Title: Revisiting evolution at the rear edge

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Abstract:

Rear-edge populations occur at species' warmer range limits, with many still occupying glacial refugia. They offer insights into evolution under changing climates, yet they are underused as models. We identify three equally likely evolutionary patterns in rear edges: high genetic diversity and differentiation, elevated genetic drift, and strong local adaptation. Multiple patterns create challenges for predicting the vulnerability, conservation value and adaptive potential of rear edges under future climates. Which factors drive these distinct outcomes, and why only some rear edges persist in former refugia, remains unclear. We propose to address these gaps by leveraging stable, receding, and trailing rear edges as evolutionary models of persistence and decline to improve predictions of species' responses to changing climates.

Highlights:

- Populations in the rear edges of species' distributions are typically relicts of glacial refugia and may offer key insights into evolution under climate warming.
- Long histories of postglacial warming may have led to the persistence, decline, or extinction of refugial populations, with resulting stable, receding, and trailing rear edges, respectively.
- The increased interest in range limits over the last two decades provides a wealth of empirical work addressing long-standing theories on rear-edge evolution. Three evolutionary outcomes to past warming can be expected at the rear edge, including the maintenance of genetic diversity, high genetic drift, and strong local adaptation.
- Evolutionary responses to climate warming are context dependent, with vulnerability to future warming and adaptive potential shaped by populations' demographic and evolutionary history.

Rear edges are natural laboratories of evolution under changing climates

A major focus of current research is to understand how **species' distributions** (see Glossary) are altered by ongoing **climate change** [1–3]. **Temperate species** are predicted to track changes in climate by migrating toward higher latitudes and/or elevations through **range expansion** at colder **range limits** and **range contraction** at warmer range limits [4]. However, whether species' ranges shift, expand, contract, or remain stable will be influenced by the interplay between environmental change and evolutionary forces [5,6]. Similar processes have driven range dynamics under past climate change, shaping present-day distributions [7–10]. Understanding the contribution of the distinct evolutionary processes that shaped species' range limits under past warming will provide insights for anticipating responses to ongoing and future climate change.

The **rear edge** of species distributions, typically composed of relict populations from the last glaciation (Fig. 1 [11]), serves as an example of evolution in response to past climate change because these populations have experienced long-duration **postglacial warming**, including, in some cases, temperatures outside of species' typical thermal niche [9,10,12]. During the last glaciation, most temperate species retreated to unglaciated areas at low latitudes and elevations where climates were mild [13], referred to as glacial **refugia**. After the **Last Glacial Maximum** (LGM; [14]), as the Earth warmed and new habitats became available, these species recolonized higher latitudes and elevations, tracking the retreat of ice sheets (i.e., the **leading edge** of species distributions; Fig. 1, [7,8]). However, outcomes were more diverse for populations in warming refugial areas (Box 1). In some cases, they persisted more or less in place in former refugia, with little demographic change while the range expanded, and now constitute a **"stable" rear edge** [11]. In other cases, **refugial populations** were extirpated and species' ranges shifted to track changing climates, with populations at the contracting warmer range limit representing a "**trailing" rear edge** [11]. Between these extremes are cases where refugial populations still exist but are in decline. We define this intermediate as a "**receding" rear edge** (Box 1). In each case, contemporary rear-edge populations represent the oldest populations across the range and are the closest relatives of refugial populations.

Rear-edge populations are an ideal model for elucidating the role of eco-evolutionary processes in shaping genetic patterns in response to changing climates. The importance of rear edges for ecological and evolutionary research was first highlighted in 2005 in a seminal review by Hampe and Petit [11]. This review provided distinct expectations for the distribution of **genetic**

diversity, demographic history, and patterns of selection and adaptation for populations in the range core and stable rear edges. We build on this work, using current evolutionary theory and empirical research on range limits, to develop a framework of evolutionary processes and resulting genetic patterns expected at the rear edge (Box 2; Fig. 2). The framework leads to the following predictions: (i) rear edges may be hotspots of genetic diversity because of their history of persistence in former refugia; (ii) Alternatively, habitat decline and fragmentation associated with long-term postglacial warming may have led to population contraction and isolation, exposing rear-edge populations to strong **genetic drift** with associated reductions in genetic diversity and **fitness**; and (iii) finally, long-term persistence in the face of postglacial warming suggests that rear-edge populations may show high **local adaptation** to the warmer rear-edge climates. Although not mutually exclusive, each prediction has distinct implications for the fate of rear edges under future warming (Box 3). Stable, receding and trailing rear edges, while sharing a common origin, are likely to have been shaped by different evolutionary processes (Box 2). Determining the frequency and characteristics of the outcomes of these evolutionary processes and associating them with distinct rear-edge types will be key in improving forecasts of species' responses to climate change (Box 3).

Developing an understanding of evolution driven by past warming from the genetic patterns in contemporary rear edges may also help refine predictive frameworks of responses to changing climates (Box 3). Rear-edge populations are generally expected to decline or go extinct as climates warm because they often coincide with a species' warmer range limit, and thus may occur near their upper thermal tolerance ([5,15] but see Ref. [16]). In addition, expectations from range-limit theory and empirical patterns suggest that rear edges often consist of small and isolated populations, occur in marginal habitats, and are sensitive to stochastic extinction events [16–22] (but see Ref. [16,20]). Yet, a growing number of reports have documented lags in expected extinctions at warmer range limits [2,16,23–25], suggesting that additional dynamics shape the **vulnerability**, **resilience**, and **adaptive potential** of rear edges. A focus on the distinct types of rear edges is a first step to revealing these dynamics.

Despite their ecological and evolutionary importance, rear-edge populations garnered little attention until Hampe and Petit's prescient review 21 years ago [11]. It is an opportune time to synthesize the new knowledge sparked by this seminal work and evaluate it in an evolutionary framework (Box 2), using an expanded definition of rear-edge types (Box 1), to update our understanding and identify areas ripe for exploration.

What do we know about patterns of diversity, drift and selection at the rear edge?

Attention to this historically understudied range limit has greatly increased, with 444 studies published in the last 21 years (see Supplementary Information online), a similar number to the leading edge (474 studies). However, much of this research focuses on characterizing ecophysiological traits linked to adaptation in warm and/or dry climates (e.g., [26]), or on models to predict responses to climate change (e.g., [27,28]). Evolutionary research on the rear edge remains scarce, representing only about 17% of recent studies (see Supplementary Information online).

We reviewed studies of evolution at the rear edge of species' distributions (see Supplementary Information online), identifying 61 studies across 58 species. Most studies explored the distribution of **genetic differentiation** and diversity (95% of species; see Supplementary Information online), largely based on a small number of neutral genetic markers. Few studies directly evaluated selection or patterns of adaptation at the rear edge. However, a synthesis of latitudinal and elevational patterns of local adaptation across multiple species [29] can serve as a strong proxy for rear-edge research. Finally, as noted by Hampe and Petit [11], research on the rear edge, and range limits in general, tends to unevenly represent the global diversity of species and geographic regions [15,30,31]. Most studies identified for this review focus on plants, occur in the Northern Hemisphere, and assess latitudinal rather than elevational distributions.

