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The geographic footprint of mutualism: How mutualists influence species’ range limits

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Abstract

Understanding mechanisms that generate range limits is central to knowing why species are found where they are and how they will respond to environmental change. There is growing awareness that biotic interactions play an important role in generating range limits. However, current theory and data overwhelmingly focus on abiotic drivers and antagonistic interactions. Here we explore the effect that mutualists have on their partner's range limits: the geographic "footprint" of mutualism. This footprint arises from two general processes: modification of a partner's niche through environment-dependent fitness effects and, for a subset of mutualisms, dispersal opportunities that lead suitable habitats to be filled. We develop a conceptual framework that organizes different footprints of mutualism and the underlying mechanisms that shape them, and evaluate supporting empirical evidence from the primary literature. In the available literature, we find that the fitness benefits and dispersal opportunities provided by mutualism can extend species' ranges; conversely, the absence of mutualism can constrain species' from otherwise suitable regions of their range. Most studies find that the footprint of mutualism is driven by changes in the frequency of mutualist partners from range-core to range-edge, while fewer find changes in interaction outcomes, the diversity of partners, or varying sensitivities of fitness to effects of mutualists. We discuss these findings with respect to specialization, dependence, and intimacy of mutualism. Much remains unknown about the geographic footprint of mutualisms, leaving fruitful areas for future work. A particularly important future direction is to explore the role of mutualism during range shifts under global change, including promotion of shifts at leading edges and persistence at trailing edges.

Keywords: mutualism, range limits, biogeography, dispersal, demography, context-dependence

Introduction

Every species has limits to its geographic distribution. This distribution is the area in which a species can persist and/or to which it can disperse (Sexton et al. 2009; Hargreaves, Samis, and Eckert 2014). The study of range limits aims to understand why distributions are where they are, and to predict how they may change with changing environmental conditions.

Abiotic factors are most often invoked as the drivers that create and maintain range limits. However, recent work has called for renewed attention to the importance of biotic interactions in setting species' ranges (Wisz et al. 2013; Louthan, Doak, and Angert 2015; Early and Keith 2019; Sirén and Morelli 2020; Alexander et al. 2022). Their importance has long been recognized: von Humboldt (Morueta-Holme et al. 2015; Humboldt and Bonpland 1807), Darwin (Darwin 1859), Connell (Connell 1961), and MacArthur (MacArthur 1984) all recognized the potential for biotic interactions to influence species' ranges. However, research in this area has focused overwhelmingly on antagonistic interactions such as competition and consumption, with far less attention paid to mutualisms, mutually beneficial interspecific interactions (Paquette and Hargreaves 2021).

The influence of mutualism on range limits has been alluded to in scattered case studies and theoretical models (Afkhami, McIntyre, and Strauss 2014; Araújo and Rozenfeld 2014; Godsoe et al. 2017). A recent review of such studies has called for a synthetic framework to organize and understand the mechanisms by which the broad spectrum of mutualistic interactions can affect range limits (Stephan, Mora, and Alexander 2021). Such a framework is even more urgent as the planet undergoes rapid environmental change, causing the ranges limits of many species to shift (Cunze, Heydel, and Tackenberg 2013; Sittaro et al. 2017; Freeman et al. 2018). Forecasting such shifts is a pressing ecological challenge, and meeting it requires a mechanistic understanding of the processes by which range limits arise. Here, we present a conceptual framework and literature synthesis to explore the role that mutualisms play in shaping species' distributions and modifying range limits — that is, the geographic footprint of mutualism.

The defining features of mutualism

To understand how mutualisms can create geographic footprints, it is helpful to first consider the natural history of these interactions, including features that unify all mutualisms as well as the axes of variation along which different mutualisms fall. We define mutualisms by the exchange of resources and services between partners in ways that reciprocally enhance fitness. We define population mean fitness as the geometric rate of population growth λ (Caswell 2001), which connects mutualism to population viability and the niche (the range of conditions that can support viable populations, i.e., $\lambda \geq 1$). Mutualism enhances fitness via demographic vital rates such as survival, growth, and reproduction, which combine to determine λ.

The resources that mutualists exchange are richly diverse, including rewards such as food or biochemical products, and services such as protection, dispersal or housing (Boucher 1985; Bronstein 2015). Providing these resources to partners incurs energetic, physiological, and/or ecological costs; the balance of costs and benefits on each side of the interaction determines the overall strength and symmetry of mutualism, as well as the likelihood that it will shift towards antagonism if costs exceed benefits for one or both partners. Mutualism manifests at the scale of a species pair (+/+), but pairs of mutualists are embedded within multi-species communities. A single mutualist can engage simultaneously or sequentially with multiple partner species that may differ in the quality of goods or services they provide (Palmer et al. 2010; Batstone et al. 2018), and entire communities can engage in complex networks of mutualistic interactions (Bascompte and Jordano 2007).

Mutualisms and mutualists vary across three axes that are likely to influence how the interaction affects range limits: dependence, specialization, and intimacy. First, mutualism may be obligate for one or both partners if the resources exchanged are required for survival or reproduction, or facultative if mutualist-derived resources are beneficial but not essential. Second, mutualists range from being highly specialized, such that possible partners are limited to one or a few species, to being generalized with many interacting partners. Third, mutualisms vary in intimacy, ranging from symbiotic (in which one partner lives in or on the other) to free-living (in which partners must find one another in space and time). These features differ depending on which partner's perspective is considered. For example, in the mutualistic symbioses between aphids and microbes (*Hamiltonella* spp.), the interaction is obligate for the symbiont but facultative for the host (Henry et al. 2015). Similarly, in pollination mutualisms, generalized plants commonly interact with specialized pollinators and vice versa (Brosi 2016). Consequently, in analyzing how mutualism affects range limits, one must be specific about which partners' range is the focus.

In the sections that follow we first take a unilateral perspective, focusing on the range limits of one focal species and contrasting its distribution with and without its mutualist(s). We then shift to a bilateral perspective, considering the feedbacks through which mutualist partners can influence each other's distribution. We focus primarily on stable species' distributions; in the Discussion we return to the idea of how mutualists may influence non-stationary ranges, which is particularly relevant for invading species or those whose ranges are shifting in response to environmental change. While our framework is intended to be general to all mutualisms, different positions along the axes of dependence, specialization, and intimacy provide different vantage points for interpreting how mutualism affects range limits, and of which mutualistic partner. We draw inspiration and support for our conceptual framework from the published literature, and cite empirical examples to illustrate particular ideas and mechanisms. We present summary results from a literature synthesis to assess empirical support for key features of our framework. We note that mutualisms in the literature may be a biased sample of mutualisms in nature. Our goal is to assess evidence for effects of mutualists on species' range limits, the direction of these effects, and the mechanisms underlying them. One key takeaway is that much of this research identifies or suggests effects of mutualism on species' ranges, but only rarely are these effects quantified. Finally, we discuss fruitful directions for future research based on gaps in current knowledge.

A General Framework: Geographic footprints of mutualism arise from niche modification and dispersal

The range limits of any given species can be understood by answering two questions: (1) What are the environmental conditions in which that species can maintain at least replacement-level population growth ($\lambda \geq 1$)? and (2) Can the species disperse to (and perhaps beyond) these suitable environments? The first question defines the limits of the niche; the second determines the extent to which the niche is "filled", i.e., how much of the environmental space where $\lambda \geq 1$ is occupied. These two elements of a species' distribution roughly correspond to the classic concepts of fundamental and realized niches, which contrast distributional limits without and with, respectively, the influences of species interactions and dispersal limitation (Pulliam 2000). However, for obligate mutualisms, these classic concepts can be difficult to apply (what is the fundamental niche of a species that cannot persist without a mutualist?). In Appendix S2, we discuss various niche concepts as they relate to mutualism and geographic distributions.

Mutualism can affect range limits via two processes: *niche modification* and *dispersal* (Fig. 1). First, niche modification refers to the change in the niche of a focal species due to mutualism; such changes reflect the fitness benefits of mutualism and how these benefits differ according to environmental conditions. For example, many facultative mutualisms enhance fitness more strongly in stressful environments than in benign ones. In this way, mutualism can ameliorate stress along environmental gradients, rendering harsh environments more suitable (Afkhami, McIntyre, and Strauss 2014) and extending or shifting niche limits of a focal partner. Niche modification has a different interpretation for obligate mutualisms because these mutualist partners serve as essential niche dimensions (Bruno, Stachowicz, and Bertness 2003; Koffel, Daufresne, and Klausmeier 2021). In these cases, the availability of partners imposes a hard limit on which environments can or cannot sustain populations. Whether through facultative benefits or obligate dependence, mutualism can alter the environmental limits of population viability ($\lambda \geq 1$) with consequences for geographic distributions (Fig. 1A).

Second, a subset of mutualisms additionally involves dispersal opportunities. The most thoroughly studied cases involve seed dispersal by frugivorous animals, in which the plants gain a fitness advantage, e.g., by being moved away from the maternal plant (Harper 1977) or by escaping enemies (Janzen 1969). For other mutualisms, dispersal may occur as a byproduct of the interaction, such as when beneficial symbionts disperse with their host (Wornik and Grube 2010). Since dispersal limitation can cause realized geographic distributions to fail to fill the niche (Sexton et al. 2009; Lee-Yaw et al. 2016), mutualisms that promote dispersal should increase the likelihood that the niche is filled, all else being equal (Fig. 1B). However, it is also important to consider dispersal biases and how mutualist-mediated movement of the dispersed partner can change across its niche. For example, frugivorous animals can deposit seeds nonrandomly in micro-environments that are favorable (Wenny and Levey 1998) or unfavorable (Gómez, Puerta-Piñero, and Schupp 2008; Razafindratsima and Dunham 2015) for plant recruitment. At large geographic scales, dispersal mutualisms may “overfill” the niche if dispersers consistently carry partners to sink environments, or “underfill” the niche if disperser movement does not allow partners to reach some suitable environments (Howe, Davis, and Mosca 1991; Foppen, Chardon, and Liefveld 2000; Pulliam 2000). Thus, we define over- and underfilling, respectively, as occurrence in environments beyond niche limits ($\lambda < 1$) and lack of occurrence in environments within niche limits ($\lambda \geq 1$).

