Title: Revisiting evolution at the rear edge

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Highlights:

- Rear-edges, relict populations from glacial refugia, may offer key insights to study evolution under climate warming, yet remains underused as models.
- Recent theoretical and empirical work reveals three equally likely evolutionary trajectories at the rear edge under past warming – maintenance of genetic diversity, loss of diversity through drift, and strong local adaptation – complicating predictions of evolutionary potential and response to future climates.
- Significant gaps remain in understanding why species follow one evolutionary trajectory over another. This may be resolved through comparative studies of rear edges with differing evolutionary histories.
- Trailing edges, rear edges where refugial populations have been lost, are rarely studied, despite their potential as models to study population extinction under climate change.

Abstract:

Rear-edge populations occur at species' warmer range limits, with many still occupying glacial refugia. They offer valuable insights into evolution under changing climates yet are underused as models. From two decades of research, we identify three equally likely evolutionary patterns in rear edges: high levels of 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 avenues to address these gaps, leveraging rear edges as models to better understand evolution under climate change and improve predictions of species' responses.

Rear edges are natural laboratories of evolution under changing climates

A major focus of current research is to understand how species' distributions are altered by ongoing climate change [1–3]. Temperate species are predicted to track changes in climate by migrating towards 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 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 comprised of relict populations from the last glaciation (Fig. 1A, [11]), serve as examples of evolution in response to past climate change due to their long histories of postglacial warming. During the last glaciation, most temperate species retreated to unglaciated refugia at low latitudes and elevations where climates were mild [12]. After the Last Glacial Maximum (LGM, ~20kya, [13]), as the Earth warmed and new habitats became available, these species colonized higher latitudes and elevations, tracking the retreat of the ice sheet ("leading edge", Fig. 1A, [7,8]). In some cases, refugial populations persisted more or less in place while species expanded their range, and now constitute a "stable" rear edge (*sensu* [11]). In other cases, refugial populations were extirpated as species' ranges shifted to track changing climates, with populations at the contracting warmer range limit representing "trailing" rear edges [11]. Therefore, rear-edge populations are often the closest relatives of refugial populations. Stable and trailing rear edges, while sharing a common origin, are likely to have been shaped by different evolutionary processes.

Rear-edge populations provide an ideal framework for elucidating the role of past eco-evolutionary processes in shaping contemporary genetic patterns across species ranges. The importance of rear edges for ecological and evolutionary research was first highlighted in 2005 in the 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 between populations in the range core and stable rear-edges. Building upon these expectations, and drawing on current evolutionary theory and empirical research on range limits, we develop a framework of three evolutionary processes expected at the rear edge and their resulting genetic patterns (Box 1). These reflect different evolutionary outcomes to past warming (Fig. 1C), and yield the following predictions, (1) Rear edges may be hotspots of genetic diversity because of their history of persistence in former refugia. (2) Alternatively, habitat degradation associated with long-term postglacial warming may have led to population contraction and decline, exposing rear-edge populations to strong genetic drift with associated reductions in genetic diversity and fitness. (3) Finally, long-term persistence in the face of postglacial warming suggests rear-edge populations may have experienced high local adaptation under warming climates. Each outcome has distinct implications for the fate of rear edges under future warming (Box 2). Determining the frequency and characteristics of these evolutionary outcomes will be key in improving forecasts of species' responses to climate change. This requires studying both stable rear edges, where refugial populations have persisted, and trailing rear edges, where refugial populations have been lost (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 ([5,14] but see [15]). Rear edges are also expected to consist of small and isolated populations, occur in marginal habitats, and thus be more sensitive to stochastic extinction events [15–19]. Yet, a growing number of reports have documented lags in expected extinctions at warmer range limits [2,15,20–22], suggesting additional dynamics shape the vulnerability, resilience and adaptive potential of rear edges. Developing an understanding of evolutionary responses driven by past warming through the resulting genetic patterns in contemporary rear edges, may help refine existing predictive frameworks of responses to changing climates (Box 2).

Despite their ecological and evolutionary importance, rear-edge populations, and warmer range limits in general, have historically represented only a small fraction of the literature on range limits, especially when compared to the leading edge or colder range limits [11]. In the 20 years since Hampe and Petit's review, research on the rear edge has caught up (Fig.1), yielding an opportune time to summarize current knowledge. Using our framework of evolutionary outcomes (Box 1), we review evidence supporting each from genetic patterns assessed in recent empirical research and we discuss the significance of these findings. Lastly, we identify gaps remaining in our understanding and propose future research directions (see Outstanding Questions).

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 (Fig 1B), with 419 studies published in the last 20 years (see Online Supplementary Material Method S1), a similar number as the leading edge (453 studies). However, most of this research focuses on eco-physiological adaptations to warm and/or dry climates (e.g. [23]), or predicting responses to climate change using modeling approaches (e.g. [24,25]). Evolutionary research on the rear edge remains scarce, representing only about 17% of rear-edge studies (Fig 1B).