Do rear edges maintain high diversity?

Rear edges may be expected to serve as reservoirs of genetic variation because of their history of persistence in former refugia (Box 2). We identified 50 species in which within-population genetic diversity at the rear edge was compared with that in central parts of the range. Thirty-six of these also evaluated patterns of differentiation among populations (see Supplementary Information online). About half of the species exhibited higher genetic diversity within populations at the rear edge than in the range core (23/50), with most of the remainder exhibiting lower diversity (21/50). In contrast, in a majority of species (69%, 25/36) there was greater genetic differentiation among populations at the rear edge than in the core. Rear edges are combined hotspots of both diversity and differentiation in only a few species (7/36), suggesting that distinct evolutionary processes led to high diversity within and between populations. Overall, rear-edge populations frequently represent hotspots of genetic differentiation, but less consistently hotspots of diversity within populations.

Are rear edges exposed to strong genetic drift?

Rear edges are also expected to be fragile, with populations expressing genetic drift following a history of small size and isolation in declining habitats (Box 2). The contribution of drift to population genetic structure at the rear edge has typically been inferred from patterns of reduced genetic diversity within populations and elevated genetic differentiation between them [17,20], (e.g., [32–36] but see Ref. [37]). This pattern was found in almost half of the species studied (16/36). Genetic drift in rear-edge populations may also be inferred from genetic signatures of **bottlenecks** [38,39], inbreeding [40], and population decline and isolation determined via demographic inference [41–43]. **Drift load**, a decrease in fitness associated with genetic drift [44–46], has rarely been tested in rear-edge populations though it is a direct measure of the fitness consequences of drift (Box 2). Notable exceptions are the lyrate rockcress, *Arabidopsis lyrata*, where genetic and phenotypic evidence of drift load increases toward the rear edge [47,48], confirming drift suggested by patterns of genetic diversity [49], and the Arizona grape *Vitis arizonica*, which shows the opposite pattern [50]. In summary, signatures of genetic drift including high population differentiation, high inbreeding, population decline, and drift load, highlight the fragility of many rear-edge populations.

Do rear-edge populations display strong local adaptation as a consequence of long-term warming?

Rear-edge populations may have persisted in place by adapting to the strong selective pressures imposed by past warming, and may thus show greater local adaptation than the expanded regions that tracked suitable habitats (Box 2). A recent meta-analysis of local adaptation inferred from transplant experiments on 135 species [29] reports a latitudinal gradient in the magnitude of local adaptation, with stronger adaptation toward the equatorial range limits. As rear edges often coincide with the lower latitudinal range limit, this suggests that stronger local adaptation at rear edges may be prevalent. While rear-edge populations are often recognized for their distinct adaptations to warmer and/or drier climates [26,51,52], we found only two studies that explicitly quantified local adaptation in rear-edge populations, both using transplant experiments, and they support stronger local adaptation at the rear edge (see Supplementary Information online [53,54]). Furthermore, genomic studies in three species found that rear-edge populations exhibit stronger local adaptation [50,55] and signatures of selection by environmental factors (see Supplementary Information online [56]), than the rest of the range. In total, despite few explicit tests, strong selection and local adaptation at the rear edge may be more prevalent than the literature suggests.

Have multiple evolutionary processes occurred at the rear edge?

The three evolutionary outcomes are not mutually exclusive, and signatures of diversity, drift and adaptation may be found in combination in rear-edge populations. For example, populations that are large and highly diverse may also demonstrate strong local adaptation, whereas in declining populations, low diversity and drift may hamper adaptation [57,58]. In addition, strong selection may come at a cost, decreasing population size and exposing populations to drift [29]. Empirical evidence of combined evolutionary processes in rear-edge populations is scarce. In the crayweed (*Phyllospora comosa*), rear-edge populations with genomic signatures of local adaptation also had genome-wide patterns of low diversity and high differentiation, supporting drift [37]. In the meta-analysis of local adaptation [29], equatorial populations showed the strongest local adaptation but also tended to perform poorly across environmental contexts suggesting drift load. Evidence for multiple evolutionary processes is likely limited because studies have typically focused on single or alternative hypotheses, that is, greater or less genetic diversity [43,59–61]. Integrating multiple hypotheses is essential to capture the complexity of processes shaping rear-edge populations, and to set the stage for applying eco-evolutionary models of range limits to the rear edge.

In addition, due to the expected age of rear-edge populations and the iterative nature of glaciations, individual rear-edge populations of the same species may exhibit signatures of distinct evolutionary processes. We found eight cases of distinct outcomes in species with multiple, geographically distinct rear edges (see Supplementary Information online) with most showing different patterns among rear edges, such as heightened diversity in one rear edge but reduced diversity in the other [12,60,62–64]. Similarly, rear-edge populations within the same broad geographic area may show distinct patterns, for example if refugial populations were established during different glacial cycles [65]. Heterogeneity among rear edges could be more prevalent than reported in the literature as many studies focus on a single refugium even if species occur in additional refugial areas. With the recent profusion of range-wide phylogeographic studies, we predict that more species will be identified with genetically distinct rear edges (e.g., [62,66]), allowing comparative studies to investigate similarities in responses to past warming.

Lack of a common evolutionary outcome complicates predictions of rear-edge evolution

There is evidence of greater diversity, drift and local adaptation in rear-edge populations. Finding all predicted patterns is both concerning and hopeful. As environments warm, the climate of rear-edge populations are expected to become more adverse, leading to maladaptation, population decline and potential loss [5]. Rear-edge populations that have experienced high levels of drift may be especially vulnerable to increasingly stressful climates (Box 3). The observation that half of the surveyed species show signatures of low diversity and high drift at the rear edge underscores pressing concerns for the long-term persistence of rear-edge populations. Yet, the fact that rear-edge populations in a similar number of species have been able to maintain high diversity, and that others have adapted to past warming, suggests that in many species these populations may not be as fragile as expected (Box 3), raising hopes for their ability to persist under future warming.

Our literature survey also revealed gaps in predicting the future trajectory of rear edges. First, the comparable frequency of diversity, drift and local adaptation in rear-edge populations casts doubt on our ability to make general predictions about the evolutionary history of rear edges and likely contributes to discrepancies between predicted and observed responses to contemporary warming [2,23–25]. The inability to generalize further complicates the assessment of conservation needs of these populations and their potential use in climate resilience efforts. Finally, it is unclear which factors lead species to follow one evolutionary trajectory over another at the rear edge, highlighting a critical gap in our understanding of how species respond to climate change. Addressing these gaps is not only key to predicting rear-edge evolution but more generally, may allow a better understanding of species' evolution under past and future climates and how past evolutionary processes shape responses to future climate change.