Through niche modification and/or dispersal, mutualism can lead to four possible outcomes, or “footprints”, at the biogeographic scale. We define a footprint as the difference in a species’ geographic distribution attributable to mutualism. Mutualism may *extend*, *contract*, *constrain*, or have *no effect* on the range limit of a focal species (Fig. 2). First, range extension should occur when the presence of mutualists (+M) allows a focal species to occupy a greater area than it could without mutualists (-M), either due to mutualist-mediated niche extension or due to dispersal mutualism that extends the distribution by moving the dispersed partner beyond niche limits, overfilling the niche (Fig. 2A). Second, mutualism can contract the partner’s range if the interaction outcome shifts from mutualism to antagonism from the range core to the range edge, particularly when partners are obligate, or if dispersers actively move propagules away from the range edge (Fig. 2B). Third, mutualism can constrain the range: instead of costly interactions contracting the range, beneficial or essential mutualists may be absent from areas that would otherwise be habitable (Fig. 2C). In this third scenario, mutualism may have beneficial effects on a species’ distribution relative to the absence of mutualists (-M vs +M), as in range extension, but at the same time lack of mutualists in potentially suitable habitat may constrain the range relative to a scenario in which partners are more widely available (+M vs ++M) (Fig. 2C). Finally, it is possible that mutualists provide strong fitness benefits or movement opportunities for the focal species within the range core, yet have no effect on range limits (Fig. 2D). This would happen if mutualism were to shift to have negligible fitness benefits towards the range edge while prevailing abiotic factors set the range limit. Which of these outcomes occur should depend on how niche modification and dispersal respond to environmental drivers that vary from core to edge. We next explore niche modification and dispersal in greater depth as they relate to these four footprints, including underlying mechanisms and evidence in the available literature.

Literature Overview

Here, we give a brief overview of the literature review that we performed (see Appendix S1 for a full description of literature review methods, results, and biases). In brief, we compiled studies published up to the end of September 2021 by searching Web of Science and following citations that examine mutualism in the context of range limits and environmental gradients, which we screened for observational and experimental studies across environmental conditions along species' ranges, corresponding to latitudinal, longitudinal, or elevational environmental gradients. To the best of our knowledge, we excluded studies of invasive species and other species principally dispersed by human activities to focus on stationary range limits assumed to be in a dynamic equilibrium with the environment. We identified 57 studies of niche-modifying mutualism and 27 studies of dispersal mutualism, which we then categorized according to their support for different footprints, as well as mechanisms by which the mutualisms contribute to those footprints. We also categorized these studies according to their degree of interaction specialization and dependence. The majority of these studies were conducted in North America or Europe (Fig. 3). In addition to geographic biases (discussed also in Stephan et al. 2021), the compiled research shows taxonomic biases: specifically, the current literature focuses nearly exclusively on the range limits of terrestrial plants (Fig. 4; Appendix S1: Table S1, Appendix S1: Table S4). Among dispersal mutualisms, studies of seed dispersal by animals, particularly by birds and ants, far outnumber other types of dispersal, comprising 26 out of 27 studies (Appendix S1: Table S4). It is important to recognize that this body of literature is not representative of the frequency and diversity of mutualistic interactions in nature. Nevertheless, these empirical examples are illustrative of key context-dependent mechanisms by which mutualists can affect species' range limits.

Context-dependent mechanisms of mutualist-mediated niche modification

"Niche modification" implies that mutualism changes which environments are suitable for replacement-level population growth (Fig. 1A). Our literature review shows that niche modification has been commonly documented and contributes to the footprints of mutualism described above (Appendix S1). Out of 57 studies of mutualist-mediated niche modification at range limits, 23 (40%) present data consistent with range extension (Fig. 2A) and 25 (44%) consistent with range constraint (Fig. 2C) (Appendix S1: Table S2). Compared to range extension, range constraint is more frequent in mutualisms that are specialized and/or obligate (Appendix S1: Table S2), in line with the findings of Stephan et al. (2021). The remaining studies are consistent with either no range effect (Fig 2D) (5 studies; 9%) or range contraction (Fig 2B) (4 studies; 7%).

The mechanisms of niche modification fall under the general umbrella of context dependence (Catford et al. 2021), whereby interactions vary in an environment-dependent manner. As a starting point, consider a mutualist that is equally available and beneficial to a focal species across its range. Such a mutualism would be context-independent. It could, in theory, expand the niche of the focal species: by elevating fitness equally across all environments, otherwise challenging edge locations may become more suitable through mutualism (Fig. 1A), leading to range extension. It is unlikely that any interaction is truly independent of context, but it is possible that some interactions may not vary meaningfully over the environments in which they occur (Chamberlain, Bronstein, and Rudgers 2014; Maron, Baer, and Angert 2014). Studies of *Astragalus utahensis,* a pollen-limited plant with population growth rates that decline with decreasing precipitation towards its northern range edge, illustrate the effects of context-independent fitness benefits (Baer and Maron 2018; 2019). Baer and Maron (2018) find that hand-pollination treatments, mimicking the effects of a consistent mutualist across environments, yield equivalent per-capita benefits across the range. The benefits from this treatment elevate population growth rates in marginal populations at the northern range edge where growth rates are near replacement levels and suggesting the pollination extends the distribution, but also elevates growth rates in the range center (Baer and Maron 2018).

A more common type of niche modification occurs when some feature of the interaction depends on environmental context. Context dependence emerges from at least four non-mutually exclusive (and often intertwined) mechanisms that can alter the niche of a focal partner: changes in interaction frequency, interaction outcome, partner diversity, and vital rate sensitivity (Fig. 5). These are the same general mechanisms of context dependence by which negative species interactions influence range limits (Louthan, Doak, and Angert 2015; Early and Keith 2019; Louthan et al. 2018). Here we discuss these mechanisms through the lens of mutualism.

Interaction Frequency: The availability of mutualist partners and thus the frequency of beneficial interactions can vary across environments. Changes in interaction frequency could be driven by changes in the abundance of partners or the number of encounters per capita. At the extreme, mutualists can be entirely absent from range-edge environments, and thus low interaction frequency may constrain the distribution of a partner that would otherwise be able to establish. Within the literature on niche modification that we reviewed, context-dependent shifts in interaction frequency were the most commonly described mechanism contributing to mutualism's geographic footprints (44 out of 57 studies; 77%) (Appendix S1: Table S3).

Pollination mutualisms provide several examples for how changes in interaction frequency modify a niche by affecting the environments in which a species successfully reproduces. Harrower and Gilbert (2018) suggest that the elevational distribution of Joshua trees (*Yucca brevifolia*) in Joshua Tree National Park is constrained by the absence of their obligate moth pollinators at high and low elevation extremes that are otherwise suitable for the plants (Harrower and Gilbert 2018). Across latitudes in North America, northern range edge populations of another yucca species (*Y. glauca*) are potentially constrained by declining abundance of their moth pollinators (Hurlburt 2001; 2002). Similar processes limit populations of Asian fig species, such as *Ficus virens*, at their northern range edge, where their obligate pollinating wasp occurs less frequently (Fig. 5A) (Zhang et al. 2014; Wang et al. 2015; Chen et al. 2018). In these examples, obligate, specialized pollinating insects provide a non-substitutable service by which plants reproduce, so the absence of mutualists at extreme altitudes or latitudes is an important constraint on the plants' range limits. Stephan et al. (2021) suggest that this type of range constraint is particularly likely for specialized interactions. However, similar patterns can also occur in more generalized mutualisms. For example, pollen limitation likely contributes to range limits of obligately outcrossing *Clarkia xantiana ssp. Xantiana* in California, for which abundance and visitation of generalist pollinators declines toward range edges, coinciding with declines in population growth rates (Moeller et al. 2012).

Interaction Outcome: Even with no change in interaction frequency, the per-capita effect of mutualism on fitness, or interaction outcome, may change across environments. The Stress Gradient Hypothesis describes how interaction outcomes may shift from negative to positive along gradients of increasing environmental stress (Bertness and Callaway 1994; Maestre et al. 2009). While heavily studied in the context of the competition-facilitation continuum within plant communities (Armas, Rodríguez-Echeverría, and Pugnaire 2011） and to a lesser degree in animal communities (Fugère et al. 2012; Beaudrot et al. 2020), ideas about interaction outcomes becoming increasingly positive with increasing stress apply to mutualisms more broadly, especially protective mutualisms that may become neutral or costly in enemy-free environments (Palmer et al. 2008; 2017).

Interaction outcomes that become more positive in stressful conditions hold the potential to shift or expand the niche and thus the geographic distribution (Fig. 2). In a landmark demonstration of mutualist-mediated range extension, Afkhami et al. (2014) show that benefits of symbiosis with a heritable fungal endophyte strengthen with increasing drought stress for the California grass *Bromus laevipes* (Fig. 5B). Consequently, plants with fungal symbionts experience higher survival than symbiont-free plants under drought conditions along a precipitation gradient, extending the host species' range limits by ~20% into regions that would otherwise be too arid to support viable populations (Afkhami, McIntyre, and Strauss 2014). Context-dependent outcomes can also work in the opposite direction, with the strongest benefits in the range core and no effect or negative effects at environmental limits (Fig. 2). For example, facultative symbiosis with algal symbionts benefits the coral host, *Astrangia poculata,* under warmer temperatures but becomes costly under colder conditions, a response that contributes to contracting the host species' northern range limit (Dimond et al. 2013).

Overall, 23 of the 57 niche modification studies we reviewed (40%) report that changes in interaction outcomes contribute to mutualism's effects on range limits (Appendix S1: Table S3), commonly contributing to range extension (9 of 23 studies; 39%) (Appendix S1: Table S3). Many of the studies consistent with range constraint (9 of 23 studies; 39%) document weaker interaction outcomes on a per-capita basis towards range edges coinciding with declines in partner frequency towards range edges (Appendix S1: Table S1). It is likely that both mechanisms contribute to these range effects, as weaker interaction outcomes can drive low interaction frequency, making the two mechanisms difficult to distinguish without experimental manipulations. Observations alone cannot tell us whether low partner frequency at range edges occurs because of negative interaction outcomes, or whether they are absent for other reasons (e.g. dispersal limitation) but would otherwise be beneficial.

Partner Identity and Diversity: Mutualism often involves guilds of interacting species (Palmer, Stanton, and Young 2003). In a geographic context, partner identity may turn over along environmental gradients. Partner turnover can determine the environments in which mutualism is more or less beneficial, since partner identity can be an important source of variation in the fitness consequences of mutualism (Batstone et al. 2018; Chomicki, Kiers, and Renner 2020). For example, the tropical plant *Embrothrium coccineum* is pollinated by both hummingbirds and bumblebees. Hummingbirds are more effective pollinators, but only bumblebees tend to persist towards dry range edges; the decline in quality of pollination service likely contributes to the species' range limit (Chalcoff, Aizen, and Ezcurra 2012). In other cases, partners may confer equivalent services, in which case partner turnover may expand rather than constrain niche opportunities for a focal species. For example, in the lichen *Lasallia pustulata*, the identity of the dominant algal symbiont turns over along latitudinal (Rolshausen et al. 2018) and altitudinal (Rolshausen et al. 2020) gradients, allowing the fungal partner to persist in a wider range of environments than would be possible with only one algal partner.

