (B) Jacopo Werther, Creative Commons; (C) Jennifer Williams (author); all photos used with permission.

why, and in what direction evolution may influence expansion variability is therefore an urgent challenge.

Here, we develop a framework for understanding how evolution may affect the variability, and thus predictability, of population expansion. This framework connects ecological theory for spreading populations with population genetics theory. We focus on intrinsic sources of variance as we expect that extrinsic (environmental) variability will only increase expansion variability. We offer a perspective that is intended to aid interpretation of current, conflicting results and illustrate a way forward for eco-evolutionary studies of invasion and range expansion.

## Spread Dynamics Are Known to Be Variable

The dynamics of spreading populations have long been recognized to be highly variable and idiosyncratic. Temporal and spatial environmental heterogeneity are pervasive in nature and it is unsurprising that these extrinsic factors contribute to variation in spread [22–24]. More surprisingly, ecologists have also discovered substantial variability in spread dynamics even in tightly controlled, constant environments [25–27]. Because spread is driven by individual-level demography and dispersal processes, intrinsic noisiness in these processes (random realizations of births, deaths, and movement) is one ingredient of expansion variability, even in constant environments. However, in a landmark study, Melbourne and Hastings [25] demonstrated that variability across replicates in laboratory-based beetle invasions exceeded what would be expected from stochastic variation in demography and dispersal, alone.

The development and testing of eco-evolutionary theory for spreading populations has suggested new sources of variance that may help explain patterns of expansion in field and lab systems. Importantly, the change in variability that has been attributed to evolutionary processes

### Glossary

**Allee effect:** positive density-dependence in components of fitness, such that population growth rate increases with increasing density in small populations where it is, for example, difficult to find mates.

**Assortative mating:** nonrandom mating in a population where some pairs of individuals are more likely to mate than others, often by phenotype. During population spread, assortative mating occurs with respect to dispersal phenotype, with strong dispersers that reach the leading edge more likely to mate with each other than with individuals at the population core.

**Density-dependent selection:** differential reproduction and survival of individuals experiencing strong intraspecific competition at high population densities, such as at the core of an expanding population or at a steep wave front. Individuals with traits that lead to increased competitive ability ('*K*-selection') are likely to be favored.

**Density-independent selection:** differential reproduction and survival of individuals experiencing weak intraspecific competition at low population densities, such as those at a shallow leading edge of an expanding population. Individuals with traits that lead to increased reproductive rate, including producing more offspring or reproducing earlier ('*r*-selection'), are likely to be favored.

**Dispersal kernel:** probability distribution of distances of offspring dispersal away from the parent.

**Effective population size ($N_e$):** the number of individuals in an idealized population; it indicates the extent to which that population experiences genetic drift. An idealized population is a population where sex ratio is equal, mating is random (thus, not assortative), and there is no natural selection, no sexual selection (i.e., unequal reproductive success among different individuals), and finally no fluctuations in census population size through time. For most organisms, one or several of these conditions will not hold, so $N_e$ is typically less than $N$.

**Expansion load:** reduced fitness of the population at the expanding front due to increase in frequency or fixation of deleterious alleles via gene surfing. Deleterious alleles may also increase in frequency due to linkage with alleles that

occurs among replicates, meaning that each realization of a spreading population may exhibit a unique trajectory (Figure 1). Melbourne and Hastings [25] also found unique trajectories across replicates, but did not quantify the contribution of evolution. In nature, of course, biological invasions and range expansions are rarely replicated. The implication of elevated among-replicate variance for natural settings is that, for any single expansion, the observed dynamics are drawn from a wider distribution of possibilities, hence increasing the challenge of forecasting the outcome for any single realization. However, if the sources of this variability can be rigorously defined then the distribution of possibilities may too be defined, facilitating the estimation of uncertainty intervals for spreading speeds even if accurate point predictions remain elusive.