Distinguishing stable, receding, and trailing rear edges matters

Stable, receding, and trailing rear edges represent distinct historical responses of refugial populations to past warming (Box 1). Accurately distinguishing rear-edge types first requires identifying rear-edge populations. These populations are expected to be the oldest populations across a species' range, which can be tested through phylogeographic analyses, with rear-edge populations basal or early diverged relative to populations in the expanded range. Rear-edge populations should also occur within former refugia (stable or receding edges) or near them (trailing edges). Refugia can be identified through species distribution model hindcasting, a technique to predict past distributions [13], or from fossil and pollen data in species leaving paleobotanical records [13,67–69]. Stable and receding edges can then be distinguished from trailing edges by testing whether the present-day rear edge overlaps with former refugial areas. Receding and stable edges may be best distinguished by evaluating decline, for example, through demographic inference or drift load.

While studies frequently integrate some aspects of phylogeography to characterize rear-edge populations, it is less common to explicitly assess their occurrence relative to putative refugia, with many relying on geographic position or occurrence at the warmer range limit (see Supplementary Information online). Moreover, studies evaluating evolution at the rear edge generally do not distinguish among rear-edge types, therefore conflating fundamentally different demographic histories and likely contributing to the apparent unpredictability of rear-edge evolution. For example, most studies exploring patterns of diversity have focused on species whose rear-edge populations occur in former refugia (see Supplementary Information online). Yet about half of these species show lower within-population diversity than central portions of the range in at least one rear edge (22/47). If these are receding rather than stable rear edges, the insight provided by identifying the type of rear edge would afford greater accuracy. Explicitly distinguishing rear-edge type will allow the development of a more flexible framework of expectations and interpretation of genetic patterns in rear-edge populations.

Stable, receding, and trailing rear edges may also be leveraged as models of evolutionary responses to climate warming, with stable edges representing persistence and receding and trailing edges representing demographic decline. However, trailing edges are understudied, with only two rear-edge studies identified in the literature where species were not present in refugia [12,41], severely limiting our understanding of evolutionary outcomes associated with range shifts out of refugia. Combined with the lack of explicit distinction among rear-edge types, this biases the study of rear edges toward systems that have persisted relative to those that have declined. The limited number of studies focused on trailing edges may be partly due to a lack of recognition that range edges outside of refugial areas may be rear edges. In addition, the perception that stable rear edges hold greater value for conservation projects and ecological and evolutionary research [11] may further bias the choice of study systems. Future research should sample trailing edges and leverage them as models of decline, complementing existing studies on receding and stable edges.

Context matters: Identifying factors driving rear-edge evolution

Our limited ability to predict evolutionary outcomes to past warming in rear edges, including no clear link to organism type or biogeographical area, suggests that they are likely the product of local ecological, climatic, and genetic contexts. Identifying the factors within those contexts that led to persistence in stable edges or drove decline under past climate change in what are now receding and trailing edges can offer practical approaches to understanding the apparent unpredictability of rear-edge evolution. These distinct demographic histories likely reflect different outcomes of selection under past warming, with persistence in stable edges linked to successful adaptation, while population decline in receding and trailing edges likely reflects a lack of adaptation (Box 2).

Factors driving success or failure of adaptation to postglacial warming at the rear edge are expected to reflect general processes affecting adaptation at range limits [70], such as a lack of standing genetic variation, small initial population size favoring genetic drift [50,58,71], and life history trade-offs [72], among others. The outcome of these processes will be influenced by interactions with environmental and ecological factors, such as the speed and magnitude of past climate change or biotic interactions. For example, rapid climate change or anthropogenic land use [73] could exacerbate limits to adaptation, and outpace the capacity of refugial populations to adapt, while buffering effects of local microrefugia may facilitate persistence [13]. Further insight into the factors that enabled or constrained past adaptation may be gained from the large body of ecological rear-edge research. These factors have yet to be integrated into our understanding of why some refugial populations persisted under postglacial warming while others declined. Patterns of selection and how they affect adaptation or maladaptation at the rear edge, remains largely unexplored.

Theoretical models and simulation studies represent a first step toward identifying potential drivers of evolution at the rear edge. These approaches have been conducted to investigate the interaction between ecological and evolutionary processes underlying range expansion, particularly the roles of genetic drift, adaptation and their interactions in shaping leading edges [74–78]. Extending these frameworks to model eco-evolutionary dynamics at the rear edge could provide powerful insights. Predictions from these models can then be tested and refined by fitting empirical genetic or phenotypic data.

Potential drivers of persistence or decline may also be identified through empirical comparisons of rear edges with different evolutionary outcomes and with different histories of persistence or decline under past warming. In particular, species exhibiting heterogeneity among rear edges across multiple glacial refugia can serve as model systems to explore contextual factors driving one or another evolutionary outcome. For example, differences in genetic patterns between former refugia have been linked to the strength of past climate change, with stronger change associated with lower diversity [63]. A comparative focus will allow the identification of cases where distinct responses among rear edges provide insight into the underlying drivers of observed patterns.

Drivers of persistence or decline may also be identified by a deeper exploration of the mechanisms underlying distinct evolutionary outcomes and their functional consequences. Neutral genetic patterns, as assessed by most of the reviewed studies, offer valuable insights into the demographic and evolutionary history of the rear edge, but only through indirect evidence. Key questions remain: does high diversity confer high adaptive potential, does low diversity necessarily reflect drift, and do such signatures of drift translate to high drift load? Integrating targeted experimental approaches to explicitly address drift load [48,79], local adaptation [29,80,81] and their effects on responses to future warming [82,83] can address these gaps. Recent innovations in genome-wide techniques to investigate demographic history [84], range-wide patterns of adaptive genetic variation [85,86], genomic vulnerability due to drift [47,50], and the consequences of evolutionary legacies for adaptive potential [87–92] move molecular genetic studies beyond documenting patterns of diversity to addressing underlying evolutionary mechanisms and their functional consequences. This broader set of approaches will help determine the legacies of evolutionary change in rear-edge populations and improve predictions of vulnerability or resilience under future warming.

Concluding remarks

Rear-edge populations provide natural laboratories to study evolutionary processes that have shaped species' responses to past climatic oscillations as well as their predicted responses to ongoing climate change. Our review of the last 21 years of research on rear-edge evolution revealed three equally likely patterns in response to past warming: the maintenance of ancestral genetic diversity, signatures of strong genetic drift, and adaptation to climate change. These distinct outcomes, independently and in combination, provide robust expectations for future exploration of evolution in rear-edge populations (see Outstanding questions). Through such studies, rear edges may serve as models for disentangling the roles of genetic diversity, demographic history, and selection in shaping range dynamics and species' responses to changing climates – past, present, and future.

