



Range edges in heterogeneous landscapes: Integrating geographic scale and climate complexity into range dynamics

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Funding information

USDA National Institute of Food and Agriculture, Grant/Award Number: 1016272; National Science Foundation, Grant/Award Number: DBI-1523866, DEB-1457827, DEB-1553053 and DEB-1637686

Abstract

The impacts of climate change have re-energized interest in understanding the role of climate in setting species geographic range edges. Despite the strong focus on species' distributions in ecology and evolution, defining a species range edge is theoretically and empirically difficult. The challenge of determining a range edge and its relationship to climate is in part driven by the nested nature of geography and the multidimensionality of climate, which together generate complex patterns of both climate and biotic distributions across landscapes. Because range-limiting processes occur in both geographic and climate space, the relationship between these two spaces plays a critical role in setting range limits. With both conceptual and empirical support, we argue that three factors—climate heterogeneity, collinearity among climate variables, and spatial scale—interact to shape the spatial structure of range edges along climate gradients, and we discuss several ways that these factors influence the stability of species range edges with a changing climate. We demonstrate that geographic and climate edges are often not concordant across species ranges. Furthermore, high climate heterogeneity and low climate collinearity across landscapes increase the spectrum of possible relationships between geographic and climatic space, suggesting that geographic range edges and climatic niche limits correspond less frequently than we may expect. More empirical explorations of how the complexity of real landscapes shapes the ecological and evolutionary processes that determine species range edges will advance the development of range limit theory and its applications to biodiversity conservation in the context of changing climate.

KEYWORDS

climatic niche, microclimate, range limit theory, range shifts, topography

1 | INTRODUCTION

I want to stand as close to the edge as I can without going over. Out on the edge you see all the kinds of things you can't see from the center.

(Kurt Vonnegut)

Range shifts are considered to be one of the most notable biological responses to climate change (Pech et al., 2017). The need to quantify

and predict range shifts with climate change has re-energized the fundamental question of the role of climate, and its interactions with other ecological and evolutionary processes, in setting species range limits (Angert, 2009; Sutherland et al., 2013). Most empirical studies of contemporary range shifts have focused on poleward shifts in latitude or upward shifts in elevation (reviewed in Lenoir & Svenning, 2015), which have already been documented in a number of taxa across the globe and are implicitly or explicitly linked to spatial gradients in temperature (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Moritz et al.,

2008; Morueta-Holme et al., 2015; Parmesan & Yohe, 2003; Wolf, Zimmerman, Anderegg, Busby, & Christensen, 2016). However, some species have not shifted their ranges at all (Doak & Morris, 2010; Zhu, Woodall, & Clark, 2012), while others have moved toward the equator or downslope, counter to expectations (summarized in Lenoir et al., 2010). The diversity of documented patterns has prompted rigorous discussion about the effects of dispersal and demographic lags, and interactions between temperature and precipitation gradients, in driving range dynamics (Harsch & Hille Ris Lambers, 2016; Rapacciuolo et al., 2014; Svenning & Sandel, 2013). There has also been a growing emphasis on understanding the importance of fine-scale climate variation—shaped by regional, topographic, and microclimatic landscape features—in setting species ranges and their biogeographic responses to global climate change (Ackerly et al., 2010; De Frenne et al., 2013; Elsen & Tingley, 2015; Loarie et al., 2009; Rapacciuolo et al., 2014; Scherrer & Körner, 2011). The potential for range-limiting processes to interact across different landscape features requires a refocusing of how we define, discuss, and quantify species range edges.

Biologists' fascination with species distributions has long motivated research that examines how climate, species interactions, disturbance, dispersal, and niche evolution shape species' range limits (MacArthur, 1972). Yet, even determining what constitutes a biologically meaningful geographic range limit of a species remains empirically difficult (Gaston, 2009; Pironon, Villellas, Morris, Doak, & García, 2015; Sexton, McIntyre, Angert, & Rice, 2009). Although standard range maps and other conventions portray a range edge as a clear-cut boundary, the multidimensional, scale-dependent nature of species' distributions across landscapes challenges this convention (Brown, 1995; Soberon, 2007). Range edges can be described at regional or local scales, at climate extremes (e.g., coolest or hottest), or in terms of dynamic changes (e.g., leading or trailing; Soberon & Nakamura, 2009; Svenning & Sandel, 2013). Importantly, the ecological and evolutionary processes that drive these various types of edges may differ (Anderegg & Hille Ris Lambers, 2019; Hargreaves & Eckert, 2019; Sexton & Dickman, 2016; Sexton et al., 2009). The difficulty of finding generalities in the drivers of range edges, and therefore also in predicting range shifts, is in part driven by the nested hierarchy of geographic features (global, regional, and local) that influence climate, and also by the multidimensional nature of climate (e.g., temperature, precipitation, snowpack).

In this paper, we evaluate how the multifaceted relationship between geography and climate unfolds in different landscape types to influence range edges and range shifts with climate change. Specifically, we examine the relationship between geographic and climate spaces. We define *geographic space* as the spatial arrangement of locations on a landscape, spanning latitude and longitude. For simplicity, in this paper, we focus on latitude and longitude as geographic axes, corresponding to the convention of range maps. We recognize that elevation is a critical driver of climate and could be considered a geographic axis. The framework we develop here could be elaborated to take this into account, and treat geographic ranges as three-dimensional hulls, rather than just two-dimensional representations on maps; this avenue may provide a productive direction for future work. We define *climate space* as the multivariate

distribution of climate variables measured for the same physical area, in *n*-dimensional space, depending on which and how many climate variables are considered. Together, geographic and multi-dimensional climate space generate complex patterns of climate across landscapes, making the link between species geographic range limits and climate variation far from straightforward. This idea has been touched on with climate velocity metrics (i.e., the ratio of the change in climate across space and change in climate through time) to generate many interesting theoretical and applied findings (Brito-Morales et al., 2018; Loarie et al., 2009; Ordóñez, Williams, & Svenning, 2016). Yet, range limit theory (and range shift predictions) still often invoke linear, unidimensional environmental variation across geography (Sexton et al., 2009), where geographic and climate space are effectively interchangeable (Figure 1a; Hargreaves,