### Evolution as a Modifier of Expansion Variability

We suggest a framework for evaluating when and how evolution may increase or decrease expansion variability based on the balance of selective processes, which lead to more consistency among replicate expansions, and drift, which leads to greater variance among replicate expansions. Spatial sorting and natural selection on life history traits during spread each have a directional, variance-reducing effect on dispersal and fitness, respectively, given heritable variation in those traits. At a low-density leading edge, in the absence of **Allee effects**, spatial sorting should favor greater dispersal ability and natural selection should favor greater reproductive rate [2,5–8,28]. Indeed, these expectations are often, but not always, supported by the experimental results described above, as well as by observational field studies that compare trait values between range-edge and range-core populations [29–33]. These directional, selective processes likely account for the highly consistent, positive effects of evolution on the average spreading speed of experimental invasions.

In addition to directional, selective processes acting on dispersal and fitness, evolution during expansion has a stochastic component that can make each realization unique. Population geneticists have recognized the potential for neutral processes to act on allele frequencies during spread [34–37], and ecologists are just now coming to grips with this phenomenon and its consequences [19,38,39]. Specifically, in spreading populations, genetic drift occurs at the expansion front due to small population size, and via the serial founder events that occur as the population moves into new territory, reducing genetic variation [40]. Furthermore, novel mutations and alleles initially rare at the leading edge can increase in frequency and become locally fixed even if they are deleterious via the process of **gene** (or mutation) **surfing** [32,33,37]. These are explicitly spatial processes that occur as an expansion wave advances by serial founder events, in which colonists at the leading edge contribute disproportionately to the genetic composition of the expanding front in subsequent generations [34,36,39]. Thus, small population size at the leading edge favors the stochastic loss or fixation of alleles, including fixation of those with deleterious fitness effects [37,41]. The increase in frequency or fixation of deleterious alleles leads to reduced fitness at the edge, or **expansion load** [35]. Importantly, the stochastic nature of gene surfing means that each realization of a population expansion would tend to fix a different set of alleles at the expanding front [42], which will tend to increase variability in speed across replicate expansions.

We propose that the eco-evolutionary dynamics of spreading populations arise from the interaction between processes that reduce variance across replicate expansions (spatial sorting of dispersal ability and natural selection on life history traits) and those that increase variance across replicate expansions (gene surfing and drift). For the remainder of this piece, we use 'selective processes' to refer to both spatial sorting and natural selection, and 'drift' to refer to changes in allele frequencies due to neutral processes. 'Selective processes' may also include **spatial selection**, the combination of spatial sorting and a low-density fitness advantage for strong

are responding to spatial sorting or natural selection.

**Expansion speed:** the speed (or velocity) at which the leading edge of an expanding population moves into previously unoccupied space. In experiments and simulations, typically quantified as number of patches colonized or distance moved per generation.

**Expansion variability:** variability across replicate spreading populations in the expansion speed or total distance colonized. Variation in speed among generations within one population also occurs, but here we specifically refer to variation across replicates (in an experiment, or between different expanding fronts of the same species in the field).

**Gene surfing:** during population spread, rare alleles or new mutations can be carried by the expanding wave front to reach high frequency at the leading edge of the population expansion. Alleles can be swept to fixation or near fixation even if deleterious, reducing fitness of the population at the expansion edge (see expansion load, above).

**Kurtosis:** describes the shape of a probability distribution, here related to the shape of the dispersal kernel. Distributions with greater excess kurtosis have a fatter tail than a normal distribution, corresponding to a greater frequency of long-distance movement, and those with negative excess kurtosis have a more truncated tail.

**Spatial selection:** at the edge of an invasion or range expansion, dispersal can evolve via a combination of spatial sorting (see definition below) and a fitness advantage at low density (collectively 'spatial selection'). At the leading edge, conspecific density can be low, and so individuals have the resources to produce more offspring than they would at the core. Together this means that the most dispersive individuals contribute more offspring per-capita, increasing the frequency of high-dispersal phenotypes at the leading edge.

