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Author for correspondence:
Seema Nayan Sheth
Tel: +1 919 515 4168
Email: ssheth3@ncsu.edu

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Seema Nayan Sheth[1], Naia Morueta-Holme[2] and Amy L. Angert[3]

[1]Department of Plant and Microbial Biology, North Carolina State University, Raleigh, NC 27695, USA; [2]Center for Macroecology, Evolution and Climate, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark; [3]Departments of Botany and Zoology and Biodiversity Research Centre, University of British Columbia, 3520-6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada

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Key words: biogeography, dispersal ability, endemism, niche breadth, niche evolution, occupancy, range filling, rarity.

Summary

Geographic range size has long fascinated ecologists and evolutionary biologists, yet our understanding of the factors that cause variation in range size among species and across space remains limited. Not only does geographic range size inform decisions about the conservation and management of rare and nonindigenous species due to its relationship with extinction risk, rarity, and invasiveness, but it also provides insights into fundamental processes such as dispersal and adaptation. There are several features unique to plants (e.g. polyploidy, mating system, sessile habit) that may lead to distinct mechanisms explaining variation in range size. Here, we highlight key studies testing intrinsic and extrinsic hypotheses about geographic range size under contrasting scenarios where species' ranges are static or change over time. We then present results from a meta-analysis of the relative importance of commonly hypothesized determinants of range size in plants. We show that our ability to infer the relative importance of these determinants is limited, particularly for dispersal ability, mating system, ploidy, and environmental heterogeneity. We highlight avenues for future research that merge approaches from macroecology and evolutionary ecology to better understand how adaptation and dispersal interact to facilitate niche evolution and range expansion.

I. Introduction

Geographic range size, the area across which a species occurs, can vary dramatically across space and among clades (Box 1; Fig. 1), and macroecologists and biogeographers have long sought to understand the mechanisms underlying such variation. Knowledge of the determinants of range size sheds light on the interplay between fundamental ecological and evolutionary processes and informs applied conservation problems. Because of the relationship between a species' ecological niche and its geographic range (Pulliam, 2000), understanding variation in range size provides insights into the processes of adaptation and dispersal. Furthermore, range size represents a major axis of rarity (Rabinowitz, 1981) and is a strong predictor of extinction risk (Schwartz *et al.*, 2006; IUCN Standards & Petitions Subcommittee, 2019), so identifying the factors that shape range size is crucial for prioritizing species and areas of

Box 1 Range size metrics

To measure the size of a species' range (Fig. 1), one must first map the range itself, for example via museum records, naturalist observations, or a species distribution model (reviewed in Gaston & Fuller, 2009). With such information in hand, macroecologists and biogeographers have most commonly measured range size as latitudinal or longitudinal extent, extent of occurrence, or area of occupancy (Gaston, 1994). Extent of occurrence represents the spatial spread of the outermost areas where a species occurs (e.g. a minimum convex polygon or bounding box encompassing all known localities; Gaston & Fuller, 2009). Area of occupancy quantifies how much area a species occupies (e.g. the number of grid cells where a species is known to occur) independent of the spatial spread of constituent populations (Gaston & Fuller, 2009). While various metrics of range size can be correlated (Sheth *et al.*, 2014), instances in which a species has a small area of occupancy relative to its extent of occurrence have stimulated research interest in range filling and why some geographically widespread species have patchy distributions (Gaston & Fuller, 2009). Range filling is commonly estimated as the ratio of realized range (based on occurrence records) to potential range (based on an ecological niche or habitat suitability model; Svenning & Skov, 2004; Paul *et al.*, 2009; Sheth *et al.*, 2014). Although narrow ranges are often synonymized with rarity, none of these metrics concerns the local abundance of individuals within populations.

