Plant Ecol (2016) 217:1331–1344
DOI 10.1007/s11258-016-0603-z

Biotic forcing: the push–pull of plant ranges

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Received: 19 September 2015 / Accepted: 11 April 2016 / Published online: 21 April 2016

Abstract Scientists now recognize the importance of species interactions for range shifts, but lack general predictions about when and how species interactions influence shifts. The 'biotic envelopes' of plant species are defined by inter-specific interactions that influence their range limits. Two prominent hypotheses describe the biotic envelopes of plants by predicting that the outcome of inter-specific interactions is determined by climate, especially temperature and aridity. The first hypothesis posits that species distributions are structured by a trade-off between competitive ability and cold tolerance, so plant species exposed to warming climates will have trailing range edges that are limited by competitive interactions. The second hypothesis proposes that the effects of competition and facilitation from neighbouring plants change within a species range, such that facilitative interactions dominate in more environmentally stressful conditions; these facilitative interactions define leading range edges in a warming climate. We incorporate these hypotheses into a common framework that allows us to identify when mismatches in dispersal rates will lead to range expansion or contraction for a focal species. We provide general predictions about the biotic envelopes of plants, and how climate change will alter these envelopes, while highlighting uncertainties in applying these predictions beyond range edges.

Keywords Biotic interactions · Cold tolerance · Geographic distribution · Plant · Range shift · Stress gradient hypothesis

Introduction

Climate change is altering the latitudinal and elevational range limits of many species, often driving poleward and upward range shifts (Parmesan 2006; Chen et al. 2011). As a result, there has been renewed interest in species ranges and their underlying determinants (Gaston 2003; Louthan et al. 2015). Despite the growing number of climate change studies, forecasting species responses is challenging because we lack quantitative examples of how physiological tolerances and species interactions combine to structure current day communities across environmental gradients (Ewanchuk and Bertness 2002; Sexton et al. 2009).

Biotic interactions and dispersal work in conjunction with abiotic conditions to structure species ranges (Parmesan 2006; Hargreaves et al. 2014). For

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Communicated by Prof. Lauchlan Fraser.

Electronic supplementary material The online version of this article (doi:10.1007/s11258-016-0603-z) contains supplementary material, which is available to authorized users.

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example, competition can limit species ranges through both short-term ecological interactions and longer-term evolutionary dynamics (MacArthur 1972; Diamond 1975; Price and Kirkpatrick 2009). Even so, the abiotic environment, especially temperature and precipitation, is known as determinants of species distributions (Cain 1944). These factors do not function independently; it is well understood that the outcomes of competitive interactions depend on the environmental arena in which species interact (Taniguchi and Nakano 2000; Schemske et al. 2009).

Ecological theory posits that local abiotic conditions influence not only the outcome of competitive interactions, but also the *type* of species interactions that occur in a community (Bertness and Callaway 1994; Schemske et al. 2009). To date, studies of range limits have focused almost exclusively on antagonistic interactions: competition, predation and herbivory (Brown et al. 1996; Sexton et al. 2009). Despite this preoccupation with antagonistic interactions, positive interactions can be important for diversity patterns (Hacker and Gaines 1997), range delimitation (Callaway et al. 2002) and even facilitate expansion of range edges (Spasojevic et al. 2014; Cavieres et al. 2014; Grassein et al. 2014). For plants in particular, interactions among neighbours have often been shown to shift from competitive to facilitative as abiotic gradients change from relatively benign to stressful, suggesting facilitative interactions may be important for many plant species at more stressful range edges (Fig. 1) (Callaway and Walker 1997; Brooker et al. 2008; Richardson et al. 2012).

The changing types and importance of biotic interactions within a species range raises the possibility that the nature of the "biotic envelope", or the types and strengths of interactions that influence the range limits of a species, may be general to many species. This type of generalization requires that the net effect of biotic interactions on the ranges of plants across an abiotic environmental gradient (here we consider latitude and elevation) be broken down into its constituent parts. We define "biotic pushes" as the negative biotic interactions—specifically competition—that limit species distributions (Fig. 1). These biotic pushes decrease the realized range of species by 'pushing' species out of habitat that would be suitable in the absence of the interactions. In contrast, "biotic pulls" are positive biotic interactions—specifically intra-guild facilitation—that create the upper bounds of species distributions by 'pulling' plant species into habitats that would be unsuitable in the absence of neighbours (Fig. 1). The combined effects of biotic pushes and pulls on a species range are analogous to the reduction and expansion of the fundamental niche that result from biotic interactions, forming the realized niche (Bruno et al. 2003).