**Spatial sorting:** ordered distribution of dispersal phenotypes from the leading edge to the core of an expanding population, with the most dispersive individuals near the leading edge, allowing for assortative mating by dispersal phenotype.

dispersers at the leading edge. The relative contributions of selective processes and drift should determine whether the net effects of evolution during spread would tend to increase or decrease expansion variability. When both selective processes and drift strongly contribute to spread dynamics, we expect an increase in speed, on average, and also elevated expansion variability. This is because, in some cases, drift in the alleles underlying dispersal and fitness would reinforce the direction of selective processes and in other cases it would oppose it. However, if the potential for drift is dampened, we expect the variance-reducing effects of selective processes to prevail, such that different realizations would tend to converge on favored trait values, leading to an increase in average speed and a reduction in expansion variability. Thus, we can make predictions about whether evolution should tend to increase or decrease expansion variability by identifying the conditions or traits that can modify the role of neutral processes relative to the directional influences of selective processes.
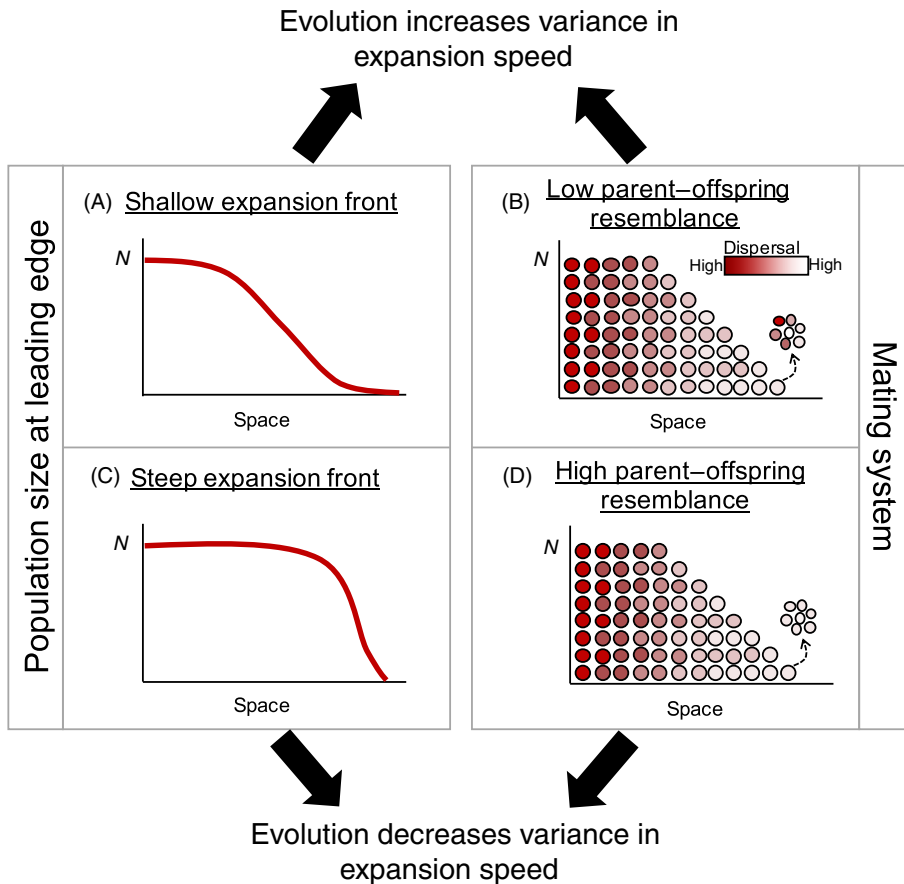
## Factors That Determine the Relative Roles of Variance-Reducing and Variance-Generating Processes

Here we develop hypotheses for factors that can tip the balance of drift versus selective processes during population expansion. We first focus on two factors that theory suggests should play an important role in this balance: population size at the expanding front and mating system (Figure 2). We then briefly consider additional factors and the potential for interactions or feedbacks. We assume throughout that dispersal and life history traits exhibit genetically based variation [43]; clearly, in the absence of trait heritability, neither selective processes nor drift can influence the dynamics of spread.

