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The evolution of plasticity at geographic range edges

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The evolution of plasticity at geographic range edges

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Abstract

Phenotypic plasticity enables rapid responses to environmental change, and could facilitate range shifts in response to climate change. What drives the evolution of plasticity at range edges, and the capacity of range-edge individuals to be plastic, remains unclear. Here, we propose that accurately predicting when plasticity itself evolves or mediates adaptive evolution at expanding range edges requires integrating knowledge on the demography and evolution of edge populations. Our synthesis shows that: (1) the demography of edge populations can amplify or attenuate responses to selection for plasticity through diverse pathways; and (2) demographic effects on plasticity are modified by the stability of range edges. Our spatially-explicit synthesis for plasticity has the potential to improve predictions for range shifts with climate change.

On the importance of plasticity at geographic range edges

Species **range edges** (see Glossary) are shifting rapidly in response to changing climate [1,2]. **Leading-edge** populations (i.e., at high-latitude and high-elevation range edges) are expanding into habitat that is now climatically suitable, whilst encountering novel non-climate conditions (e.g. in photoperiods [3] or biotic communities [4]). Range-edge populations can cope with these new conditions by adaptive evolution [5]. The ability and need for edge populations to adapt to environmental change, however, is affected by **phenotypic plasticity**– rapid responses that enable individuals to adjust their phenotype within a single or few generations [6–9].

Decades of research have allowed for comprehensive syntheses of factors influencing adaptation to new conditions in edge populations (reviewed in [5]). However, the relative paucity of studies focusing on plasticity at range edges has hampered the formulation of unifying theories (but see [10–12]), despite the fact that plasticity itself can evolve and can respond to selection over multiple generations (Box 1) [13]. Lack of synthesis predicting when edge populations will evolve higher or lower plasticity is a major gap in our ability to anticipate responses to climate change. Importantly, variation in plasticity may not solely reflect patterns of environmental selection [12,14,15] (but see [11,16,17]). Rather, it may also be shaped by demographic and evolutionary processes that can operate with different strengths toward **species range** edges [18–20] (Box 1).

Plasticity evolution at range edges should be affected by the same processes that govern the formation of range edges. Thus, much of the theory on evolution at range edges can be used to predict the evolution of plasticity. However, plasticity is more complex than most traits. First, rather than being a single quantifiable trait, like body size or photosynthetic capacity, plasticity pervades all traits, and the degree of plasticity can vary among traits within an individual [21]. Second, by altering the phenotype, plasticity mediates the interaction between the genotype and environment, and therefore feeds back to affect selection in complex ways [22]. Plasticity can either hinder adaptation by reducing the genetic response to selection or, by contrast, facilitate adaptation if initial plastic changes promote subsequent selection for genetic adaptation (i.e., the plasticity-first hypothesis) [23][24]. Additionally, while plasticity can dampen or facilitate evolutionary responses, existing plasticity at range edges could facilitate range shifts without the need for any genetic adaptation. In turn, range edges may affect the expression and evolution of plasticity in unique ways. Range edges often involve gradients in environmental heterogeneity, demography, and **gene flow**, all of which influence the evolution of plasticity. Developing a clearer framework for understanding plasticity at range edges is a challenging but critical step toward predicting species' responses to climate change.

Here, we unify theoretical and empirical work to address the expression and evolution of plasticity at species' leading range edges. We describe how plasticity might vary at range edges given the ecological and evolutionary processes that: (i) can limit species' geographic ranges; and (ii) occur during range expansion. We enumerate key hypotheses for patterns of plasticity evolution toward range edges (Box 2), highlighting gaps in empirical work and paths forward for testing them.

Plasticity evolution at species' range limits

Limits and costs to plasticity evolution at range edges

Empirical evidence suggests that habitat quality declines across ~75% of species' range edges [25]. Plasticity is advantageous in low-quality habitats if it helps organisms adaptively regulate their environmental tolerances or phenology to improve fitness [26]. However, predicting whether plasticity will evolve adaptively requires a consideration of its limits and costs [27]. At **stable range edges** where edge populations are unable to expand their range due to reduced fitness (Box 1), our synthesis below predicts plasticity to be both limited and costly (Hypothesis 1; Box 2).

If adaptive evolution at range edges is constrained by low **effective population size** (Box 1), then edge populations might lack adaptive variation in all traits, including **genetic variation for plasticity** (GxE; [11,28]). Even where genetic variation for plasticity is present and there is selection for increased plasticity, the evolution of plasticity can be costly at range edges. While environmental stress towards range edges (Box 1) could impose costs to any trait regardless of plasticity, it should be particularly demanding to the often complex physiological and metabolic mechanisms involved in the production, expression, maintenance, and cue perception required to evolve and express plasticity [29–31]. Furthermore, the adaptive response in stressful environments may involve phenotypic buffering, where traits involved in fitness maintenance and physiological homeostasis are favoured to be constant across environments to reduce costs of plasticity [32]. Phenotypic buffering will thus manifest as flat **reaction norms** and may be common at range edges [32]. There is evidence for reduced plasticity in response to stressful conditions at range edges [33–36]; but see [37,38]. For example, climatic stress can correlate negatively with the magnitude of plasticity across space [15,39–41], such as with cold stress limiting plasticity in physiological traits for terrestrial plant species towards the poles [15].