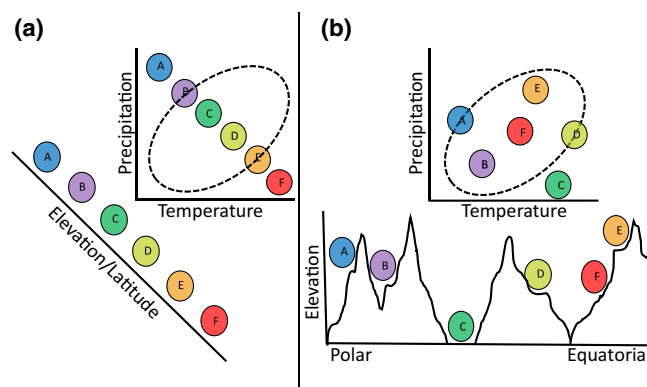


FIGURE 1 Cartoon of a species range shown in both geographic (latitudinal and/or elevational gradients) and climate space (temperature vs. precipitation). Circles represent populations across the species entire range. The climatic niche of the hypothetical species is represented by the dashed line in the climate space inset. (a) Range limit theory often invokes linear, unidimensional environmental variation across geography with the edge of a species range in geographic space being at the edge or beyond (if considering sink populations) in climate space. (b) Real-world landscapes are much more topographically complex and can have multiple topographic gradients simultaneously shaping species distributions. Imagine a species that has a latitudinal distribution that follows a north–south mountain range. The northern- and southernmost populations may initially seem to be the most obvious to be considered at geographic range limits. However, the lowest elevation population, which may be in the center of the latitudinal range, may inhabit the most extreme climate conditions. Topographic complexity, such as the interacting effects of latitude and elevation (Population C), aspect (Populations D and F), and valleys with cold-air pooling (Population B), influences the environmental variation experienced by populations. Therefore, there can be populations at both a geographic range edge and a climatic niche edge (Population A), or at geographic range edge, but not a climatic niche edge (Population F), or at a climatic niche edge, but not a geographic range edge (Population D). Population C, despite being at the geographic center, is beyond the climatic niche and is either a sink population or slated for eventual extinction, challenging our assumptions of range edge populations as the most vulnerable to a changing climate

Samis, & Eckert, 2014; Lee-Yaw et al., 2016). In this scenario, the edge of a species range in geographic space will also represent an edge in climate space. However, the topographic complexity of many real-world landscapes can cause climate space and geographic space to become decoupled, leading to incongruence between geographic and climate thresholds across a species' distribution (Figure 1b; Pironon et al., 2015). For example, topographic variation across a species range can cause geographically central populations to occur in climatically extreme habitats, and vice versa (Chardon, Cornwell, Flint, Flint, & Ackerly, 2015), decoupling population location and sensitivity to climate change. Slope, aspect, elevation, geology, soils, micro-topography, and effects of vegetation on microclimates, as well as the consideration of additional climate variables, can further decouple climate and geographic edges of a species range.

With the distinction between geographic and climate space in mind, we posit that three critical factors—climate heterogeneity, degree of collinearity among climate variables, and spatial scale—shape the spatial structure of climate at range edges, and in turn the ecological and evolutionary processes that determine current and future range limits. We first review how species range edges have been previously described and then use data on species distributions in contrasting landscapes to investigate how climate heterogeneity, collinearity among climate variables, and spatial scale influence range dynamics by decoupling climate and geographic space. We are optimistic that this perspective has the potential to extend our understanding of range limits to more broadly explain the diversity of distributional patterns and temporal shifts in response to climate change that exist across landscapes.

2 | WHAT (AND WHERE) IS A SPECIES RANGE EDGE?

At the largest spatial scales, for example, across latitudes and elevations, species range edges have often been attributed to physiological limits at climate extremes. A classic example is the Saguaro cactus being absent beyond a limit set by a critical number of continuous frost hours (MacArthur, 1972). Populations at the edges of a species' geographic range or climatic niche are often predicted to be characterized by smaller individuals, lower abundance, lower occupancy, lower or higher genetic variation, higher variability in population growth rate, and lower population growth rates (Ehrlen & Morris, 2015; Pulliam, 2000; Sagarin, Gaines, & Gaylord, 2006; Sexton et al., 2009). However, there is limited empirical support that a population's proximity to a geographic range or ecological niche edge is a consistent predictor of these characteristics (Abeli, Gentili, Mondoni, Orsenigo, & Rossi, 2014; Aikens & Roach, 2014; Dallas, Decker, & Hastings, 2017; Oldfather & Ackerly, 2018; Pironon et al., 2015, 2016; Santini, Pironon, Gardens, & Maiorano, 2018; Sexton et al., 2016). In most cases, there are likely to be many interacting physical, ecological, and evolutionary processes that determine the physiological and demographic limits to where a species occurs, and where it does not (Sexton et al., 2009; Willi & Van Buskirk, 2019).