### Population Size at the Expanding Front

Population size at the expanding front is likely one of the most important determinants of how variable replicate expansions might be. What matters most is not simply the census population size ($N$), but the **effective population size ($N_e$)**, which is typically smaller than $N$, often by half [44,45]. The term 'population' can take on several meanings in a spatial spread context, from an individual patch at the smallest, local scale to the complete collection of occupied patches at the largest scale. We use 'population size at the expanding front' in reference to an intermediate scale: the group of individuals nearest the leading edge and within a shared mating neighborhood that, collectively, generate most of the colonists of new patches in the next generation. Conceptually, this is similar to Wright's neighborhood size applied to an expansion front [46,47]. Population size at the expanding front will be influenced in part by the same life history traits and drivers that influence $N_e$. For example, species with larger body sizes, high variability in number of offspring, or skewed sex ratios (e.g., with polygynous mating systems) tend to have smaller effective population sizes [44,48–50].

For expanding populations, the shape of the expanding wave is likely to be an important driver of $N_e$, from shallow (small leading-edge populations, often with a long tail of low-density patches) to steep (large leading-edge populations) (Figure 2). For small leading-edge populations, drift can be a potent factor determining allele frequency, such that even beneficial alleles can be lost and deleterious ones fixed [51]. Thus, stochastic fixation of alleles due to drift will sometimes reinforce the direction of selective processes and sometimes oppose them, increasing expansion variability. In contrast, for larger leading-edge populations, the dynamics of common alleles are more likely dominated by selective processes, with favorable alleles increasing and unfavorable alleles decreasing, and less contribution from drift [51,52]. It is noteworthy, however, that expansions with large leading-edge populations may also have different selective optima, since natural selection for increased reproductive rate and spatial selection leading to increased dispersal both rely on escape from negative density dependence at the leading edge. Very large edge populations

Evolution increases variance in expansion speed

Population size at leading edge

(A) Shallow expansion front

(B) Low parent–offspring resemblance

(C) Steep expansion front

(D) High parent–offspring resemblance

Mating system

Evolution decreases variance in expansion speed

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Figure 2. Hypotheses for Factors That Determine Whether Evolution Would Tend to Increase or Decrease Expansion Variability. (A,C) Population size at the leading edge of expansion should affect the potential for stochastic fixation of alleles through genetic drift and gene surfing. A 'shallow' expansion front (A) with a long tail of low-density patches should be strongly influenced by drift and may therefore exhibit increased dissimilarity across realizations of spread due to evolution. In contrast, a 'steep' front (C) with higher densities near the leading edge would be less sensitive to neutral evolutionary processes. Instead, selective processes (natural selection on life history traits leading to increased fitness and spatial sorting leading to increased dispersal) would act more efficiently on larger range-edge populations, leading to convergence on favored phenotypes and reduced variability, relative to a no-evolution scenario. (B,D) Mating system should influence the extent to which leading edge individuals generate phenotypically similar offspring, including with respect to dispersal ability (shown with shading, where a gradient from low to high dispersal ability reflects the potential for spatial sorting of dispersal phenotype). In a sexually reproducing species, recombinant offspring may be phenotypically dissimilar from parents (with positive or negative trait deviations); this should weaken responses to selective processes and diversify the alleles and phenotypes present at the leading edge, setting the stage for stochastic allele fixation. The reduced efficiency of selective processes and increased opportunity for drift would tend to increase variance. Alternatively, a clonally reproducing species with high parent–offspring similarity may, in the short term, increase the efficiency of selective processes, such that multiple realizations of spread converge on the same 'fast' clonal genotypes, a variance-reducing process.

with little escape from density dependence may be dominated by **density-dependent selection** rather than **density-independent selection**, though either type can be variance-reducing. Thus, in applying the classic view of drift-selection balance to a spatial context, we expect that selective process will act more efficiently and be more likely to overwhelm the role of drift in larger populations [51], that is expansions with steep wave fronts, and this should tend to promote convergence across realizations.