Beyond partner identity, partner diversity may be consequential for fitness across species' ranges if the community of mutualist partners as a whole provides benefits to a focal species that exceed the additive effects of single partner species (Palmer et al. 2010; Batstone et al. 2018). When the community of mutualists has synergistic effects on the fitness of a shared partner, the gain or loss of diversity towards the edge of a species distribution has the potential to influence the shared partner's range limit. For example, surveys of root-associated fungal diversity for two Eastern North American tree species show declines in partner diversity from the center to the edge of their ranges, which is hypothesized to contribute to constraining the species' range limit (Lankau and Keymer 2016).

Twenty-nine of 57 studies we reviewed (51%) report changes in the community of partner species or partner diversity that contribute to mutualism's effects on range limits (Appendix S1: Table S3), frequently among more generalized and facultative interactions (Appendix S1: Table S1). By interacting with a community of mutualists, partner turnover affects fitness through changes in the frequency of interactions with each partner over an environmental gradient. Thus, a diverse portfolio of partner species may allow a focal mutualist to persist across a broader range of environments, as in the lichen example. This is reflected in our literature search: shifts in the availability of diverse partners across conditions most often contribute to range extension (17 of 29 studies; 59%) (Appendix S1: Table S3).

Vital Rate Sensitivities: The final mechanism by which mutualism can alter the niche in a context-dependent manner does not require any changes in mutualism at all. Mutualists enhance fitness via their effects on demographic vital rates (θ), which collectively determine fitness. The sensitivity of fitness to these underlying vital rates ($d\lambda/d\theta$) can vary across different parts of a species' geographic range (Angert 2006; Angert 2009) even if the effect of mutualism on vital rates ($d\theta/dM$) does not. Because the overall fitness effect of mutualism ($d\lambda/dM$) incorporates both the sensitivity of vital rates to mutualism and the sensitivity of fitness to vital rates ($d\lambda/dM \cong d\theta/dM \times d\lambda/d\theta$), effects of mutualists on vital rates may be constant across the range but the effect of mutualism on fitness may nonetheless vary due to variable vital rate sensitivities (Fig. 5D).

Empirical studies that examine the contributions of vital rate sensitivities to the demographic effects of mutualism are rare (only 3 of 57 studies; Appendix S1: Table S3). In one such study, simulating increased pollination of *Hibiscus meyeri* along an aridity gradient does not improve population growth towards the drier end of its distribution due to decreased demographic sensitivity to seed production at the range edge (Fig 3D) (Louthan et al. 2018). It is unclear whether changes in vital rate sensitivity are less important than other context-dependent mechanisms, or just less studied because they require a more complete demographic analysis.

Context-dependent mechanisms of mutualist-mediated dispersal

Thus far, we have focused on the fitness-enhancing aspects of mutualism that alter the niche and thus geographic limits of a focal species. Dispersal mutualisms enhance fitness, of course, but they hold additional potential to influence the other element of geographic range limits: the ability of the dispersed partner to reach areas throughout and beyond its niche. Unlike niche modification, which is general across all types of mutualisms, dispersal is limited to a subset of mutualisms. The most familiar of these are food-for-dispersal mutualisms in which one partner provides rewards in exchange for movement; although best studied in plants and seed dispersers (e.g., Gómez et al. 2022), dispersal is a benefit in other interactions as well (e.g. the movement of fungal spores by mammals (Kotter and Farentinos 1984); the movement of nectar microbes by pollinators (Russell et al. 2019); and the movement of algal symbionts by coral reef fish (Grupstra et al. 2021)). While the fitness implications of movement and handling of propagules by dispersers may be diverse (Beckman et al. 2019; Shaw, Narayanan, and Stanton 2021), we focus on mutualist-mediated movement *per se*. Throughout this section, the focal species is the partner that is dispersed by a mutualist. The vast majority of our dispersal literature review involved seed dispersal (Appendix S1: Table S4), and so most often we focus on the range limits of the plant partner.

Whether and how dispersal mutualism affects range limits depends on where dispersers carry their partner (or their partner's offspring) relative to that partner's niche. Mutualistic dispersal has the potential to extend range limits of the focal species by filling its niche, or potentially overfilling it by maintaining the presence of the dispersed partner in sink habitats ($\lambda<1$; Fig. 1B). For example, simulations suggest that the distributions of many large-seeded tree species in South America are overfilled relative to their niche limits as a result of substantial seed dispersal by large-bodied herbivores (Doughty et al. 2016). By contrast, dispersal may underfill the niche when areas outside of the realized distribution are suitable for population persistence ($\lambda\geq1$) but are not accessible, a phenomenon true of dispersal generally and not only mutualist-mediated dispersal (Seliger et al. 2021).

Consider a mutualistic disperser that is widely available and equally effective throughout the range of a sessile, focal partner species. All things equal, increased movement provided by dispersers should tend to increase the probability of occurrence of the sessile partner across its niche (Fig. 1B). For example, a suite of plants that have been adopted by Indigenous peoples in the Southwestern US for agriculture more completely fill their climatic niches than congeners that have not been adopted for agriculture (Flower et al. 2021). Rapid plant migrations into habitats abandoned after agricultural use provide evidence for the ability of dispersers to increase movement and facilitate niche-filling at biogeographic scales. For example, movement of *Trillium grandiflorum* seeds by deer has contributed to post-agricultural forest re-colonization throughout the plant's North American range (Vellend et al. 2003). Extinctions of disperser species similarly show the role that dispersers play in promoting a partner's occupancy of suitable habitat (Rogers et al. 2021).

Dispersal by mutualists clearly holds the potential to increase occurrence within a species' niche, but often in ways that are non-random, leading to uneven patterns of occurrence across niche space (Gómez et al. 2022). These biases in the magnitude and direction of dispersal arise from behaviors and habitat preferences of dispersers (Zwolak 2018). Within forest sites in Madagascar, for example, dispersal by frugivorous lemurs moves seeds into a broader set of habitats than would have been achieved without lemur dispersal; however, random seed dispersal would have moved seeds to an even broader set of habitats (Razafindratsima and Dunham 2015), suggesting that the dispersal mutualism, while beneficial, leaves the plant's niche underfilled. Such disperser biases can also affect movement over larger-scale environmental gradients. For example, seasonal fruiting phenology causes Asiatic black bears (*Ursus thibetanus*), the primary dispersers of Japanese cherry (*Prunus verecunda*), to consistently move seeds upslope, potentially facilitating upslope climate migration (Naoe et al. 2016). However, a broader suite of mammal dispersers across elevation gradients in Japan tend to move seeds downhill (Naoe et al.

2019). In these cases, biased dispersal would tend to overfill the distribution in one direction (Fig. 2A).

For these reasons, rigorously evaluating the geographic footprint of dispersal mutualism requires understanding where dispersers move partners (or their offspring) relative to the partner's niche. However, this is not always known at spatial scales relevant to geographic distributions. Among the 27 studies we found that empirically tested the effects of dispersal mutualism on species' range limits, 18 (67%) relate dispersal outcomes to the niche of the dispersed partner (Appendix S1: Table S4). Among these studies, ten (56%) reported evidence of niche underfilling (Appendix S1: Table S5) (transplants or propagules could persist when brought beyond the range edge), suggesting that dispersal mutualism constrains or contracts range limits (Fig. 2B-C). Three studies (17%) provided evidence of overfilling by dispersers, consistent with range extension (Fig. 2A), and five (28%) found that dispersers filled but did not overfill their partners' niches (Fig. 2D).

Next, we describe mechanisms that underlie how environmental context within local habitats or across large-scale environmental gradients can shape dispersal distance and direction and thus influence distributional limits. Environmental drivers can lead to changes in the frequency, outcome, and diversity of dispersal interactions (Fig. 6), in ways similar to how those drivers contribute to niche modification. With respect to dispersal, we do not discuss vital rate sensitivities because this mechanism of context dependence is explicitly tied to fitness effects.

<u>Interaction Frequency</u>: It is well-documented that the frequency and availability of dispersal partners of plants can vary among habitat types and across environmental gradients (Jordano 1993). Overall, change in partner frequency from range-core to edge is the most commonly documented mechanism of context dependence in our collected literature (23 out of 27 dispersal

studies (85%)) (Appendix S1: Table S6). Dispersal may occur more frequently in environments with increased disperser abundance and vice versa. For example, declines in the abundance of the tropical seed predator/disperser *Heteromys desmarestianus* towards higher elevations coincide with the low abundance of the palm species *Astrocaryum mexicanum* that it consumes (Klinger and Rejmánek 2010). The authors hypothesize that low frequency of dispersal may drive declining abundance of the plant at high elevation (Fig. 6A). However, the opposite may also be possible, suggesting the need for experimental manipulations that can disentangle cause and effect (Klinger and Rejmánek 2010). Similarly, the range of the perennial herb *Sternbergia clusiana* is restricted at least in part by the lack of its ant seed dispersers beyond its range edge along a latitudinal soil moisture gradient. As a consequence, *S. clusiana* is not found in areas where it could persist if established, and its environmental niche is therefore underfilled (Ben-Zvi, Seifan, and Giladi 2020). This study is one of the few that measures the effects of dispersal while also conducting transplant experiments to measure the niche (Appendix S1: Table S4). Of the 18 studies that quantify the niche, 10 (56%) are consistent with changes in interaction frequency leading to underfilled niches, and thus range constraint (Appendix S1: Table S6).

<u>Interaction Outcome</u>: Environment-dependent patterns in movement may also occur if dispersers are distributed equally across the range but change their movement direction or distance depending on local conditions. For instance, spotted nutcrackers (*Nucifraga caryocatactes)* can fly long distances and act as dispersers of Swiss stone pine (*Pinus cembra*), but tend to cache seeds only within the current elevational distribution of the tree (Fig. 6B) (Neuschulz et al. 2018; Merges et al. 2020). A similar dynamic has been observed for Clark's nutcracker (*Nucifraga columbiana*) with Whitebark pine (*Pinus albicaulis*) (Tomback 1982; Richardson, Brunsfeld, and Klopfenstein 2002). For Swiss stone pine, although spotted nutcrackers were potentially present

beyond the range edge and the pines had high germination beyond the upper range limit, the nutcrackers' movement patterns influenced the outcome of dispersal and restricted the range limits of the tree. Across studies in our literature review, these types of movement outcomes are the least common mechanism recorded as contributing to geographic footprints (7 of 27 studies (26%)) (Appendix S1: Table S6), although this likely reflects the difficulty in quantifying the movement outcomes of dispersal (Schupp, Jordano, and Gómez 2010; Beckman et al. 2019).