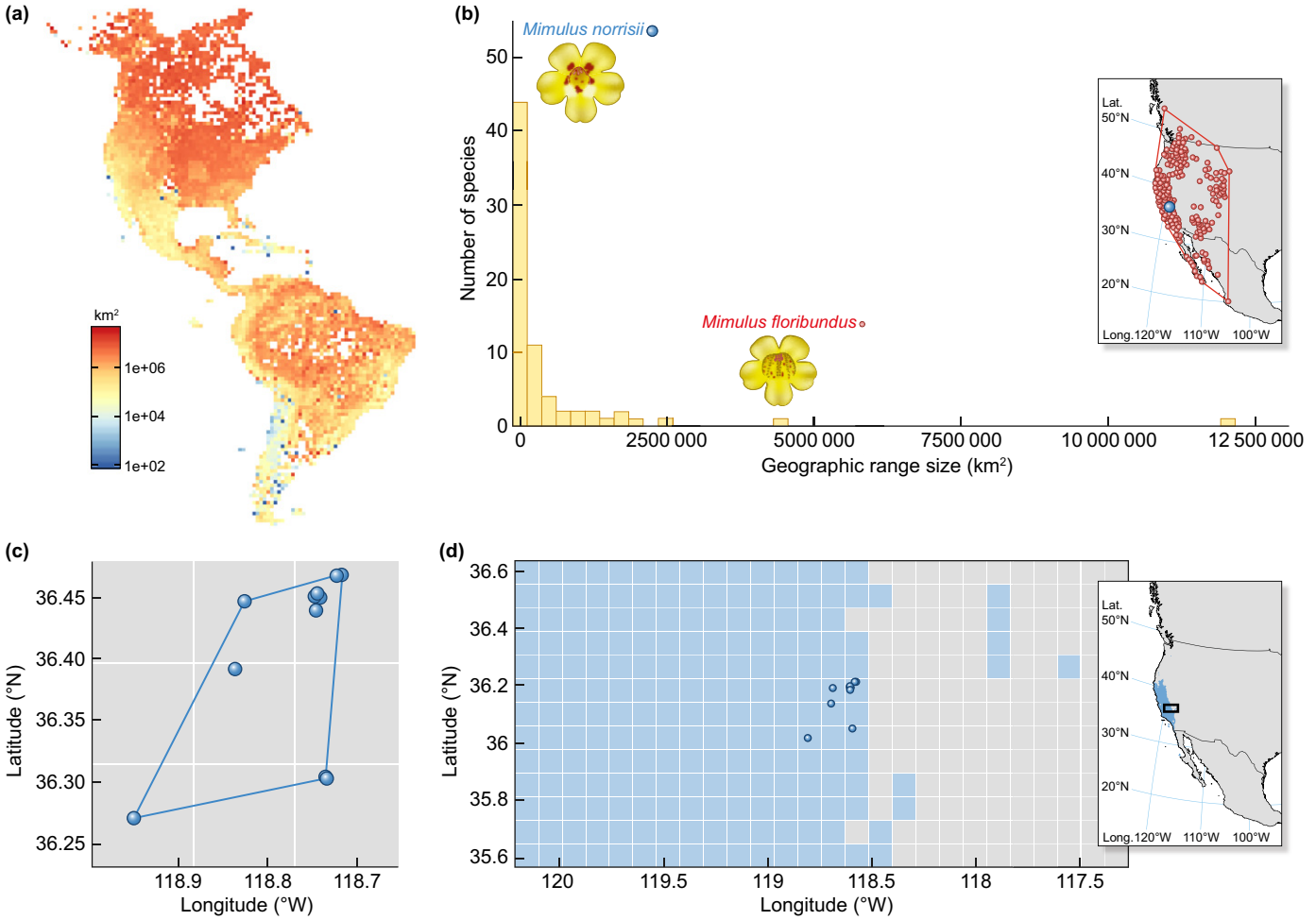

Fig. 1 (a) Geographic variation in mean range size (measured as the extent of occurrence and shown on a $\log_{10}$-scale) of New World plants (redrawn from Morueta-Holme *et al.*, 2013). Colors in the map correspond to the mean range size of species recorded in each grid cell. (b) Frequency distribution of range size for species of western North American monkeyflowers (redrawn from Sheth *et al.*, 2014). As observed in many species assemblages, most species have small geographic ranges, and only a small number of species have large geographic ranges, but range size can vary dramatically even among closely related species. Inset shows two closely related species within the same subclade of *Mimulus* that have markedly different range sizes (measured as the extent of occurrence). (c) Extent of occurrence (area of minimum convex polygon) and area of occupancy (number of 30-second grid cells), based on locality data derived from herbarium specimens (blue dots) of *Mimulus norrisii*. (d) Inset shows climatically suitable habitat (blue shading) based on a niche model for *M. norrisii*. Range filling is often estimated as the proportion of suitable habitat (shaded blue grid cells) in which a species is known to occur (blue dots). For (b–d), see Sheth *et al.* (2014) for more information.

conservation concern, forecasting shifts in geographic distributions in response to climate change, and predicting the spread of invasive species via dispersal and/or niche evolution.