The diversity of outcomes at the rear edge in response to past warming reveals new challenges, as it is unclear why species experience specific evolutionary outcomes or combinations of outcomes. This unpredictability may be resolved with the recognition that rear edges may be stable, receding or trailing. Employing comparative approaches across these rear-edge types will illuminate drivers of evolutionary history. Further research should also expand experimental and analytical techniques for holistic assessments of evolutionary outcomes. Finally, exploration of the ecological and genetic context for response to ongoing climate change in rear edges is key to identifying the conservation needs of these populations, their potential as sources of adaptive genetic diversity, and their vulnerability to future climatic oscillations (see Outstanding questions).

Outstanding questions:

- Are there specific patterns of past climate change that tend to be associated with stable, receding and trailing rear edges?
- Do eco-evolutionary models suggest different microevolutionary processes underlie stable, receding and trailing rear edges?
- If stable rear-edge populations are well adapted, why are these populations limited in size and density in rear edge habitats?
- What drives decline in trailing and receding rear edges? Do they lack adaptation to local environments or harbor drift load?
- Is genetic diversity at the rear edge associated with demographic stability and/or local adaptation?
- Does strong local adaptation to rear edge climates indicate further adaptive potential to warming? Or, on the flip side, is it associated with an exhaustion of adaptive potential?
- Is a history of strong genetic drift associated with low fitness through drift load and restricted adaptive potential to future climate change?

Text Boxes:

Box 1: Defining the rear-edge continuum: stable, receding and trailing rear edges

Rear edges come in many forms reflecting different responses to past warming (Fig. I). For ease of study, we identify three distinct types of rear edges within this continuum, expanding the original framework set by Hampe and Petit [11]. Distinguishing these three edge types is key to setting expectations for evolutionary outcomes (Box 2), assessing conservation needs and predicting evolutionary potential of rear-edge populations (Box 3).

Stable rear edges represent cases where historic refugial populations have persisted in place and remained demographically stable under past warming. Populations in stable rear edges are direct descendants of refugial populations, located in refugial areas and show evidence of demographic stability through time.

Receding rear edges are direct descendants of refugial populations that have declined in number and size following habitat degradation and rarefaction caused by postglacial warming. Populations in receding rear edges are expected to be small, isolated, overlap with former refugia and show evidence of demographic decline.

Trailing rear edges represent cases where refugial populations became extinct, and contemporary rear-edge populations are descendants of early expansion out of refugia, often those closest to refugia at the warmer range limit. Extinction in former refugia was likely due to habitat degradation from past warming leading to contraction at the rear edge and a range shift. Trailing rear-edge populations may show evidence of demographic decline if habitat degradation and contraction are ongoing.

Over long periods of time, individual rear edges are likely to transition among these three types, from stable, through receding to trailing edges if environments become increasingly less suitable. As such, these categories reflect the current condition rather than an inherent feature of a population.

Box 2: Evolutionary outcomes to past warming expected at the rear edge.

Three possible evolutionary outcomes to warming at the rear edge were derived from theory and are often assessed in empirical studies (Fig. 2; see literature review).

1. Rear edges are reservoirs of genetic variation within and among populations. Rear edges may have elevated within-population genetic diversity relative to the expanded range [13] as expansion often involves bottlenecks and **founder events** that reduce diversity [93]. Range-edge populations are also generally sparse [17,20], with long-term isolation at the rear edge leading to greater genetic differentiation among rear-edge populations than expected in the younger expanded range [11]. This differentiation will be greater if species persisted in multiple refugia (e.g., [66,94–98]), as individual refugia likely have distinct histories, including potentially harboring populations through earlier glaciations [99]. Population genetic estimates of diversity and differentiation, typically derived from neutral molecular markers, are used to assess whether rear edges are reservoirs of genetic variation.

2. Rear-edge populations are exposed to drift and are fragile. Gradual habitat decline and fragmentation under postglacial warming [11] are expected to lead to smaller populations and greater isolation at the rear edge [17,20], resulting in strong genetic drift [100–102]. Strong drift will erode genetic diversity within populations and exacerbate genetic differentiation between them [17,103]. Studies assess patterns consistent with drift in the structure of neutral genetic markers [32–36]. Genetic drift is also expected to reduce fitness as mildly deleterious mutations increase in frequency, resulting in drift load [44–46,104]. Drift load directly estimates genetic drift with fitness reduction assessed using hybrids [48] and deleterious mutations quantified with molecular techniques [47].

3. Rear edges have unique adaptations following selection under past warming. Rear-edge populations occur in distinct and warmer habitats than those in the expanded range [16] and often exhibit unique phenotypes (e.g., [26,51,52]). This suggests that rear edges have experienced substantial adaptation as a result of strong selection under continuous postglacial warming [29,81]. This local adaptation likely exceeds that in the expanded range [29,50,58] where population spread tracked suitable habitats. Local adaptation is assessed through transplant and climate manipulation experiments [29,80,81], as well as genomic approaches that associate allele frequencies with environmental variation [85,86,92].

Expectations for distinct edge types: we expect stable rear edges to harbor more genetic variation and less drift load than receding or trailing rear-edge populations. The persistence of stable rear edges despite warming climates has likely been facilitated by adaptation, whereas the decline and loss of refugial populations in receding and trailing edges suggest inadequate adaptation [10,57].

Box 3: Implications of evolutionary outcomes to past warming for future climates

Legacies of past evolutionary processes may influence the response of rear-edge populations to future climate change.

1. Unique diversity is at risk at rear edges and may be crucial for persistence under future climates. Rear edges may retain ancestral diversity that has been lost elsewhere in the range. Assessing the risk of decline at the rear edge under future warming is therefore crucial, as their loss may disproportionately reduce a species' overall genetic diversity. The higher diversity may be linked to higher resilience, including greater evolutionary potential under future warming. Whether diversity in rear edges is adaptive under future warming is, however, uncertain.

2. Strong genetic drift may precipitate extinction at warmer range limits. Genetic drift makes small rear-edge populations particularly vulnerable, as drift load reduces fitness [44–46], and is exacerbated by environmental stress such as warming climates [83]. Drift also reduces adaptive capacity by eroding genetic diversity and reducing the efficacy of positive selection [57,58,71,77]. Together, drift may reduce population fitness below critical thresholds [104,105].

3. Local adaptation may be a double-edged sword under future warming. Adaptation to past warming at the rear edge could have selected for alleles that confer an advantage under future warming, rendering these populations less sensitive to future change than other parts of the range [5,37,51]. As such, these populations could serve as a genetic resource for conservation or restoration projects to improve climate resilience in expanded portions of the range [37,106–108]. In particular, they are expected to be important for implementing assisted migration strategies [5,106]. However, strong selection under past warming may reduce adaptive potential to future change [109,110], as such rear-edge populations may be more vulnerable to continued warming.

Implications for distinct edge types: Stable edges, likely to have high diversity and successful adaptation to past warming, may be more resilient to future climate change than receding and trailing edges that have experienced decline under past warming and may be particularly vulnerable due to high drift load, low diversity and therefore low adaptive potential.

