














CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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Eco-evolutionary dynamics of range expansion

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Abstract. Understanding the movement of species' ranges is a classic ecological problem that takes on urgency in this era of global change. Historically treated as a purely ecological process, range expansion is now understood to involve eco-evolutionary feedbacks due to spatial genetic structure that emerges as populations spread. We synthesize empirical and theoretical work on the eco-evolutionary dynamics of range expansion, with emphasis on bridging directional, deterministic processes that favor evolved increases in dispersal and demographic traits with stochastic processes that lead to the random fixation of alleles and traits. We develop a framework for understanding the joint influence of these processes in changing the mean and variance of expansion speed and its underlying traits. Our synthesis of recent laboratory experiments supports the consistent role of evolution in accelerating expansion speed on average, and highlights unexpected diversity in how evolution can influence variability in speed: results not well predicted by current theory. We discuss and evaluate support for three classes of modifiers of eco-evolutionary range dynamics (landscape context, trait genetics, and biotic interactions), identify emerging themes, and suggest new directions for future work in a field that stands to increase in relevance as populations move in response to global change.

Key words: *biological invasion; dispersal evolution; eco-evolutionary dynamics; life history evolution; range expansion.*

INTRODUCTION

The movement of species' range edges is a key determinant of distribution and abundance and a pervasive feature of the Anthropocene, including the spread of introduced species and distributional shifts by native

species. All spreading populations are united by the interplay of two processes at the individual scale: demography and dispersal. "Demography" includes all the life history transitions underlying lifetime reproductive success, and "dispersal" refers to spatial displacement from an individual's natal site. Combined, these processes may give rise to population densities that expand in space and time, often in the form of a wave. Mathematical theory has been developed to predict the speed of an expansion wave from demography and dispersal traits

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(Skellam 1951, Shigesada and Kawasaki 1997, Kot et al. 1996). Nonetheless, understanding and predicting the dynamics of expansion remain grand challenges, made difficult by substantial intra- and interspecific variability, the sources of which are poorly resolved (Hastings et al. 2005, Melbourne and Hastings 2009).

Traditional theory focuses on population-wide averages of demographic and dispersal traits. As in other areas of ecology, studies of range expansion are coming to terms with the prevalence and consequences of heterogeneity among individuals in ecologically important traits. Heritable variation in demographic and dispersal traits sets the stage for the interaction of ecological and evolutionary processes—eco-evolutionary feedbacks (Kinnison and Hairston 2007, Hendry 2017, Reznick et al. 2019)—to influence spread dynamics (Fig. 1). Until recently, most theoretical and empirical work in this area has focused on the genetic consequences of expansion (reviewed in Excoffier et al. [2009]). A surge of theory development, field studies, and laboratory experiments has considered both sides of the eco-evolutionary coin, from evolutionary processes

to ecological outcomes and back (Fig. 1). The goal of this article is to synthesize and interpret lessons emerging from these advances. While previous reviews have addressed different subsets of the literature on evolution during range expansion (Excoffier et al. 2009, Phillips et al. 2010, Kubisch et al. 2014, Chuang and Peterson 2016, Nadeau and Urban 2019, Williams et al. 2019), we aim to provide a comprehensive conceptual synthesis that brings together theory and data spanning these and other sub-topics.

Like any evolutionary process, evolution during range expansion includes deterministic and stochastic elements. For spreading populations, these elements have a spatial twist because the leading edge of a traveling wave creates unique conditions for selection and drift. The study of eco-evolutionary dynamics has historically focused on ecologically important traits that evolve by natural selection, which has a deterministic influence on ecological outcomes. We emphasize that understanding the eco-evolutionary dynamics of range expansion additionally demands consideration of neutral evolutionary processes, which contribute stochasticity (Williams et al.

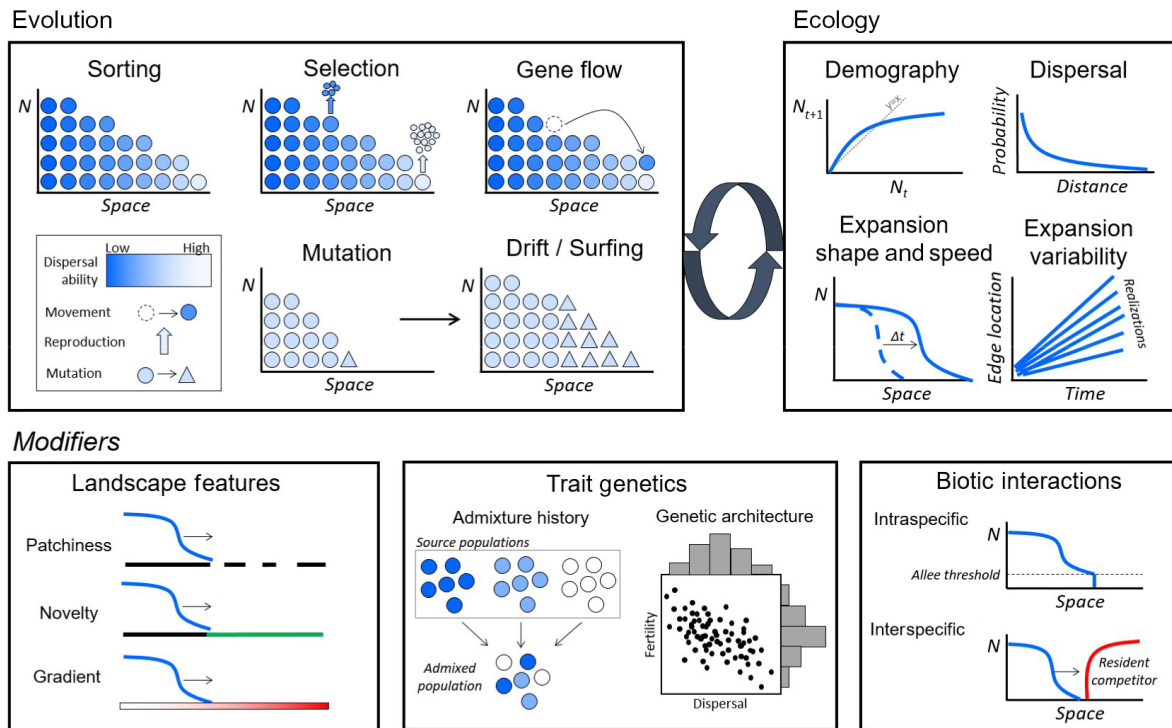


FIG. 1. Conceptual diagram of eco-evolutionary feedbacks during range expansion and three classes of modifying factors. Top left: Evolutionary processes relevant to range expansion include spatial sorting, natural selection (and spatial selection, the combination of natural selection and spatial sorting, as depicted), gene flow, mutation (a neutral mutation is shown for example), and genetic drift/ gene surfing (surfing of the neutral mutation is shown). Top right: Ecological processes include demography (low-density reproductive potential and response to density, shown as a recruitment curve with dashed line $y = x$), dispersal (shown as a probabilistic distance kernel), expansion speed (displacement of the wave front per unit time) and shape (spatial decay of local density), and expansion variability (heterogeneity in speed across realizations given identical starting conditions). Modifying factors (bottom) include: (1) landscape features, (2) trait genetics, and (3) biotic interactions including intraspecific density dependence (this example shows an expansion wave subject to strong Allee effects) and interspecific interactions [this example shows a resident competitor].