Density dependence in either population growth or dispersal (or both) can influence wave shape. For example, over-compensatory density dependence in population growth or strong Allee effects can cause expanding populations to have steep edges [53,54]. Recent theoretical work demonstrates that Allee effects can not only generate steep waves, but also promote greater genetic variation at the range edge, since edge composition is influenced by core individuals, leading to reductions in drift [38,39,55,56]. Positive density-dependent dispersal, where organisms are more likely to disperse when they are crowded, can also lead to steep wave fronts with expected reductions in drift [55]. We expect something similar where the steepness of an environmental gradient leads to a steep expansion front because the population cannot increase as environmental quality declines [41]. In contrast, shallow wave fronts often correspond to expansions driven by dispersal and fecundity from the previously colonized low-density region, with expected lower $N_e$ and genetic diversity. However, it is possible for a shallow wave front to instead be pushed by density-dependent dispersal from the core, in which case genetic diversity and $N_e$ would be higher than expected, that is more similar to a steep front. Thus, quantifying wave shape is a first step to identifying the balance between variance generating and reducing factors, but further disentangling the underlying drivers, in particular, the role of density on fecundity and dispersal, will improve predictability.

Wave shape can also be influenced by dispersal characteristics of the organism, quantified as **kurtosis** of the **dispersal kernel** [5]. For example, wind- versus animal-dispersed plants may exhibit differences in kurtosis [57]. Dispersal kernels with greater excess kurtosis ('fatter tails' corresponding to low-probability, long-distance movement) should lead to shallower expansion fronts and thus greater opportunity for stochastic fixation of local allele frequencies. This expectation can be more complex when long-distance dispersers from the core instead increase genetic diversity at the leading edge [50,58]. Conversely, kernels describing a more uniform distribution of dispersal distances (negative excess kurtosis) should generate steep expansion fronts with high local densities at the leading edge and thus greater opportunity for responses to selective processes.

### Mating System

Second, we consider the role of mating system, which can be considered along a continuum from species that reproduce clonally to those that reproduce sexually. This axis of variation could equivalently be framed as a continuum of genetic resemblance from parent to offspring (Figure 2). Other factors will also influence whether offspring might be more similar or more different to their parents, including the degree of **assortative mating** [51]. In stationary populations, over the long term, sexual reproduction facilitates adaptation [59–61], at least in part because recombination allows beneficial alleles to combine within individuals, creating fitter phenotypes on which selection can act, and deleterious alleles to combine within other individuals, facilitating their removal from the population ('purging of deleterious mutations') [62]. In contrast, over just a few generations, adaptation can proceed faster in asexual populations because the allele combinations underlying favored phenotypes are not broken up by recombination [62]. Thus, one clone with a favorable combination of alleles can rise to dominance quickly, though this evolutionary advantage of asexual reproduction does not last over the long term [59], and how sex affects the repeatability of evolution is complex and still being explored [63].

Extending these results to expanding populations, we hypothesize that sexual reproduction at the leading edge will increase variation among replicates, with recombination producing unique mixes of phenotypes with higher and lower trait values than the parents. In contrast, a fast-moving or rapidly reproducing clone in an asexual population could reach the leading edge over a few generations and then dominate due to selective processes because it breeds true [37]. Thus,

when a particular clone is favored by selective processes at the leading edge, it is likely to dominate across replicates, leading to convergence in expansion speed and reduced expansion variability.