We reviewed 20 years of empirical studies evaluating the three evolutionary outcomes in the rear edge (Method S1, Box 1). We identified 57 studies across 55 species that describe genetic patterns in rear-edge populations (Online Supplementary Material Table S1). Overall, the genetic patterns most frequently explored were the distribution of diversity and differentiation (93% of species). Few studies directly evaluated signatures of selection or patterns of local adaptation at the rear edge. However, a synthesis of latitudinal patterns of local adaptation over multiple species [26] can serve as a strong proxy for rear edge research. 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 [14,27,28]. Most studies identified for this review focus on plants, occur in the northern hemisphere, and assess latitudinal rather than elevational distributions (Table S1).

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 1). We identified 48 species in which within-population genetic diversity in the rear edge was compared to that in the rest of the range. Thirty-four of these also evaluated patterns of differentiation among populations (Table S1A). Half of the species exhibited higher genetic diversity within populations at the rear-edge than in the core (24/48), with the other half largely exhibiting lower diversity (20/48). In contrast, a majority of species (68%, 23/34) exhibited greater genetic differentiation among populations at the rear edge than among populations elsewhere in the range. In aggregate, these results indicate that rear-edge populations mostly represent hotspots of diversity between populations, but also often pools of diversity within populations. Few species showed both high diversity and differentiation (7/34), suggesting that distinct evolutionary processes lead to high diversity within and between populations.

Are rear edges exposed to strong genetic drift?

Alternatively, rear edges are expected to be fragile populations exposed to drift following a history of small size and isolation in declining habitats (Box 1). The contribution of genetic drift to population genetic structure at the rear edge was demonstrated by reduced genetic diversity within populations and elevated genetic differentiation between them. This pattern has classically been interpreted as a signature of genetic drift at range limits [16,19], including the rear edge (e.g. [29–33] but see [34]), and was found in almost half of the species studied (15/34). Four of these showed additional genetic signatures of drift including population decline and bottlenecks. Genetic signatures of greater inbreeding in and differentiation among rear edge populations provide additional evidence for genetic drift in one species [35]. Demographic inference found signatures of population decline and isolation at the rear edge in three species [36,37]. Finally, *Arabidopsis lyrata*, a species with low diversity in and high differentiation among rear edge population [38], also shows increased genetic and phenotypic signatures of drift load in rear edge compared to core populations [39,40]. In summary, across studies, signatures of genetic drift including low diversity, high inbreeding, population decline and drift load, highlight the fragility of rear-edge populations.

Have rear edges been exposed to strong selection, leading to high local adaptation?

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 in expanded regions that tracked suitable habitats (Box 1). A recent metanalysis of local adaptation inferred from transplant experiments on 135 species [26] reports a latitudinal gradient in the magnitude of local adaptation, with stronger local adaptation towards the equatorial range limits. As rear edges often coincide with the lower latitudinal range limit, this suggests 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 [23,41,42], we found only two studies that explicitly quantified local adaptation in rear-edge populations, and both support stronger local adaptation at the rear edge (Table S1B, [43,44]). Further, genomic studies in two species found rear-edge populations exhibit stronger genetic signatures of selection by environmental factors (Table S1B, [45]), and of local adaptation [46], compared to 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.

Do multiple evolutionary processes occur at the rear edge?

Due to the expected age of rear-edge populations and the iterative nature of glaciations, rear-edge populations may have signatures of multiple evolutionary processes. We found seven cases of heterogeneous genetic patterns, all among refugia in species with multiple, geographically distinct rear edges (Table S1A). For five of the species, distinct rear edges showed different patterns, such as heightened diversity in one rear edge but reduced diversity in the other [47–50]. Heterogeneity among rear edges could be more prevalent than reported in the literature; many studies focus on a single refugial area despite the species occurring in additional refugial areas. With the recent profusion of range-wide phylogeographic studies, we predict more species will be identified with geographically distinct rear-edges (e.g.[49,51]). These can serve as case studies to explore the frequency of heterogeneous evolutionary outcomes of rear-edges.

Multiple possible outcomes complicate predictions of rear-edge evolution

Increased diversity, drift and local adaptation, the three evolutionary outcomes predicted in rear-edge populations, are all well supported by the literature. This result is both concerning and hopeful. Rear-edge populations are generally of concern because they are expected to experience adverse future climates, leading to maladaptation, population decline and ultimately loss [5]. Rear-edge populations suffering from high drift may be especially vulnerable to increasingly stressful climates (Box 2). The observation that half of the surveyed species show signatures of low diversity and high drift at the rear edge underscores the pressing concern 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, with yet others adapted to past warming, suggests that in many species these populations may not be as fragile as expected (Box 2), raising hopes for their ability to persist under future warming.