Author contributions

All authors contributed to the conceptualization of the review. A.P. and O.J.K. conducted the literature review. A.P. and L.F.G. wrote the manuscript.

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Declaration of interests

The authors declare no competing interests.

Glossary:

Adaptive potential: the capacity of a population to evolve in response to selection, for example, due to a shift in climate; requires genetic variation.

Bottlenecks and founder events: sharp reductions in population size (bottlenecks) or establishment of new populations by a few individuals (founder events), both lead to reduced genetic diversity and altered allele frequencies.

Climate change: long-term shifts in temperature, precipitation, or other climate factors, driven by natural processes or human activities.

Drift load: reduction in population fitness due to the accumulation of deleterious mutations under genetic drift.

Fitness: the survival and reproductive success of an individual or population, often measured as its contribution of offspring to the next generation.

Genetic differentiation: difference in genetic makeup between populations.

Genetic diversity: variation in genetic makeup within a population.

Genetic drift (drift): change in allele frequency due to chance that reduces genetic diversity within populations and increases differentiation among populations; especially strong in small populations.

Last Glacial Maximum (LGM): the most recent time when ice sheets reached their maximum extent (~ 20,000 years ago).

Leading edge: region of a species' geographic range where populations have most recently established during range expansion.

Local adaptation: process by which populations evolve in response to selection to improve fitness in their local environment.

Postglacial warming: the rise in global temperatures following the LGM, leading to ice-sheet retreat, climate change and large-scale species range shifts.

Range contraction: decrease in the size of a species' distribution by population loss at range limits, often due to changes in environmental conditions (abiotic and / or biotic factors).

Range expansion: colonization of populations in previously unoccupied areas, typically at the leading edge of the range.

Range limit: the edge of a species' geographic distribution.

Rear edge: a region of a species' range composed of populations that are descendants of historic refugial populations, often the warmer range limit.

Receding rear edge: a type of rear edge where populations are direct descendants of refugial populations, occur in refugial areas, but are declining in size or number due to warming.

Refugia (glacial): unglaciated areas that provided suitable habitats for species to persist during glacial periods.

Refugial population: historic populations that occurred in refugia during the LGM.

Resilience: the capacity of a population to recover from perturbations.

Species distribution: the geographic arrangement of populations of a species across space.

Stable rear edge: a type of rear edge where populations are direct descendants of refugial populations, occur in former refugial areas, and have been demographically stable since the LGM.

Temperate species: species whose distributions are centered in temperate climate zones and therefore have been strongly affected by past glacial cycles.

Trailing rear edge: a type of rear edge where populations are the earliest descendants of those established in the expansion out of refugia (no populations remain in refugia); populations may be stable but are often in decline.

Vulnerability: the susceptibility of a population to decline or extinction due to stochastic demographic changes or due to environmental change.

Figures:

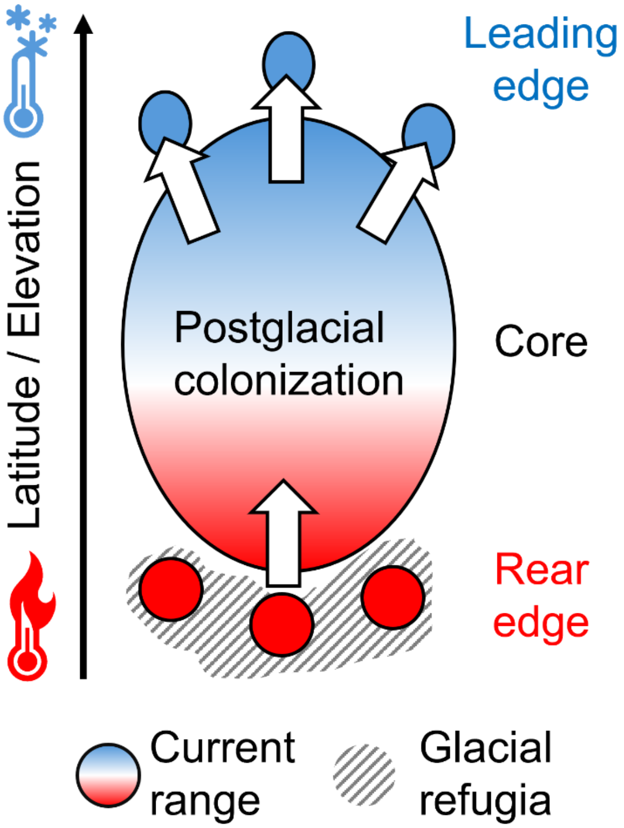

Figure 1: Postglacial range expansion results in rear and leading range edges. Many temperate species were constrained in lower latitude and elevation refugia during the LGM. After the LGM, as the Earth warmed, these species' ranges expanded toward higher latitudes and elevations. As a result, the contemporary cooler range limit often coincides with the range expansion front, termed the leading edge. Whereas the warmer range limit, or rear edge, is often composed of descendants of refugial populations. LGM: Last Glacial Maximum

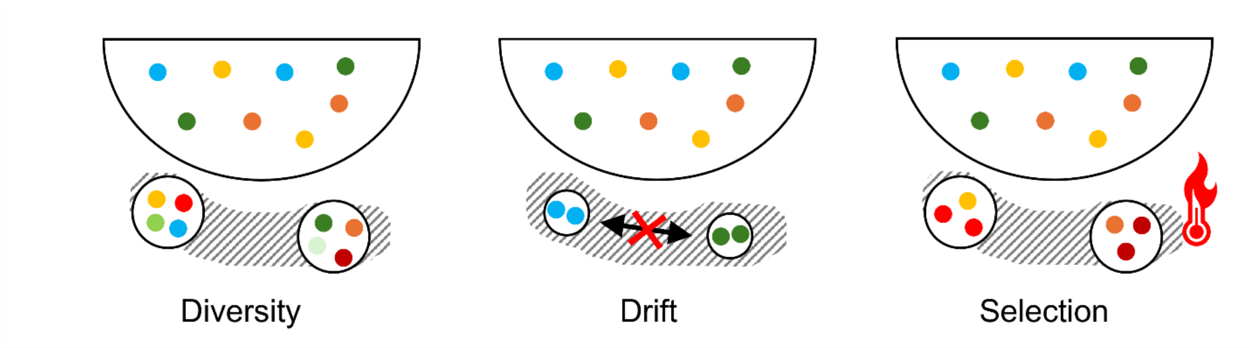

Figure 2: Three main evolutionary outcomes expected at contemporary rear edges. Rear-edge populations may represent reservoirs of *diversity* within and between populations due to a history of persistence in glacial refugia, reflect strong genetic *drift* following a history of decline under past climate change, or show high local adaptation in response to strong *selection* imposed by past climate warming (Box 2).