Lastly, empirical evidence suggests an association between range edges and increased environmental variation for certain species [42,43]; but see [44,45]. If the relative influence of environmental fluctuations on demography and fitness is stronger at the range edge than at the range core [46,47], the cost of environmental mismatch (i.e., of expressing the wrong phenotype at the wrong time) may also increase towards range edges [12,22]. Overall, genetic variation for plasticity may be limited and plasticity costly to evolve in edge populations, particularly where populations and habitats are of low quality (Figure 1).

Whilst limited genetic variation and increased costs should hold for any trait at a stable range edge, this is particularly crucial to plasticity for at least two reasons. First, based solely on assumptions that environmental variation increases towards range edges [43], one might predict increased adaptive plasticity at range edges without consideration of demographic and evolutionary constraints. However, populations at stable range edges may lack capacity to respond to selection for adaptive plasticity even if its fitness benefits are predicted to increase at the range edge [18,19,36]. Second, demographic and genetic constraints on the evolution of plasticity at range edges may further promote the formation of range limits by decreasing overall environmental tolerances at the range edge [19]. Considering how these constraints on the evolution of plasticity are overcome will therefore be key to understanding the importance of plasticity during climatic range shifts. An interesting exception is species where populations at range edges become increasingly clonal [48,49]. For clonal individuals, plasticity may be important at the range edge [50] to compensate for the loss of genetic variation [51,52].

Dispersal, gene flow and plasticity evolution at range edges

The prevalence of plasticity at range edges can also be influenced by the magnitude and direction of dispersal and gene flow. Selection for plasticity during dispersal is analogous to selection from temporal environmental variability in that plasticity can confer a fitness benefit for organisms experiencing spatially variable environments [53–56]. Here, plasticity is advantageous over **specialisation** when dispersal across varying environments selects against individuals specialized to one environment, due to mismatches with their new environments [54]. Plasticity would therefore become more common in populations that experience regular or repeated immigration of individuals across divergent environments.

Lower dispersal rates between isolated edge populations could reduce the likelihood of adaptive plasticity (Figure 1) if there is less opportunity for selection from spatial variability to act when dispersal across environments is rare [54]. Theoretical models also suggest that, under specific circumstances (Table 1), selection can favour adaptive plasticity in populations experiencing **gene swamping** if the plastic response is in a direction that mitigates fitness loss that arises due to the introduction of maladaptive alleles [18]. For example, if edge populations reproduce sexually and experience gene swamping from central populations [57], adaptive plasticity could evolve at range edges in specific cases where plasticity mitigates **genetic load** [18]. While empirical work has found evidence that edge populations can be fragmented and dispersal-limited [58–60], empirical evidence for gene swamping at range edges is generally weak [5,61]. Overall, in isolated edge populations, limited dispersal could therefore provide weak selection for plasticity from spatial environmental variation, contributing further to reduced plasticity at stable range edges (Hypothesis 1; Box 2).

There are few empirical tests of whether plasticity increases with higher rates of gene flow (Table 1; but see [62–64]). In the frog *Rana temporaria*, plasticity in metamorphosis rates is adaptive and highest in populations from ponds that experience higher fluctuations in water availability and in populations that experienced greater dispersal from islands that were environmentally dissimilar [63]. However, whilst studies have tested how gene flow affects the degree of local adaptation at species' range edges [61], we are not aware of empirical tests of how gene flow might affect the evolution of plasticity at range edges (see Outstanding Questions).

Plasticity evolution during range expansion

Range boundaries are dynamic, with periods of both stasis and expansion [65–67]. We next focus on how demographic and evolutionary processes occurring during range expansion could shape spatial variation in plasticity (Table 1).

Demography and evolution of plasticity during range expansion:

During range expansion, the evolution of adaptive plasticity at the leading edge should depend on the balance between demography and selection from the environmental gradient across space (Figure 1; Hypothesis 2, Box 2). First, during the initial stages of colonisation, selection is weak relative to genetic drift due to small population sizes [68]. However, dispersal during range expansion could subsequently alleviate evolutionary constraints on adaptive plasticity due to the accumulation of colonising individuals at the leading edge, increasing genetic variation [69] (although see "Genetic load and the evolution of plasticity" for dispersal during range expansion leading to the fixation of deleterious variants).