Comparable levels of support for each distinct evolutionary outcome reveals key knowledge gaps about the future trajectory of rear edges. First, these results raise concerns about our ability to predict the evolutionary history of rear edges. Rear-edge populations are equally likely to represent pools of high diversity as to be genetically depauperate. The inability to generalize about genetic diversity complicates assessment of conservation needs of these populations and their potential use in climate resilience efforts. It also leads to uncertainty in predicting the fate of rear-edge populations under future warming. High diversity and adaptation to warm climates may allow populations to persist longer than expected. However, drift could accelerate population decline (Box 2). Contrasting implications associated with distinct evolutionary outcomes may partly explain discrepancies between predicted and observed responses to contemporary warming at the warmer range limits [2,20–22], and call for a better integration of genetic patterns and evolutionary potential into forecasts of future range shifts (see Outstanding Questions). Second, these results highlight a critical gap in our understanding of how species respond to climate change. Specifically, it is unclear why species follow one evolutionary trajectory at the rear-edge over another. Resolving these gaps is not only crucial to understand and predict 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.

Leveraging stable and trailing rear edges as models of persistence and decline under warming climates

Predicting evolutionary outcomes and associated genetic patterns in rear-edge populations requires a better understanding of past evolution in these populations. Stable and trailing rear edges may be leveraged as models for such studies, with stable rear edges as models of persistence under climate warming, and trailing edges as models of decline and extinction (Box 3). Stable and trailing edges can be distinguished by testing for an overlap between present day rear-edges and refugial areas, typically inferred through species distribution model hindcasting, a technique to predict past distributions [12], or from fossil and pollen records. Surprisingly few studies (26/56 species) evaluate whether rear-edge populations represent stable or trailing edges (Table S1). Of these, almost all (25/26) report an overlap between putative refugia and present-day rear-edge populations, aligning with stable rear edges. Among the studies in which the location of former refugia has not been explicitly tested, rear-edge populations broadly overlap with areas known to be refugia in other species (24/31 species, Table S1, Method S1), again suggesting stable rear edges. In sum, evolution at the rear edge has almost entirely been studied in stable edges.

Trailing edges have been studied only in two species (Table S1), revealing a large gap in our knowledge of their evolution. In *Chondrus crispus,* rear-edge populations occur in two distinct geographical areas, with one showing overlap with former refugia (i.e. stable), and the other occurring at higher latitudes than presumed refugia, thus representing a trailing edge [47]. For *Puccinellia phryganodes* [36], the whole range of the species occurs in areas covered by ice sheets during LGM, suggesting that the species shifted its range after the last ice age and refugial populations have been lost; contemporary rear-edge populations thus representing a trailing edge. The lack of studies focusing on trailing edges may partly stem from the perception that stable rear edges hold greater value for conservation projects and ecological and evolutionary research [11]. Glacial refugia have historically been viewed as centers of high biodiversity and evolutionary innovation [12,52–54], and populations persisting in these refugia provide compelling models to study adaptation to warming climates [41]. Another reason for the lack of studies on trailing edges may be that rear edges are rarely considered in cases of postglacial range shifts. "Trailing edge" is more often used to describe warmer, xeric or contracting range limits (e.g. [2]), than populations closest to glacial refugia. Finally, trailing edges may be harder to detect than stable rear edges, as the loss of ancestral populations may blur phylogeographic signals [12].

Stable, receding and trailing edges each provide unique insights into evolutionary dynamics and conservation priorities. Comparing them may help explain why rear edges in some species have persisted under past climate warming, while others have experienced extinctions. By extension, this may facilitate identifying factors accelerating extinction at warm range limits [55,56] or contributing to the observed extinction lags under contemporary climate change [2,20–22]. Comparing stable and trailing edges may also help link genetic patterns of areas with histories of persistence or decline under past warming (Box 3), with implications for their vulnerability and conservation needs under future climates [47]. We therefore advocate that research sample trailing edges and leverage their potential as models of decline under past warming (see Outstanding Questions).

Context matters: Identifying factors driving rear-edge evolution

Which of the three evolutionary processes populations undergo is likely the product of ecological, climatic, and genetic context. Identifying factors that drove persistence or decline under past climate change may offer practical approaches to address the apparent unpredictability of rear-edge evolution. Particular attention should be given to factors facilitating persistence in stable rear edges, as persistence likely reflects successful adaptations to past warming. Similarly, attention should be given to factors constraining adaptation in trailing edges as past population decline is likely to have resulted from limited adaptive capacity to warming climates. Many ecological and evolutionary processes may affect adaptation at range limits [57], and in early stages of postglacial warming, such as a lack of standing genetic variation, small initial population size favoring genetic drift [58–61] and life history trade-offs [62], among others. Alternatively, the speed and magnitude of past climate change could also have outpaced the capacity of refugial populations to adapt. These processes have yet to be integrated in a framework for understanding why some species experienced range shifts versus range expansion during postglacial warming. In general, the evolutionary dynamics of selection under past warming, and how they affect local or mal-adaptation, remain largely unexplored at the rear-edge.

Theoretical models and simulation studies may represent a first step in 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 [63–67]. Extending theoretical and simulation frameworks to model eco-evolutionary dynamics at the rear edge could provide powerful insights. Predictions from these models may then be tested and refined by fitting empirical genetic or phenotypic data.