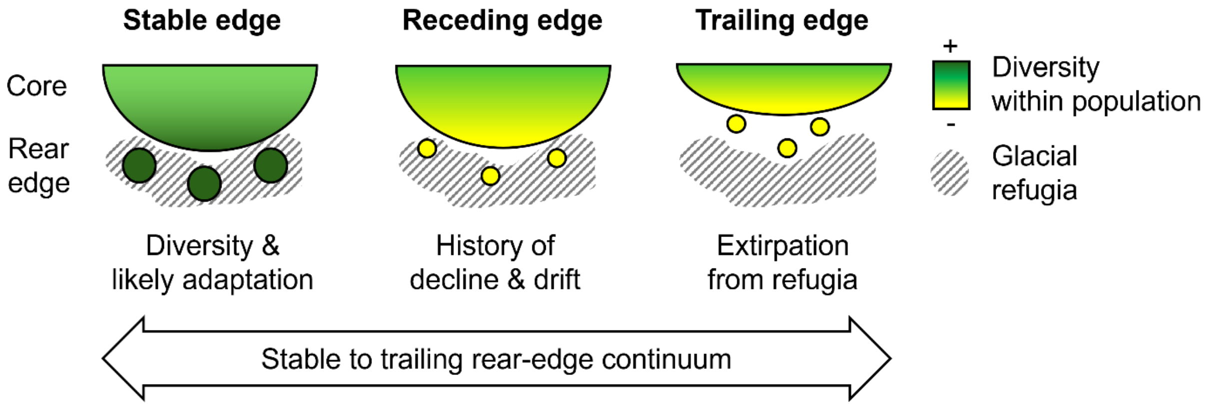

Figure I: The stable – trailing rear-edge continuum. The link between a history of decline or persistence under past warming and genetic patterns at the rear edge. **Stable edges** consist of populations that persist in former glacial refugia and typically have high diversity relative to the rest of the range. **Receding edges** consist of declining refugial populations, with decreases in population size and drift associated with reductions in genetic diversity. **Trailing edges** are outside of former refugia and consist of populations that are the earliest descendants of postglacial range expansion and may be experiencing decline due to climate stress and genetic drift.

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Supplemental Information

Revisiting evolution at the rear edge

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Table S1A. List of species in testing for signatures of higher diversity or drift at the rear edge.

Kingdom	Organism type	Common name	Species name	Location	Gradient	Rear edge diversity	Rear edge differentiation	Other signatures	Overlap with refugia	Study
Animal	Insect	Meadow grasshopper	*Chorthippus parallelus*	Europe	Latitude	Higher †	-	-	Inferred	[S1]
Animal	Insect	Scotch argus	*Erebia aethiops*	Europe	Latitude	Higher	Higher	-	-	[S2]
Animal	Mollusk	Owl limpet	*Lottia gigantea*	N America	Latitude	Higher	Higher	-	Tested	[S3]
Animal	Insect	Apollo butterfly	*Parnassius apollo*	Europe	Elevation	Lower	Higher	Stronger decline	Tested	[S4]
Animal	Insect	Large blue	*Phengaris arion*	Europe	Latitude	Lower	Higher	-	Inferred	[S5]
Animal	Mamal	Gray long-eared bat	*Plecotus austriacus*	Europe	Latitude	Higher	Higher	-	Tested	[S6]
Animal	Reptile	Common wall lizard	*Podarcis muralis*	Europe	Latitude	Higher	Lower	-	Tested	[S7]
Animal	Bird	Western capercaillie	*Tetrao urogallus*	Europe	Latitude	Lower	Higher	Bottleneck	Inferred	[S8, S9]
Animal	Reptile	Common lizard	*Zootoca vivipara louislantzi*	Europe	Elevation	Similar	Higher	Higher FIS	Inferred	[S10]
Plant	Coniferous tree	Silver fir	*Abies alba*	Europe	Latitude	Higher	-	-	Tested $	[S11]
Plant	Deciduous tree	Black alder	*Alnus glutinosa*	Europe	Latitude	Higher & lower	-	-	Inferred	[S12]
Plant	Herb	Rock cress	*Arabidopsis lyrata*	N America	Latitude	Lower	Higher	Higher drift load	Inferred	[S13–S15]
Plant	Herb	Silverweed	*Argentina anserina*	N America	Elevation	Higher	Lower	Higher Ne, lower FIS	-	[S16]
Plant	Herb	-	*Bupleurum euphorbioides*	Asia	Latitude	Lower	Lower	Bottleneck	Tested	[S17]
Plant	Herb	Black sedge	*Carex nigra*	Europe	Latitude	Higher	Lower	-	Inferred	[S18]
Plant	Herb	Princes' pine	*Chimaphila umbellata*	Asia	Latitude	Lower	Higher	-	Inferred	[S19]

Kingdom	Organism type	Common name	Species name	Location	Gradient	Rear edge diversity	Rear edge differentiation	Other signatures	Overlap with refugia	Study
Plant	Red macroalgae	Irish moss	*Chondrus crispus*	Europe	Latitude	Higher & lower	-	-	Tested #	[S20]
Plant	Seagrass	Little Neptune grass	*Cymodocea nodosa*	Europe	Latitude	Higher	-	-	Inferred	[S21]
Plant	Herb	Eight petal mountain-avens	*Dryas octopetala*	Circumboreal	Latitude	Lower	Higher	-	Inferred	[S22, S23]
Plant	Herb	Grassy bells	*Edraianthus tenuifolius*	Europe	Latitude	Higher	-	-	Inferred	[S24]
Plant	Herb	Irish spurge	*Euphorbia hyberna*	Europe	Latitude	Higher	-	-	Tested	[S25]
Plant	Deciduous tree	European beech	*Fagus sylvatica*	Europe	Latitude & elevation	Higher	Higher	No bottleneck	Tested $	[S26]
Plant	Deciduous tree	Narrow-leaved ash	*Fraxinus angustifolia*	Europe	Latitude	Lower	-	-	Inferred	[S27]
Plant	Deciduous tree	European ash	*Fraxinus excelsior*	W Asia	Latitude	Higher	Similar	-	Inferred	[S28]
Plant	Brown macroalgae	Horned wrack	*Fucus ceranoides*	Europe	Latitude	Higher	Higher	-	Inferred	[S29]
Plant	Brown macroalgae	Saw wrack	*Fucus serratus*	Europe	Latitude	Lower	-	-	Inferred	[S30]
Plant	Brown macroalgae	Bladder wrack	*Fucus vesiculosus*	N Atlantic	Latitude	Lower	Higher	-	Tested	[S31]
Plant	Red macroalgae	Worm Wart Weed	*Gracilaria vermiculophylla*	China sea	Latitude	Higher	Lower	-	Inferred	[S32]
Plant	Herb	Amur Daylily	*Hemerocallis middendor*	Asia	Latitude	Lower	Higher	Past decline	Tested	[S33]
Plant	Herb	lizard orchid	*Himantoglossum hircinum*	Europe	Latitude	Higher	-	-	Inferred	[S34]
Plant	Herb	Baltic rush	*Juncus balticus*	Europe	Latitude**	High & low	-	-	Tested	[S35]
Plant	Brown macroalgae	Oarweed	*Laminaria digitata*	N Atlantic	Latitude	Higher	Lower	-	Tested $	[S36]