Here, we define a *geographic range edge (limit)* as a spatially extreme landscape position beyond which abundance drops to 0 (e.g., the northernmost individual) at a specific point in time. Importantly, species' distributions are more often patchy than contiguous, generating different geographic range edges at different scales (Figure 2; Brown, 1995). As a result, the line between the presence and absence of a species can be drawn at the edge of an individual, stand, population, or at the maximum extent of all populations of the species. Range edges may be described with reference to a geographic axis (e.g., northernmost, southernmost), or along any edge defined by connecting occupied points (i.e., alpha hull; Figure 3). Taking a different perspective, edges may also be described with

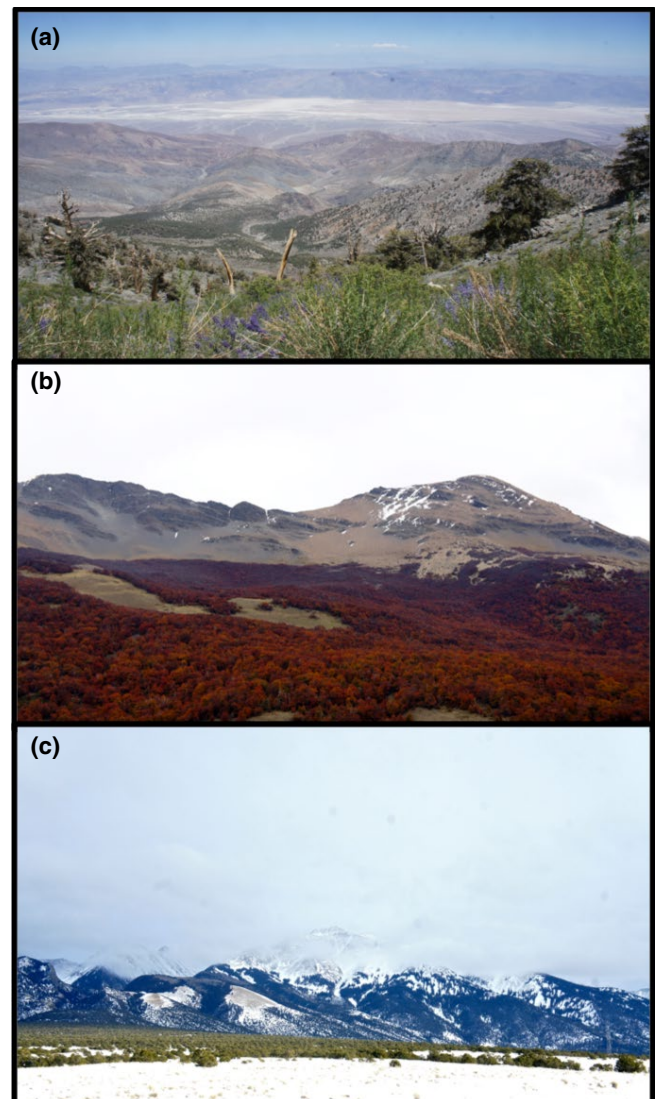


FIGURE 2 Examples of species' distributions at different spatial scales. (a) Topoclimatic differences drive patchy range edges of *Lupinus* and *Pinus* from Telescope Peak to Death Valley in California, United States. (b) Noncontinuous treeline of the deciduous *Nothofagus* in Patagonia, Argentina, due to microclimatic differences. (c) A shared range limit at the transition from shrubs to trees in Great Sand Dunes National Park in Colorado, United States due to a broad-scale steep elevation gradient