### Additional Factors, Interactions, and Feedbacks

We have focused on leading-edge population size and mating system because theory suggests that these factors can affect the balance between variance-reducing and -generating processes at expansion fronts, but additional intrinsic factors likely contribute. For example, genetic architecture, including covariance and linkages among traits, is likely to play a role, since multivariate genetic constraints may dampen responses to selection [64], or deleterious alleles may increase in frequency due to linkage with alleles responding to spatial sorting or natural selection. Further, while here we have considered each factor separately, they are unlikely to operate in isolation, and there may be feedbacks between drivers and outcomes of range expansion. For example, the accumulation of deleterious alleles due to drift can slow down range expansion, which feeds back to limit further drift and strengthen the role of selection [37]. A further challenge is that factors may cause variance to increase or decrease on different time scales that, at least in an
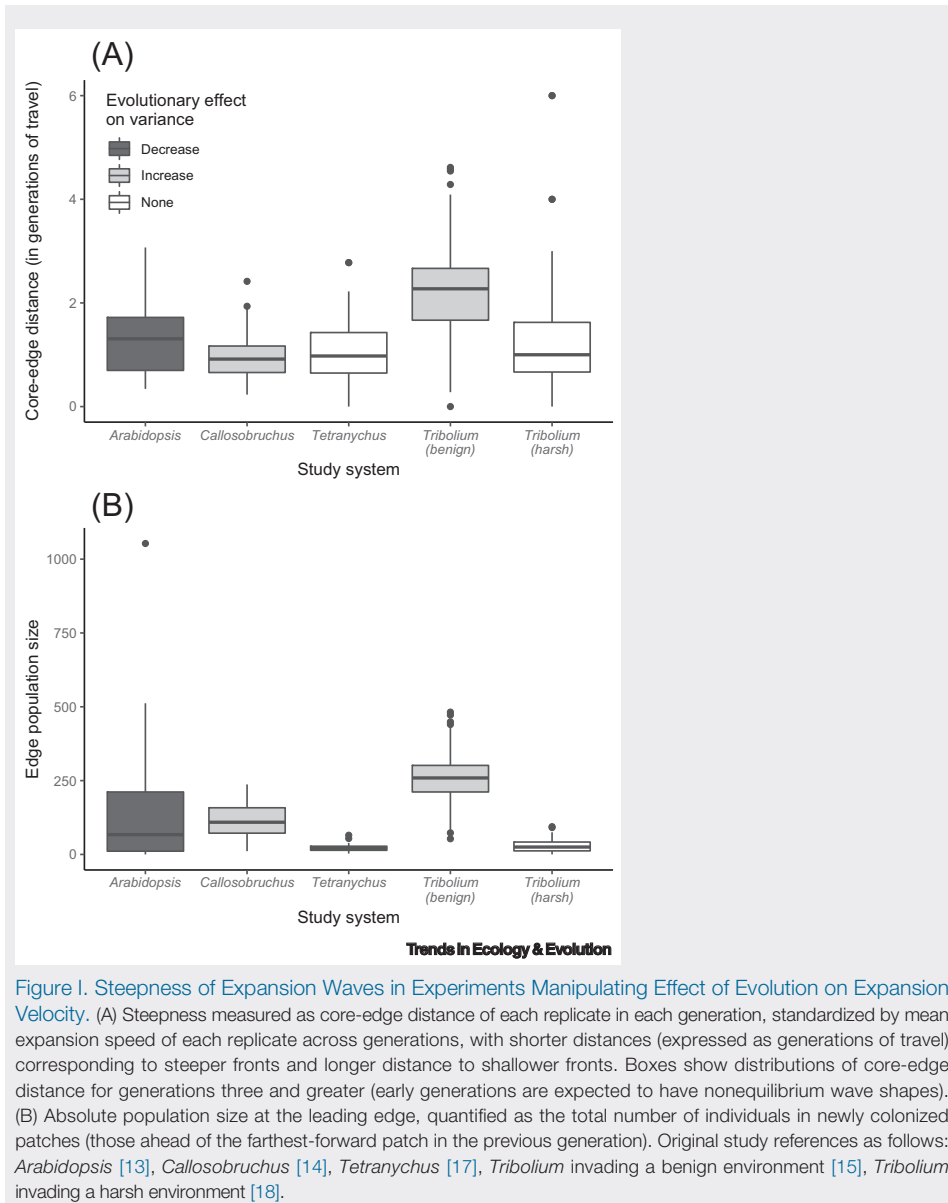
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**Box 1. Steepness of the Expanding Wave and Variance**

The shape of the leading edge of an expanding wave (wave front) has consequences for population size at the front. Most simply, steep fronts, with a relatively short distance from leading edge to core, have larger edge populations than shallow fronts, with a relatively long distance. Quantifying the shape of the expanding wave in a standardized way allows for comparisons across experimental systems. All else being equal, we expect that species with shallower fronts (greater core-edge distances and small edge population sizes, and therefore a strong role of drift relative to selective processes) should be subject to an evolutionary increase in expansion variability, whereas species with steeper fronts (shorter core-edge distances, larger edge population sizes, and thus a dominant role of selective processes) should be subject to an evolutionary decrease.