Second, models of plasticity evolution and colonisation suggest that environmental gradients impose strong selection for adaptive plasticity if that plasticity promotes tolerance to, and establishment in, new environments [68,70]. However, whether plasticity or specialisation is favoured at the leading edge depends on dispersal rates (see Dispersal, gene flow and plasticity evolution at range edges) and whether range expansion involves dispersal into new environments. For the latter, recent modelling work shows that when dispersal occurs into environments that are within the species niche (i.e., non-novel environments), higher dispersal can introduce genotypes already suited to the environment at the leading edge [20]. When the environment is novel, higher dispersal can favour plasticity (adaptive or non-adaptive) over specialisation, as none of the genotypes introduced by dispersal are specialised to the new environment at the leading edge [20].

While theory suggests that range expansion can select for increased adaptive plasticity, some empirical results suggest that maladaptive plasticity can also arise during range expansion [71–74]. This occurs when populations encounter increasingly stressful or novel environments that limit expression of adaptively plastic phenotypes. Evidence from spatial variation in **transcriptional plasticity** [72,74,75] and lab-based experimental range shifts [73] suggests that maladaptive plasticity during range expansion can, counterintuitively, enhance adaptation to environments being colonised. Maladaptive plasticity could promote adaptive evolution by increasing: 1) the strength of directional selection as a result of lower relative fitness; and 2) the response to selection by increasing fitness variance [72,74–76]. Therefore, both adaptive and maladaptive plasticity are predicted to have key roles in promoting colonisation during range expansion (Hypothesis 3, Box 2).

Empirical data on plasticity evolution during native range expansions is limited (but see [77–79]. Instead, most evidence for plasticity evolution during range expansion comes from invasive species, which have found that many traits evolve differences between leading-edge populations compared to populations further behind the expansion front, though both plasticity and fixed genetic differences can contribute to such differences [80]. Invasive populations experience different demographic and environmental conditions than would be typical of climate-driven range shifts, as the former tends to involve a few founding individuals colonising new communities and environments [68]. Understanding plasticity evolution in the context of native ranges will be critical for predicting how plasticity evolves to facilitate or inhibit range expansion in response to climate change (see Outstanding Questions).

Genetic load and the evolution of plasticity

During range expansion, sequential founder events can lead to strong genetic drift and therefore increased genetic load [81]. Plasticity in particular can accumulate genetic load during range expansion when plasticity is controlled by conditional, environmentally-induced gene expression. This occurs because selection for plasticity can be relaxed during range expansion when there is spatial heterogeneity in the environment that induces plasticity such that plasticity is not expressed consistently across space [82]. This can subsequently lead to mutation accumulation in conditionally expressed genes that regulate plasticity [82,83]. Although there is no empirical evidence testing whether plastic traits accumulate genetic load during range expansion, there is theoretical evidence that environmentally induced genes are especially susceptible to load as a result of relaxed selection [83]. This is especially relevant for many plastic traits that have specific, environmental cues such as for phenological plasticity in response to temperature or day length [12]

Looking forward: testable hypotheses for plasticity at species' range edges

Our synthesis suggests that to predict levels of plasticity in range-edge populations, one must look beyond measures of environmental variability and incorporate the interactive effects of demography and evolution (Table 1; Figure 1). Importantly, synthesising the effects of demography and evolution alters predictions of spatial variation in plasticity based solely on environmental variability, and provides alternative mechanisms for currently unexplained patterns. We highlight these key, testable hypotheses on range-edge plasticity that emerge from our synthesis in Box 2.

Empirical approaches for testing hypotheses on plasticity at range edges

We highlight that empirical tests comparing the different ecological and evolutionary drivers of plasticity in range-edge populations are limited (but see [11]). Our synthesis of drivers of plasticity shows major gaps in testing the demographic drivers of plasticity (Table 1). This sort of test is inherently difficult because plasticity is challenging to measure and responds to a variety of co-occurring environmental gradients. Nevertheless, such studies will be paramount to understand how plasticity will influence species responses to global change.

Plasticity is typically estimated by sampling individuals from populations and measuring trait change at the individual level across environments (e.g., in common gardens with two or more environmental treatments; Figure 2A; [10]). More recently, modern genomic tools have allowed quantification of plasticity at the transcript level [75,84]. To identify predictors of plasticity at the range edge, one must then link differences in the magnitude of plasticity to variation in environmental, demographic, and evolutionary processes occurring at the population level (Figure 2B). Specifically, we propose that sampling designs should focus on measuring and contrasting plasticity at both range core and edge populations (Figure 2B).

To test whether plasticity is limited and costly in smaller and isolated range-edges (Hypothesis 1) studies could compare levels of genetic variation for plasticity (e.g. in climate-related traits) between range core and range edge populations, or across range-edge populations that differ in connectivity and population size. This can be done, for example, by directly identifying loci associated with plasticity [85], or by quantifying whether selection is acting to maintain plasticity in edge populations (summarised in [28]), although we note that these quantitative genetics studies require larger experiments. New studies may be designed based on prior knowledge of a system, for example, by focusing on environmental predictors and traits important for persistence at the range edge. Existing studies that quantify local adaptation at stable range limits [5] are also ripe for testing hypotheses on plasticity at range edges. These studies have also quantified the effect of gene flow on the degree of local adaptation at the range edge (e.g., [86]), the effect of which on plasticity is unclear (Table 1; Outstanding Questions).