Interaction Diversity: The diversity of dispersal partners may have a large influence on how dispersers move propagules across the distribution of a focal species. As in niche-modifying mutualisms, turnover in partner identity may affect range limits. For example, two ant species that differ in their phenology and ability to disperse shared plant partner species occupy warmer (southern) and colder (northern) regions of the Southeastern US; the southern ants, *Aphaenogaster rudis*, which forage later in the season, have shifted their ranges with warming temperatures to the north, displacing the northern, early-season foraging ant species, *Aphaenogaster picea* (Warren and Chick 2013). In transplant experiments across this boundary, the dispersal of early-seeding plant partners is limited due to phenological mismatch between the plants and the late-foraging ants, constraining the plant species' range limit (Warren and Bradford 2014). It may often be difficult to distinguish between the effects of partner turnover and dispersal partner diversity *per se*. For instance, the diversity of seed-dispersing ant species declines across elevation, likely driven by decreasing temperatures, potentially affecting plant range edge dynamics (Fig. 6C) (Sanders et al. 2007; Zelikova, Dunn, and Sanders 2008).

A bilateral perspective: interdependence of mutualist ranges

We have focused thus far on the range limits of one focal mutualist, mirroring the emphasis of most existing studies in our synthesis of the literature, and indeed most studies of mutualism

(Bronstein 1994; 2015). However, to fully understand the footprint of mutualism, it is necessary to consider distributions and niche limits of both partners simultaneously. Here we extend our conceptual framework to consider the interdependence between partner species' distributions.

Mutualists can differ in their responses to environmental variation in ways that influence the potential of co-occurrence. That is, the environmental tolerances of two partner species might or might not match. Across their ranges, species' niches may be mismatched when their individual physiological requirements do not completely overlap, hindering their ability to interact in some environments (Pateman et al. 2012; HilleRisLambers et al. 2013). Niche mismatch is implicit in our discussion of shifts in interaction frequency, where a focal mutualist gains or loses interactions with a partner species in different parts of its distribution (Fig. 5A; Fig. 6A). In addition to the niche of each partner species being set by its own environmental tolerances, the presence of mutualists themselves may set their partner's niche (Koffel, Daufresne, and Klausmeier 2021). This mutual dependence and the match or mismatch of environmental tolerances holds potential to generate feedbacks between the ranges of partner species, and the strength of these feedbacks should depend on the symmetry of their dependence and specialization.

A bilateral perspective is essential in reciprocally obligate mutualisms, those in which both species require their partners for survival and/or reproduction. The changes in interaction frequency leading to range constraint in the case of *Yucca brevifolia* across elevations in Joshua Tree National Park (Harrower and Gilbert 2018), for example, might be explained by niche mismatch. In that study, the moth partners were observed to occupy a narrower elevation range than the plants and may have a narrower abiotic tolerance (Fig. 7A). It may be useful to measure the physiological tolerances of partners independently. This has been done in growth chambers under high (Huxman et al. 1998) and low temperature extremes (Loik et al. 2000) for the yucca, but not, to our knowledge, for the moth pollinators. In cases like this, where partners depend on each other obligately and symmetrically, their joint distribution -- and thus the mutualism -- should occur only over the environments that are within their shared environmental limits. Peay (2016) called this shared niche space the "mutualistic niche", to contrast to the "individualistic niche" that characterizes species' physiological requirements independent of mutualism (Appendix S2).

The influence of positive feedbacks between mutualists on range limits is likely weaker when their dependence is asymmetric. A specialized mutualist is likely to be limited by the physiological tolerance of its partner, but the reverse is less likely to be true if its partner is a generalist (Fig 7B). For example, specialized oil-secreting orchids are limited by low pollinator visitation at the edge of their distribution (Pauw and Bond 2011). However, the bees that pollinate these orchids tend to be generalists, such that the distribution of the pollinators likely constrains the range of the plant but not vice versa.

A bilateral perspective is also essential for dispersal mutualisms, in which feedbacks between the ranges of partners are likely to arise in cases of strong and symmetric dependence. Many seed dispersers track their food resources in ways that suggest feedbacks between plant and animal range limits, including birds (Galetti, Laps, and Pizo 2000), primates (Tutin et al. 1991), and other mammals (Naoe et al. 2019). In the cases of pine seed dispersal by nutcrackers, a specialized mutualism (Tomback 1982), the birds disperse seeds up to but not beyond the range limits of the trees. In these specialized interactions, plants may influence the distribution of their dispersers as much as the other way around (Richardson, Brunsfeld, and Klopfenstein 2002;

Merges et al. 2020). These feedbacks should be weaker when dispersal is more generalized, where dispersers do not track specific resources (Baltzinger, Karimi, and Shukla 2019).

Discussion and Synthesis

We have presented a conceptual framework that integrates mechanisms of environmental context dependence into demographic theory to explore the role of mutualism in influencing species' range limits. It is clear from this framework and from our synthesis of a growing body of research that mutualism can generate a geographic footprint. On the one hand, the fitness benefits and dispersal opportunities of mutualism can expand a focal partner's niche and contribute to filling or overfilling the niche, respectively -- extending range limits in ways that mirror the negative range effects of antagonistic interactions. On the other hand, lack of mutualism constrains geographic ranges, especially when partners provide essential and non-substitutable goods or services. This tension generates questions that we expect will stimulate further research. We structure the following discussion around three overarching questions that emerge from our conceptual and empirical synthesis.

How large or small is the geographic footprint of mutualism?

While theory and data point to a potentially important influence of mutualism on range limits, this influence has almost never been quantified. Instead, the empirical literature primarily documents mechanisms, such as trends in interaction frequency or outcome across environmental gradients (Schupp, Jordano, and Gómez 2017; Rogers et al. 2019; Beckman et al. 2019; Gómez et al. 2022) that are qualitatively suggestive but not quantitatively demonstrative of geographic patterns. The study of *Bromus laevipes* and its fungal endophyte is the sole study, to our knowledge, that provides a quantitative estimate for how and where mutualism changes a species' range (Afkhami, McIntyre, and Strauss 2014). Across the many studies documenting patterns consistent with range constraint, none has quantified how much of a species' potential range is unoccupied due to lack of mutualism, information that would be useful in decision-making for conservation and management as partner species shift their ranges (Dawson et al. 2011; Kerr 2020). Even the qualitative inferences we are able to glean from the literature -- how often mutualists are likely to extend, contract, constrain, or have no effect on the range limits of their partner (Tables S3,S6) -- will be strongly influenced by representation of different types of mutualism in the literature (e.g., specialized and obligate mutualisms are commonly associated with range constraint but may be over-represented in the literature relative to their occurrence in nature) and by submission or publication biases against "non-significant" results (i.e., the finding of "no effect on range limits" is relatively rare in the literature). Thus, on a fundamental level, the geographic footprint of mutualism and its distribution across systems are not well known.

We see two main avenues of opportunity for advancing understanding of how mutualism affects range limits: through experiments and through modeling. Experimental approaches are essential for disentangling whether changes in the interaction between mutualists approaching range limits are a cause or a consequence of those limits. For example, the observation that birds disperse seeds up to but not beyond a plant's range limits (Neuschulz et al. 2018; Merges et al. 2020) could mean that dispersers generate the range limit, respond to a limit generated by some other process, or a combination of the two. Elucidating the role of mutualists in range limits will require experimental designs that accommodate the potential for both extending and/or constraining effects. Most current experimental approaches either add or exclude mutualists from a focal partner, but not both. Combining addition and exclusion treatments in a single experimental design, and replicating this across environmental gradients from range core to range edge, could be highly informative in systems where those treatments are feasible. Improved range-edge performance under mutualist addition would suggest a constraining influence of mutualism, while depressed range-edge performance under mutualist exclusion would suggest an extending influence (e.g., Hargreaves, Weiner, and Eckert 2015). There is also an important role for beyond-edge transplant experiments (Stanton-Geddes and Anderson 2011; Warren and Bradford 2014), as has been recognized in studies of range limits more generally (Sexton et al. 2009; Hargreaves, Samis, and Eckert 2014). Data from these transplant studies can be used to quantify whether a species' range limit is dispersal-limited and the degree to which a species' distribution is filling its niche. In cases where lack of mutualists constrains range limits from otherwise suitable habitat, this may be impossible to detect without bringing the focal species beyond its observed range limit and adding or simulating the service of its mutualist. Transplant experiments conducted in parallel with dispersal studies will also be valuable for understanding whether dispersal mutualism fills, overfills, or underfills the niche. Similar approaches have been employed in dispersal studies at small spatial scales (Razafindratsima and Dunham 2015), but are rarely conducted across the large geographic scales relevant to species' range limits (Warren and Bradford 2014; Neuschulz et al. 2018; Mortelliti et al. 2019; Ben Zvi, Seifan, and Giladi 2020; Merges et al. 2020).

Experimental manipulations may suggest a direction in which mutualism affects a species' range. However, quantifying that influence will almost always require modeling approaches that translate empirical results into geographically explicit predictions. The *Bromus laevipes* case study (Afkhami, McIntyre, and Strauss 2014) relied on species distribution modeling (SDM) to contrast host geographic distributions with and without symbiotic mutualists. While more data-intensive than SDMs, mechanistic range models based on demographic responses to environmental variation (Merow et al. 2014; Miller and Compagnoni 2022) will be an essential next step in this field. Mechanistic range models can embed the influence of mutualism on specific vital rates into the context of the complete life cycle and provide a more rigorous platform for predicting the consequences of future environmental change. Such approaches have been widely applied to study antagonistic interactions (Morris et al. 2020), but have been under-used in mutualism research. Mechanistic range models can also integrate local demography with dispersal (Neubert and Caswell 2000) and therefore provide a quantitative vehicle for integrating both niche-modifying and dispersal mutualism.

A final challenge to estimating the geographic footprint of mutualism is to go beyond the influence of single pairings of mutualists and integrate the total influence of mutualism *per se*. Any given species may participate in many different mutualisms with partners that provide complementary functions. Leguminous plants, for example, may engage with N-fixing bacteria, mycorrhizal fungi, ant defenders, insect pollinators, and vertebrate seed dispersers (Janzen 1981; Ossler, Zielinski, and Heath 2015; Baer and Maron 2018). Many species are likely to engage in both niche-modifying and dispersal mutualisms, yet we know little about their relative influence in systems where both types of range effects occur. Few studies have explored the combined influence of multiple mutualist guilds on a species' range (Benning and Moeller 2019; 2020), which is an important next step given the potential for synergy or interference between guilds (Batstone et al. 2018; Afkhami, Friesen, and Stinchcombe 2021).