We used two metrics to quantify wave shape from published studies. First, we estimated the distance between the range edge (defined as the farthest-forward patch that contains at least one individual) and the range core (defined as the farthest-forward patch that meets or exceeds the 50th percentile of local population size; results are the same for other percentile thresholds). Because distance is measured in different units across systems, we standardized the comparison by dividing core-edge distance by the mean expansion speed (distance/generation) for each replicate of each system. This means that standardized core-edge distance is expressed in generations of travel (where, again, greater values correspond to shallower waves). Because wave positions are defined as percentiles of population density, this metric standardizes for differences in absolute densities across systems. Second, as a measure of leading-edge population size, we tallied the total number of individuals in newly colonized patches (those ahead of the farthest-forward patch in the previous generation). This metric is in the units of absolute number of individuals. Both metrics were estimated separately for each replicate in each generation.

Neither wave steepness measure was strongly associated with the evolutionary effect on expansion variability, though some results were consistent with predictions (Figure I). Specifically, *Tribolium* invading a benign environment [13] had the shallowest fronts, consistent with a strong evolutionary increase in variance in this system. However, other experiments with contrasting evolutionary effects on expansion variability had similar core-edge distances, corresponding to ca. one generation of travel (Figure IA). Similarly, leading-edge population sizes were variable across systems with no apparent relationship with expansion variability (Figure IB). In fact, the *Tribolium*-benign system had the largest edge population sizes despite also having the greatest core-edge distances. Clearly, wave shape alone cannot explain the differences in variability in speed across these systems.

Why might these steepness metrics not correspond with the results for evolutionary effects on expansion variability? The sizes of the mating and competition neighborhoods could vary even for expansions with the same steepness. For example, a shallow front could have enough individuals and genetic diversity to respond to strong selection, while a relatively steep one could have a smaller mating neighborhood. Taking mating neighborhood into account in metrics of steepness would be a fruitful next step. Additionally, our analysis of leading-edge population size was limited to census population size ($N$), but what matters more for evolutionary sources of variance is effective population size ($N_e$). Any differences across systems in the ratio of $N$:$N_e$ (due to sex biases at the leading edge, for example [26]) would complicate the comparisons in Figure IB. To our knowledge, no experimental invasion studies have estimated both $N$ and $N_e$. This could be a valuable direction for elucidating mechanisms underlying evolutionary effects on variance.

Figure I. Steepness of Expansion Waves in Experiments Manipulating Effect of Evolution on Expansion Velocity. (A) Steepness measured as core-edge distance of each replicate in each generation, standardized by mean expansion speed of each replicate across generations, with shorter distances (expressed as generations of travel) corresponding to steeper fronts and longer distance to shallower fronts. Boxes show distributions of core-edge distance for generations three and greater (early generations are expected to have nonequilibrium wave shapes). (B) Absolute population size at the leading edge, quantified as the total number of individuals in newly colonized patches (those ahead of the farthest-forward patch in the previous generation). Original study references as follows: *Arabidopsis* [13], *Callosobruchus* [14], *Tetranychus* [17], *Tribolium* invading a benign environment [15], *Tribolium* invading a harsh environment [18].

experimental context, might make one factor appear more important than another in the short term but not in the longer term.

## Revisiting Empirical Results for Variability in Range Expansion

Theoretical predictions outlined above and differences in biology suggest that both steepness of the expanding front and mating system contributed to whether evolving populations had more variability across replicates (flour beetles, *Tribolium castaneum*, and bean beetles, *Callosobruchus maculatus*) or less (thale cress, *Arabidopsis thaliana*) (Figure 1). To evaluate whether wave steepness relates to the extent to which evolution affected expansion variability across systems, steepness needs to be quantified in a standardized way. In Box 1, we propose two metrics for such a comparison. We find that neither metric supports the hypothesis that wave

shape can fully explain differences in expansion variability across systems, highlighting that population size at the leading edge is only one contributor.