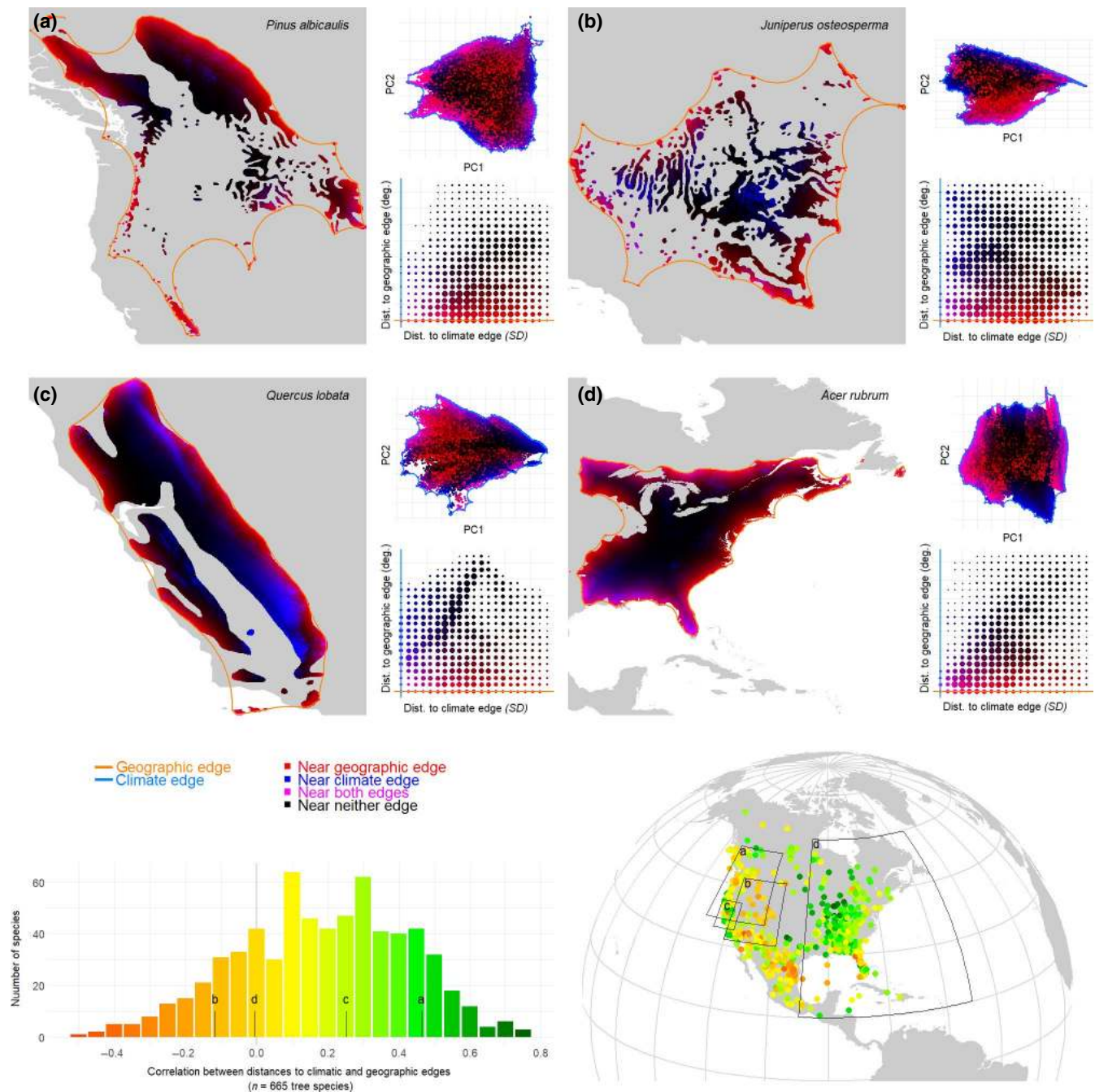


FIGURE 3 Ranges of four species (a–d) illustrating the range of correlation between geographic edges and climate edges. In both geographic space (map on left) and climate space (scatterplot on right), blue represents points close to a climate edge, red represents points close to geographic edges, and magenta points represent those that are at both geographic and climate edges. The climate or geographic edge is outlined in orange or light blue, respectively. Distance to the climate or geographic edge of a point is calculated as the distance of that point from the nearest edge of the alpha hull. The histogram shows correlations between distance to geographic and climate edges for all North American tree species (Little/USGS expert range maps). Hemispheric map shows the species ranges of the North American tree species as boxes that encompass the entire species range for the four focal species, as well as points at the centroid of the species range for all species. The colors of the points match the histogram, indicating how the correlation between climate and geographic edges varies spatially. In a simplified view, if a species can reach all locations with suitable climate, this will result in a coherent range in climate space, occupying all locations up to the climatic niche limits, while the geographic range may be patchy, corresponding to patchiness in underlying climate variables. Alternatively, if a species range is limited by dispersal from a central location (e.g., an expanding invasive), the range may be coherent in geographic space, while distributions in climate space will incidentally reflect the mapping between geography and climate. As discussed in the main text, the balance of spatial (i.e., dispersal) and climatic (i.e., niche-related) processes lead to a complex array of possibilities between these two simple cases. See Methods S1 for further details on this analysis

reference to a climate axis (e.g., hottest, driest, coldest, wettest); we define this as the *climate edge* of a species range, that is, an extreme position along a climate axis (or alpha hull in climate space) beyond which abundance drops to 0. When a species geographic range is transposed into climate space, we can use similar methods to identify individuals or populations that occupy edges in relation to climate gradients (Figure 3, see discussion below). The number of dimensions of climate space is limited only by our creativity in calculating climate metrics and our ability to identify informative climate variables that we expect to have a causal effect on the physiology, demography, and persistence of a species.

Much of range limit theory has been developed around the assumption that geographic range limits are equivalent to climatic niche limits (Gaston, 2009; Kirkpatrick & Barton, 1997; Pulliam, 2000; Sexton et al., 2009). Here, we define the *climatic niche limit* as the climatically extreme condition in multidimensional climate space, along a particular axis, at which the long-term population growth rate is greater than or equal to one (Soberon, 2007). Unlike climate edges described above, which are based on correlations between species' occurrences and climate variables, defining climatic niche limits requires information about whether population growth is stable, increasing, or declining. Geographic limits and climate niche limits can be spatially de-coupled due to dispersal limitation, biotic interactions, demographic lags—all of which are shaped by the complex patterns of climate across landscape features, the focus of this study (Angert, 2009; Hargreaves et al., 2014; Lee-Yaw et al., 2016; Pironon et al., 2015). Local adaptation of populations across a species range may drive individual populations to have different climate niche limits, greatly modifying how climate is shaping current and future range dynamics (Peterson, Doak, & Morris, 2018). Geographic and climate niche limits may also be decoupled in time if dispersal lags limit the rate at which individuals can colonize climatically suitable habitat, or track shifting climate regimes (e.g., leading or trailing edges; Diez, Giladi, Warren, & Pulliam, 2014; Hampe & Petit, 2005; Rehm, Olivas, Stroud, & Feeley, 2015; Svenning & Sandel, 2013).

Topographic complexity will influence the degree to which geographic range edges and climate edges align (Figure 1; see Section 3). We can examine this quantitatively by testing for congruence in the geographically peripheral and climatically extreme occurrences across species distributions. Using regional occurrence data for 662 tree species in North America (Figure 3; see Methods S1 for analysis details), we calculated the distance from each point to the edge of its respective species distribution in geographic and in climate space. In this analysis, the mean correlation between these geographic and climate distances across all species was approximately 0.25, demonstrating a surprisingly weak relationship between the two; that is, geographic edges and climate edges are *not* closely aligned. There are also quite a few species with negative correlations, meaning that climate edges occur in the interior of a species range (Figure 3). These patterns support the notion that populations that occupy the edge in relation to geography (e.g., northernmost) often may not occupy a climate edge, due to the complex patterns of climate across the landscape (Pironon et al., 2016).

The lack of congruence between geographic range edges and climate edges may be driven by unmeasured climate variables, edaphic constraints, biotic interactions, dispersal limitation, or other mechanisms of disequilibrium between the geographic range edge and climatic niche limits (Chardon et al., 2015; Svenning & Sandel, 2013). In this dataset, variation in elevation also likely influences this lack of congruence, highlighting the importance of considering additional landscape features when evaluating range–climate relationships. Lastly, if considering only cases where geographic and climate marginality do align (e.g., Figure 3a), we may expect more support for generalizable edge population characteristics (e.g., reduced population growth rates).