Kingdom	Organism type	Common name	Species name	Location	Gradient	Rear edge diversity	Rear edge differentiation	Other signatures	Overlap with refugia	Study
Plant	Brown macroalgae	Golden kelp	*Laminaria ochroleuca*	N Atlantic	Latitude	Higher	Higher	-	Tested $	[S37]
Plant	Herb	Dutchman's pipe	*Monotropa hypopitys*	Europe	Latitude	Higher	-	-	Tested	[S38]
Plant	Herb	Sidebells wintergreen	*Orthilia secunda*	Europe	Latitude	Higher	-	-	Tested	[S38]
Plant	Brown macroalgae	Chanelled wrack	*Pelvetia canaliculata*	N Atlantic	Latitude	Higher & lower	-	-	Tested	[S39]
Plant	Seagrass	Torrey's surfgrass	*Phyllospadix torreyi*	N America	Latitude	Lower	Higher	-	Tested	[S40]
Plant	Brown macroalgae	Crayweed	*Phyllospora comosa*	Australia	Latitude	Lower	Higher	-	-	[S41]
Plant	Coniferous tree	European spruce	*Picea abies*	Europe	Latitude*	Higher & lower	Higher & lower	No bottleneck	Inferred & tested	[S42, S43]
Plant	Coniferous tree	Maritime Pine	*Pinus pinaster*	Europe	Latitude	Lower	Higher	-	Inferred	[S44]
Plant	Coniferous tree	Scots pine	*Pinus sylvestris*	Europe	Latitude	Lower	Higher	-	Tested $	[S45]
Plant	Deciduous tree	Quaking aspen	*Populus tremuloides*	N America	Latitude	Lower	Higher	-	Inferred	[S46]
Plant	Deciduous tree	Japanese wingnut	*Pterocarya rhoifolia*	Asia	Latitude	Higher	-	-	Tested	[S47]
Plant	Herb	Creeping alkali grass	*Puccinellia phryganodes*	Europe	Latitude	Lower	Similar	Lower Ne	Tested #	[S48]
Plant	Deciduous tree	Algerian oak	*Quercus canariensis*	N Africa	Latitude**	-	-	Low Ne	Inferred	[S49]
Plant	Deciduous tree	Portuguese oak	*Quercus faginea*	N Africa	Latitude**	-	-	Low Ne	Inferred	[S49]
Plant	Deciduous tree	Pedunculate oak	*Quercus robur*	Europe	Latitude	Mixed	Higher	-	Inferred	[S50]
Plant	Brown macroalgae	Furbellow	*Saccorhiza polyschides*	N Atlantic & Mediterranean	Latitude	Higher †	Higher †	-	Tested	[S51]

Kingdom	Organism type	Common name	Species name	Location	Gradient	Rear edge diversity	Rear edge differentiation	Other signatures	Overlap with refugia	Study
Plant	Shrub	Halberd willow	*Salix hastata*	Europe	Latitude**	High & low	-	-	Tested	[S35]
Plant	Shrub	Dwarf willow	*Salix herbacea*	Europe	Latitude	Lower	Higher	-	Inferred	[S52]
Plant	Brown macroalgae	-	*Sargassum thunbergii*	Asia	Latitude	Lower	Lower	-	Tested	[S53]
Plant	Shrub	-	*Sibiraea angustata*	Asia	Latitude	Higher	similar	Stable Ne	Inferred	[S54]
Plant	Coniferous tree	Japanese thuja	*Thuja standishii*	Asia	Latitude	Lower	Higher	Lower Ne	Tested	[S55]
Plant	Vine	Arizona grape	*Vitis arizonica*	N America	Latitude	-	-	Lower drift load	Tested	[S56]
Plant	Seagrass	Eelgrass	*Zostera maritima*	Europe	Latitude	Lower	Higher	-	Inferred	[S57]

For each species, *gradient* indicates the axis of comparison between the rear edge and the expanded range. For some species, only rear-edge populations were assessed and compared with populations elsewhere in prior studies (*) or not at all (**). Patterns of genetic *diversity* and *differentiation* are reported for the rear edge compared to the range core. Some species showed mixed patterns within a rear edge, divergent patterns between distinct rear edges (higher & lower) or showed the same pattern to varying degrees (†). For each species, we report whether overlap between contemporary populations and former refugia were tested or inferred. Overlap was assessed through SDM hindcasting, or from comparison with fossil pollens or macrofossils. Some studies report locations of refugia from prior studies ($). If the location of refugia was not reported by the authors, we inferred overlap based on whether rear-edge populations occur in known refugial areas. In most cases, contemporary populations overlapped with former refugia, with two exceptions where populations occurred outside refugia (#). Cases where overlaps could not be inferred are left blank.

Table S1B. List of species testing for signatures of strong selection and/or local adaptation at the rear edge

Kingdom	Organism type	Common name	Species name	Location	Gradient	Signature of selection	Overlap with refugia	Study
Plant	Herb	Buckler-mustard	*Biscutella laevigata*	Europe	Elevation	Divergent selection	-	[S58]
Plant	Brown macroalgae	Bladder wrack	*Fucus vesiculosus*	Europe	Latitude	Higher local adaptation	Tested	[S59]
Plant	Deciduous tree	Lenga beech	*Nothofagus pumilio*	S America	Elevation	Higher local adaptation	-	[S60]
Plant	Deciduous tree	Balsam poplar	*Populus balsamifera*	N America	Latitude	Higher turnover of climate-adaptive alleles	Tested	[S61]
Plant	Vine	Arizona grape	*Vitis arizonica*	N America	Latitude	Higher number of climate-adaptive alleles	Tested	[S56]
-	-	-	*135 species*	-	Latitude & elevation	Higher local adaptation	-	[S62]

For each species, *gradient* indicates the axis of comparison between the rear edge and rest of the range. Signatures of selection and/or local adaptation are reported for the rear edge compared to the range core. For each species, we report whether overlap between contemporary populations and former refugia were tested or inferred. In all cases, contemporary populations overlapped with former refugia. Cases where overlap could not be inferred were left blank.