Despite widespread acknowledgement of the importance of biotic interactions for species ranges (Davis et al. 1998; Urban et al. 2012; Svenning et al. 2014), there has been a lag in experimental work applying these ideas to range shifts. For example, a recent meta-analysis provided evidence for the role of biotic interactions in structuring plant ranges, with negative interactions limiting species at lower range edges more than at upper range edges (Hargreaves et al. 2014). However, even this meta-analysis lacked sufficient studies to formally test the impact of biotic interactions at leading and trailing edges. Our own literature search of the most recent published literature on plant range limits revealed similar patterns (Fig. S1; Table A1). Of the sixteen manipulative experiments investigating plant ranges that were published since January 2013, four considered plant–plant interactions and only one of these transplanted species beyond both leading and trailing range edges. Despite the lack of experimental tests, almost every paper referred to the importance of biotic interactions in structuring ranges. Overall, this suggests that a general predictive framework could help motivate experimental work to test how biotic interactions at leading and trailing edges mediate range shifts.

Our objective is to explore how plant–plant interactions influence range shifts. We generalize plant range shift predictions by considering hypotheses concerned with the nature of species interactions across environmental gradients. The first, the Cold-Tolerance Competition Hypothesis (CTCH), posits that species' are limited by competitive interactions at the warmer range limit and intolerance to stressful cold conditions at the cooler range limit (Darwin 1859; Dobzhansky 1950; MacArthur 1972; Pianka 1966). The second is the stress gradient hypothesis (SGH), which states that the intensity of facilitative interactions increases with environmental stress (Bertness and Callaway 1994). Both relate specifically to the physiological tolerance limits of plants to temperature, and how temperature shapes the types and strengths of species interactions. Together, these hypotheses

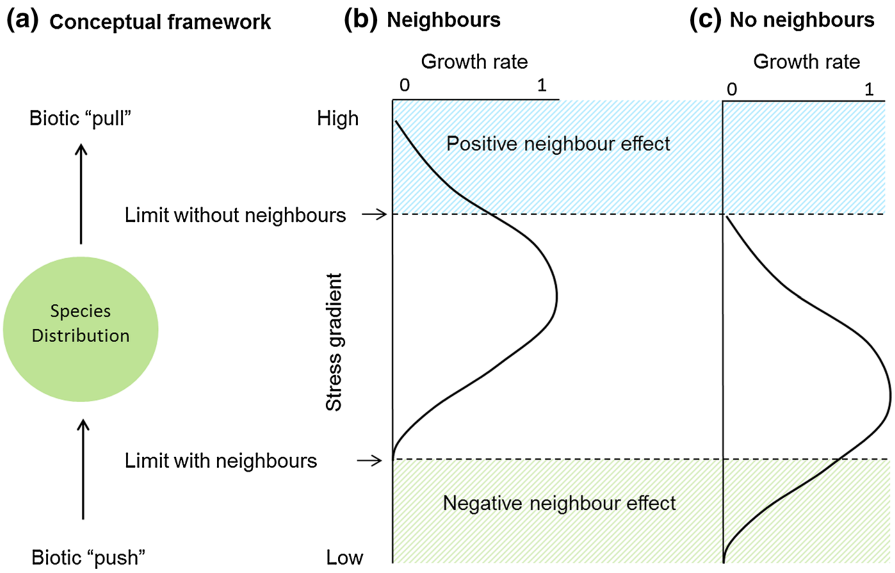

Fig. 1 Schematic depicting the relative impact of species interactions and abiotic stress (e.g. cold temperatures) on species distributions. **a** The southern portion of a species distribution is constrained by the competitive environment. This biotic "push" causes a negative growth rate, pushing the population towards local extinction. With climate change this could ultimately drive a contraction of the trailing edge of a distribution due to competitive interactions. The northern portion of a species distribution is governed by a biotic "pull". Here, facilitation reduces abiotic stress experienced by benefactors, expanding the northern distributional limit. **b** A hypothetical species distribution across a latitudinal or elevational gradient with neighbours. Here, the species can persist despite a negative growth rate in the absence of neighbours (*blue hashed area*). **c** The same hypothetical species as in **b** but with neighbours removed. The lower or southern limit of the distribution expands when competitive interactions are removed (*green hashed area*), whereas the upper (northern) limit of the distribution shrinks. The net effect of neighbour removal is a downward (southward) shift in the distribution of the species. (Color figure online)

generate the prediction that species interactions may not only exclude populations at the trailing edge of a species range, but also facilitate populations at the leading edge when ranges are structured by temperature gradients. In addition, the general predictions of the SGH suggests that it may apply to a broader range of climate change scenarios, such as areas in which range shifts are driven by increasing drought or other physical or abiotic stressors.

In this article, we present a testable conceptual model designed to stimulate experimental work on species interactions and plant range shifts. Below, we review evidence for the hypotheses that underlie the model and present a framework for empirical tests to characterize how biotic envelopes influence range shifts. We argue that differences in the dominant types of plant–plant interactions across environmental gradients will be influenced by climate change and affect range dynamics. Our framework deals specifically with plant–plant interactions and how these may be generalized across species ranges, but we also discuss how other types of interactions, such as plant-soil microbe interactions, can be incorporated into this framework.