2019). Theory for the deterministic influence of selective processes and the stochastic influence of neutral processes in spreading populations has developed largely independently. Thus, a second goal of this article is to promote synthesis between these perspectives.

Much of the work on eco-evolutionary dynamics of range expansion has assumed or employed simple, idealized settings (homogenous landscapes, simple modes of trait inheritance, etc.). As a starting point, we invoke similar assumptions to describe current understanding. In later sections, we relax these assumptions to accommodate realistic sources of complexity and contingency. Finally, we identify new emerging themes and discuss needs for further research.

THEORETICAL EXPECTATIONS

Theoretical expectations for eco-evolutionary dynamics of expansion have been derived from verbal models (Phillips et al. 2010, Shine et al. 2011), analytical theory (Phillips and Perkins 2019, Peischl and Gilbert 2020), and individual-based simulations (Travis and Dytham 2002, Peischl et al. 2015), though some relevant processes were foreshadowed by earlier work (Cwynar and MacDonald 1987). At the core of this newly developed theory is one key concept that is unique to moving populations: space itself promotes distinct deterministic and stochastic evolutionary processes. These processes involve several steps and variations; the vocabulary is summarized in Appendix S1.

Deterministic evolutionary processes can accelerate range expansion

The starting point is “spatial sorting”: the endogenously generated, ordered distribution of dispersal phenotypes across space (Shine et al. 2011). (We assume here and throughout this section that the landscape is homogeneous.) As long as dispersal traits are heritable, spatial sorting creates spatial genetic structure that concentrates high-dispersal alleles at the leading edge. Spatial sorting also reduces the likelihood of mating between weak and strong dispersers and thus promotes assortative mating that further concentrates high-dispersal alleles at the expansion front. Through time, spatial sorting is expected to favor the evolution of increased dispersal ability at the leading edge, thus increasing expansion speed through a positive feedback. Spatial sorting is a selective process but it does not require any association between dispersal and fitness. In this sense, spatial sorting can be viewed as the spatial analogue of natural selection (Shine et al. 2011, Phillips and Perkins 2019), acting on dispersal traits to drive changes in allele frequency in space in the same way that natural selection acts on lifetime reproductive success to drive changes in allele frequency in time. We focus on spatial sorting as a process unique to expanding populations, but dispersal can also evolve by natural selection via its influence on

fitness, instead of or in addition to spatial sorting (Travis et al. 2013, Kubisch et al. 2014).

While differential reproductive success is not necessary for spatial sorting, dispersers that reach the leading edge may indeed experience a reproductive advantage. The expected gradient of densities in a spreading population, decreasing from core to edge, promotes two additional evolutionary processes that can amplify the accelerating effect of spatial sorting, alone. First, if strong dispersers that reach the expansion front escape density-dependent competition, as expected for pulled expansion waves (Appendix S1), then “spatial selection” will favor the evolution of increased dispersal ability via greater reproductive output of strong dispersers. Second, with a release from negative density dependence at the leading edge of pulled waves, natural selection may favor demographic traits that result in high reproductive rates at the expense of traits that promote tolerance of competitive environments: essentially *r*-selection (Phillips et al. 2010). Because theory predicts that the speed of expansion is controlled by demographic and dispersal traits, evolutionary mechanisms that enhance these traits are expected to accelerate expansion. This accelerating influence represents an eco-evolutionary feedback whereby ecological processes (population growth and wave expansion) affect and are affected by evolutionary processes acting on ecologically important traits and operating on the same time scale (Fig. 1).

Gene surfing generates stochasticity in expansion outcomes

Evolution during spread also has a neutral component that can affect the stochasticity in expansion outcomes. A key stochastic process during range expansion is “gene surfing” (Edmonds et al. 2004, Klopstein et al. 2006), the spatial analogue of genetic drift (Peischl and Gilbert 2020). A pulled expansion wave is driven by serial founder events, where few individuals colonize the leading edge and their offspring will likely go on to colonize the next generation’s leading edge (Moreau et al. 2011). Through these sequential colonization bottlenecks, alleles initially present at or near the leading edge, or those that arise there by mutation, can “surf” to high frequency on the expanding front simply by chance. This is true for neutral alleles, the best studied case (Klopstein et al. 2006, Hallatschek and Nelson 2008, Marculis et al. 2017). It is also true for non-neutral alleles, including beneficial alleles that enhance demographic or dispersal traits and whose rise in frequency is reinforced by natural selection or spatial sorting. In fact, gene surfing can act as an evolutionary “jackpot,” such that beneficial variants increase in frequency more strongly due to the extra boost of gene surfing at the expansion front (Gralka et al. 2016). On the other hand, deleterious alleles that would be rapidly eliminated from a well-mixed population may be able to persist in a spatially

structured population by surfing (Burton and Travis 2008, Peischl et al. 2015). Gene surfing is essentially a spatial priority effect and therefore has analogues in studies of evolutionary priority effects in community assembly (e.g., De Meester et al. 2016).

Since gene surfing can promote the fixation of non-neutral variants at the expansion front, it stands to reason that this process could also modify expansion speed. Thus, gene surfing is not only a consequence of range expansion, it is also a driver; theory has begun to explore this feedback. For example, the accumulation of mutations with deleterious fitness effects at the expansion front (“expansion load”) can slow down range expansion (Peischl et al. 2013, Gilbert et al. 2017). The build-up of expansion load can result in long-term fluctuations in speed, as edge populations periodically reach low enough fitness to slow or even stop expansion until higher fitness genotypes catch up to the expansion edge (Peischl et al. 2015, Andrade-Restrepo et al. 2019).