Potential drivers may also be identified through detailed 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 found across multiple glacial refugia, may serve as model systems to explore contextual factors driving one or another evolutionary outcome. For example, the strength of past climate change has been linked to differences in genetic patterns between former refugia, with the lowest diversity populations having experienced stronger change in the past [50]. A comparative focus among rear-edge populations from multiple putative refugia in future studies will allow the identification of cases where distinct responses among rear edges can allow for exploration of underlying drivers.

Concluding remarks

Rear-edge populations provide natural laboratories to study evolutionary processes that have shaped species' responses to past warming, and may provide insight into responses to ongoing and future climate change. Our review of the last 20 years of research on rear-edge evolution revealed three common evolutionary outcomes for rear-edge populations: the maintenance of ancestral genetic diversity, exposure to strong genetic drift, and adaptation under past warming. This set of distinct outcomes provides robust expectations for future studies of evolution in rear-edge populations (see Outstanding questions). Furthermore, with this set of outcomes, 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 also reveals new challenges for identifying the conservation needs of these populations, their potential as sources of adaptive genetic diversity, and their vulnerability under future climate change. Further, it is yet unclear why species experience one or another outcome. This presents a fundamental challenge for predicting long-term evolutionary responses to changing climates. Addressing this challenge will require a nuanced understanding of the impact of past and present ecological and genetic context on the response of rear edges to ongoing and future warming (see Outstanding questions).

Outstanding questions:

1) **What can trailing edges teach us about population decline under climate change?** Trailing edges have received almost no study and could provide insight into what drives local extinction or persistence under changing environments.
2) **What drives specific evolutionary outcomes at the rear edge?** Understanding the factors driving each outcome is crucial for predicting evolutionary responses to changing climates. These factors can be identified through theory, simulation, and comparative analysis of environmental and historical contexts of rear edges with different genetic patterns.
3) **How does evolutionary history affect future range shifts or persistence?** Improving forecasts of species' responses to climate change may require combining population genetic patterns with dynamic species distribution models. This integration depends on resolving key questions about the impact of genetic structure on rear-edge population's response to environmental changes: Is the high diversity observed in some rear edges adaptive? How does drift impact response to climate change? Does strong local adaptation indicate further adaptive potential to warming or its exhaustion?
4) **What can rear edges teach us about adaptation to warming climates?** Stable, well adapted rear edges are natural laboratories to study successful adaptation to climate change. Future studies should explicitly test for local adaptation at the rear edge, investigate its phenotypic and genetic basis, and evaluate whether these adaptations remain effective under future warming.
5) **Can rear-edge populations serve as models of climate resilience?** Conservation and restoration projects increasingly aim for climate resilience. Exploring adaptive potential in relation to genetic patterns in rear-edge populations will be key in determining their conservation value and in identifying source populations for climate resilience in other parts of the range.

Author contributions

All authors contributed to the conceptualization of the review. A.P. and O.J.K. performed 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.

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Text Boxes

Box 1: Evolutionary outcomes in response to past warming

1. Rear edges are reservoirs of genetic variation within and among populations

Range expansion is often accompanied by bottlenecks and founder effects that reduce genetic diversity [68]. Rear edges may therefore have elevated within-population genetic diversity relative to expanded portions of the range (Fig. 1C *Diversity*, [12]). This may be especially true for stable edges, that have persisted in place since the LGM, compared to trailing edges, where populations experienced contractions [50]

Range-edge populations are generally sparse [16,19], resulting in isolation from gene exchange. Long-term isolation may lead to stronger genetic differentiation at the rear edge than in the younger expanded range [11]. This differentiation will be greater in species that persisted in multiple refugia (e.g. [51,69–73]), as separate refugia likely have different histories, including LGM refugia that also functioned as refugia during earlier glaciations [74].

2. Rear edges are fragile populations exposed to drift

Gradual habitat decline and fragmentation under postglacial warming is expected at the rear edge [11]. This will lead to smaller populations and greater isolation [16,19]. Population decline and long-term isolation is likely to result in strong genetic drift (Fig. 1C *Drift*; [75–77]. Strong drift will erode genetic diversity within populations and exacerbate genetic differentiation between populations [16,78]. High drift has been hypothesized for stable rear edges [11,79], yet trailing edges may show stronger signatures of drift as they are comprised of populations that undergo gradual decline prior to disappearing.

3. Unique local adaptation following selection under past warming

Rear-edge populations often exhibit remarkable and unique phenotypes (e.g. [23,41,42]), and occur in distinct and warmer habitats than those in the expanded range [15]. This suggests that rear edges have experienced substantial local adaptation as result of strong selection under continuous post-glacial warming ([26,80], Fig. 1C *Selection*). Indeed, local adaptation may be greater in rear edges than in the expanded range [26,58,60,61] where populations tracked the availability of suitable habitats. Stable rear edges, where populations have persisted in place despite warming climates, are expected to experience stronger selection and hence local adaptation than trailing edges where populations have tracked suitable habitats [10,81].