Interactions across environmental gradients

Trade-offs in competitive ability and cold tolerance

Trade-offs in competitive ability and cold tolerance are often invoked to explain the distributional limits of species (Menge and Sutherland 1976; Case et al. 2005; Normand et al. 2009). Darwin was the first to suggest that the intensity of competitive interactions could be structuring communities to differing degrees across a latitudinal gradient, with latitude acting as a surrogate for temperature among other factors (Darwin 1859). Dobzhansky further advanced the CTCH by developing conceptual models of how harsh environments selected for species that could tolerate broad ranges of abiotic conditions but were weak competitors (Dobzhansky 1950; Pianka 1966). More recently, Grime presented this trade-off with an additional axis, disturbance, to explain the ecological distributions of species (the CSR model of plant strategies; Grime 1974, 1977). These arguments, in conjunction with coevolutionary models, provide a general mechanism that can account for greater diversity and greater competitive ability in warmer climates (Shemske 2009).

There are potentially many physiological constraints that could cause a trade-off between competitive ability in non-stressful environments and tolerance to stressful environments. For instance, tree species have been shown to have a trade-off between elevated freezing tolerance and growth rates, which has been interpreted as support for the CTCH (Loehle 1998; Koehler et al. 2011). Annual plants have shown similar trade-offs along water gradients, where competitive species dominate when rainfall is frequent, but are replaced by drought-tolerant species when rainfall is sparse (Novoplansky and Goldberg 2001). Similarly, annual plant species that experience variable rainfall among years often develop seed banks that ensure long-term persistence even when some years result in reproductive failure. This bet-hedging strategy lowers the mean and variance in population growth rates among years (Cohen 1968; Ellner 1985; Venable 2007). Importantly, while seed banks ensure survival in fluctuating, harsh environments, they reduce population growth rates in more stable environments, generating a trade-off between tolerance and competitive ability. Together these trade-offs support the role for physiological trade-offs between stress tolerance and competitive ability that underlie both the SGH and CTCH.

The CTCH is a compelling hypothesis for range distributions because it provides predictions that can be tested both within and among species. In the CTHC, 'cold tolerance' is interpreted broadly as any strategy that allows a species to persist in cold environments, from physiological adaptations to freezing, to resistance to breakage by snow loading, to an herbaceous perennial strategy that avoids aboveground exposure in winter months. When considering multiple species, the trade-off between cold tolerance and competitive ability could map directly to species range distributions (Fig. 2a), with these different factors quantified using population growth rates with and without competitors. Within species, the CTHC predicts that species should be limited at lower latitudes by competitive interactions with neighbours (Fig. 3; antagonistic interactions), and at higher latitudes by abiotic stresses associated with the cold climate, such as a short growing season and frost damage.

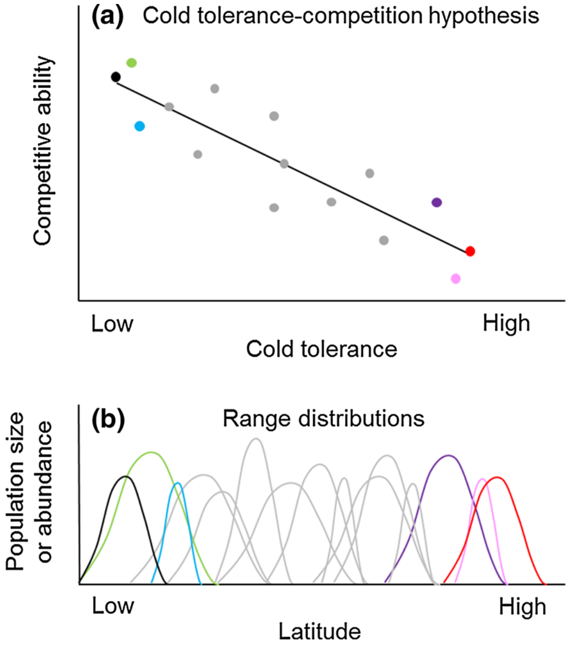

Fig. 2 **a** The cold-tolerance competition hypothesis (CTCH) can be tested for large numbers of species by evaluating a trade-off between cold tolerance (fitness in the absence of competitors) and competitive ability (fitness in the presence of competitors). **b** species' distributions, here drawn as unimodal distributions for simplicity, reflect this trade-off with lower range limits defined by low competitive ability (i.e. species' are displaced because population growth rates are negative with competitors but positive in the absence of competition). Species in **a** are drawn in the same horizontal position in **b**, with species at either end *marked* with specific *colours* for clarity. (Color figure online)