Integrating deterministic and stochastic components of evolution during range expansion

Spatial sorting and gene surfing are expected to play out simultaneously, yet theory has only recently begun to consider the interaction of these processes. Studies that consider both deterministic and stochastic processes show that mutations enhancing demographic or dispersal traits are likely to surf the expansion front (Travis et al. 2010, Gralka et al. 2016), and that evolution of dispersal via spatial sorting can limit the accumulation of expansion load (Peischl and Gilbert 2018). Results such as these highlight how the interaction between deterministic and stochastic processes can influence genetic composition and trait evolution but do not address outcomes for expansion speed. Phillips (2015) was among the first to make that connection, demonstrating that gene surfing can add substantial variation to range expansion: while deterministic forces acting on demography and dispersal traits can indeed increase expansion

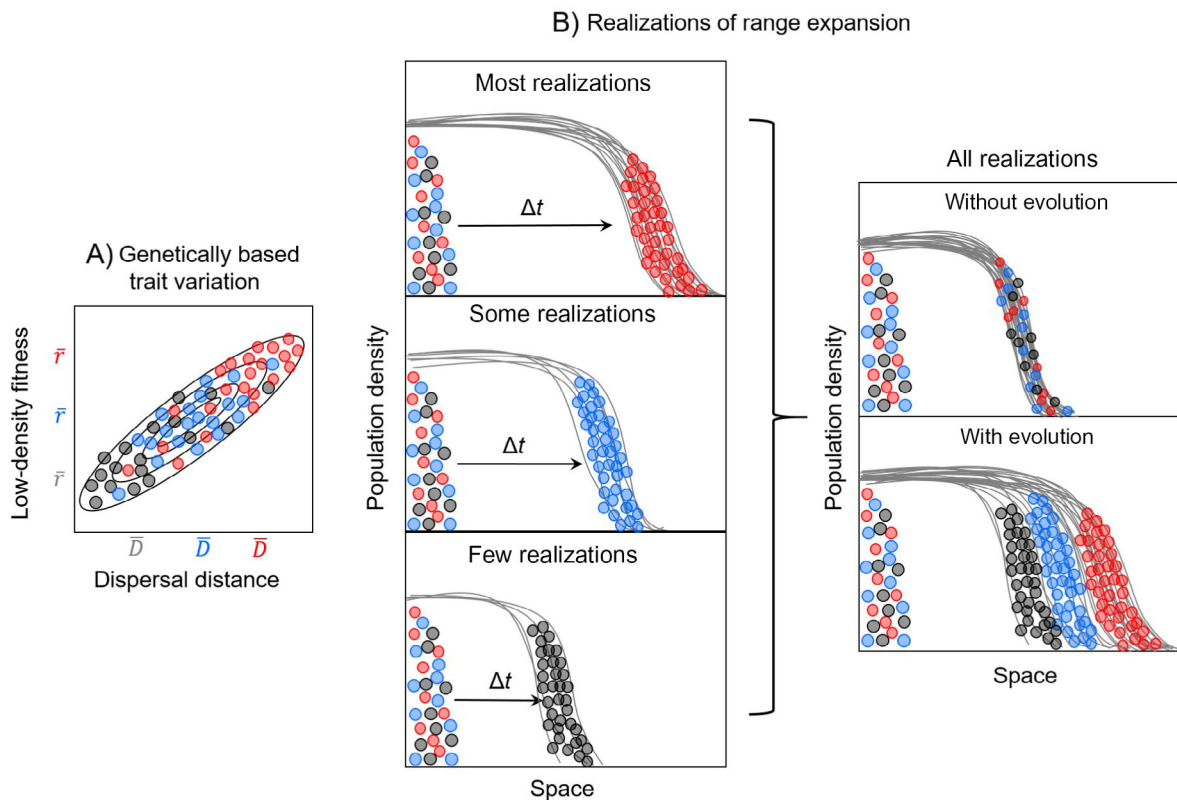


FIG. 2. Conceptual framework for how eco-evolutionary feedbacks can increase the speed and variability of range expansion. (A) Genetically based variation in low-density fitness and dispersal distance for three hypothetical genotypes (colors) in a founding population. In this example, there is a positive genetic correlation between the two traits, though this need not be the case generally. (B) Alternative eco-evolutionary outcomes for different realizations of expansion from identical starting conditions; lines show different realizations, colored points show the genotype that dominates the expanding front in a single realization, and Δt is meant to emphasize differences in wave expansion over the same amount of time. Across all realizations, range expansion with eco-evolutionary feedbacks is accelerated, on average, but also more variable, relative to hypothetical expansions without the influence of spatial genetic structure, where the initial genetic makeup persists at the expanding front.

speed they are “pushed through a strong stochastic filter.”

The integration of spatial sorting and natural selection as accelerating processes and gene surfing as a variance-generating process is illustrated in Fig. 2. The central idea is that multiple realizations of range expansion from the same starting conditions should more or less conform to a deterministic expectation but will sometimes deviate from this expectation due to chance events that promote evolution of trait values not favored by selective processes. Interestingly, and a little paradoxically, the very conditions that promote evolved increases in demographic and dispersal traits via selective processes (a high-fitness, low-density edge, colonized by strong dispersers, that propagates forward through serial colonization) simultaneously weaken responses to selection and favor a strong role of drift (Weiss-Lehman et al. 2019). Combined, the interaction of these processes is expected to result in range expansion that is, on average, accelerated by rapid evolution but also made more variable across realizations.

EMPIRICAL EVIDENCE

While theory clearly indicates that eco-evolutionary feedbacks can influence expansion speed and variability, decomposing the contribution of evolutionary processes to expansion outcomes in empirical systems is challenging. It requires evidence for evolved trait changes during spread and a reciprocal influence of trait evolution on expansion speed. Empiricists have evaluated one or (more rarely) both of these criteria with a variety of approaches, generating a body of evidence that generally supports the qualitative predictions described in the previous section, but also includes some surprises.

Deterministic evolutionary processes: spatial sorting and natural selection

The majority of empirical work has focused on the expectations of enhanced dispersal ability and reproductive rate in range-edge populations relative to range core. Chuang and Peterson (2016) reviewed core-edge contrasts for a variety of morphological, behavioral, and physiological traits from field studies of native and introduced species (though not all ranges were actively expanding). Overall, they found abundant evidence for core-edge trait differences, often (but not always) in the expected direction. While such trait contrasts suggest a signature of evolution during range expansion, they are necessarily retrospective and cannot discern how trait evolution affected expansion. Even where trait differences are clearly shown to have a genetic basis, it is difficult to diagnose whether selective or neutral evolutionary processes generated them, and whether the difference reflects evolution of increased dispersal at the range edge and/or evolution of decreased dispersal in the range core.