Box 2: Implications of evolutionary outcomes under future climates

1. *Unique diversity is at risk at rear edges, and may be crucial for persistence under future climates*

Rear-edges, as descendants from refugial populations, may retain ancestral diversity that has been lost elsewhere in the range. This may be especially true for stable rear edges that have persisted in place since LGM. The loss of these populations due to future warming may therefore disproportionately reduce a species' overall genetic diversity. At the same time, high genetic diversity may contribute to the resilience of these populations, and be crucial for allowing them to persist under future warming. Rear edges are of high value for biodiversity conservation, both for their potential as source of (adaptive) diversity, and because of the potential loss of that diversity under future warming.

2. *Strong genetic drift may precipitate population extinction at warmer range limits*

Strong drift may negatively impact persistence of rear-edge populations under future climates. Strong drift in long-term small populations reduces adaptive capacity by eroding genetic diversity and reducing the efficacy of positive selection [58,59,66,81]. Drift may further reduce fitness as selection is inefficient at purging deleterious mutations from small populations [82–84]. Expression of this drift load has been shown to be exacerbated by environmental stress [60,85], such as found in warming rear-edge populations, and may reduce population fitness below critical thresholds [86,87].

3. Local adaptation may be a double-edged sword under future warming

Distinct local adaptation at the rear edge makes these populations valuable for improving outcomes of species' responses to future climates. Past warming 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 [5,34,41]. These populations could also serve as a source of genetic material for conservation or restoration projects aimed at improving climate resilience of populations in expanded portions of the range [34,88–90]. However, strong local adaptation may also have limitations. Populations that are strongly adapted to current climates may be maladapted under future climates [91,92]. In addition, strong selective sweeps under past warming may have reduced genetic diversity [93,94] and exhausted adaptive potential to respond to future changes.

Box 3: Histories of persistence and decline: stable, receding and trailing edges

Stable rear edges, where populations persist in glacial refugia until current times despite postglacial warming, are expected to have elevated genetic diversity, while trailing rear-edges, those outside of refugial areas, are expected to show signatures of drift (Box 1). Yet, our literature review found about a third of stable rear edges (18/49, Table S1) have lower within population diversity than central portions of the range. Therefore, occurrence in former refugia is not necessarily synonymous with the maintenance of diversity, or perhaps even demographic stability.

We propose rear edges of species distributions would be better understood by conceiving of them as dynamic, occurring along a "stable to trailing" continuum (Fig. I). This framework allows for more flexible expectations of past and future evolution than a strict dichotomy between the two. Here, stable rear-edge populations that have persisted under past warming, maintained high diversity, and are likely locally adapted, represent one extreme of the continuum. Trailing edges, where refugial populations went extinct under past warming, represent the other extreme. We suggest that rear-edge populations in refugial areas with a history of drift represent intermediates, and term them "receding" rear edges. They occur in former refugia, hence appear to be "stable," but the signatures of genetic drift suggest that population sizes are likely small. As such, receding rear-edge populations are expected to be in decline, potentially over long periods of time, due to a combination of maladaptation to warming environments compounded by the genetic load associated with drift. Therefore, receding edge populations are likely to face extirpation in the future.

Distinguishing receding edges from stable rear edges will be crucial to accurately assess conservation needs and evolutionary potential of these populations. Populations that have successfully maintained population sizes under past warming (i.e. stable edges) may be less at risk of population decline and extinction under future warming than populations that have already experienced decline. Furthermore, stable rear edges may be valuable sources of diversity, while receding and trailing edges may be of high conservation concern. Moving forward, we suggest systematically evaluating whether rear edges under study are stable, receding or trailing.