Plants effectively reproduced clonally in the *Arabidopsis* experiments [13], allowing for the fastest clonal genotype to dominate the expanding front across replicates, and we hypothesize that the clonal mating system contributed to evolving populations exhibiting less variability. In contrast, in two of the beetle experiments (*Callosobruchus* [14] and *Tribolium* [15]), sexual recombination may have generated trait heterogeneity at the leading edge (especially if mating occurred before or during dispersal), disrupting the assortative mating of strong dispersers, which would weaken short-term responses to natural selection and spatial sorting and allow for a relatively greater role of drift. An intermediate result, with no or little change in variance with evolution was observed in the spider mite (*Tetranychus urticae*). We propose that its ability to reproduce both sexually and asexually might lead this system to fall somewhere in between in terms of the influence of evolution on variability, as it does [17] (Figure 1). Thus, across these systems, differences in mating system seem one likely explanatory factor of divergent effects of evolution on expansion variability.

## Advancing the Leading Edge of Eco-evolutionary Spread Dynamics

Here we focus on what we see as two fruitful future directions to advance understanding of how evolution modifies variability in expansion speed and the underlying traits of expanding populations (see Outstanding Questions).

First, no theoretical framework exists to evaluate and predict the effects of evolutionary processes on the variability of spread rates. While a few individual-based simulations exist for special cases [65], and progress has been made on the underlying stochastic processes [19,37,66], an analytical approach to this problem has not yet been developed, and this presents a key opportunity for mathematical biologists. This gap in theory stands in strong contrast with well-developed ecological theory for processes that determine mean expansion speed [2,5–8]. Our hypotheses for when evolution should increase or decrease variance are based on conceptual theory and deductive reasoning; rigorous mathematical theory is an essential next step to explore these hypotheses further and to motivate experimental tests. Integrating this work with theory related to the broader question about repeatability or predictability of evolution is also a valuable direction for understanding expansion outcomes.

Second, evidence for evolutionary effects on expansion variability is limited to experiments in tightly controlled laboratory settings. There is a need to better understand these processes empirically in variable environments. This includes natural settings, where populations face heterogeneous landscapes that vary over time and space with respect to both biotic and abiotic factors, as well as laboratory experiments that incorporate different aspects of environmental variability (e.g., [12]). One approach to this problem in nature would be to compare across replicate expanding fronts of the same species, including species deliberately introduced for biological control. Investigations into differences in expansion speed across replicate fronts could be accomplished through monitoring ongoing invasions or range expansions, or using historical records to approximate distance moved. Lastly, work that examines the intersection of theory and data by evaluating the extent to which different hypotheses explain results from the lab or field will be fruitful.

## Concluding Remarks

Predicting how quickly species will expand their ranges, whether in response to changing climates or introduction to a new range, is a pressing challenge. Here we have argued that it is not enough to understand the extent to which evolution can increase the mean spread velocity, but that it is critical to also understand variability in speed of future range expansions, and to do

### Outstanding Questions

What population characteristics and environmental conditions determine the balance of variance-reducing processes (natural selection and spatial sorting) and variance-generating processes (drift and gene surfing) in range expansions?

What is the relative importance of natural selection on life history traits and spatial sorting in dispersal as processes that contribute to evolutionary effects on expansion speed and variability?

How do genetic architecture, trait covariance (e.g., genetic correlations between dispersal and reproductive rate), and potential trade-offs between investments in dispersal and reproduction modify the roles of drift versus selective processes on expansion speed and variability?

How do variance-reducing and variance-generating processes differ between expansion waves that are 'pulled' (negative density dependence in fitness and/or no density dependence in dispersal) versus 'pushed' [positive density dependence in fitness at low density (Allee effects) and/or positive density dependence in dispersal]?

Do expectations for evolutionary effects on expansion variability in one-dimensional experimental landscapes generalize to higher-dimensional landscapes?

How do evolutionary sources of expansion variability interact with other sources of variation (spatial and temporal environmental heterogeneity) typically found in natural settings?

How repeatable are spread dynamics at different expanding edges of the same species in nature?

so requires assessing the balance of selective processes and drift at leading expansion edges. The hypotheses we consider, population size at the leading edge and mating system, are by no means exhaustive. Identifying additional factors that can tip the balance between these variance-generating and variance-reducing processes, as well as inserting realism into future studies, will be essential to predicting expansion variability. We are optimistic that outstanding questions can be addressed with a combination of new theoretical work, along with carefully designed experiments and field studies, enabling assignment of bounds to future range expansions (see Outstanding Questions).

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