To test whether adaptive and maladaptive plasticity can both facilitate range expansion at the leading edge (Hypothesis 2 and Hypothesis 3) studies on plasticity evolution during the expansion of native ranges (as opposed to invasive ranges) are much needed. Over-the-edge transplant experiments, employed to test whether persistence is possible just beyond the range edges of native populations, could be used to test whether selection favours adaptive plasticity, or if environments at sites beyond the edge trigger the expression of non-adaptive plasticity [72]. Laboratory-based experimental range expansions [73,87] are another tractable approach to explore the evolution of plasticity in real-time. We note that combining genomics and transcriptomics (e.g., DNA and RNA mapping) with demography (e.g., common gardens and experimental transplants) is a promising avenue for exploring the genetics of plasticity and its complex drivers in nature [75,84].

Concluding remarks

We stress the importance of bridging two well-established bodies of work: the evolution of plasticity and the evolutionary ecology of species' ranges. By uniting these two fields, we provide a synthesis for the importance of plasticity at range edges. Crucially, this synthesis offers a richer array of mechanisms beyond temporal environmental variability, and provides improved predictions for when and how plasticity should vary at stable and expanding range edges. We highlight that these drivers have been previously overlooked in studies of plasticity in nature.

Our synthesis shows that plasticity at the range edge can be shaped by diverse eco-evolutionary pathways, and that plasticity can be enhanced or attenuated by the demography of expanding and stable range-edge populations. While much work has focused on climate-driven selection for plasticity, a fuller consideration of mechanisms (Table 1) suggest that these predictions may be oversimplified. Predictions arising from our unified perspective lay the foundation for much needed empirical tests and quantitative syntheses (see Outstanding Questions). A synthetic approach to plasticity evolution is necessary to better assess when edge populations are able to respond plastically to rapid environmental change or face local extinction.

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Figure Legends

Figure 1. Underlying mechanisms that drive variation in the evolution and expression of plasticity at stable and expanding range edges. In Panels A and B, we illustrate how **reaction norms** (the difference in a trait expressed by a single genotype or individual across environments) can be compared across edge (yellow or orange in map) and core (grey in map) populations, and the different ways in which the demography of edge populations can affect the mean and variance (histograms) of reaction norms. Panel C shows specific predictions for reaction norms and their drivers at (i) stable and (ii) expanding range edges based on hypotheses in Box 2. (A) From individuals across range-core populations (grey dots), we can measure plasticity as the slope of reaction norms across testing environments (A and B) and derive a hypothetical variance distribution of reaction norms (grey histogram). The width (σ) of this histogram represents the amount of genetic variation for plasticity in the core population. (B) By using the distribution of reaction norms obtained from the core population as a reference, we can compare how changes in demography and evolution impact the mean and variance of reaction norms in edge populations (orange histogram). A change in the magnitude of plasticity is represented by a shift in the population mean plasticity ($\bar{x}$), whilst a change in the genetic variation for plasticity is represented by changes in variance (σ). Additionally, a change in the population size is represented by changes in the integral ($\int$) of the histogram. (C_i-C_{ii}) We show our hypothesised distribution of reaction norms and their drivers for stable and expanding range edges, respectively. We highlight that plasticity should be limited by demography at stable range edges, while both adaptive and non-adaptive plasticity may increase at expanding range edges (Box 2). For illustration purposes, we assume that the variance distribution is normal.

Figure 2. Empirical framework to identify the environmental, demographic and evolutionary drivers of plasticity at range edges. (A) To encompass differences in demographic rates and evolution and their influence on plasticity, we suggest sampling replicate populations at both the range core (grey dots) and the stable (yellow) or expanding (orange) range edge. We may also utilise existing demographic and evolutionary studies of populations across the species range (hatched), to incorporate estimates of plasticity at core and edge sites. (B) For individuals from each population, plasticity can be quantified in a variety of ways, for example, by measuring trait change across two or more environments (e.g. Environment A and B) and parameterizing reaction norms for sampled individuals. From here, we can derive population-level estimates of the mean and variation in reaction norms at the range edge (stable or expanding, represented by yellow or orange histograms) and the range core (grey). (C) Ideally, studies would quantify parameters of interest in environmental, demographic, and/or evolutionary genetic predictors at the range core and edge populations. (D) Spatial patterns in plasticity at the range edge and core can then be linked to population-level patterns and processes to test hypotheses on plasticity evolution (Box 2). Studies could focus on one driver, or use a variety of multivariate approaches (e.g., variance partitioning, generalised linear models, generalised dissimilarity modelling, and non-parametric multidimensional scaling) to test the relative importance of different factors at the core and edge. Experimental tests (e.g. reciprocal and over-the-edge transplants) can further confirm the role of each driver and whether they promote adaptive or non-adaptive plasticity.