3 | GEOGRAPHIC AND CLIMATE SPACE ACROSS LANDSCAPES

The distribution of climate across landscapes is shaped by physical geography and topography at a range of spatial scales. Globally, latitude and radiative energy balance are the dominant factors. At large regional scales, other features, such as proximity to the ocean, influence maximum and minimum temperatures (due to oceanic buffering) as well as water availability (due to storm tracks and fog inputs; Torregrosa, Combs, & Peters, 2016). Precipitation varies at the scale of mountain ranges due to orographic rainfall on the windward side and the rain-shadow effects on leeward sides. At regional scales (e.g., mountain ranges), elevation largely determines the temperature and precipitation at any location, with cooler and wetter conditions at higher elevation. However, at fine spatial scales, the effects of elevation on climate can be reversed, with cooler minimum temperatures and wetter conditions in valley bottoms due to cold-air pooling, temperature inversions (Fridley, 2009), and hydrologic accumulation (McLaughlin et al., 2017). At midlatitudes, polar-facing aspects and steeper slopes have lower solar radiation loads than equatorial-facing locations, resulting in higher maximum temperatures and water deficits on the latter (Bennie, Hill, Baxter, & Huntley, 2006; Bennie, Huntley, Wiltshire, Hill, & Baxter, 2008; Flint, Flint, Thorne, & Boynton, 2013; Geiger, Aron, & Todhunter, 2009). Snowpack, a major determinant of species distributions of mountain taxa (Körner, 2003; Stewart, Wright, & Heckman, 2017), is heavily influenced by the interaction between wind patterns and local topography (Mott and Lehning, 2010). Finer scale microtopography can also have large effects on temperature, particularly in mountain systems (Fridley, 2009; Scherrer & Körner, 2011). Lastly, underground geology and edaphic factors can have a strong influence on soil moisture, generating spatial patterns in water availability that are decoupled from above-ground conditions (McLaughlin et al., 2017). While edaphic effects are not climatic factors in the narrow sense, their strong influences on plant growth and habitat structure may lead to range edge effects at a variety of scales.

These geographic and topographic effects can be captured in three general categories that help to untangle the conceptual relationship between climate and geographic edges: climate heterogeneity, climate collinearity, and spatial scale. Collectively,