Further, it would be worthwhile to consider the effects of biotic interactions generally on species range limits across the spectrum from mutualism to antagonism. In this review, we focused on mutualism, and so we did not include studies of facilitation or commensalism (interactions in which only one species benefits). However, from the perspective of the benefitting species, effects on range limits can be driven by the same context-dependent mechanisms we have described for mutualisms. Even among studies ostensibly about mutualism, most interactions are examined unilaterally, focusing only on one partner, and so it is unknown how consistently the fitness effects of many of the mutualisms included in this review are reciprocally beneficial. Given the relative lack of attention to commensalisms, despite their commonness in nature (Mathis and Bronstein 2020), we see a need for more attention paid to these lesser studied interaction types and to consider that many interactions may span across interaction types in different places and times. Considering these interactions, which are frequently more generalized and more facultative than the most commonly studied mutualisms, would help to broaden understanding of how species interactions influence range limits.

When and where is the influence of mutualism on range limits most important?

There are likely to be complex contingencies regarding the conditions under which mutualism affects range limits, and if so, how strongly. Our literature synthesis and that of Stephan et al. (2021) already hint at such contingencies. For instance, the nature of specialization and dependence between partners influences the effect of mutualists on range limits and which underlying mechanisms are at play. Another dimension of contingency relates to *which* range edges are likely to be strongly influenced by mutualism relative to other biotic and abiotic processes. We have emphasized the footprint of mutualism as the shift in species' range limits with and without the interaction. However, not all range edges are equal in terms of the mechanisms driving reductions in fitness and/or occurrence. This may be an important point of divergence between mutualistic and antagonistic biotic interactions.

A dominant conceptual paradigm for how species' interactions influence range limits -- the Species Interactions - Abiotic Stress Hypothesis (SIASH) -- predicts that "species interactions" (but predominantly competition and consumption) are important constraints on distributions under benign abiotic conditions and have little influence at edges limited by harsh abiotic environments (Louthan, Doak, and Angert 2015; Louthan et al. 2018; Lynn, Miller, and Rudgers 2021). A recent meta-analysis of transplant studies examining the role of biotic and abiotic drivers found that biotic interactions tend to contribute more at species' warm range edges relative to cool edges, supporting a key prediction of SIASH (Paquette and Hargreaves 2021). However, only 14 of the 338 collected studies consider mutualism, leaving open the question of whether mutualism and antagonism are similar in terms of the conditions under which biotic interactions affect distributional limits.

We hypothesize that mutualisms are different. Because mutualists may confer protection against both biotic and abiotic factors, there is no *a priori* reason to expect mutualism to be more important at certain types of range edges. In fact, mutualists often confer benefits in the face of multiple types of stressors. For example, context-dependent outcomes of fungal endophyte symbiosis in grasses may improve host fitness under drought stress (Afkhami, McIntyre, and Strauss 2014; Donald et al. 2021) -- the benefit that expands the distribution of *Bromus laevipes* by 20% -- but also provide protection against biotic stressors such as herbivores (Fuchs and Krauss 2019), competitors (Vázquez-de-Aldana et al. 2013), and pathogens (Pérez et al. 2020). In other systems, different guilds of mutualists may offer benefits to a focal partner along different axes of environmental stress; for example, corals benefit from their symbiotic relationship with photosynthetic algae and can also be defended from herbivores by crustaceans (McKeon et al. 2012). Thus, the potential for mutualism to influence range limits defined by either abiotic or biotic stress is an important point of departure from range-limit theory involving antagonistic interactions. However, no studies to our knowledge have yet explored whether mutualism can expand geographic distributions via protection from biotic interactions that negatively influence fitness, as has been demonstrated for abiotic stress (Afkhami, McIntyre, and Strauss 2014).

The multi-dimensional nature of “context” -- the different axes of environmental variation that strengthen or weaken mutualism -- is important to consider because the factors that elicit beneficial outcomes of mutualism may or may not be the same factors driving range limits, and this should be another key source of contingency in the geographic footprint of mutualism. Range limits are most likely to be extended when the environmental drivers of context-dependent declines in fitness toward the range edge are the same drivers that maximize the fitness benefits of mutualism. Mutualists that confer defense against natural enemies, for example, are unlikely to affect range limits set by climatic constraints, and vice versa. We currently do not have evidence for how often the environmental drivers of mutualist-derived benefits align with the drivers of range limits. Incorporating manipulations of biotic and abiotic environmental stressors into experiments and models along range-core/range-edge gradients could help reveal the (mis)alignments of the drivers of range limits and drivers of mutualism.

How does mutualism affect non-stationary range limits under global change?

Finally, we have discussed range limits in the context of stable range edges, assuming species’ distributions are in some dynamic equilibrium with the geographic template of abiotic and biotic environmental variation. The effect that mutualists have on non-stationary range limits, i.e. those that are moving because the species’ distribution is out of equilibrium with suitable environments, may be different, however. These could include invasive species expanding into available habitat, or range shifts in response to climate change. The same mechanisms of context-dependence will likely contribute to the effect of mutualism on both stationary and non-stationary range limits, but it is unclear whether certain mechanisms may take on different importance for shifting range edges. For example, it may be the case that novel climatic conditions could alter the outcomes of mutualism for species shifting to keep pace with climate change, or that the availability (or lack) of suitable partners could take on heightened importance for invasive species outside their native ranges. Many distributions are likely to come to be (or already are) in disequilibrium with their environments due to climate change (Svenning and Sandel 2013). Predicting the extent of this disequilibrium and which species are more or less influenced by their mutualists is a major challenge. Ranges may shift via expansion at a leading edge and/or contraction at a trailing edge, and mutualism may play different roles in each setting.

At leading edges, the ability to colonize suitable habitat may be limited by dispersal, both for native species shifting into newly suitable climate environments (Alexander, Diez, and Levine 2015) and for exotic species invading novel environments (Traveset and Richardson 2014). Therefore, we hypothesize that the role of dispersal mutualism may be amplified at the leading edges of non-stationary ranges, relative to its influence on stationary range limits. The invasion biology literature provides examples of seed dispersers facilitating the spread of invasive plants (Padrón et al. 2011; Spotswood, Meyer, and Bartolome 2012), and similar processes may influence range expansion of native species. Globally, the extinctions of dispersers are estimated to have reduced the capacity of animal-dispersed plants to shift their ranges on pace with climate change by 60% (Fricke et al. 2022).

The role of mutualism is likely to be different at trailing edges, particularly those of native species whose ranges are falling out of equilibrium due to climate change. Range shifts at trailing edges, where environments become increasingly inhospitable, are driven by local extinction of edge populations (Lenoir and Svenning 2015). Mutualism could modulate the occurrence or pace of trailing-edge contraction by promoting population resilience in the face of increasing environmental stress. Niche-modifying mutualisms may be particularly influential at trailing edges and may decelerate range shifts by buffering fitness against negative effects of environmental change through interaction outcomes that are more beneficial with increasing stress. However, trailing-edge dynamics of mutualism are poorly studied relative to leading-edge dynamics, and we currently do not know how commonly or strongly mutualism may retard range contraction at trailing edges. Lankau et al. (2015) contrast tree species hosting ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) fungi at the leading and trailing edges of their North American ranges; EM fungi tend to be more morphologically and functionally diverse than AM fungi, leading the authors to hypothesize that EM fungi may be better able to buffer their hosts against changing environmental conditions. They find that EM-associated species showed reduced contraction at trailing edges, consistent with a buffering influence of mutualism in the face of increasing climate stress. As these authors acknowledge, this study, the only one of its kind, was based on relatively coarse correlative patterns and lacked mechanistic detail, highlighting a need for experimental approaches and mechanistic modeling to rigorously evaluate the footprint of mutualism on trailing-edge range shifts. Given widespread projections of range contractions, particularly at lower latitudes and altitudes of species' ranges (typically "warm edges"), exploring the influence of mutualism on population viability in these settings will be an important area for future work.

Bilateral and multilateral perspectives that incorporate feedbacks between mutualist partners may be particularly important to consider in non-stationary ranges. Forecasting species' distributions under future climate scenarios is a pressing ecological objective. There is growing awareness that incorporating biotic interactions may be an important component of this process, as global change holds potential to generate assemblages characterized by novel species compositions and interactions (Gilman et al. 2010; Veloz et al. 2012). For species with obligate dependence on mutualists, it may be impossible to predict their future range shifts without also accounting for possible shifts in their mutualists (HilleRisLambers et al. 2013). One way to address this challenge is by incorporating physiological measurements into niche models (Gamliel et al. 2020; Briscoe et al. 2019). Measurements of physiological performance of partner species under a broad spectrum of environmental conditions (Buckley et al. 2010; Kingsolver, Diamond, and Buckley 2013) could inform whether mutualists will shift their ranges at a similar direction and pace with respect to environmental change. To our knowledge, only one study has used these types of physiological measurements to inform species distribution modeling efforts of mutualists (Dimond et al. 2013). It is currently unknown whether and under what conditions global change is likely to increase or decrease the geographic overlap of mutualist partners given their independent physiological requirements. This knowledge would add a valuable geographic dimension to broader questions about whether mutualisms will strengthen or break down under global change (Kiers et al. 2010).

Conclusion

Understanding the processes underlying geographic range limits and predicting shifts in these limits under environmental change are grand challenges in ecology. While interest in the role of biotic interactions in generating and maintaining range limits is long-standing, incorporation of mutualism into theory of range limits is long overdue. Our general conceptual framework and literature synthesis illustrate the potential for mutualism to leave a geographic “footprint” via the two fundamental ingredients of species’ ranges: niche limits and the ability to (over/under) reach them. Here we have shown that mutualism can extend range limits, yet (just as often in the available literature) *lack of mutualism* may constrain range limits from otherwise suitable habitat; these contrasting footprints are strongly related to dependence and specialization. As this body of research continues to grow, further experimental and modeling work is needed to rigorously quantify the footprint of mutualism and identify its sources of variation. Given ongoing environmental change and human redistribution of species, there is both powerful opportunity and urgent need to explore how mutualism (or lack thereof) will modify leading- and trailing-edge dynamics of rapidly shifting ranges.

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Conflicts of Interest Statement

The authors have no conflicts of interest to declare.