Box 1. Linking plasticity evolution to species range dynamics

Plasticity is the ability of a genotype to produce different phenotypes in varying environments. Adaptive plasticity refers to phenotypic variations in response to alternative environments that increase fitness [22]. Whether increased plasticity can evolve in response to environmental selection depends on the temporal or spatial scale over which populations experience alternative environments (reviewed in [14,23]). However, the evolution of increased plasticity may not solely reflect patterns of environmental selection [6,14]. Its evolution can also be shaped by **genetic drift** and gene flow, which depend on demographic processes related to population size and connectivity (see Table 1 for a synthesis of processes shaping plasticity).

Theory on the evolution of range limits often posits that habitat quality and quantity decrease toward range edges, resulting in declining population size and connectivity [24]. Empirical studies show that, while not universal, most range edges overlie gradients in habitat quality [25], genetic quality of populations [26], and declines in demography [27] (sometimes referred to as the abundant centre hypothesis [28]). Declines in effective population size and connectivity should increase the magnitude of genetic drift relative to selection at a **stable range edge** [29]. The relative importance of drift, selection and gene flow can further depend on whether range edges are stable or expanding [29,30]. While eco-evolutionary dynamics at range edges shape the role of plasticity at **expanding range edges**, studies of plasticity evolution and species ranges have often advanced disparately, despite decades of prominent work on species ranges and their response to changing environments.

Box 2. Hypotheses on plasticity that incorporate demography and evolution at range edges.

Here, we outline three hypotheses for the evolution and expression of plasticity that explicitly incorporate the demography and evolution of stable and expanding geographical range-edges. Our hypotheses show that demography interacts with environmental heterogeneity to augment or attenuate spatial patterns in plasticity, and how it does so depends on the stability of range limits.

Hypothesis 1: Demography at stable range limits can constrain plasticity

At stable range edges, there will be greater limits and costs on the evolution of plasticity due to demography (Fig 1Ci). First, although there may be increased selection for plasticity if environments at range edges are suboptimal or more variable (but see [49]), response to selection should be limited by demographic constraints and reduced genetic variation for plasticity (GxE). This is especially pertinent for smaller, isolated edge populations that experience strong genetic drift. Second, even with sufficient genetic variation for plasticity, lower habitat quality and increasing environmental stress at the range edge could result in higher costs for expressing and evolving plasticity. Third, dispersal could be limited among more isolated edge populations, resulting in reduced selection for plasticity from spatial environmental variation.

Hypothesis 2: Demography during range expansion can enhance plasticity

At expanding range edges, there will be increased expression and evolution of plasticity due to demography's interaction with evolutionary processes (Fig 1Cii). First, demographic limits to plasticity evolution should be overcome when increased dispersal and gene flow during range expansion introduces genetic variation for plasticity and increases population sizes at the range edge. Second, selection for plasticity is predicted to be strong due to individuals experiencing spatiotemporal variation in the environment during dispersal (Table 1).

Hypothesis 3: Both adaptive and non-adaptive plasticity are critical for colonisation at the expanding range edge

At expanding range edges, both adaptive and maladaptive plasticity is important for colonisation (Fig 1Cii). Adaptive plasticity could facilitate colonisation when plasticity confers increased tolerance to these environments. Maladaptive plasticity could facilitate adaptive evolution by increasing the strength of selection or fitness variance [22, 78–80], thus allowing colonisation of new environments where plasticity is unsuited. As the environment experienced by a colonising individual will be a function of the rate and directionality of dispersal, whether adaptive or non-adaptive plasticity is expressed at the leading edge depends on dispersal and the degree of environmental heterogeneity across the landscape. For example, when range expansion occurs across divergent landscapes with long-distance dispersal, increased exposure to novel environments may trigger the expression of non-adaptive plasticity during range expansion.

Glossary

Climate variability hypothesis: Populations and species exposed to greater climate variation will evolve greater tolerance (conferred through plasticity or niche evolution) to climatic change

Effective population size: The size of an idealised population (i.e., a population that meets Hardy-Weinberg assumptions) at which populations experience genetic drift, which is inversely proportional to the efficiency of natural selection. Also described as corresponding to the number of breeding individuals in a population).

Expanding range edge: The edge of a species range where populations are expanding across space

Gene flow: The transfer of alleles between populations through dispersal and subsequent interbreeding

Gene swamping: The decrease in frequency of locally adaptive alleles in a population due to introduction of alleles from differently adapted populations

Genetic drift: The random loss of genetic variation due to repeated, random sampling of alleles

Genetic load: reduction in mean fitness of a population relative to an idealized population composed only of individuals with optimal genotypes

Genetic variation for plasticity (GxE): Genotypes in a population differ in their magnitude or direction of plasticity when responding to the environment

Leading edge: Populations at the front of the expanding range

Phenotypic plasticity: The ability of one genotype to produce different phenotypes in response to environmental variation within a single generation or across multiple generations (i.e., transgenerational plasticity).