Research in one particular empirical system, the well-documented expansion of cane toads in northeast Australia, has taken core-edge contrasts further. The rate of cane toad expansion has accelerated from 10–15 km/yr following their introduction in the mid-1930s to 50–60 km/yr in recent years (Phillips et al. 2006, Urban et al. 2008, Perkins et al. 2013). This increase in speed is associated with, and was likely driven by, evolved changes in a suite of behavioral and morphological traits that promote elevated dispersal and demographic rates at the expanding edge (Phillips et al. 2008, Perkins et al. 2013, Brown et al. 2014). The connection between trait evolution and spread dynamics has been possible in this system by coupling eco-evolutionary models with field-based parameter estimates, allowing the contributions of evolutionary processes to be quantitatively partitioned (Perkins et al. 2013) and providing the most compelling evidence to date that trait evolution can importantly affect expansion speed in field settings.

Despite substantial progress, retrospective studies inevitably fall short of a “gold standard” in testing the consequences of eco-evolutionary feedbacks, because the feedbacks cannot be turned off (except in silico). This is where a surge of laboratory-based experiments has filled a key gap, leveraging the power of experimental evolution in controlled environments. While obviously a simplification of range expansion in nature, these experiments have provided proof of concept for how space, per se, can drive evolutionary change that feeds back to influence population dynamics, controlling for other selective pressures in ways that field studies cannot. Fronhofer and Altermatt (2015) used a freshwater ciliate to track the real-time evolution of increased dispersal ability at expanding population edges in the lab, corroborating many field-based core-edge contrasts. More recently, laboratory-based studies have gone farther to articulate the connections between trait evolution and expansion speed. Critically, many of these experiments followed a qualitatively similar experimental design that disrupted spatial genetic structure in a subset of replicates. We conducted a small meta-analysis to quantify how eco-evolutionary feedbacks modified expansion speed across experimental studies, focusing on those studies that contrasted expansions with (feedbacks on) and without (feedbacks off) spatial genetic structure (Williams et al. 2016a, Ochocki and Miller 2017, Szűcs et al. 2017, Weiss-Lehman et al. 2017, Van Petegem et al. 2018). Manipulations to suppress genetic structure involved either replacement from a source pool or a “shuffle” treatment to randomly distribute alleles across landscapes. Most of these experiments considered spread through constant, benign, and one-dimensional environments using a variety of plant and animal model organisms. Literature search and meta-analytic methods are provided in Appendix S2.

Collectively, results of these new experiments strongly support the hypothesis that eco-evolutionary feedbacks increase mean expansion speed (Fig. 3A). Each reported

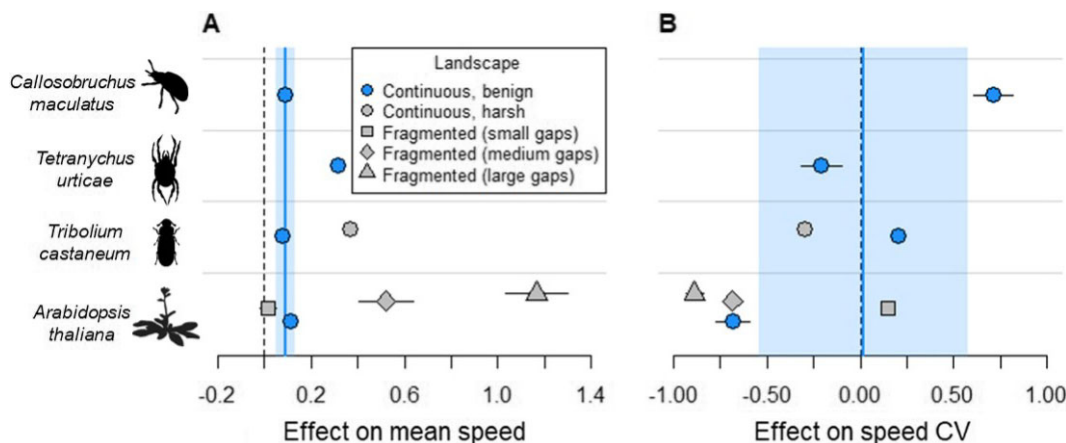


FIG. 3. Log response ratio of (A) mean and (B) coefficient of variation (CV) in range expansion speed between replicated expansions with and without spatial genetic structure (eco-evolutionary feedbacks “on” and “off,” respectively). Points correspond to mean within-study estimates, with error bars corresponding to the sampling variance (sometimes obscured by the points). Blue points and lines correspond to benign, continuous landscapes (blue line represents the pooled effect size in benign landscapes, and blue shading represents the 95% CI across studies). Some studies included other landscape types, which were included in the analysis as covariates: gray point for *T. castaneum* is from a separate study that used a harsh environment, and gray points for *A. thaliana* are patchy landscape treatments with small (circle), medium (diamond), and large (triangle) gap sizes. Organisms used in the studies are as follows: Ochocki and Miller (2017), *Callosobruchus maculatus*; Szűcs et al. (2017) and Weiss-Lehmann et al. (2017), *Tribolium castaneum*; Van Petegem et al. (2018), *Tetranychus urticae*; Williams et al. (2016a), *Arabidopsis thaliana*. Meta-analysis methods are provided in Appendix S2.

significantly faster range expansion in replicates with spatial genetic structure, with an overall effect size estimate across studies showing a 9.7% increase in mean speed (95% CI: 5.3% to 14.3%). Through follow-up common garden studies or genotyping, these studies have further elucidated the traits that evolved to increase expansion speed. Interestingly, despite the consistency in population-level outcomes, trait evolution during expansion was idiosyncratic. In some cases, increased expansion speed was driven by the evolution of increased reproductive rate (Szűcs et al. 2017, Van Petegem et al. 2018) while in others it was evolution of increased dispersal ability (Ochocki and Miller 2017, Weiss-Lehman et al. 2017) or a combination of traits contributing to dispersal and competitive ability (Williams et al. 2016a). In addition to these directional effects indicated by mean outcomes, replicated laboratory experiments also provide important insights into stochastic components of evolution during range expansion, as we explore next.