Evidence for the CTHC is mixed, in part because it is rarely fully evaluated in empirical studies. Competition has been shown to form range limits in a number of studies (Case et al. 2005), but comparisons of the importance of abiotic and biotic factors at northern and southern limits (as proposed by the CTCH) are lacking (Sexton et al. 2009). For example, consistent with a trade-off, studies testing for an association between temperature and occurrence across an environmental

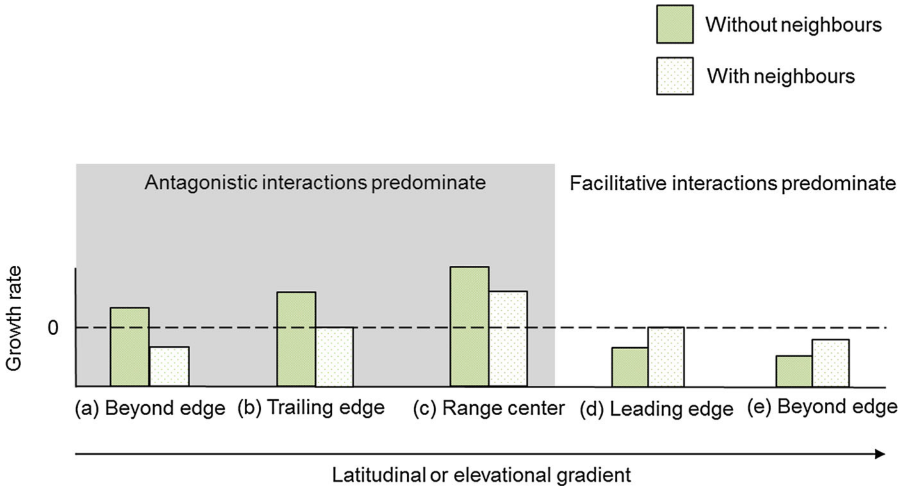

Fig. 3 Predictions for the response of plant populations to the presence or absence of a neighbour across a stress gradient, here we consider a latitudinal or elevational gradient. We consider 'range center' to measure viable populations between the range edges. Plant communities originate from populations across their latitudinal or elevational range. The focal species is grown at a common density in the presence or absence of a neighbour across their range. For each range location, the predictions are as follows: (*a*) beyond the trailing edge, the focal species has a positive growth rate only in the absence of neighbours, (*b*, *c*) at the trailing edge and range centre, the focal species has a greater, positive growth rate in the absence of neighbours, (*d*) at the leading edge the growth rate becomes negative in the absence of a neighbour, and (*e*) beyond the leading edge, in the absence of neighbours, growth rate decreases further

gradient have found that low temperatures and high snow pack often limit distributions at the northern and high elevation range limits (MacDonald et al. 2000). However, they normally do not explicitly test how local factors such as competition impact distributions, therefore failing to appropriately test for a trade-off (Lavergne et al. 2010; Ettinger et al. 2011; Hargreaves et al. 2014).

Despite the lack of formal tests in the literature, there are several examples of trade-offs in response to environmental conditions that inform the generality of the CTCH. For example, Ettinger and colleagues studied adult trees to test the biotic and abiotic drivers of range limits across an elevation gradient on Mt. Rainier, U.S.A. (Ettinger et al. 2011; Ettinger and HilleRisLambers 2013). The authors found some evidence that was consistent with predictions of the CTCH, but results varied among species. For instance, high elevation species were strongly limited by climate at the upper edge of their distribution but not at the lower edge. However, this pattern did not hold for lower elevation species (Ettinger et al. 2011). Similarly, of three species tested for the effects of competition, only one showed evidence that competition was more limiting at the lower edge (Ettinger and HilleRisLambers 2013). The approach taken by Ettinger and colleagues, which is similar to a single species approach (Fig. 3), can be expanded to examine competitive abilities among species as well as cold tolerance. Indeed, as such studies increase, they may present the opportunity to compare cold tolerance and competitive ability among large numbers of species, thus offering a robust test of the trade-off that underlies the CTCH (Fig. 2a).

Positive interactions and range shifts

Facilitative interactions are rarely invoked to explain range sizes (Brooker et al. 2007; Le Bagousse-Pinguet et al. 2014), yet it is well understood that plants in some communities facilitate neighbours by ameliorating the local environment (Brooker et al. 2008). The SGH proposes that the net effects of facilitative and competitive interactions vary inversely across abiotic stress gradients, with facilitation increasing in high stress conditions (Bertness and Callaway 1994).