Range edge: A population at or near the spatial periphery of a species' geographical distribution

Range expansion: When a population expands into space previously unoccupied by that species

Reaction norms: Range of traits a genotype can express under different environmental conditions

Specialisation: Populations or species adapted to a restricted, local environment (i.e., the evolution of a narrow ecological niche breadth)

Species' range: The geographical area within which all individuals of a species occurs

Stable range edge: The point in space at the limit of a species range beyond which population growth rates are negative.

Transcriptional plasticity: Changes in gene expression in response to environmental change

Table 1. Synthesising drivers of plasticity at range edges. Our synthesis shows a lack of both theoretical and empirical studies that test how various demographic and evolutionary processes (other than selection from environmental variability) drive plasticity evolution, particularly in a spatial context. These gaps highlight that we are missing critical processes that shape plasticity at range edges, limiting our ability to predict the capacity of plasticity to facilitate responses to rapid environmental change. † Temporal environmental variability increasing plasticity towards poleward edges is commonly argued as part of the **climate variability hypothesis** [88] despite mixed evidence for a latitudinal cline in climatic variables. We suggest that it is critical to go beyond broad-scale metrics of environmental variability, and explore other environmental predictors relevant to theoretical models for plasticity evolution (e.g., scale of spatiotemporal fluctuations, extremes and autocorrelation, as recently explored in [22]).

Drivers of plasticity	**Predicted pattern in plasticity at range edges**	**Explanation**	**Adaptive or non-adaptive plasticity?**	**Predictions for stable or expanding range edges?**	**Theoretical evidence**	**Empirical evidence**
Habitat quality	Lower towards edges	When habitat quality declines at range edges (e.g., if range limits reflect niche limits), this can impose a metabolic or physiological cost on plasticity.	Adaptive plasticity reduced	Stable	[9,29–31,53]	[15,36,39–41]

Population size and genetic variation	Lower towards edges	When effective population size and genetic variation decrease towards range edges, this will reduce genetic variation for plasticity (GxE) and the potential for plasticity evolution.	Adaptive plasticity reduced	Stable	[11,18,19,28]	[11,28,35,89, 90]
Dispersal and gene flow	1. Lower in more isolated edge populations	Dispersal is limited among isolated edge populations. Limited dispersal can lead to specialisation over plasticity evolution.	Adaptive plasticity reduced	Stable	[11,18,54–56]	[11,62,64]
	2. Greater for edge populations experiencing gene swamping	Reduced fitness due to constant gene swamping can increase directional selection in edge populations. If there is enough genetic variation for plasticity, adaptive plasticity can evolve to mitigate this fitness loss	Adaptive plasticity increased	Stable	[18]	
Selection during range expansion	Greater towards leading edge	Range-expanding individuals likely encounter new conditions. Plasticity can promote tolerance and establishment during colonisation.	Adaptive plasticity increased	Expanding	[20,68]	[66,71,77–79,91–93]

		Maladaptive plasticity expressed at the leading edge may aid colonisation by increasing the strength of directional selection and/or increasing fitness variance.	Non-adaptive plasticity increased	Expanding	[94]	[72–75]
Genetic load during founder events	Lower towards the leading edge	Repeated founder effects lead to strong genetic drift and the accumulation of genetic load. This could increase the cost of plasticity. Loci for plasticity could further accumulate deleterious mutations due to relaxed selection on conditionally expressed genes.	Adaptive plasticity reduced	Expanding	[19,82,83]	[95]
Temporal environmental variability †	Greater towards poleward edges	Temporal variability increases towards the poles. Plasticity confers tolerance to environmental variability.	Adaptive plasticity increased	Stable and expanding	[13,18,96–98]	[14,15,88,99–102]

Highlights

Populations at species geographical range edges are experiencing rapid environmental change, driving consequent shifts in species spatial distributions.

Although phenotypic plasticity can facilitate range shifts and responses to environmental change, little is known about how the demography and evolution of range-edge populations influence the evolution and expression of plasticity.

We show diverse pathways by which population dynamics at range edges interact with environmental variation to shape plasticity. Critically, demography of stable range edges may constrain plasticity, whilst that of expanding range edges favor increases in both adaptive and non-adaptive plasticity.

Demography therefore alters where and when we predict plasticity to be important, providing a fuller perspective for the role of plasticity at range edges and its capacity to facilitate responses to climate change.

Outstanding Questions

When do spatial patterns in plasticity emerge as the by-product of demographic processes (e.g., constraints in population size and the stability of range edges) as opposed to direct responses to spatially varying natural selection?

How does genetic variation for plasticity (G×E) vary across the range and is it limited at stable range edges? Is lower G×E associated with lower habitat quality at the range edge?

How do patterns of gene flow drive the evolution of plasticity at range edges?

How important is maladaptive versus adaptive plasticity during range expansion?