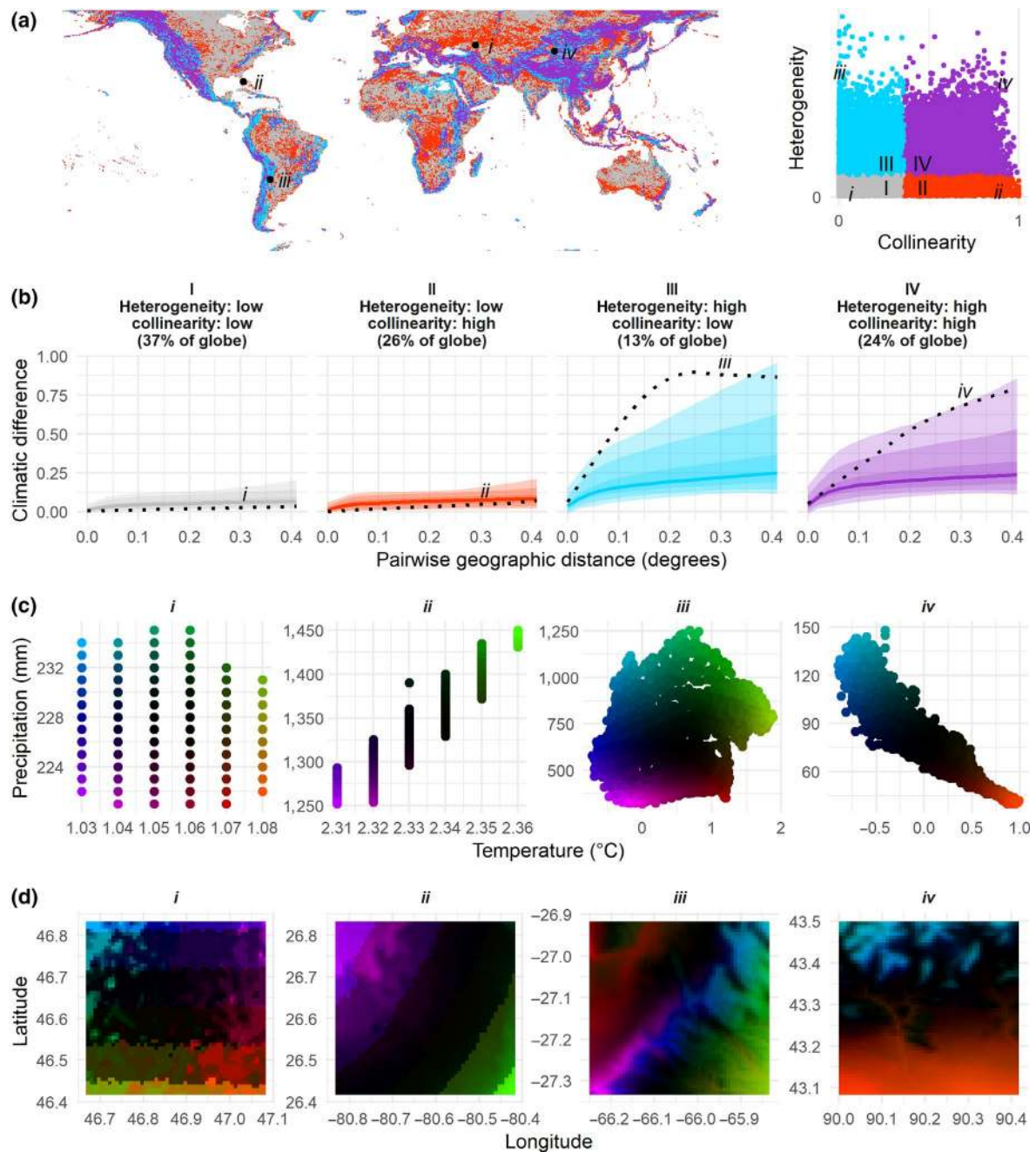


FIGURE 4 Global patterns, and representative examples, of landscape climate heterogeneity and collinearity. Climate is represented by mean annual temperature and log mean annual precipitation. Landscapes are defined at a single scale—50 × 50 km areas with climate conditions quantified for each 1 km × 1 km pixel with the landscape. See Methods S2 for further details on this analysis. (a) Patterns of climate heterogeneity and collinearity for landscapes globally. Heterogeneity is quantified as standard deviation of climate within each landscape. Collinearity is quantified as the squared correlation between the two climate variables across each landscape. Heterogeneity and collinearity are split up into four combinations of high and low values shown on the associated scatterplot with region I (gray) representing low heterogeneity and low collinearity, region II (red) representing low heterogeneity and high collinearity, region III (blue) representing high heterogeneity and low collinearity, and region IV (purple) representing high heterogeneity and high collinearity. Placement of example landscapes (shown in panel b) of these combinations is indicated by the location of the representative lowercase letters on the map and scatterplot. (b) Relationships between pairwise geographic distance and climate distance for all landscapes globally for each of the four categories of collinearity and heterogeneity. Splines were fit for each landscape; the solid line represents the median spline fit across all landscapes in each category (I–IV), while shaded areas summarize these fits for the median 50%, 90%, and 98% of global landscapes. Dashed lines represent the example landscapes highlighted in panels (c) and (d). (c) Temperature versus precipitation of each grid cell in the four representative landscapes. A two-dimensional color ramp is applied to these scatterplots, serving as the legend for the corresponding maps in panel (d). (d) Geographic climate patterns for the four representative landscapes. The color mapped onto geographic space represents the climate of each pixel in the landscape as shown in the associated climate space figure in panel (c)

these three factors describe the spatial structure of the environment that is critical for defining a spectrum of landscapes. *Climate heterogeneity* includes both the overall range of climate variables over a certain spatial domain (extent) and the likelihood of nearby patches having different climate conditions (patchiness). These two components determine the variation in climate conditions that an individual may experience across a landscape; the overall difference in climate between two sites could be increased by a steeper climate gradient or higher patchiness (i.e., very different conditions between the two sites). *Climate collinearity* describes the degree of statistical dependence between pairs of climate variables across a landscape (e.g., mean annual temperature and precipitation), such that climate variables with high collinearity exhibit similar spatial patterns. The relationships between climate variables can range from entirely collinear to orthogonal (statistically independent). *Spatial scale* describes the geographic extent (e.g., local, regional, global) being considered. Both the climate heterogeneity and collinearity measured across a landscape will depend on the suite of climate variables considered, which will vary across spatial scales; therefore, spatial scale acts as a modifier of climate heterogeneity and collinearity. For example, at regional scales, elevation gradients may drive strong collinearity between temperature and precipitation, whereas at more local scales, temperature may be less collinear with precipitation due to changes in aspect and cold air pooling.

An analysis of climate heterogeneity and collinearity metrics of landscapes globally at a single spatial scale elucidates how these factors influence the spatial structure of the climate in different landscapes (Figure 4; see Methods S2 for analysis details). Specifically, climate heterogeneity and collinearity both independently and simultaneously drive large variation in the relationships between climate space and geographic space (Figure 4b). Landscapes with high heterogeneity and low collinearity have the largest variation in the shape of the relationship between geographic space and climate space. Although there is a general pattern for climate differences to increase with increasing geographic distance, there is substantial variation in both the magnitude of change in climate conditions across short distances (initial slope) and the distance at which the change in climate becomes minimal (distance at which the slope flattens). Furthermore, by qualitatively considering scale as a modifier of both heterogeneity and collinearity, more potential relationships between these two spaces become possible. This variation in the relationship between geographic and climate space across a landscape suggests that geographic edges, climate edges, and climatic niche limits have the potential to be more independent of one another than currently appreciated.

4 | RANGE DYNAMICS OVER COMPLEX LANDSCAPES WITH CHANGING CLIMATE

We propose that the three factors discussed above—climate heterogeneity, climate collinearity, and spatial scale—critically influence

range dynamics. We examine the influences of these factors in turn and discuss how these dynamics may unfold across realistically complex landscapes in the context of a changing climate.

4.1 | Spatial heterogeneity in climate

Regional climate interacts with topography, soils, hydrology, and vegetation to generate complex patterns of climate variation across landscapes (Bramer et al., 2018; Dobrowski, 2011). Some regions are topographically simple, and therefore more spatially homogenous in climate (e.g., flat plains), while others are climatically complex due to topographic variation (e.g., mountainous regions; Figure 4). In examining how spatial climate heterogeneity influences species range edges, we are predominantly concerned with the total range of climatic variation that occurs in a given area, and the extent of patchiness in those conditions across the landscape (i.e., the likelihood of nearby patches having different climatic conditions).

Climate heterogeneity will influence whether species respond to a changing climate through persistence, movement, plasticity, and/or evolutionary adaptation. Climate refugia, which are areas that are decoupled from regional climate change patterns in complex landscapes, may reduce the local extirpation risk for organisms (Dobrowski, 2011). The potential for spatial buffering to reduce extinction risk has been shown to be especially important in areas with greater warming, for species that are most physiologically sensitive to changes in climate, and for species with limited dispersal (Suggitt et al., 2018). Furthermore, if nearby populations experience different climatic conditions due to high heterogeneity, dispersal among populations may lead to demographic inputs that promote population persistence despite unsuitable sink conditions in some locations (Gomulkiewicz, Holt, & Barfield, 1999). The scale of climate patchiness relative to species' dispersal distances also has important consequences for the potential for species to track climate change through range shifts. With a changing climate, shorter dispersal distances may be required for species to track their climatic niche in climatically heterogeneous landscapes (Ackerly et al., 2010; Scherrer & Körner, 2011). However, climatically heterogeneous landscapes may also lead to increasing fragmentation and isolation of suitable climatic conditions (Graae et al., 2018). At the scale of mountain ranges, valleys can act as significant dispersal barriers for species that are restricted to high-altitude conditions (Alexander et al., 2018; Dobrowski & Parks, 2016; White, 2016). Patches that are closest in geographic space (e.g., immediately downslope) may have very different climate regimes than patches that are further away (e.g., at the top of the next mountain).