The first global test of the SGH provided some of the most compelling support for a shift from negative to positive interactions as elevation increased, supporting the hypothesis that cold-related environmental stress increases facilitation (Callaway et al. 2002). Using neighbour removal experiments, the authors showed that focal species had higher biomass, fecundity and survival at high elevations when neighbours were present but that neighbours generally depressed performance at low elevations. Although evidence for the SGH across elevational gradients is not ubiquitous (e.g. de Bello et al. 2011), meta-analyses show that positive interactions increase on average at higher elevations and latitudes (Kikvidze et al. 2011; He et al. 2013). For species at or close to their range limits, these trends suggest that facilitative interactions could expand range limits in stressful conditions (e.g. higher latitude or higher elevation) beyond those that would occur in the absence of species interactions.

In semi-arid regions, water availability often determines plant ranges, and climate change is predicted to alter this stress gradient in many parts of the world (IPCC 2013). In these systems, facilitative interactions often come in the form of shading, where shrubs ameliorate hot conditions for seedlings or herbaceous plants by reducing rates of evaporative water loss and increasing soil moisture levels (Gómez-Aparicio et al. 2004). For example, the leading edge of Scots pine occurs in northern Europe where low temperatures determine northern range limits (James et al. 1994). However, the southern distribution extends into the Mediterranean basin in south-eastern Spain where relic populations persist on mountain tops—in these environments, shrubs facilitate seedling survival and as a result, recruitment occurs where shrubs are present (Castro et al. 2004). Despite many such examples, facilitative interactions need not increase at lower rainfall in semi-arid environments (Maestre and Cortina 2004; Maestre et al. 2005; Lortie and Callaway 2006), in part because some species respond to gradients other than moisture (Lortie and Callaway 2006; He et al. 2013). The results of work in semi-arid environments suggest that the importance of facilitation depends on the degree to which species are limited by the abiotic gradient studied, but overall shows an increase in facilitation with stress (Lortie and Callaway 2006; He et al. 2013).

Although the SGH has been tested by ecologists in many habitats, it has only recently been recognized that facilitative interactions may be important for range shifts (He et al. 2013; Michalet et al. 2014; Spasojevic et al. 2014). Importantly, tests of the SGH provide evidence for increased competitive interactions in more favourable environments as well as evidence for facilitative dynamics in stressful environments (He et al. 2013). This is because experiments testing the SGH are designed to isolate the net effect of plant interactions across a stress gradient. Indeed, the SGH approach of quantifying fitness with and without neighbours across a gradient is similar to that required for testing the CTHC when abiotic stress is driven by a colder climate at one range edge (Fig. 3b–d). Although incorporating facilitation into range shift hypotheses may appear to make an already-complex problem intractable, the generality of the SGH and thus the predictability of competitive and facilitative dynamics with environmental change promise to simplify predictions (see *How biotic interactions affect species range shifts* below). Recent consideration of facilitative interactions for range limits (Brooker 2006; Spasojevic et al. 2014) promises to follow a more general shift in the ecological literature that incorporates positive interactions into existing ecological paradigms (Bruno et al. 2003).

How biotic interactions affect species range shifts

Testing the generality of biotic pushes and pulls across species ranges

The incorporation of biotic interactions into range shift hypotheses has been slow, in part because the strength and nature of species interactions can vary by location and species. Our conceptual framework generalizes the biotic envelope that encompasses species' ranges in terms of the strength of biotic pushes and pulls along latitudinal or elevational gradients (Fig. 1a). Although other interactions clearly impact species distributions (see "Expanding the biotic envelope" below), we propose this framework as a method to test long-standing ecological hypotheses and generate predictions for species range shifts.

When cold-associated abiotic stress limits species ranges, negative species interactions are hypothesized to depress the population growth rate of the focal species at low latitudes, and the strength of this negative interaction increases as this stress decreases. This elevated competitive environment creates the trailing edge of the focal species' range (Fig. 1b). Importantly, because the competitive effect creates negative growth rates at the trailing edge, experimental removal of neighbours would allow the establishment and persistence of the focal species beyond its lower range limit (Figs. 1c, 3a, b). Although this hypothesis follows from the CTCH, it has not been tested sufficiently (Hargreaves et al. 2014). In contrast, at the high latitude edge of the range, plants experience relatively high abiotic stress that is ameliorated by facilitative interactions (Fig. 1b). Here, neighbours increase the survival and growth of the focal species in marginal habitats, as has been shown in several studies of the SGH (He et al. 2013). This effectively pulls the distribution to higher latitudes or elevation, meaning that removing neighbours would drive local extirpation of the focal species at its current upper range limit (Figs. 1c, 3d, e).