Figure legends

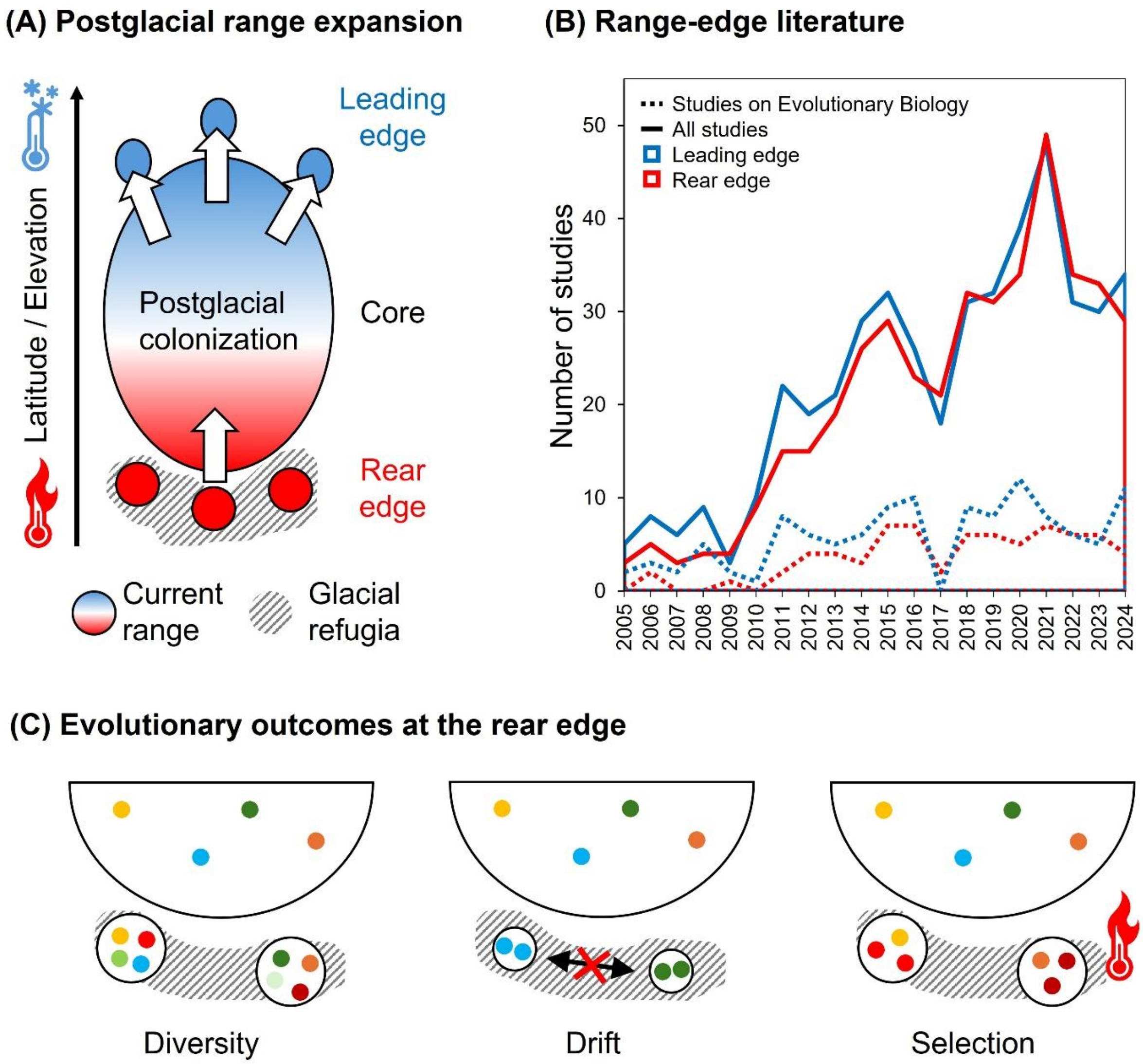

Figure 1: Evolution at the rear edge. (A) Schematic depiction of postglacial range expansion and resulting types of range edges. **(B)** Review of research on range edges based on a literature search over the period of 2005 - 2024 (Method S1). The total number of studies focusing broadly on range edges is represented in full lines, dashed lines represent the subset of studies focusing on evolution. Literature focusing on leading edges is depicted in blue, rear edges in red, and both edges added to the count of each type. **(C)** Three main evolutionary outcomes expected at contemporary rear edges with populations representing reservoirs of *diversity* within and between populations due to a history of persistence in glacial refugia, reflecting strong *drift* following a history of decline under past climate change, or high local adaptation in response to strong *selection* imposed by past climate warming.

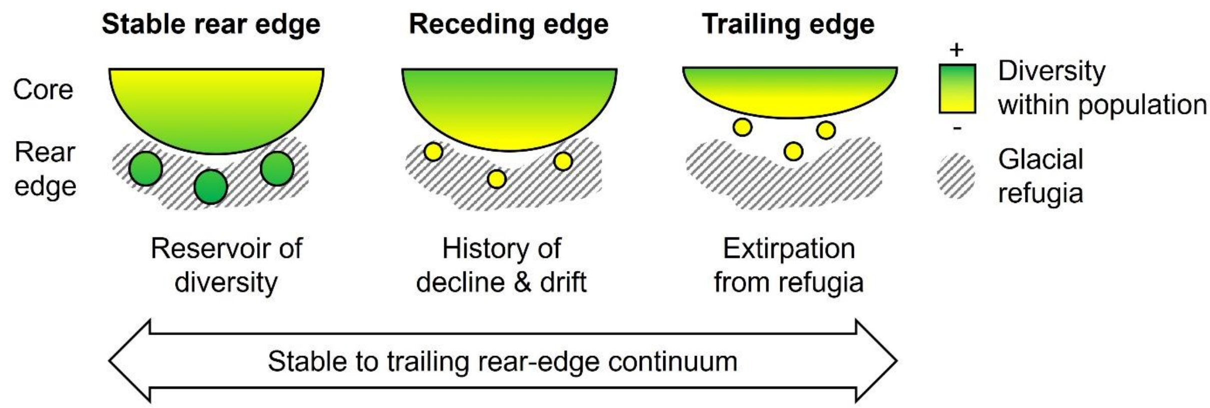

Figure I: The stable – trailing rear-edge continuum. Schematic description of the link between a history of decline or persistence under past warming and genetic patterns. **Stable rear edges** consist of populations that persist in former glacial refugia and typically have high diversity within populations relative to the rest of the range. **Receding edges** consist of refugial populations on their way to extinction, with drift associated declines in genetic diversity and population size from past warming. **Trailing edges** are rear edges in species' distributions that have shifted under past climate change due to the loss of refugial populations, and may still be experiencing recession due to climate stress and drift.