Amplifications in the rate of climate change across topographic gradients (e.g., elevation-dependent warming; McCullough et al., 2016; Oyler, Dobrowski, Ballantyne, Klene, & Running, 2015; Pepin, Bradley, & Diaz, 2015) will destabilize the relationship between climate gradients and topographic gradients in heterogeneous terrain.

Nearby sites may become either more or less climatically similar (Walter et al., 2017). If climate becomes more homogenous, species' dispersal distances may need to increase to track their climatic niche as they move across broader spatial gradients (Scherrer & Körner, 2011). However, if changing climate increases climate heterogeneity (i.e., the isolation among regions with similar climates), selection may favor strategies that reduce dispersal, potentially generating an "ecological trap" in fragmented contracting range edges (Hargreaves & Eckert, 2014). Gene flow among climatically dissimilar populations is more likely in heterogeneous landscapes, but the magnitude of climate differences between adjacent patches will influence whether gene flow hinders or facilitates adaptation (Holt, 1996). In heterogeneous landscapes where climatically dissimilar environments may be in close geographic proximity, gene flow from geographically distant populations may be more likely to be beneficial (i.e., genetic rescue; Bontrager & Angert, 2018; Hufbauer et al., 2015; Whitlock, Ingvarsson, & Hatfield, 2000).

4.2 | Collinearity among climate variables

Collinearity describes the degree of statistical dependence among pairs of climate variables. Several factors will influence the degree of collinearity among climate variables, including latitudinal position, maritime-continental gradients, local variability in elevation, and which climate axes are being considered (Geiger et al., 2009). Collinearity will often be high for variables that are strongly and monotonically influenced by elevation and in areas where mountain terrain is the primary determinant of climate variation (e.g., the negative correlations between temperature and precipitation that occur across elevation in many mountain ranges; Körner, 2007), though the climate variables can be decoupled when leeward and windward sides of a mountain range are considered together (Körner, 2003). In contrast, orthogonality will be high when variables are controlled by different geographic factors; for example, temperatures decline with latitude in the North American Midwest, but rainfall varies east to west due to the dominant influence of the Rocky Mountain rain shadow. This variation in collinearity across landscapes will also be influenced by topographic complexity when climate variables exhibit different responses to latitudinal, elevational, and more fine-scaled topographic gradients (Barry & Blanken, 2016).

A more careful consideration of the multidimensional nature of climate, and specifically the collinearity among different climate axes, may help explain the apparently idiosyncratic patterns of range shifts that have occurred in response to climate change (Gibson-Reinemer et al., 2015; Lenoir & Svenning, 2015; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; VanDerWal et al., 2012). Recent work shows that multivariate climate experiments are crucial for determining population responses to climate change, as the response to one climate axis (e.g., temperature) can be highly dependent on another (e.g., moisture availability; Nicolaus, Wijmenga, Kempaers, & Dingemanse, 2018; Winkler, Chapin, & Kueppers, 2016). Furthermore, different life history stages may vary in their sensitivities to different

climate variables, so that range-wide population stability is determined by the interaction among multiple climate gradients (Oldfather & Ackerly, 2018; Pironon et al., 2018). As the climate variables driving range dynamics change through time, the relationship between climate variables (e.g., from collinear to orthogonal)—and therefore the relationship between climate and geography—may also change.

The complex relationships among multiple climate variables and species' climatic niches will impact the direction, velocity (Dobrowski et al., 2013; Ordonez et al., 2016), and magnitude of range shifts. Theoretically, if species have different sensitivities to different climate variables, even the ordering of species along a climate gradient can be reversed in response to climate change (Jackson & Overpeck, 2000). When climate variables are highly collinear across a landscape, range shifts in one direction (e.g., up or downhill) will result in strong changes along the dominant environmental axis, while movement in an orthogonal direction (e.g., along elevation contours) will proceed along climate isoclines. In contrast, range shifts in landscapes where climate variables are orthogonal will necessarily result in species experiencing a change in one or more climate variables. Where climate variables are highly correlated, range shifts may compensate for climate change if the two variables shift in time in the same way they are correlated in space (Ordonez et al., 2016). For example, where temperature declines and precipitation increases with elevation, an upward range shift can offset a warmer and drier climate. However, if conditions become warmer and wetter in the future, a species would need to move upward to offset the temperature change, and downward to offset the precipitation change, making it impossible to optimally track both climate variables in some landscapes. In a landscape with orthogonal variables, all combinations of different climate values could occur somewhere, potentially facilitating range shifts that can offset any future climate change (if dispersal is not limiting).

To illustrate the potential likelihood of collinear climate variables limiting species ability to biogeographically respond to climate change, we quantified the alignment between (a) the sign of the correlation (negative or positive) between two climate variables (mean annual temperature and total annual precipitation) across landscapes and (b) the sign of the correlation between two climate variables in the direction of predicted climate change, across multiple general circulation model (GCM) scenarios (Figure 5; see Methods S2 for analysis details). In landscapes with high alignment values, the climate collinearity and predicted change in climate allow for species to track suitable conditions in both climate dimensions with movement across the landscape. In divergent landscapes (low alignment values), the predicted change in climate runs counter to the spatial relationship between the climate variables so that tracking one of the climate variables would be in direct conflict with tracking the second. Sixty-two percent of landscapes globally exhibit divergence for more than half of GCMs, while 27% exhibit alignment for more than half (1% are tied). Highly divergent landscapes (exhibiting divergence across most future climate change scenarios) are most common in higher latitudes. If collinearity among climate variables hinders species' abilities to track suitable climate conditions via range shifts, they will need to rely on evolutionary adaptations to novel combinations of climate variables to avoid extinction.