The experimental set-up outlined in Fig. 3 can also be used to clarify how the relative strength of fitness differences and stabilizing differences (sensu Chesson 2000) shift across a species range. At the coarsest level, growing a species at low abundance in the presence of neighbours determines whether a species can establish when locally rare; this is the definition of the invasion criteria for the focal species and has been used to predict persistence of species in many types of ecological communities (reviewed in Siepielski and McPeek 2010). The invasion criteria is the basis for Chesson's framework for coexistence, and this measure therefore captures the net effect of fitness and stabilizing differences from the perspective of the focal species (Chesson 2000; Levine and Hille Ris Lambers 2009). Importantly, unless the focal species experiences an allee effect, which can generate priority effects, the invasion criteria also predict whether a species could persist at even higher densities (Mordecai 2011). In addition, a species' maximum rate of increase is often assessed by growing a focal species in the absence of competition (Levine and Hille Ris Lambers 2009). This measure is correlated with a species absolute fitness (Godoy and Levine 2014). Finally, comparing the focal species growth rate in the presence and absence of competition across the range allows the researcher to quantify the impact of intra-specific competition across the range (Alexander et al. 2015), which is another component of fitness (Godoy and Levine 2014). In other words, the experimental design proposed in Fig. 3 is well suited to understanding whether the invasion criteria is met for a focal species, but does not provide an estimate of the invasion criteria for the extant community if the focal species were to invade.

Geographic variation in the nature of species interactions can be implicitly incorporated into our conceptual model (Fig. 1) by recognizing that most range edges correspond to changes in the abiotic environment (Hargreaves et al. 2014). As a result, the abiotic gradient can be expanded to include other forms of stress, such as drought, so long as there is a species-level trade-off between stress tolerance and competitive ability that is analogous to the CTCH trade-off (Fig. 3). For example, research on annual plant species in the Sonoran desert has shown a trade-off among species in water use efficiency and relative growth rate that is consistent with this hypothesis (Huxman et al. 2008; Angert et al. 2009). The convergence of water use efficiency rates across biomes suggests that this trade-off may also be conserved across biomes (Huxman et al. 2004), and thus be applied as generally as the CTHC. Because precipitation and temperature singly or jointly limit vegetative growth (Schultz and Halpert 1993), incorporating these two factors into a common framework for range limits could allow an assessment of general trends. Nonetheless, the manner in which these limiting abiotic factors covary and interact needs to be considered for the correct implementation of this framework, and large-scale analyses of vegetation dynamics provide a starting point for these considerations (Schultz and Halpert 1993; Potter and Brooks 1998).

Determining how climate change modifies the strength of the biotic pushes and pulls

When abiotic conditions change across a species' range, the importance of facilitative and competitive interactions on a population's growth rates at each edge of the range are also expected to change. This process could shift the entire biotic envelope if any increase in facilitative dynamics at the leading range edge is matched by an increase in competitive impacts at the trailing edge. Alternately, the changes to the relative importance of facilitative and competitive interactions may not be symmetric, causing either facilitation or competition to dominate the process of range shifts through subsequent expansion or contraction. For example, if competition in the trailing edge has a larger negative impact than facilitation or relaxed competition in the leading edge, we would observe a shift towards competitive exclusion that causes the range size to contract across the biotic envelope (Alexander et al. 2015).

The direct effects of temperature change may well alter biotic envelopes through changes in temperature variation and heterogeneous changes in mean temperature around the world. For example, variation in temperature is predicted to increase in many parts of the world, and this variation is often more stressful to species even if they experience an identical mean temperature (Vasseur et al. 2014). As a result, the proportion of the biotic envelope that is dominated by biotic pulls may increase because of increased variation in temperature. Spatial patterns of temperature change may also systematically alter the biotic envelope, as mean increases in temperature are amplified in polar regions (IPCC 2013). In this case, species biotic envelopes are expected to experience greater change towards negative interactions at high latitudes relative to low latitudes, thus decreasing the overall importance of biotic pulls across the range. Climate change driven shrub expansion in the arctic tundra is an example of dynamics that are consistent with this phenomenon (Elmendorf et al. 2012b). The impact of shrubs on vegetation can vary by species and life form (Walker et al. 2006; Pajunen et al. 2011). For shade intolerant species, shrubs alter competitive dynamics by increasing competition for light. The results of a recent global analysis provide support for the increased role of competitive interactions in shrub understories, with superior competitors for light increasing in abundance over the last 30 years (Elmendorf et al. 2012a). The concurrent reduction in abundance of many shade intolerant and more northerly species (mainly lichens and mosses) suggests that the biotic envelopes of this functional group are shifting to greater competition. Whether there are also shifts in facilitation with shrub expansion for more southerly species is yet to be determined in these systems.