Stochastic evolutionary processes: genetic drift and gene surfing

Laboratory systems, particularly with microbial models, have provided some of the best empirical evidence for stochastic fixation of alleles at expanding range edges, strongly supporting theoretical expectations for gene surfing (Appendix S2: Table S1). In an elegant and visually striking set of experiments, Hallatschek et al. (2007) showed that a well-mixed starting population of two fluorescently labeled but otherwise identical strains of bacteria or yeast will eventually be dominated by one

or the other strain as colonies expand. This experiment showed that gene surfing can act on standing neutral variants to generate differences in leading-edge genetic composition that arise solely by chance.

In addition to standing variants, subsequent studies have further shown that gene surfing can affect the fate of mutations that arise during expansion, including non-neutral ones (Bosshard et al. 2019). In a rare field study, Willi et al. (2018) showed that range-edge populations of *Arabidopsis lyrata* carried genomic signatures of expansion load and reduced fitness relative to range-core populations. This study serves as a cautionary example for core-edge contrasts, since the direction of fitness difference was the opposite of expectations based on selective processes, and may be driven instead by the surfing of deleterious mutations. In a laboratory setting, Bosshard et al. (2017) showed that high-mutation-rate strains of *E. coli* usually (but not always) evolved reduced fitness during expansion due to accumulation of expansion load. In contrast, low-mutation strains showed increased fitness, as expected under deterministic theory.

To fully explore the intersection of deterministic and stochastic evolutionary processes during expansion, we return to the replicated laboratory experiments that “turned off” spatial genetic structure (Fig. 3) for insight into the (in)consistency of eco-evolutionary outcomes across repeated realizations. As described qualitatively by Williams et al. (2019), effects of evolution on variability among replicates differed in direction and magnitude across experiments (Fig. 3B). In two independent experiments using beetles (Ochocki and Miller 2017, Weiss-Lehman et al. 2017, 2019), evolutionary acceleration of

expansion speed was accompanied by significant increases in expansion variability: while many replicates were made faster by evolution, some were made slower, consistent with gene surfing acting as a variance-generating process (Fig. 2). However, in other experiments, the change in variance was closer to zero or there was a significant *decrease* in variance with spatial genetic structure (Fig. 3B). Overall, our analysis shows an effect size of eco-evolutionary feedbacks on expansion variability centered near zero with a wide 95% confidence interval (Fig 3B). Such heterogeneity in outcomes is not predicted by current theory. Williams et al. (2019) hypothesized that contrasting eco-evolutionary effects on variance may reflect differences across studies in factors such as mating system and effective population size, which may alter the balance between variance-reducing effects of selective processes and the variance-generating effects of gene surfing. Understanding the traits or conditions that tip this balance is an open problem for future theory and empirical tests.

MODIFIERS OF ECO-EVOLUTIONARY RANGE EXPANSION DYNAMICS

Much of our current understanding of the eco-evolutionary dynamics of range expansion is tied to simplifying assumptions and idealized settings. Advancing the conceptual framework will require that we investigate how realistic sources of variation—attributes of the species and/ or environment—can modify expectations. We discuss three classes of such modifiers, highlighting what is known and unknown about their influence on deterministic and stochastic components of rapid evolution during range expansion (Fig. 1).

Landscape context

Here we consider expansion through three common contexts of landscape structure (Fig. 1, lower left). First, nearly all expanding populations must move through mosaics of favorable and unfavorable habitat. Ecological models predict that expansion speed should usually be slower through patchy landscapes (Shigesada et al. 1986), though some dispersal behaviors can reverse this prediction (Lutscher and Musgrave 2017). Much of the evolutionary research focuses on dispersal evolution by natural selection, demonstrating that dispersal can increase or decrease with fragmentation (Ronce and Olivieri 2004, Cote et al. 2017). Both avenues of research have focused mainly on deterministic processes and tend to ignore eco-evolutionary feedbacks during expansion. Theory exploring selection for traits during expansion demonstrated that gaps in suitable habitat can cause the build-up of population density in leading-edge patches, favoring the evolution of increased competitive ability (*K*-selection) instead of rapid reproduction (Williams et al. 2016b). For this reason, evolutionary acceleration of range expansion was predicted to be weaker in

patchier landscapes. However, subsequent experimental work with *Arabidopsis* (Fig. 3; Williams et al. 2016a) showed that patchiness can strengthen the accelerating effect of evolution, likely due to joint evolution of competitive ability that leads to increased speed in patchy landscapes and dispersal ability that allows colonists to cross gaps. Both theory and experiments reveal a role for gene surfing (Williams et al., 2016a, b) and recent evidence suggests that landscape heterogeneity may generally amplify the importance of chance events (Gralka and Hallatschek 2019). Collectively, the literature on expansion into patchy landscapes paints a complex picture where details of landscape structure, density dependence, and life history trade-offs can all affect evolutionary outcomes and their influence on expansion speed.

Second, many spreading populations encounter novel or harsh environmental conditions, particularly introduced species transported great distances by humans (though some of these “escape” into more favorable, enemy-free environments). For introductions into environments that are harsh relative to source conditions, adaptation to novel conditions may interact with or even override evolutionary processes that arise solely from spatial genetic structure. For example, using experimental expansions of flour beetles in a harsh, novel habitat, Szűcs et al. (2017) showed that adaptation to the environment was the dominant process leading to evolutionary acceleration of expansion, overwhelming any effect of dispersal evolution via spatial sorting. Adaptation to harsh environments may generally slow down range expansion (García-Ramos and Rodríguez 2002) and also dampen stochastic fixation of alleles at the leading edge (Gilbert et al. 2017), making replicated expansions less variable relative to expansions in benign environments (compare *T. castaneum* expansion in benign vs. harsh environments: Fig. 3). While more work is needed, current evidence suggests that, for expansion into strongly selective environments, adaptation to environmental conditions may play a stronger role than evolutionary processes that arise from spatial genetic structure.