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Figure Legends

Fig. 1 Two processes by which mutualism can influence range limits of a focal species. The niche is defined as the range of environments that could support stable or growing populations ($\lambda \geq 1$). (A) Fitness effects of mutualism can modify the niche of the focal species by changing the range of environments in which population growth is above replacement level. In this example, fitness benefits for the focal species are facultative ($\lambda \geq 1$ is possible without mutualism) and consistent across environments. (B) Dispersal by mutualists may influence the realized occurrence of the focal species (filled and open circles show occupied and empty habitat patches, respectively) relative to its niche. In this example, dispersal mutualism overfills the focal species' niche.

Fig 2. Four possible geographic footprints of mutualism. Thick black lines represent the range limits of a focal species with its mutualist partner relative to its distribution in the absence of mutualism (gray area). Both niche modification and dispersal have the potential to generate these geographic footprints. (A) Mutualism leads to range extension when context-dependent interactions extend the niche, such that the niche without mutualists (-M) is smaller than the niche with mutualists (+M), or when dispersers "overfill" the niche by consistently carrying propagules into sink habitat beyond niche limits. (B) Mutualism may contract range limits when interactions provide benefits in the range core, but become costly in range edge habitats, restricting the niche or, when dispersers provide biased or weaker benefits beyond range edges, reducing occupancy in edge environments where the focal species could otherwise persist. (C) Range constraint can occur when a focal species is missing essential partners in environments that would be otherwise suitable, potentially having no available niche space without their partners (flat line, -M); This dependence means that the niche of the focal species should occur where mutualists are available (solid line, +M) but may be constrained relative to having mutualists available in all potentially suitable habitats (++M). Similarly, species that rely on dispersers can only be moved and occupy habitats where their dispersers are available (i.e. dispersal limitation). (D) Finally, it is possible for mutualism to be beneficial without influencing range limits. This may occur when fitness effects are stronger in range-core than range-edge environments, or when dispersal mutualism promotes greater occupancy within a species' niche, but not beyond it.

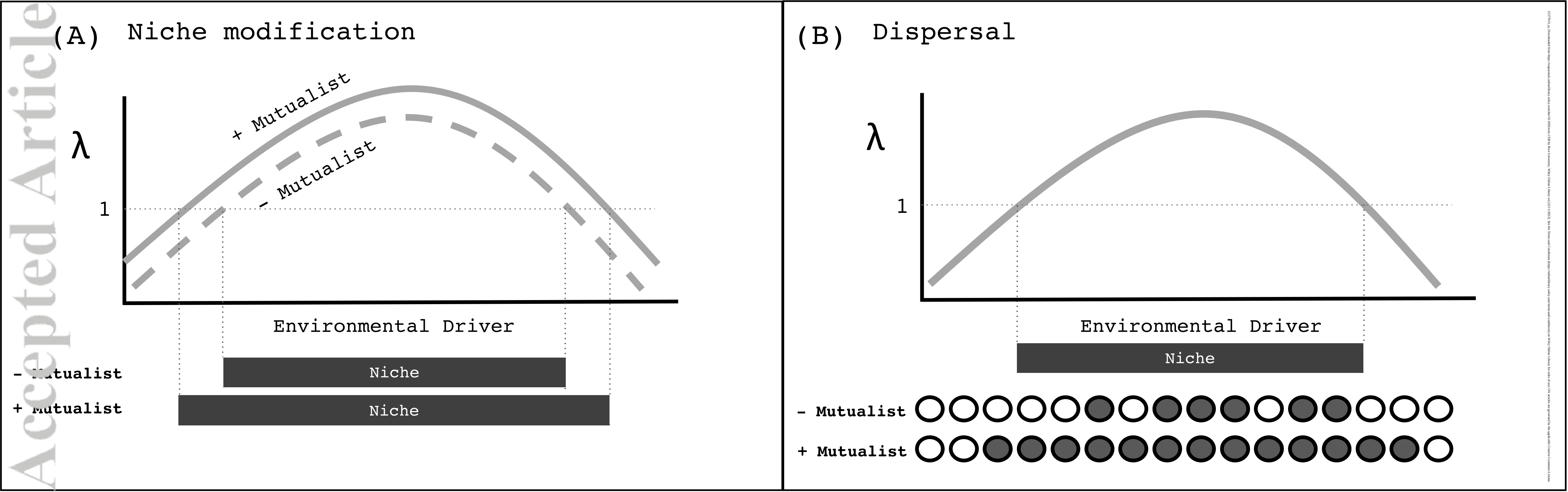
Fig. 3 Locations of compiled studies on the effects of mutualism on species' range limits. Approximate locations taken from site descriptions within studies or the average GPS coordinates of study sites when available. Crosses represent studies of niche-modifying mutualism and circles represent studies of dispersal mutualism.

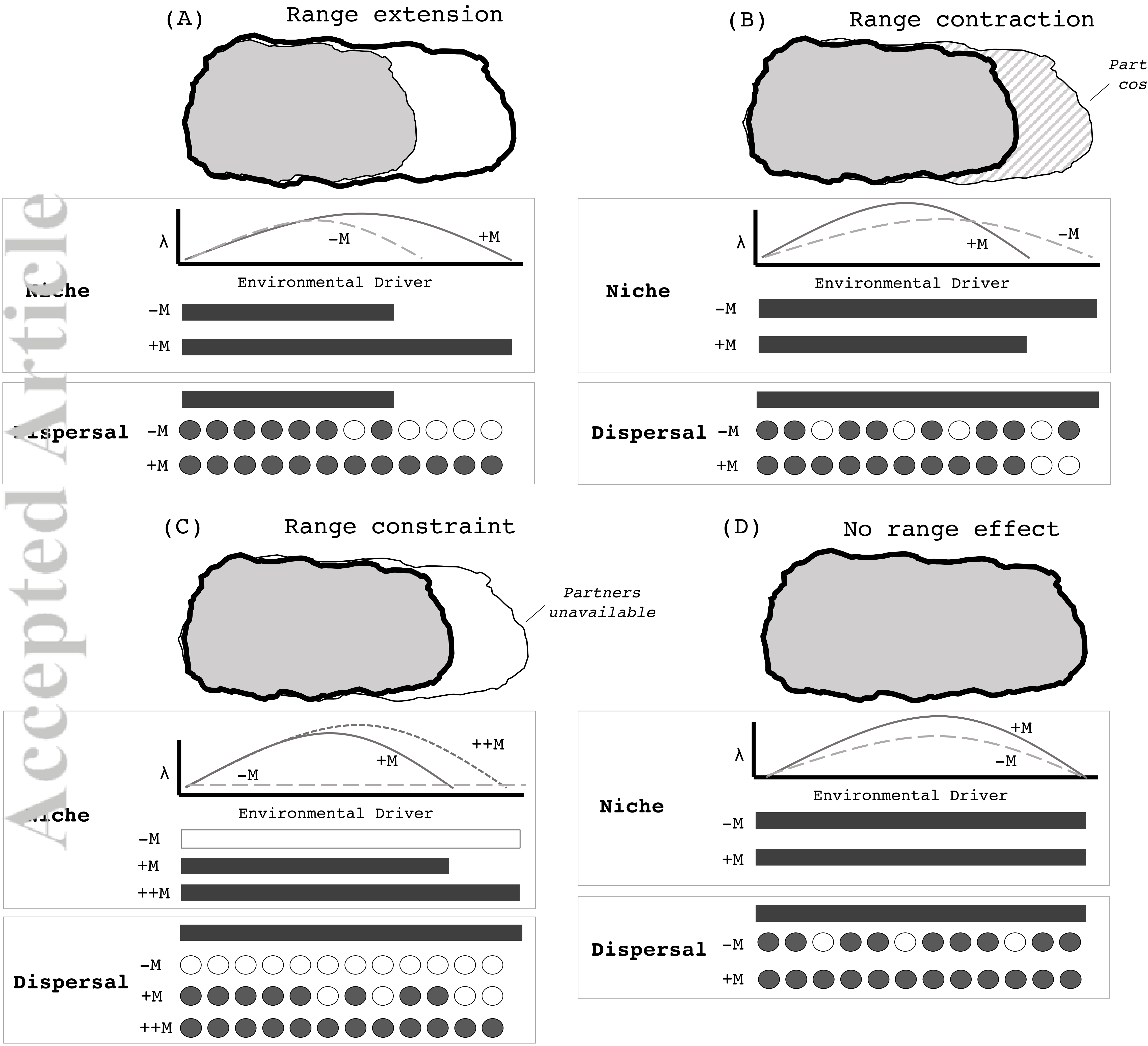
Fig. 4 Counts of focal partner taxa (the partner whose range limit is being assessed) and their interacting mutualists across the studies compiled in this review. For studies with multiple taxa of mutualist partners, each partner is tallied separately.