The second process that affects the biotic envelopes of species is a difference in the rate of movement of interacting species (e.g. Urban et al. 2012, 2013). In the simplest case, interacting species will experience equal rates of movement, and the strength of biotic pushes and pulls will reflect abiotic constraints unless the strength of interactions within the recipient community shift (e.g. Alexander et al. 2015). However, asymmetries in dispersal rates can change the biotic envelope, potentially creating temporal lags in which the negative effects of biotic pushes are relaxed for a period, increasing range size or biotic pulls disappear, causing range sizes to collapse. These asymmetries depend on the relative movement rates of a focal species, its competitors and facilitators, and the velocity of climate change across the species range (Brooker et al. 2007; Loarie et al. 2009; Alexander et al. 2015). As an example, imagine a mid-latitude plant species that is unable to track the velocity of climate change and has lower dispersal ability than its lower-latitude competitors. As higher temperatures push communities' poleward, competitors increasingly compress the range of the focal species through competitive interactions (Alexander et al. 2015). In extreme cases, this effect can drive the extinction of the focal species by encompassing its entire range in the biotic push zone (Urban et al. 2012). The same phenomenon can occur at the poleward range limit, but in this case, it would require the facilitating species to have a small initial range size and lower dispersal (Brooker et al. 2007).

Although in many cases, climate change will push species distributions poleward, it is important to recognize that in some situations, climate change is expected to move species away from areas that were previously dominated by biotic pulls. As an example, many arid regions are expected to become drier with climate change (Schlesinger et al. 1990; Cook et al. 2004; IPCC 2013). Stress amelioration via facilitation is important for species persistence in these ecosystems and could buffer the impact of climate change in these regions (Bellot et al. 2001; Brooker et al. 2008). In this scenario, the trailing edge, and its maintenance, will depend on the rate of movement of facilitating species. If the presence of facilitator species' such as nurse plants maintain positive growth rates, the rate of range contraction at the trailing edge will be dampened (Schöb et al. 2013; Michalet et al. 2014; Cavieres et al. 2014). As a result, the dispersal rates of the facilitating species in these regions will determine how ranges contract at the trailing edge.

Expanding the biotic envelope

One of the greatest challenges for ecologists is to determine the structure of the biotic envelope. The framework we have presented is powerful for plants because of its generality. However, the focus on plant–plant interactions that forms the SGH and CTHC does not account for other types of species interactions that also influence the biotic envelope (e.g. Bruno et al. 2003; Weber et al. 2005; Memmott et al. 2007; Nathan et al. 2008). Although the effects of interactions with other groups of species have not been generalized across environmental or latitudinal gradients, there are a number of these interactions that appear important to species ranges (Gaston 2003; Case et al. 2005; Holt and Barfield 2009). We explore three of the prominent interactions that plants experience: interactions with animal dispersers, local microbial partners and herbivores. Plant-pollinator interactions, which are also important determinants of the biotic envelope for many plant species, have been fully reviewed elsewhere (Memmott et al. 2007; Hegland et al. 2009; Burkle et al. 2013).

The facilitation of dispersal

Seed dispersal by animals is an underappreciated aspect of plant ranges (Urban et al. 2013), despite its importance for population dynamics (Nathan et al. 2008). In many cases, animal dispersers carry seeds very short distances (Howe and Smallwood 1982). However, rare long-distance dispersal events by animals are important and have often been invoked to explain rapid expansion of tree ranges following glacial retreat (Clark et al. 1998). In addition, long-ranging species that only occasionally ingest a focal plant's seeds may generate infrequent long-distance dispersal events (Fragoso 1997; Vellend et al. 2003). For example, deer occasionally dispersed trillium seeds more than three kilometres, despite some seeds being destroyed in the deer gut (Vellend et al. 2006). These cases of long-distance dispersal provide a solution to Reid's paradox, the asymmetry between post-glacial ranges of temperate plants and their limited mean dispersal distances (Reid 1899; Clark 1998), and suggest that the ability of plants to track climatic conditions will be mediated by interactions with their dispersers.

When plant and animal species respond similarly to climate change, the fidelity of animals to the plants they disperse could lead to differences in plant colonization rates. On one hand, generalist feeders that forage broadly may have a reduced impact on plant range dynamics, at least in the short-term, for two reasons (Angert et al. 2011). First, each species makes up a small proportion of the animal's overall diet, and the likelihood of dispersal may therefore be low. Second, even when animals disperse beyond the range of their plant food source on a shorter timescale, the timing of foraging within the plant's extant range must coincide with the production of fruit, which is unlikely unless the animal is actively targeting the focal plant. In contrast, specialist animal dispersers could enhance range shifts (Cunze et al. 2013), effectively acting as a biotic pull by accelerating range expansion. For example, the passenger pigeon is hypothesized to have facilitated range expansion in a number of eastern North American nut trees following glacial retreat, and these nuts provided an important part of their autumn diet (Webb 1986). To date, the implications of animal dispersal on the range shifts of plants remain unclear but it is amenable to comparative tests, and its potential importance raises questions about biogeographic patterns of dispersal modes.