The last landscape feature we consider is one likely to arise with increasing frequency under climate change: shifting environmental gradients or shifting windows of suitable habitat, where environmental limits on species’ ranges move directionally (e.g., poleward or altitudinally). This situation falls between two well studied extremes. At one extreme, movement of an environmental limit is much faster than the population’s expansion speed, so the creation of suitable habitat ahead of the range edge should cause expansion to approximate the simple case of spread into a benign, non-selective environment (Fig. 2). If the entire window of suitable habitat is moving (e.g., both lower and upper altitudinal limits), natural selection may act on dispersal ability to keep up with it (Pease et al. 1989, Boeye et al. 2013). At the other extreme, environmental limits on a species range are not shifting, so evolutionary dynamics are dominated by the

balance of adaptation to range-edge environmental conditions, core–edge gene flow, and stochastic effects of drift in edge populations that limit further adaptation and expansion (Kirkpatrick and Barton 1997, Kubisch et al. 2013, Polechová and Barton 2015). Many situations in nature likely fall in between these extremes, where environmental shifts and population spread play out on similar time scales, such that all of the above processes combine. Several theoretical studies show that fitness declines toward the edges of slow-moving environmental gradients can slow expansion speed and create a “pushed wave” dynamic where migration from the range core promotes genetic diversity at range edges (Fig. 4), which may limit the role of drift and promote responses to selection (Gilbert et al. 2018, Lewis et al. 2018). The expected maintenance of genetic diversity along shifting gradients suggests potential for adaptive evolutionary responses to moving climate envelopes, a hypothesis that merits further theoretical work and could be amenable to experimental tests in laboratory systems.

Trait genetics

Genetic variation in demographic and dispersal traits is a prerequisite for eco-evolutionary feedbacks during expansion. Historical factors that influence genetic variation may therefore be an important source of contingency. For example, due to genetic bottlenecks associated with introduction, non-native species expanding into a novel range may be subject to stronger evolutionary constraints than resident species expanding in response to climate change. However, many successful biological invasions by non-native species stem from the

admixture of multiple independent introductions that bring together genetically distinct populations, which may elevate genetic variance in ecologically important traits (Dlugosch and Parker 2008).

Genetic admixture has been hypothesized to promote evolutionary acceleration of expansion due to stronger responses to selection in populations with elevated genetic diversity. However, in a laboratory experiment with beetles, Wagner et al. (2017) found little support for this hypothesis: evolution of increased dispersal ability due to spatial sorting occurred in both admixed and single-source populations, consistent with observations that single introductions do not necessarily deplete additive genetic variation underlying quantitative traits (Dlugosch and Parker 2008). While multiple introductions are often implicated as drivers of expansion due to increased evolutionary potential, there is yet little evidence that evolutionary acceleration of spread is any less likely for single-source expansions subject to strong bottlenecks than for admixed expansions. (Notably, the Australian invasion of cane toads stemmed from 101 individuals from a single source; Sabath et al. 1981.)

Covariance between demographic and dispersal traits can also modify eco-evolutionary dynamics of expansion. This has been most commonly explored in the form of genetically based trade-offs, which are often suggested in observational core-edge contrasts (Chuang and Peterson 2016) and experimental evolution studies (Fronhofer and Altermatt 2015). Several theoretical studies have included trade-offs between low-density fitness and the ability to tolerate competition, the axis of classic r/K selection. These studies show that selective processes generally tip the balance in favor of increased reproductive rate at the expanding front (Burton et al. 2010),

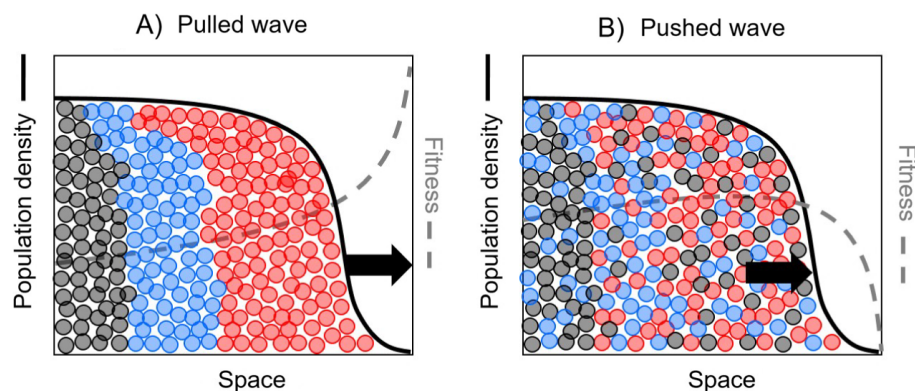


FIG. 4. Contrasting eco-evolutionary dynamics of pulled vs. pushed expansion waves. (A) Pulled waves are characterized by fitness that decreases monotonically with increasing density. In such cases, reproduction by low-density leading-edge colonists and dispersal of their offspring pulls the expansion forward. Due to selective processes that favor strong dispersal/fast reproduction and bottlenecks associated with serial founder events, genetic diversity is reduced at the expanding front. (B) Pushed waves are characterized by declines in fitness at the low-density leading edge. This may be due to Allee effects (positive density dependence at low density) or environmental stress at range edges for species expanding along an environmental gradient. For pushed waves, dispersal from the range core plays an important role in moving the population forward. Genetic contributions from a greater number of individuals (and/or more heterozygous individuals) result in a more diverse genetic composition of the range edge relative to a pulled wave.

though the optimal strategy may switch to competitive ability once the wave front passes (Perkins et al. 2016), or when landscapes are patchy (Williams et al. 2016b).

Trade-offs along the r/K axis need not affect expansion speed since evolved increases in demographic rates should similarly accelerate spread whether or not they are associated with reduced competitive ability, assuming pulled-wave conditions. In contrast, trade-offs between demography and dispersal could play a more important role because these traits control the rate of spread. Such trade-offs have been widely documented, where evolved dispersal at the expanding front comes at the cost of reduced fecundity (Hughes et al. 2003, Simmons and Thomas 2004). In cane toads, for example, strong dispersers at the expansion front have reduced reproductive success (Hudson et al. 2015). For species at range equilibrium, trade-offs between dispersal and reproduction may be maintained by metapopulation structure, where high-dispersal strategies are favored early in patch colonization (Olivieri et al. 1995). By maintaining high-dispersal phenotypes, metapopulation structure may therefore be an important precursor to rapid range expansion (Duckworth 2008).

Recent work suggests that demography–dispersal trade-offs (and covariance, more generally) can affect both deterministic and stochastic components of evolution during expansion. Ochocki et al. (2020) showed with individual-based simulations that negative genetic correlations between demographic and dispersal traits cause weaker acceleration of range expansion than expected if the traits evolve independently, echoing long-standing hypotheses that genetic architecture may act as an evolutionary constraint (Walsh and Blows 2009, but see Agrawal and Stinchcombe 2009). Strongly negative genetic correlations can even lead to evolutionary *deceleration* of expansion, if the strong dispersers that dominate the front have poor reproductive performance. Deforet et al. (2019) developed an analytical rule to predict which of two strains on opposite ends of a demography–dispersal trade-off will dominate the expanding edge based on comparison of their respective expansion speeds. Genetic correlations can also modify stochastic processes, with negative correlations decreasing and positive correlations increasing variability in expansion speed across realizations (Ochocki et al. 2020).