Despite the importance of understanding the mechanisms underlying range size, the relative importance of the hypothesized determinants of range size remains largely unknown. Here, we

assess support for various hypotheses that have been proposed to explain variation in range size among species and across space. This topic has been relatively understudied in plants, which have minimum range sizes that are far smaller than the smallest ranges of birds and mammals (Brown, 1984). Mechanisms that shape variation in range size among plant species may be unique given plants' sessile nature, diversity of mating systems and ploidy levels, and prevalence of hybridization and sympatric speciation. First, we describe extrinsic (i.e. features of the external environment such as dispersal barriers or habitat stability) and intrinsic (i.e. characteristics of an organism or taxon such as dispersal ability or niche breadth) hypotheses about variation in range size under assumptions that species' geographic range and ecological niche limits are stable over time, and highlight key studies testing these hypotheses. Second, we discuss support for extrinsic and intrinsic hypotheses about why range size might change over time. Next, we synthesize results from a meta-analysis attempting to evaluate the relative importance of factors hypothesized to explain variation in range size among species. We conclude by highlighting promising future avenues to advance our understanding of the ecology and evolution of range size in plants.

II. Equilibrial limits: variation in ranges that are static through time

1. Extrinsic ecological limits

Hypotheses related to extrinsic ecological limits on range size focus on the availability of suitable habitats in space and external barriers to the dispersal of species between suitable habitats. If 'everything is everywhere, but the environment selects' (Baas Becking, 1934; in O'Malley, 2008), a species' range size would equal the area of suitable habitat worldwide. However, external boundaries such as mountains, rivers, biomes, and the land–sea transition limit the geographic space available and may pose barriers to dispersal to suitable habitats beyond the boundary. What constitutes a dispersal or habitat boundary, and how impermeable a boundary is, is species-specific and scale-dependent (e.g. a river is a stronger boundary to an ant-dispersed than to a wind-dispersed plant species). We describe how boundaries at small and large spatial scales, habitat availability, and climate variability drive patterns of geographic range size among species and across space.

At small spatial scales, boundaries can limit the local or regional availability and connectivity of habitat area and explain range sizes. Mountains act as barriers to range expansion, but can also create unusual and/or diverse environmental conditions. Steep terrains can pack many small habitat areas that accumulate small-ranged species specialized to rare conditions (Rahbek *et al.*, 2019). Indeed, hotspots of small-ranged and endemic species often occur in mountains (Ohlemüller *et al.*, 2008; Morueta-Holme *et al.*, 2013), supporting the importance of topographic diversity in determining range shapes and sizes (Letcher & Harvey, 1994). At even smaller spatial scales, the rarity of other abiotic factors such as soil conditions can limit range sizes, as is the case for species adapted to rare serpentine soils (Safford *et al.*, 2005).

At broader spatial scales, the *geometric constraints hypothesis* asserts that continental boundaries create a mid-domain effect (Colwell & Hurtt, 1994; Weiser *et al.*, 2007) for range sizes, simply due to the exclusion of the largest range sizes towards the boundaries. For uni-dimensional latitudinal range extents, this null model predicts that the largest range extents should be found closer to the equator. Yet, observed range extents deviate from this mid-domain expectation. For instance, woody plants in the Americas show a bimodal distribution with peaks in mean range size in north temperate and equatorial regions, and minima in subtropical regions (Weiser *et al.*, 2007). The *geometric constraints hypothesis* can be expanded to two dimensions, with range sizes predicted to peak at the center of continents or biomes (Weiser *et al.*, 2007). Thus, the observed increase in range size with latitude in North America (consistent with Rapoport's rule, the tendency of range size to increase with latitude; Stevens, 1989), and reversed pattern in South America (counter to Rapoport's rule), have been argued to result from the covariance of latitude and land area. Although range sizes can be simulated simply as a null response to land mass area (Saupe *et al.*, 2019), the lack of expected pattern for animal taxa in parts of the Palearctic suggests that land area alone is not a general explanation (Gaston *et al.*, 1998). Instead, there might be stronger selection for broader niches – and thus larger ranges – in large continents like North America because of an interaction between land mass and environmental gradients, which are weakened by the buffering effect of oceans in smaller continents like South America (Gaston & Chown, 1999). Studies of range shape (e.g. relative longitudinal and latitudinal extent) can help disentangle the importance of barriers compared to environmental gradients (Brown & Maurer, 1989). For instance, a study of gradients in range shape for mammals and birds found that the geometric constraints caused by the continental shape of South America and Africa indeed limit longitudinal range extents stronger than climate gradients (Castro-Insua *et al.*, 2018). To our knowledge, there are no similar studies of global gradients in plant range shapes. However, an interaction of land area (influenced by land shape) with other climate factors is supported for patterns of mean range size of plants across the Americas (Morueta-Holme *et al.*, 2013).

The *habitat area hypothesis*, which encompasses multiple mechanisms across spatial scales, proposes that the combination of a species' niche position (relative to regional conditions) and the availability of conditions should set the theoretical limit for range expansion (Ohlemüller *et al.*, 2008; Morueta-Holme *et al.*, 2013). Thus, a species inhabiting conditions that are common in the world can have a larger range than a species preferring rare conditions. Supporting the *habitat area hypothesis*, large-ranged species in South America and Australia are prevalent where both available land area and mean annual temperatures are high (Gaston & Chown, 1999; Gallagher, 2016).