Supplementary material

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	Species	Location	Gradient	Rear edge diversity	Rear edge differentiation	Other signatures	Edge type	Study
Animal	*Chorthippus parallelus*	Europe	Latitude	Higher †	-	-	Stable #	[S1]
Animal	*Erebia aethiops*	Europe	Latitude	Higher	Higher	-	-	[S2]
Animal	*Lottia gigantea*	N America	Latitude	Higher	Higher	-	Stable	[S3]
Animal	*Parnassius apollo*	Europe	Elevation	Lower	Higher	Stronger decline	Stable	[S4]
Animal	*Phengaris arion*	Europe	Latitude	Lower	Higher	-	Stable #	[S5]
Animal	*Plecotus austriacus*	Europe	Latitude	Higher	Higher	-	Stable	[S6]
Animal	*Podarcis muralis*	Europe	Latitude	Higher	Lower	-	Stable	[S7]
Animal	*Tetrao urogallus*	Europe	Latitude	Lower	Higher	Bottleneck	Stable #	[S8, S9]
Animal	*Zootoca vivipara louislantzi*	Europe	Elevation	Similar	Higher	Higher FIS	Stable #	[S10]
Plant	*Abies alba*	Europe	Latitude	Higher	-	-	Stable $	[S11]
Plant	*Alnus glutinosa*	Europe	Latitude	Higher & lower	-	-	Stable #	[S12]
Plant	*Arabidopsis lyrata*	N America	Latitude	Lower	Higher	Higher drift load	Stable #	[S13–S15]
Plant	*Argentina anserina*	N America	Elevation	Higher	Lower	Higher Ne, lower FIS	-	[S16]
Plant	*Bupleurum euphorbioides*	Asia	Latitude	Lower	Lower	Bottleneck	Stable	[S17]
Plant	*Carex nigra*	Europe	Latitude	Higher	Lower	-	Stable #	[S18]
Plant	*Chimaphila umbellata*	Asia	Latitude	Lower	Higher	-	Stable #	[S19]
Plant	*Chondrus crispus*	Europe	Latitude	Higher & lower	-	-	Stable & trailing	[S20]
Plant	*Cymodocea nodosa*	Europe	Latitude	Higher	-	-	Stable #	[S21]
Plant	*Dryas octopetala*	Circumboreal	Latitude	Lower	Higher	-	Stable #	[S22, S23]
Plant	*Edraianthus tenuifolius*	Europe	Latitude	Higher	-	-	Stable #	[S24]
Plant	*Euphorbia hyberna*	Europe	Latitude	Higher	-	-	Stable	[S25]
Plant	*Fagus sylvatica*	Europe	Latitude & elevation	Higher	Higher	No bottleneck	Stable $	[S26]
Plant	*Fraxinus angustifolia*	Europe	Latitude	Lower	-	-	Stable #	[S27]
Plant	*Fraxinus excelsior*	W Asia	Latitude	Higher	Similar	-	Stable #	[S28]
Plant	*Fucus ceranoides*	Europe	Latitude	Higher	Higher	-	Stable #	[S29]
Plant	*Fucus serratus*	Europe	Latitude	Lower	-	-	Stable #	[S30]
Plant	*Fucus vesiculosus*	N Atlantic	Latitude	Lower	Higher	-	Stable	[S31]