Finally, mutations can introduce genetic variation in ecologically relevant traits, and therefore increased mutation rate could increase opportunity for trait evolution during expansion. For example, an individual-based model including mutations in dispersal genes showed that higher mutation rates could promote evolution of increased dispersal relative to spatial sorting acting on standing variation alone (Phillips et al. 2008). On the other hand, mutations with negative fitness effects could surf expanding fronts, slowing down expansion and leading to the accumulation of expansion load, as has been shown experimentally (Bosshard et al. 2017); importantly, though, this same study showed that

sometimes beneficial mutations surfed, highlighting the variability that can arise across realizations (Fig. 2). Thus, the ecological consequences of mutations during spread depend on their frequency, the sign and magnitude of their effect, position along the wave front, and the traits affected.

Biotic interactions

Last, we consider ecological interactions within and between species. Intraspecific interactions, specifically the nature of density dependence, play a key role as a modifier of both deterministic and stochastic evolutionary processes. First, spatial sorting and natural selection are most potent for pulled expansion waves, where fitness is maximized as density approaches zero, promoting an increase in frequency of alleles carried by long-distance dispersers that colonize vanguard areas (Fig. 4). In contrast, Allee effects (positive density dependence at low density) can generate a pushed expansion. Due to costs for rare colonists at the leading edge, Allee effects can dampen or even reverse the predicted effects of selective processes based on strictly negative density dependence, causing evolutionary deceleration due to selection against dispersal (Travis and Dytham 2002, Shaw and Kokko 2015). It is worth noting, however, that at least one of the experimental systems that showed evolution of increased dispersal and accelerated spread (the beetle *C. maculatus*, Fig. 3; Ochocki and Miller 2017) is known to experience strong mate-finding Allee effects that cause local extinction at the expanding edge (Miller and Inouye 2013). Shaw and Kokko (2015) showed that evolutionary deceleration may be more likely for species with monogamous than polygamous mating systems due to the difference in severity of mate limitation; this may help explain results for the polygamous *C. maculatus*. Thus, even a strong Allee effect (extinction below a density threshold) does not necessarily override the accelerating effect of spatial sorting, and additional theory is needed to better understand the conditions under which it does.

Second, in addition to its influence on deterministic evolutionary processes, intraspecific density dependence can also modify the potential for gene surfing. Pulled-wave conditions that promote selective processes at low-density fronts can simultaneously result in increased genetic drift (Fig. 4). By reducing or eliminating the reproductive contributions of the low-density edge, Allee effects can limit opportunities for stochastic fixation of alleles. Positive density dependence in dispersal similarly generates pushed waves (Sullivan et al. 2017) and dampens gene surfing (Birzu et al. 2019). Thus, pushed waves, where dispersal from behind the leading edge plays the most important role in population expansion, generally harbor greater leading-edge genetic diversity than pulled waves (Marculis et al. 2017, Birzu et al. 2019, Gandhi et al. 2019).

Expanding populations also encounter interspecific interactions. Interspecific competition, in particular,

may be an important component of stable range edges (Price and Kirkpatrick 2009, Kubisch et al. 2013) and may also affect the speed of expanding ranges and the traits that are favored during spread. Burton et al. (2010) showed that resident competitors can limit dispersal evolution and evolutionary acceleration of spread, favoring life history strategies at the leading edge that are more competitive, less dispersive, and less fecund. Resident competitors may also generate resistance to colonization in a way that mirrors the pushed-wave dynamic of expansion along a gradient of abiotic stress (Roques et al. 2015). The majority of eco-evolutionary theory for range expansion assumes that focal populations encounter empty landscapes. Relaxing this assumption to account for novel biotic interactions will be an important direction for future work.

EMERGING THEMES AND NEW DIRECTIONS

In theory, eco-evolutionary feedbacks can accelerate or decelerate expansion

Empirical evidence strongly supports the hypothesis that rapid evolution of dispersal and demographic traits can accelerate range expansion, on average (Fig. 3). At the same time, our review of modifying factors reveals several mechanisms that may, under some conditions, cause evolutionary *deceleration* of expansion. These include the accumulation of expansion load due to gene surfing, Allee effects at low density that select against long-distance dispersal, and negative genetic correlations between dispersal and fertility. Is evolutionary deceleration of expansion a theoretical curiosity that resides in obscure corners of parameter space, or a likely outcome waiting to be documented empirically? A first step toward answering this question would be to experiment with laboratory models, where key parameters can be tuned to test whether a system can switch from evolutionary acceleration to deceleration as predicted by theory.

Pushed waves arise by diverse mechanisms and have consistent eco-evolutionary consequences

Classic ecological theory of range expansion and many of the more recent eco-evolutionary predictions assume pulled-wave conditions. However, as we highlight above, pushed expansion waves can arise by diverse mechanisms and may exhibit very different eco-evolutionary dynamics. Positive density dependence in demographic or dispersal traits, expansion into territory occupied by competitors, and ranges that track clines of environmental stress can all lead to pushed waves. Just as pulled waves select for increased dispersal and reproduction but simultaneously create opportunities for the diversifying effects of gene surfing, pushed waves do the opposite, whatever their cause: they dampen (or even reverse) selection on demographic and dispersal traits

but simultaneously facilitate the maintenance of genetic diversity at range edges (Fig. 4). We predict that these contrasting features should make eco-evolutionary feedbacks more likely to elevate the mean and variance of expansion speed under pulled-wave than pushed-wave conditions, all else equal. This may contribute to the diversity of eco-evolutionary effects on range expansion, especially expansion variance, seen in experimental studies (Fig. 3) (Williams et al. 2019). Theory development to distinguish pulled vs. pushed expansions (Gandhi et al. 2016) offers a promising avenue for testing this and related hypotheses.