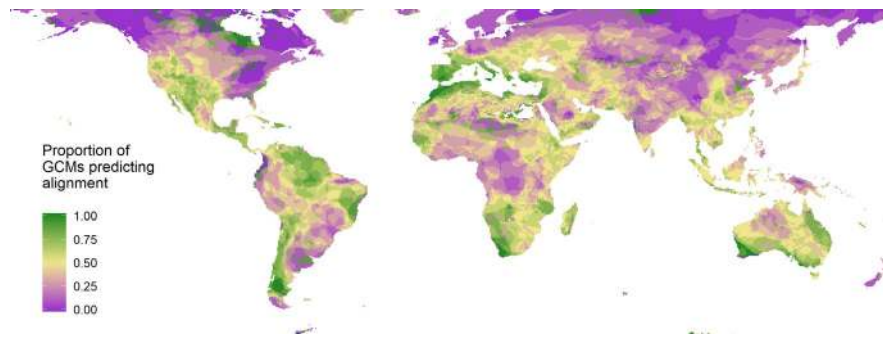


FIGURE 5 Alignment between the sign (negative or positive) of spatial climate collinearity of temperature and precipitation across a landscape and the sign of the direction of predicted temporal change in climate conditions. Values represent the proportion of general circulation models (GCMs) in an ensemble that predict alignment for a given landscape. Landscapes with high alignment values are expected to allow species to track suitable conditions in both climate dimensions with movement across the landscape. In contrast, landscapes with low alignment values limit species' ability to track suitable conditions as the tracking one of the climate variables would be in direct conflict with tracking the second. See Methods S2 for further details on this analysis

4.3 | Spatial scale

Spatial scale influences the relationship between geographic and climate spaces across landscapes by modifying climate heterogeneity and climate collinearity (Figure 4). The scale at which climate influences a species' distribution can be species-specific (Lembrechts, Nijs, & Lenoir, 2018) and depends on the ecology and mobility of the species (Soberon & Nakamura, 2009). Some have argued that studies investigating the role of climate in driving range edge dynamics should be at the spatial scale at which climate influences the population dynamics of the species of interest (McLean, Lawson, Leech, & Pol, 2016), as range dynamics will occur with local population extirpation and expansion in response to climatic, not geographic, conditions (Ehrlén & Morris, 2015). However, the predictions for future population persistence across a species range depend heavily on the extent to which populations across the species range are in equilibrium or disequilibrium with current climate (Hampe & Petit, 2005; Svenning & Sandel, 2013).

The magnitude of disequilibrium with climate can vary dramatically across scales due to shifts in the relative importance of different ecological and evolutionary processes determining range shifts. Constraints on species ranges due to reaching a niche limit are hypothesized to be more prevalent at smaller scales where environmental gradients are steeper, whereas dispersal may play a larger role in mediating species range limits at regional and global scales (Angert, Bayly, Sheth, & Paul, 2018; Hargreaves et al., 2014). Habitat availability or biotic interactions may be dominant drivers of population-scale range limits, whereas climate and dispersal limitation may be the primary drivers of range limits at larger spatial scales (Anderegg & Hille Ris Lambers, 2019; Sexton & Dickman, 2016). Both of these scenarios present the potential for disequilibrium dynamics between species distributions and climate, but vary in the processes likely driving these dynamics.

There are also many scenarios where the processes that limit a species range at one scale would interact with processes that drive range edges at other scales. For example, the location of an edge at local (population or subpopulation) scales may depend on proximity

to a broader scale range edge (e.g., shifts in species distributions to poleward-facing slopes at the low rainfall edge of the range; Boyko, 1947). At species-level range limits, responses of individual populations to climate change are predicted to shift to topo- or microclimates driven by fine-scale topography (Bennie et al., 2008). These fine-scale distribution shifts may lead to some counterintuitive responses to changing conditions at the scale of the entire species range: individuals that occupy the coolest topographic positions within a local landscape may be among the most vulnerable regionally, as they are at physiological limits and the dominant, surrounding warm-adapted species may easily outcompete them (Ackerly, 2003; Ackerly et al., 2020; Graae et al., 2018). Lastly, interactions among range-limiting processes across scales generate important feedbacks that are overlooked when only one spatial scale is considered at a time. For example, the magnitude of a broadscale disturbance may reduce the impact of fine-scale climatic heterogeneity on population persistence (Heffernan et al., 2014).

5 | CONCLUSIONS

Studies of species range edges often predict that geographically marginal populations are the most likely to expand or contract in response to climate change (Chardon et al., 2015; Hardie & Hutchings, 2010; Hargreaves et al., 2014; Vucetich & Waite, 2003). We challenge that notion, arguing that diverse relationships between geographic and climate space have important consequences for how species' climatic niches, dispersal, and biotic interactions unfold across a species range and ultimately determine where the range ends. We found that geographic and climatic edges are only weakly concordant across species ranges (Figure 3) and that climate heterogeneity and climate collinearity drive large variation in the possible relationships between climate and geographic distance even at a single scale (Figure 4). Furthermore, populations at geographic edges may represent a climate edge only in some parts of a species range (Figure 3), leading to high

extinction risk for species geographic range edge populations with a changing climate in some regions, but not others (Boakes, Isaac, Fuller, Mace, & McGowan, 2018). Consequently, a more nuanced understanding of the range-limiting processes themselves, and how they behave and interact in both geographic and climate space across realistically complex landscapes, may be necessary for the prediction of range shifts with climate change. We call for more empirical studies to consider how climatic heterogeneity, collinearity, and scale impact range dynamics, and the processes that drive them, when investigating species range shifts with a changing climate.

ACKNOWLEDGEMENTS

The authors thank K. Carscadden, M. Peterson, and two anonymous reviewers for helpful comments on earlier versions of this manuscript. This work was supported by NSF DEB-1553053, DEB-1457827, DEB-1637686, and DBI-1523866, as well as USDA National Institute of Food and Agriculture Hatch project 1016272. MMK was supported by an NSF Graduate Research Fellowship.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Oldfather MF, Kling MM, Sheth SN, Emery NC, Ackerly DD. Range edges in heterogeneous landscapes: Integrating geographic scale and climate complexity into range dynamics. *Glob Change Biol.* 2020;26:1055–1067. <https://doi.org/10.1111/gcb.14897>