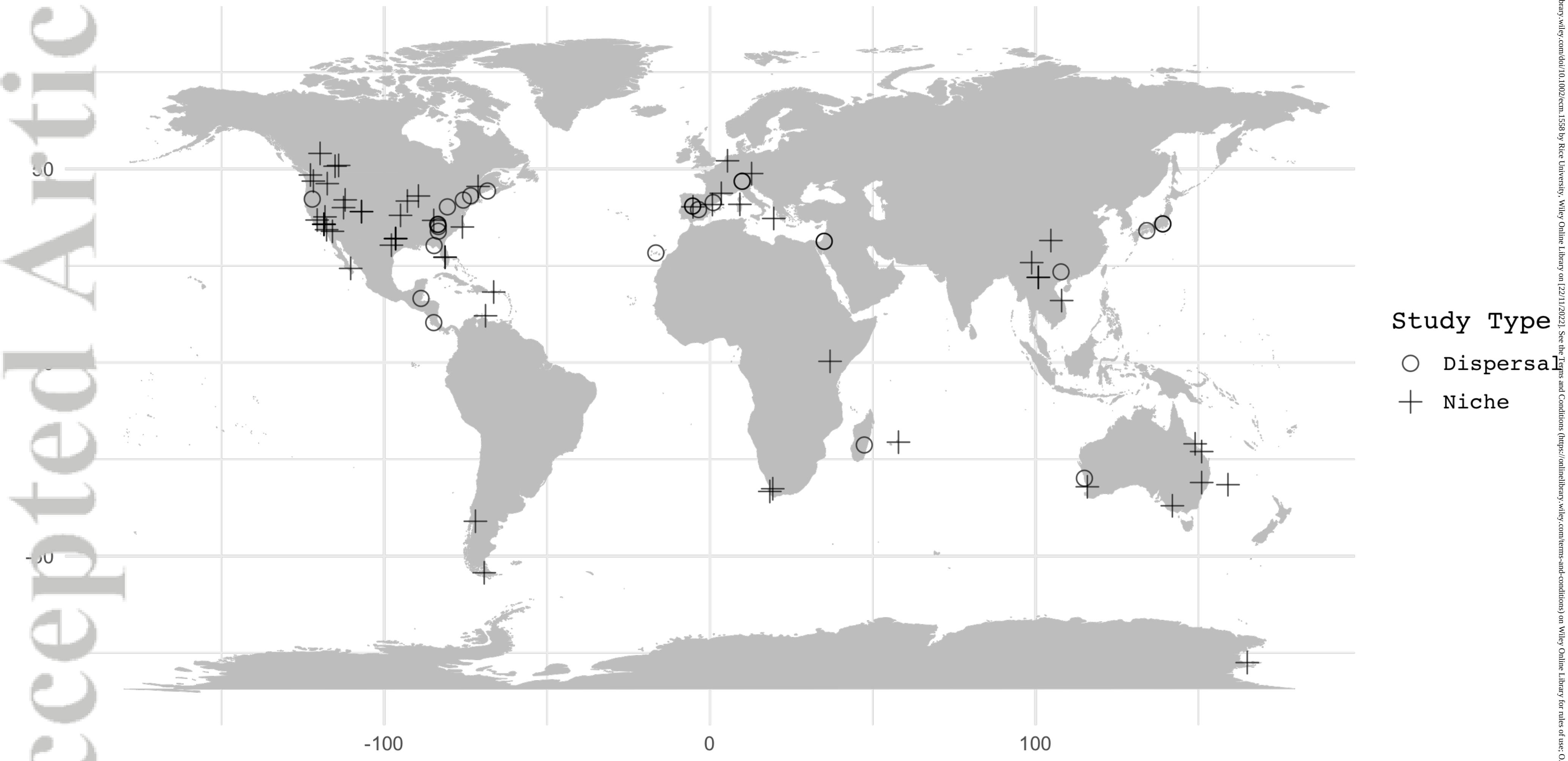
Fig. 5 Four case studies of context-dependent mutualist niche modification, depicting idealized relationships for each mechanism. (A) Interaction frequency: Declining pollinator abundance constrains a plant's northern range limit in the specialized mutualism between *Ficus virens* and its fig wasp pollinator; (B) Interaction outcome: Increased mutualism benefits to survival from *Epichlöe* fungal endophytes under drier conditions extend the distribution of the grass host, *Bromus laevipes*, into drier environments (silhouette modified from '*Bromus laevipes*' by Cindy Roché © Utah State University); (C) Interaction diversity: Different haplotypes of algal symbionts have different environmental tolerances, so partner turnover extends the distribution of the lichenized fungus, *Lasallia pustulata*, across altitudes; (D) Vital rate sensitivity: Declining sensitivity to simulated increases in pollination towards the arid range edge of *Hibiscus meyerii* indicate that pollination has no effect on the range limit.

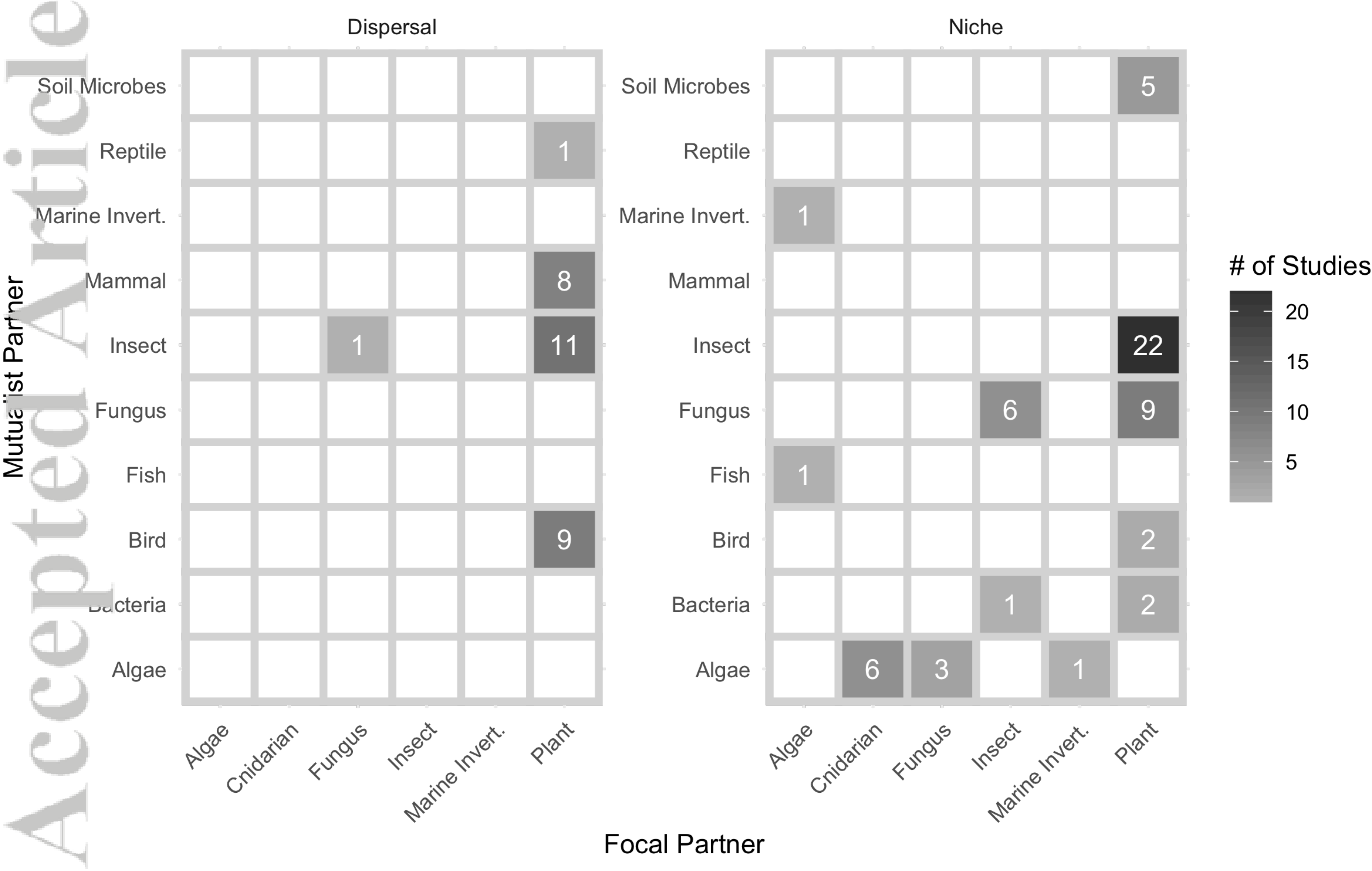
Fig. 6 Three case studies of context-dependent dispersal, depicting idealized relationships for each mechanism. (A) The abundance of the rodent seed predator/disperser, *Heteromys desmarestianus*, decreases towards high elevation along with the abundance of the tropical palm species, *Astrocaryum mexicanum*; (B) The distance of dispersal by spotted nutcrackers (*Nucifraga caryocatactes*) decreases towards high elevations constraining the range edge of the pine tree, *Pinus cembra*; (C) Seed-dispersing ant species diversity declines towards high elevations, constraining the range of the specialized plant, *Trillium undulatum*.

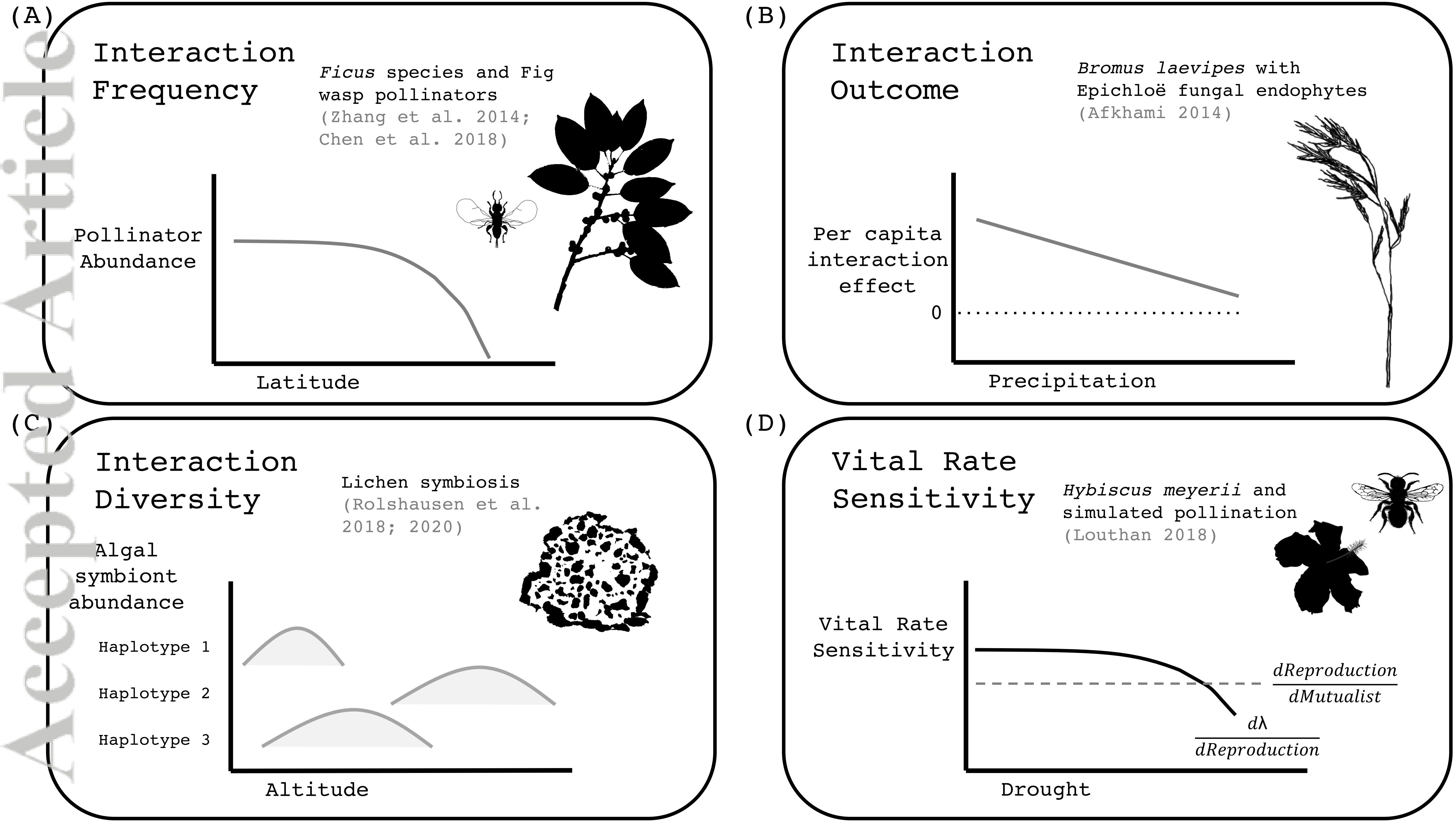
Fig. 7 A bilateral perspective of the effects of mutualists on species niches. (A) Feedbacks between the ranges of mutualist partners can shape species distributions when partners are essential for completing each other's life cycles, such as between yuccas and their moth pollinators (after Harrower and Gilbert 2018). The individual environmental tolerances of both partners influence and are influenced by their dependence on their partner, leading to a shared distribution. (B) When the dependence is asymmetrical, such as an obligately pollinated orchid pollinated by generalist bees (after Pauw and Bond 2011), these feedbacks should be weaker in that the plant is likely influenced by its pollinators, but not vice versa.