Herbivory and range dynamics

Recent research has recognized that herbivory should be integrated into range shift studies (Holt and Barfield 2009). Herbivores directly impact plant performance (Crawley 1989; Maron and Crone 2006) and sometimes even delimit plant range edges (Scheidel and Bruelheide 1999; Lavergne et al. 2005). For example, Bruelheide and Scheidel (1999) transplanted *Arnica montana* populations below their altitudinal range limit in the Harz mountains of Germany. The authors found that mollusc herbivory resulted in up to 70 % leaf damage compared with 8 % at higher elevations, where populations naturally persist. In a separate study, the same group conducted palatability trials comparing the preferences of three slug species to twenty co-occurring plants. They determined that *A. montana* was among the most preferred by molluscs (Scheidel and Bruelheide 1999). Together, these studies suggest that range limits can be driven by trophic interactions and could therefore modify the dynamics of range shifts.

Herbivore pressure has long been hypothesized to increase towards the equator (Dobzhansky 1950; Schemske et al. 2009), suggesting that it could be systematically incorporated into range shift predictions. However, a recent meta-analysis shows no support for this hypothesis, with rates of natural herbivory being no different on average across latitude (Moles et al. 2011). Studies included in this meta-analysis and other studies have shown clear latitudinal trends in herbivore pressure for specific species, but they appear to be idiosyncratic and suggest that herbivory can impact both the leading and trailing edges of plant distributions (Dyer and Coley 2002; Salazar and Marquis 2012).

Plant-soil feedbacks and range expansion

Plant-soil feedback experiments have demonstrated the importance of soil microbes for community membership (Weber et al. 2005; Kardol et al. 2006; Fukami and Nakajima 2013), dominance relationships (Klironomos 2002) and invasion (Pringle et al. 2009). The role of soil biota in mediating range shifts is less understood (Van Grunsven et al. 2007). Recently, the enemy release framework, where escape from soil pathogens allows non-native species to establish in novel habitats, has been extended to temperature-induced range shifts (Van Grunsven et al. 2010). Because plants disperse faster than the soil microorganisms they are associated with, range expansion could allow individuals at the leading edge to enjoy a period of enemy release.

In the first study to apply these concepts to native species shifting their ranges poleward, Van Grunsven and colleagues manipulated the soil biota of a range expanding species, *Tragopogon dubius* and its widely spread congener *T. pratensis*, across their latitudinal ranges in Europe (Van Grunsven et al. 2010). They found a reduction in the negative plant-soil feedback for *T. dubius* in its newly colonized range, whereas the widespread *T. pratensis* experienced negative feedbacks across its range. The specific mechanism remains unknown as both a reduction in plant specific pathogens (Klironomos 2002) or an increase in the effectiveness of arbuscular mycorrhizal fungi (Bever et al. 1997) could cause the observed pattern. However, this study stresses the importance of belowground interactions for the expanding ranges of plants and represents a biotic pull that can operate in concert with climate change. Just as slow dispersal of pathogenic soil microorganisms can aid range expansion, specialized plant-soil feedbacks that increase the fitness of a plant can be left behind the range front of a shifting species (Levine et al. 2006). In these cases, the biotic pull that would be exerted by the mutualist are absent, which can slow the expansion of the focal species range (Weber et al. 2005).

Conclusion

Incorporating species interactions into tests of range limits and range shifts is important for understanding the mechanisms that maintain species distributions and thus how climate change will modify ranges. Our framework attempts to address this by merging the impact of the abiotic environment on species distributions with the nature of species interactions across environmental gradients to predict how climate change will modify range boundaries. There are a variety of ways in which species interactions and responses to the abiotic environment can combine to alter population dynamics, population persistence and species ranges (Gilman et al. 2010; Gilbert and O'Connor 2013; HilleRisLambers et al. 2013; Jones et al. 2013; Gilbert et al. 2014). We propose that the relative strengths of pushes and pulls that make up the biotic envelope change predictably across plant species ranges in many ecosystems, and explain how this hypothesis is both general and testable.

Our framework can also be expanded to generate new hypotheses about the consequences of climate change on range shifts when there is specific information about how the climate is changing. For example, the strength of biotic pushes at the trailing edge are predicted to increase at higher temperatures, elevating the risk of extinction through competition at the trailing edge of many species ranges. Although careful experimental manipulations are required to test these hypotheses, recent studies have proposed exciting new approaches in plant ecology (e.g. Alexander et al. 2015). By reframing existing hypotheses to explicitly link changes to species distributions and the nature of species interactions, we will be better positioned to isolate the proximate causes of extant range limits and more accurately predict range shifts.

Acknowledgments We would like to thank Marc Johnson and Andrew MacDougall for providing helpful feedback on a previous version of this paper. We also thank NSERC for funding (BG, Discovery Grant) as well as Ontario Graduate Scholarships (NTJ).

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