Is selection for plasticity at the range edge stronger during range expansion than at stable range edges?

Figure

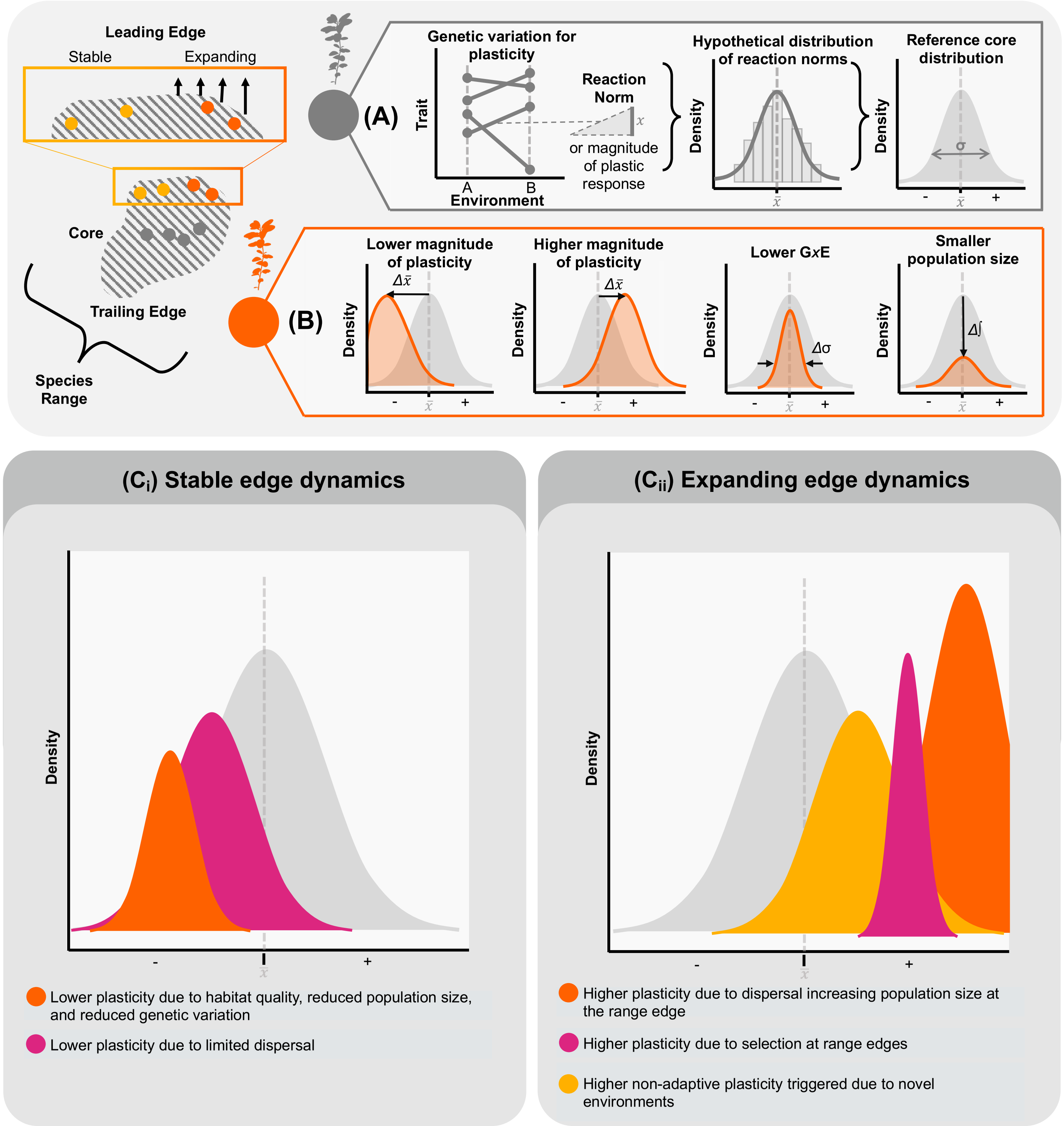
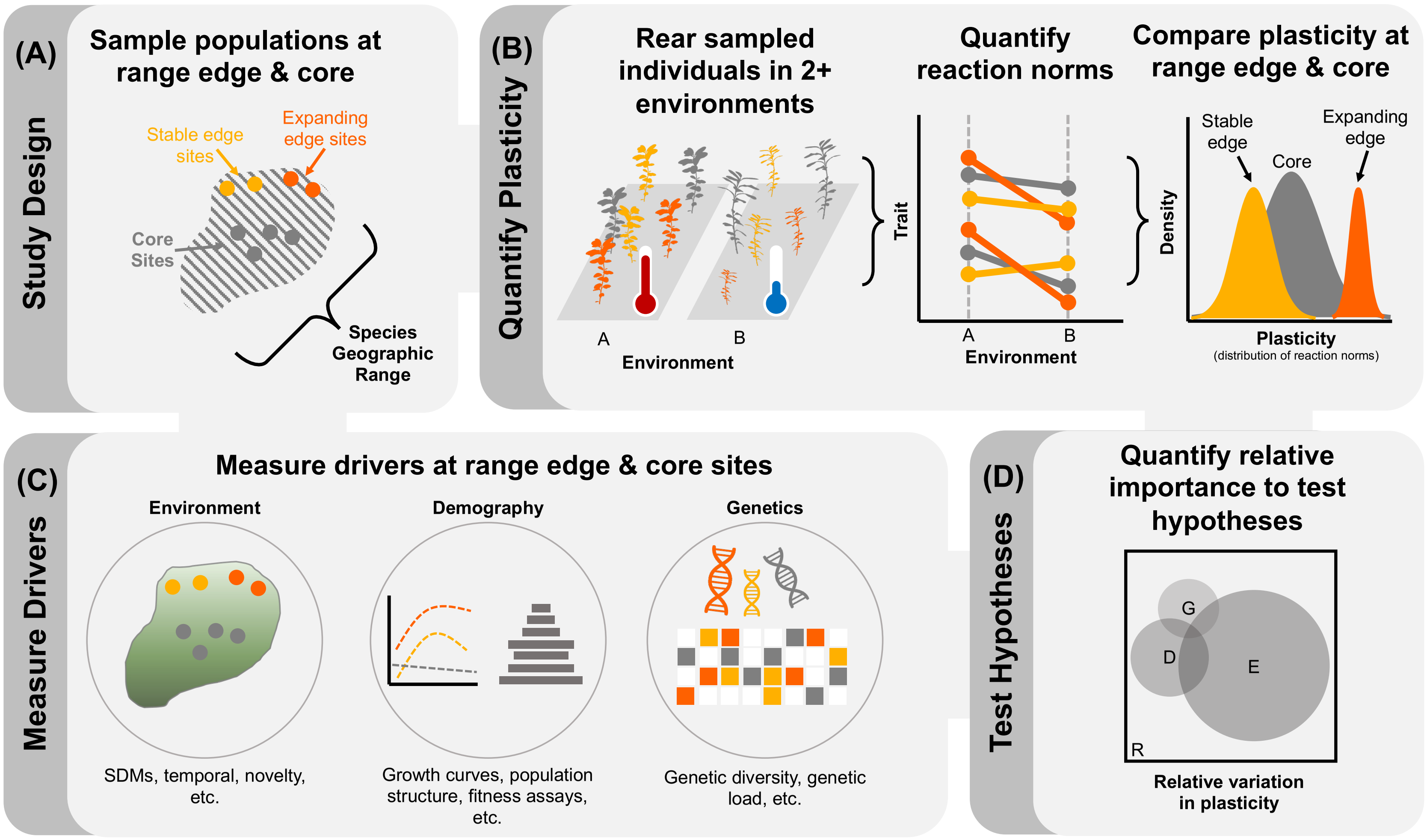