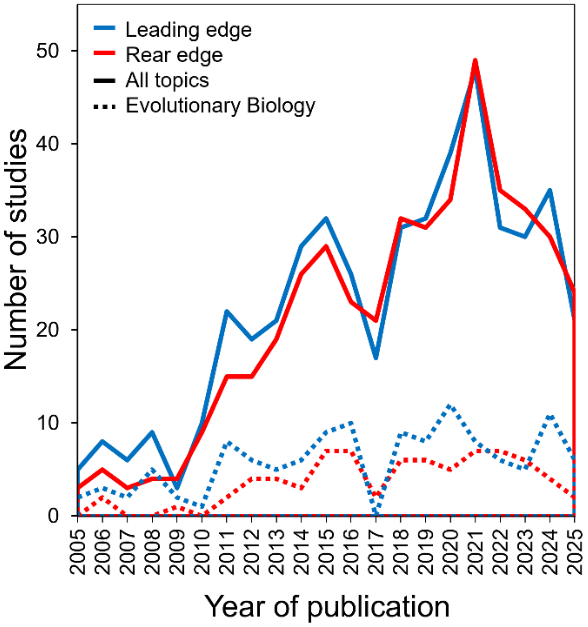

Figure S1: Review of research on range edges based on a literature search over the period of 2005 - 2025. The total number of studies focusing broadly on range edges is represented in solid lines, dashed lines represent the subset of studies categorized under "evolutionary biology". Literature focusing on leading edges is depicted in blue, rear edges in red, and both edges added to the count of each type.

Method S1:

Rear-edge literature search

We conducted a literature search to identify studies on the rear edge of species distributions using the Web of Science platform (https://www.webofscience.com, accessed 31/12/2025). The search was restricted to studies published between April 2005 and December 2025, representing 21 years of literature since the foundational review by Hampe and Petit in 2005 [S63]. The query for studies on the rear edge included either "rear edge" or "trailing edge" in the title, abstract or keywords ("topic" field), and was found in at least one of the following Web of Science categories: Ecology, Forestry, Biodiversity Conservation, Plant Sciences or Evolutionary Biology. These categories were used to restrict studies to those associated with range limits (omitting spurious results, e.g. from engineering). This initial search resulted in 371 studies with the keyword "rear edge", 357 with the keyword "trailing edge" (34 overlapping). We performed a similar search to find studies focusing on the leading edge, using as topics "leading edge" (2154 studies) or "expansion edge" (1373 studies, with 646 overlapping), in the same categories as above.

The results of these initial searches were pruned to keep only research publications in journals (Publication type: "J" & Document type: "Article", i.e. excluding reviews, book chapters, editorial material, etc.). Some research articles were categorized as reviews and were manually reassigned to the correct category. We then removed duplicates within rear and leading-edge searches and manually excluded studies that were not relevant to leading or rear edges broadly defined. Pruning was performed by assessing the relevance of studies based on study title, or for studies with ambiguous titles, by reading the abstract. Excluded studies typically included the search keyword in a different context (e.g. edge effects, habitat edges or ecotones, urban expansion). We also excluded studies focusing on postglacial colonization dynamics (e.g.

"leading-edge" model of colonization) but not the actual range limit, studies focusing on a range limit without clear information about it being leading or rear edge, and studies focusing on range expansion in a different context than addressed in this review (e.g., biological invasions, re-introductions, pest outbreaks, or range dynamics in theoretical, simulation or experimental evolution frameworks). Finally, some studies were manually re-assigned to the correct edge. For example, some rear-edge studies showed up by searching for "leading edge" and vice-versa, and some studies assessed both edges but were identified only for one type of edge. Finally, two relevant studies were added from personal knowledge [S4, S43]. This resulted in a final list of 716 studies, with 242 studies focusing on the rear edge, 272 on the leading edge, and 202 dealing with both. Of these, 159 studies belonged to the Web of Science category "Evolutionary Biology," with 35 on the rear-edge, 84 leading-edge, and 40 on both edges.

Empirical support of evolutionary outcomes

We then evaluated all 444 studies on the rear edge (242 rear edge + 202 dealing both edges) to identify those that report patterns of genetic diversity, drift, selection and local adaptation. Some studies supported multiple patterns. We limited inclusion to those where rear edge populations were compared to the rest of the range (core or whole range, in the study itself, or using data from prior studies), omitting those that focused on the rear edge only. One exception was Jimenez-Alfaro et al. 2016 [S35], as it compared among rear edges with different postglacial histories. We further excluded studies with unclear results, where the designation of rear-edge populations was unclear, and studies conducted on species that were heavily influenced by recent human activity (e.g. re-introduction, admixture between natural and domestic populations, etc.). In total, 18 studies were excluded. Three additional studies were included that supported a history of drift at the rear edge by assessing demographic patterns [S49] or signatures of drift load [S14, S15]. This resulted in a total list of 61 rear-edge studies across 58 species [Table S1; S1–S61], and one meta-analysis assessing latitudinal patterns over 135 species [S62].

Our search strategy may not have captured the full scope of published knowledge on rear-edge evolution. For example, relevant data may be embedded in range-wide phylogeographic studies that do not explicitly identify rear-edges and may thus not have been included in the Web of Science search. Conversely, only a small subset of the studies reviewed here [S7, S8, S13, S45] were included in broader reviews of genetic patterns at range limits [S64, S65]. This is likely due to differences in focus, as previous reviews emphasized the center–periphery hypothesis, not the rear edge. The lack of overlap underscores the limited recognition of rear-edge populations in synthetic literature.

Of the studies that assessed diversity or drift, we scored patterns of within-population genetic diversity as well as differentiation among populations (rear edge vs central populations: higher, lower, similar, or mixed patterns). These studies employed a wide range of molecular markers, but most rely on a limited number of neutral markers (e.g. single sequence repeats, small sets of short nuclear or plastid sequences). Few of these studies have evaluated genome-wide patterns of genetic variation [S3, S4, S14, S16, S41, S44, S56]. Studies employed a variety of metrics to assess genetic variation, such as heterozygosity, allelic richness, and nucleotide diversity. Differentiation among populations was typically evaluated using F_{ST} and related statistics, AMOVA, and other measures of among-population structure. We also recorded any additional supporting results such as demographic patterns, inbreeding, or estimates of drift load. In addition, for each species, we assessed whether the study tested for an overlap of contemporary rear-edge populations with potential glacial refugia. For species where past distributions, i.e.

glacial refugia, were not explicitly addressed (about half of the studies), we compared the present-day distribution to known glacial refugia associated with similar present-day distributions in other studies (e.g. Iberian, Italian and Balkan peninsulas in Europe, Hyrcanian forests in Western Asia, the gulf coast in the eastern U.S.). Most studies evaluating evolution at the rear edge appear to have been conducted on stable or receding rear edges. Among studies that explicitly evaluate location relative to refugia, almost all report an overlap (28/29 species, Suppl. Info). For studies where this is not evaluated, rear-edge populations often broadly overlap with areas known to be refugia in other species (26/31 species). In contrast, trailing edges are understudied. We found only two studies where rear-edge populations are found outside of refugia. In one, there were two distinct rear edges, one overlapping with former refugia and the other at higher latitudes than presumed refugia, i.e., a trailing edge [S20]. In the other study, the contemporary range is in areas covered by ice during last glaciation [S48], suggesting the loss of refugial populations consistent with a trailing edge.

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