Plant	*Gracilaria vermiculophylla*	China sea	Latitude	Higher	Lower	-	Stable #	[S32]
Plant	*Hemerocallis middendor*	Asia	Latitude	Lower	Higher	Past decline	Stable	[S33]
Plant	*Himantoglossum hircinum*	Europe	Latitude	Higher	-	-	Stable #	[S34]
Plant	*Juncus balticus*	Europe	Latitude**	High & low	-	-	Stable	[S35]
Plant	*Laminaria digitata*	N Atlantic	Latitude	Higher	Lower	-	Stable $	[S36]
Plant	*Laminaria ochroleuca*	N Atlantic	Latitude	Higher	Higher	-	Stable $	[S37]
Plant	*Monotropa hypopitys*	Europe	Latitude	Higher	-	-	Stable	[S38]
Plant	*Orthilia secunda*	Europe	Latitude	Higher	-	-	Stable	[S38]
Plant	*Pelvetia canaliculata*	N Atlantic	Latitude	Higher & lower	-	-	Stable	[S39]
Plant	*Phyllospadix torreyi*	N America	Latitude	Lower	Higher	-	Stable	[S40]
Plant	*Phyllospora comosa*	Australia	Latitude	Lower	Higher	-	-	[S41]
Plant	*Picea abies*	Europe	Latitude*	Higher	Lower	No bottleneck	Stable #	[S42]
Plant	*Pinus sylvestris*	Europe	Latitude	Lower	Higher	-	Stable $	[S43]
Plant	*Populus tremuloides*	N America	Latitude	Lower	Higher	-	Stable #	[S44]
Plant	*Pterocarya rhoifolia*	Asia	Latitude	Higher	-	-	Stable	[S45]
Plant	*Puccinellia phryganodes*	Europe	Latitude	Lower	Similar	Lower Ne	Trailing #	[S46]
Plant	*Quercus canariensis*	N Africa	Latitude**	-	-	Low Ne	Stable #	[S47]
Plant	*Quercus faginea*	N Africa	Latitude**	-	-	Low Ne	Stable #	[S47]
Plant	*Saccorhiza polyschides*	N Atlantic & Mediterranean	Latitude	Higher †	Higher †	-	Stable	[S48]
Plant	*Salix hastata*	Europe	Latitude**	High & low	-	-	Stable	[S35]
Plant	*Salix herbacea*	Europe	Latitude	Lower	Higher	-	Stable #	[S49]
Plant	*Sargassum thunbergii*	Asia	Latitude	Lower	Lower	-	Stable	[S50]
Plant	*Sibiraea angustata*	Asia	Latitude	Higher	similar	Stable Ne	Stable #	[S51]
Plant	*Thuja standishii*	Asia	Latitude	Lower	Higher	Lower Ne	Stable	[S52]
Plant	*Zostera maritima*	Europe	Latitude	Lower	Higher	-	Stable #	[S53]

For each species, *gradient* indicates the axis of comparison between the rear edge and rest of the range. For some species, only rear-edge populations were assessed and compared with core populations in prior studies (*) or not at all (**). Patterns of genetic *diversity* and *differentiation* are reported for the rear edge compared to the rest of the range. Some species showed divergent patterns between distinct rear edges (higher & lower) or showed the same pattern to varying degrees (†). Each species was assigned an *edge type*, with stable edges representing cases where the contemporary rear edge overlaps with former glacial refugia, and trailing edges representing cases where the species occurs entirely outside of former refugia. In most cases, overlap was assessed in each study 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 were not tested or reported by the authors, rear-edge type was inferred based on whether rear-edge populations occur in known refugial (stable) or glaciated (trailing) areas (#). Cases where rear edge type 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	Species	Location	Gradient	Signature	Edge type	Study
Plant	*Biscutella laevigata*	Europe	Elevation	Divergent selection	-	[S54]
Plant	*Fucus vesiculosus*	Europe	Latitude	Higher local adaptation	Stable	[S55]
Plant	*Nothofagus pumilio*	S America	Elevation	Higher local adaptation	-	[S56]
Plant	*Populus balsamifera*	N America	Latitude	Higher turnover of climate-adaptive alleles	Stable	[S57]
-	*135 species*	-	Elevation	Higher local adaptation	-	[S58]

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 rest of the range. Each species was assigned an *edge type*, with stable edges representing cases where the contemporary rear edge overlaps with former glacial refugia. Cases where rear edge type could not be inferred are left blank.

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 21/01/2025). The search was restricted to studies published between April 2005 and December 2024, representing 20 years of literature since the foundational review by Hampe and Petit in 2005 [S59]. 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 352 studies with the keyword “rear edge”, 341 with the keyword “trailing edge” (32 overlapping). We performed a similar search to find studies focusing on the leading edge, using as topics “leading edge” (2005 studies) or “expanding edge” (1266 studies, with 600 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 post-glacial colonization dynamic (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, one relevant study was added from personal knowledge [S4]. This resulted in a final list of 678 studies, with 225 studies focusing on the rear edge, 260 on the leading edge, and 193 dealing with both. Of these, 151 studies belonged to the Web Of Science category "Evolutionary Biology," with 33 on the rear-edge, 79 leading-edge, and 39 on both edges.

Empirical support of evolutionary outcomes

We then evaluated all 418 studies on the rear edge (including the 193 dealing with both edges) to identify those that report patterns of genetic diversity, drift, selection and local adaptation. Some studies supported multiple outcomes. We limited inclusion to those where rear edge populations were compared to the rest of the 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), 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 [S47] or signatures of drift load [S14, S15]. This resulted in a total list of 57 rear-edge studies (Table S1) across 55 species [S1–S57], and one meta-analysis assessing latitudinal patterns over 135 species [S58].

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 the rest of the range: higher, lower, similar, or mixed patterns). We also recorded any additional supporting results such as demographic patterns or inbreeding. In addition, for each species we determined whether the rear edge is stable, i.e. present day populations overlap glacial refugia, or trailing, with the whole range occurring at a higher latitude or altitude than former refugia. For species where past distributions, i.e. glacial refugia, were not explicitly addressed (about half of the studies), the present-day distribution was compared 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.).

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