Leading Edge
Stable
Expanding
Core
Trailing Edge
Species Range
(A)
Genetic variation for plasticity
Trait
A
B
Environment
Reaction Norm
x
or magnitude of plastic response
Hypothetical distribution of reaction norms
Density
$\bar{x}$
Reference core distribution
Density
σ
-
$\bar{x}$
+
(B)
Lower magnitude of plasticity
Density
$\Delta\bar{x}$
-
$\bar{x}$
+
Higher magnitude of plasticity
Density
$\Delta\bar{x}$
-
$\bar{x}$
+
Lower GxE
Density
$\Delta\sigma$
-
$\bar{x}$
+
Smaller population size
Density
$\Delta\int$
-
$\bar{x}$
+
(C$_i$) Stable edge dynamics
Density
-
$\bar{x}$
+
Lower plasticity due to habitat quality, reduced population size, and reduced genetic variation
Lower plasticity due to limited dispersal
(C$_{ii}$) Expanding edge dynamics
Density
-
$\bar{x}$
+
Higher plasticity due to dispersal increasing population size at the range edge
Higher plasticity due to selection at range edges
Higher non-adaptive plasticity triggered due to novel environments

Figure 2


(A)
Study Design
Sample populations at range edge & core
Stable edge sites
Expanding edge sites
Core Sites
Species Geographic Range
(B)
Quantify Plasticity
Rear sampled individuals in 2+ environments
A
B
Environment
Quantify reaction norms
Trait
A
B
Environment
Compare plasticity at range edge & core
Density
Stable edge
Core
Expanding edge
Plasticity
(distribution of reaction norms)
(C)
Measure Drivers
Measure drivers at range edge & core sites
Environment
SDMs, temporal, novelty, etc.
Demography
Growth curves, population structure, fitness assays, etc.
Genetics
Genetic diversity, genetic load, etc.
(D)
Test Hypotheses
Quantify relative importance to test hypotheses
G
D
E
R
Relative variation in plasticity