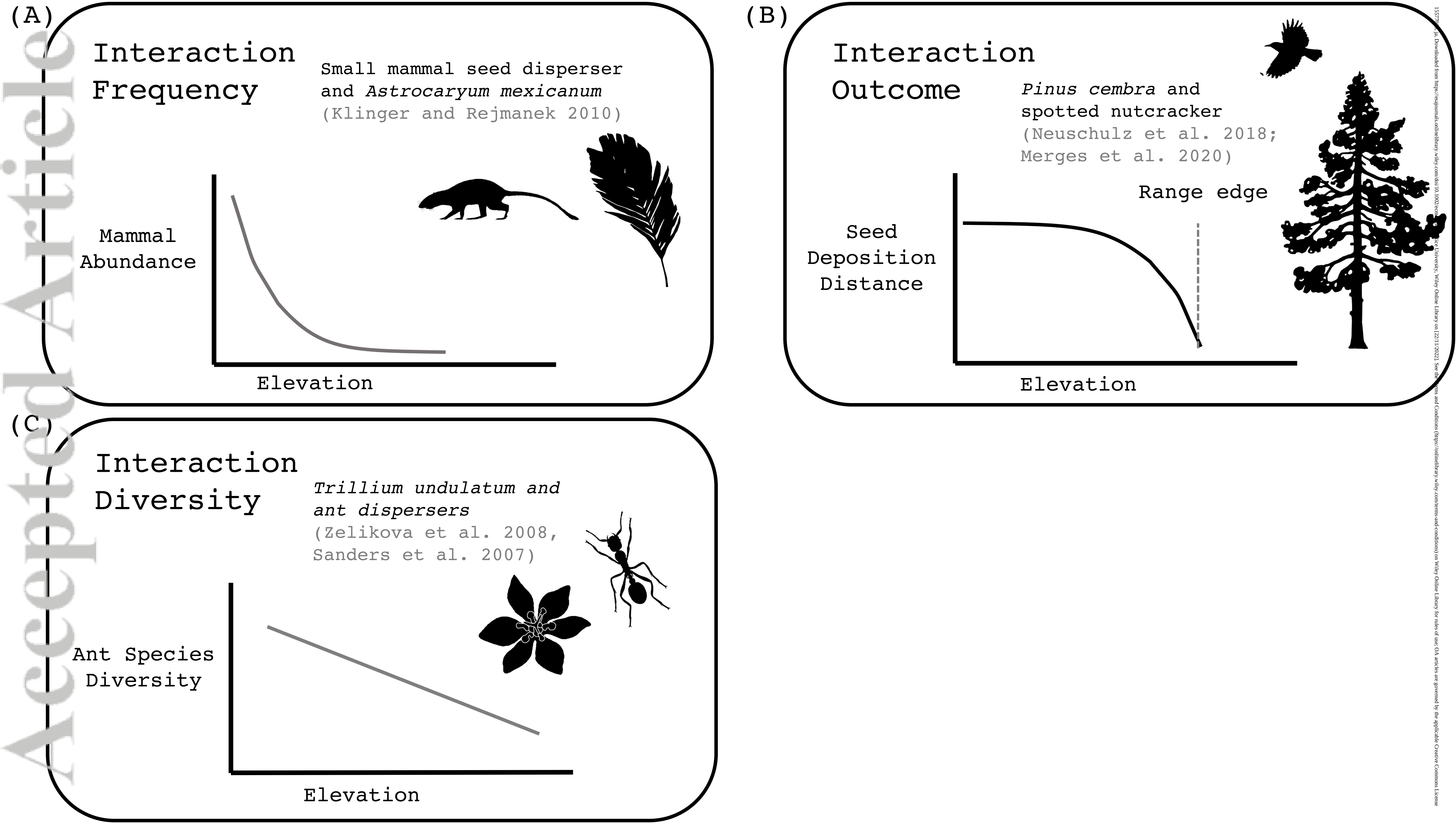

(A) Niche modification
+ Mutualist
- Mutualist
λ
1
Environmental Driver
- Mutualist
+ Mutualist
Niche
Niche
(B) Dispersal
λ
1
Environmental Driver
Niche
- Mutualist
+ Mutualist

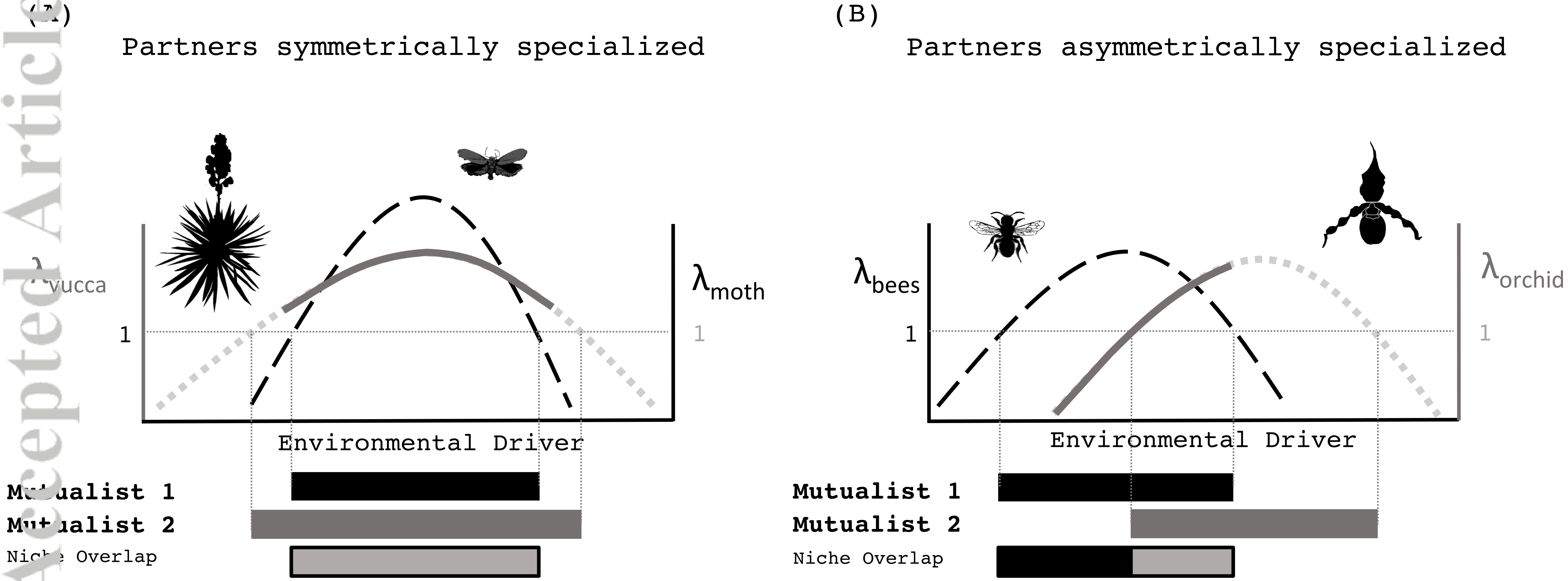

(A)
Range extension
λ
-M
+M
Environmental Driver
Niche
-M
+M
Dispersal
-M
+M
(B)
Range contraction
Partners costly
λ
+M
-M
Environmental Driver
Niche
-M
+M
Dispersal
-M
+M
(C)
Range constraint
Partners unavailable
λ
++M
+M
-M
Environmental Driver
Niche
-M
+M
++M
Dispersal
-M
+M
++M
(D)
No range effect
λ
+M
-M
Environmental Driver
Niche
-M
+M
Dispersal
-M
+M


50
-50
-100
0
100
Study Type
Dispersal
Niche


Dispersal
Niche
Mutualist Partner
Soil Microbes
Reptile
Marine Invert.
Mammal
Insect
Fungus
Fish
Bird
Bacteria
Algae
Focal Partner
Algae
Cnidarian
Fungus
Insect
Marine Invert.
Plant
1
8
1
11
9
5
1
22
6
9
1
2
1
2
6
3
1
# of Studies
20
15
10
5


(A)
Interaction Frequency
Ficus species and Fig wasp pollinators
(Zhang et al. 2014; Chen et al. 2018)
Pollinator Abundance
Latitude
(B)
Interaction Outcome
Bromus laevipes with Epichloë fungal endophytes
(Afkhami 2014)
Per capita interaction effect
0
Precipitation
(C)
Interaction Diversity
Lichen symbiosis
(Rolshausen et al. 2018; 2020)
Algal symbiont abundance
Haplotype 1
Haplotype 2
Haplotype 3
Altitude
(D)
Vital Rate Sensitivity
Hybiscus meyerii and simulated pollination
(Louthan 2018)
Vital Rate Sensitivity
$\frac{dReproduction}{dMutualist}$
$\frac{d\lambda}{dReproduction}$
Drought


(A)
Interaction Frequency
Small mammal seed disperser and *Astrocaryum mexicanum*
(Klinger and Rejmanek 2010)
Mammal Abundance
Elevation
(B)
Interaction Outcome
Pinus cembra and spotted nutcracker
(Neuschulz et al. 2018; Merges et al. 2020)
Range edge
Seed Deposition Distance
Elevation
(C)
Interaction Diversity
Trillium undulatum and ant dispersers
(Zelikova et al. 2008, Sanders et al. 2007)
Ant Species Diversity
Elevation


(A)
Partners symmetrically specialized
λyucca
λmoth
1
1
Environmental Driver
Mutualist 1
Mutualist 2
Niche Overlap
(B)
Partners asymmetrically specialized
λbees
λorchid
1
1
Environmental Driver
Mutualist 1
Mutualist 2
Niche Overlap