Similarities and differences between expansions of introduced and native species

Studies of range expansion often invoke invasion by introduced species and climate change-induced expansion by native species as interchangeable ecological settings. However, the modifying factors we discuss suggest how expansion by native and introduced species may be subject to different historical contingencies that can affect their eco-evolutionary dynamics. Distributions of native species are likely to be near equilibrium with environmental constraints (Lee-Yaw et al. 2016), where range edges reflect ecological factors that reduce population viability approaching environmental limits and evolutionary processes that prevent adaptation beyond those limits. As environmental limits shift in response to global change, expansion by native species should be characterized by relatively high genetic diversity, reflecting historical core-edge gene flow and reinforced by reduced fitness at the leading edge (Fig. 4). In contrast, introduced species should, in principle, experience a loss of genetic diversity through the introduction bottleneck that reduces evolutionary potential (though evidence is mixed) and are more likely to be in disequilibrium with their environmentally determined distributional limits. Thus, we predict that expansions by native species are more likely to be pushed, including a role for adaptation to environmental extremes (which may be facilitated by elevated genetic diversity at the edge, but perhaps impeded by maladaptive alleles from the range core), while expansions by introduced species, lacking systematic environmental resistance, are more likely to be pulled, such that space per se and available genetic variation are the key drivers of eco-evolutionary dynamics. Following the logic developed for pushed vs. pulled waves, this may lead to very different eco-evolutionary effects on the means and variances of native and introduced expansion speeds that warrant further study and comparative analyses.

New directions for theory and experiments

Theoretical models of evolution during range expansion have relied heavily on individual-based models (IBMs). There are exciting opportunities to develop

analytical approaches that would generalize existing IBMs and suggest new avenues for empirical work. For example, a rigorous analytical solution for the variance of expansion speed accounting for eco-evolutionary feedbacks could help resolve the diversity of evolutionary effects on the variability of range expansion seen in experimental studies (Fig. 3). Similarly, new analytical theory may help explain why the main driver of evolutionary acceleration is spatial sorting of dispersal traits in some systems and natural selection on demographic traits in others.

On the empirical side, experiments in laboratory systems are well poised to test hypotheses for modifiers of eco-evolutionary outcomes, as illustrated by studies of habitat fragmentation or heterogeneity (Williams et al. 2016a), environmental novelty (Szűcs et al. 2017), genetic admixture (Wagner et al. 2017), and Allee effects (Gandhi et al. 2019). As new experiments are pursued, it is worth asking how developments in theory could inform experimental design. For example, predictions for evolutionary effects on variance of expansion speed may suggest an allocation of experimental effort that favors increased replication and post-expansion studies that test for phenotypic and genetic divergence across replicates, approaches that might not be considered with a focus on deterministic processes alone. Similarly, theoretical results for important differences between pulled vs. pushed expansions may focus experimental efforts on characterizing density-dependent population growth and dispersal.

While current laboratory systems have fairly good taxonomic representation (Appendix S2: Table S1), they likely over-represent “weedy” life histories with short generation times. These systems may be biased in favor of an important role for rapid evolution relative to organisms with complex life histories, long-lived adult stages, and reproductive delays. A more diverse set of experimental systems would broaden the scope of inference and may help develop a trait-based framework for predicting variation in eco-evolutionary outcomes. At the same time, given the heterogeneity among weedy species (Fig. 3), additional taxonomic replication within life history types would be valuable for strengthening inferences about life history differences.

There is also a need to better connect results from studies of micro- and macro-organisms, which present different opportunities and limitations. Laboratory studies of plants and arthropods have focused on spatial sorting of dispersal phenotypes, and experimental manipulations in these systems have been designed to disrupt the resulting spatial genetic structure. On the other hand, most microbial studies have used non-motile species or strains that do not have dispersal phenotypes, such that spatial sorting is not possible; in these systems, range expansion occurs by cell division and the composition of the range core is “frozen” once the front passes through due to compact growth and resource depletion (Korolev et al. 2012). Greater use of microbial models

with dispersal ability (Fronhofer and Altermatt 2015, Deforet et al. 2019), experimental contrasts with and without spatial genetic structure, and more consistent measurement of ecological outcomes (expansion speed and variability) would strengthen the parallels with studies of macroorganisms. Conversely, studies with macroorganism models should follow the lead of microbial systems with greater use of genetic resources (Weiss-Lehman et al. 2019) to couple the genetic consequences of expansion with ecological outcomes.

Bridging theory, experiments, and field data

Our synthesis of the literature suggests a need to better connect conceptual understanding from theoretical and laboratory models to expansion dynamics in nature, a need that is recognized for eco-evolutionary dynamics more generally (Hendry 2019). The case study of the cane toad is a lonely pillar in our understanding of how rapid trait evolution due to spatial genetic structure can influence ecological dynamics in field settings. Work in additional field systems, quantifying changes in speed and traits over the course of expansion, is needed to understand how commonly and under what conditions deterministic processes accelerate expansion and stochastic processes diversify outcomes. We also suggest that “planned” expansions (e.g., reintroductions, biocontrol releases), could be exploited for this purpose, particularly since these are cases where factors such as founder number and source diversity are known or could be experimentally manipulated.

One of the key challenges for empirical work in field systems is exploring the fixation of leading-edge alleles and traits due to gene surfing. While laboratory experiments have shown that this process can amplify heterogeneity across replicates, range expansion in nature is rarely, if ever, truly replicated. The implication of elevated among-replicate variance is that any single realization of expansion in nature is but one draw from a wider range of possibilities (Williams et al. 2019). This idea could be pursued in field settings by testing for convergence/divergence of genetics, traits, and speed at multiple fronts of the same expansion (White et al. 2013, Merwin 2019). Heterogeneity in environmental conditions may complicate comparisons across different fronts but, if quantified, could also present an opportunity: gene surfing can affect expansion variability in constant environments but it is unknown whether such effects are overwhelmed by the substantial spatial and temporal environmental heterogeneity expected in field settings.

CONCLUSIONS

Research over the past decade has advanced understanding of space as an agent of evolutionary change; reciprocally, it is now understood that rapid evolution of demographic and dispersal traits can alter the ecological dynamics of expansion (Fig. 1). Our synthesis of theory

and evidence for deterministic and stochastic evolutionary processes during range expansion reveals that eco-evolutionary feedbacks can be expected to accelerate expansion, on average, but also have the potential to affect expansion variability in curiously diverse ways (Figs. 2, 3). As in all of ecology and evolution, history and context matter. Much remains unknown about the modifiers we have identified (Fig. 1) and other types of contingency likely remain to be discovered. The collective weight of evidence indicates that eco-evolutionary feedbacks may be a default outcome of range expansion, to be expected whenever genetically based trait variation provides opportunity for the development of spatial genetic structure. As ecologists increasingly track the movement of range edges as a hallmark of global change, there is both an opportunity and a need to account for rapid evolutionary change as a driver and consequence of expansion.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3139/supinfo>

DATA AVAILABILITY

Associated data and code are available on Zenodo: <http://doi.org/10.5281/zenodo.3886962>.