The *climatic variability hypothesis*, first proposed to explain Rapoport's rule, posits that high temperature seasonality selects for broad thermal tolerances (Dobzhansky, 1950; Janzen, 1967; Stevens, 1989). Thus, the stronger seasonality towards the poles favors generalist species, which can spread over a broader range of climatic zones (see 'Niche breadth' section below). Conversely, the

more stable tropics allow for the persistence of niche specialists with smaller ranges. The hypothesis has been rejected for many organism groups, with the main critique being that the pattern itself – Rapoport's rule – is only a regional and not global phenomenon (Gaston *et al.*, 1998). In summary, these extrinsic hypotheses are not mutually exclusive, and can interact with intrinsic properties to shape patterns of range size.

2. Intrinsic ecological limits

Hypotheses for intrinsic ecological limits on range size focus on differences among species in the ability to colonize new habitat. Successful colonization requires several steps (Estrada *et al.*, 2018): first, emigrating from an occupied site and arriving at a new, unoccupied location (the *dispersal ability hypothesis*; Hanski *et al.*, 1993) and second, tolerating new conditions well enough to establish a viable population and proliferate (the *niche breadth hypothesis*; Brown, 1984). The former requires consideration of not just movement per se but also life-history traits such as fecundity and abundance that affect propagule pressure (Fagan *et al.*, 2009). The latter can involve traits related not only to dimensions of the abiotic and biotic niche but also mating system, which affects the strength of Allee effects (Allee, 1931) in small founding populations, and life history, which affects rates of population growth and ecological tolerance. Leger & Forister (2009) cleverly assessed colonization ability directly based on the rate at which lichens colonized gravestones (whose date of 'habitat' origin was known precisely). They found that the best colonizers occupied the largest geographic ranges, likely due to a combination of mechanisms involving movement, abundance, and tolerance of unweathered substrate. Yet, spore size (a common index of movement potential) was unrelated to colonization rates. The dividing lines between colonization ability, dispersal ability, and niche breadth can be somewhat arbitrary because some functional and life-history traits affect multiple aspects of colonization. Further adding confusion, different authors use different terminologies and distinctions. For example, Penner & Rödel (2019) created a 'dispersal index' that included aspects of fecundity and habitat specialization, while Lester *et al.*'s (2007) *site colonization hypothesis* focused only on dispersal ability as the driver of differences in colonization rates. In the sections that follow, we describe and evaluate evidence for two intrinsic hypotheses: dispersal ability and niche breadth.

Dispersal ability The *dispersal ability hypothesis* posits that, all else being equal, species with greater dispersal ability reach a greater number of areas and hence achieve larger range sizes (Hanski *et al.*, 1993). A positive association between dispersal ability and range size could also result from reversed causation: species with small ranges could undergo selection for low dispersal ability to prevent dispersing out of suitable habitat (Kunin & Gaston, 1997). However, dispersal distances tend to be a very small fraction of species' range sizes, making this mechanism unlikely for all but the most narrowly distributed species (Lester *et al.*, 2007). Finally, low dispersal ability could lead to greater population differentiation and propensity to speciate into small-ranged species (Gutiérrez & Menéndez, 1997; Section III.3).

Despite the intuitive simplicity of this hypothesis, it is difficult to test because dispersal is an emergent property that involves morphology, physiology, life history, and behavior (even for plants, which often rely on animal vectors), and it is strongly influenced by extrinsic factors like habitat connectivity. Morphological proxies for movement ability are often used instead (e.g. mass and buoyancy of mangrove seeds; Clarke *et al.*, 2001). Many studies have found positive (though often weak) associations between proxies for movement ability and range size in animals, particularly insects (e.g. Lester *et al.*, 2007; Rundle *et al.*, 2007). Studies in plants are less numerous and only sometimes support a positive relationship between movement potential and range size, although several recent large-scale studies do find support (dispersal distance index based on vector and morphology for 1276 European plants: Estrada *et al.*, 2015; seed mass for 1600 European plants: Sonkoly *et al.*, 2017).

The net effects of seed size on colonization are particularly complicated to predict due to trade-offs in dispersal and establishment success. Passively dispersed, small-seeded species are expected to travel farther and make more propagules due to size/number trade-offs (predicting a negative relationship between seed mass and colonization), yet small seeds are likely to have lower per capita recruitment success (predicting a positive relationship between seed mass and colonization). For this reason Eriksson & Jakobsson (1998) hypothesized that the greatest colonization ability occurs at intermediate seed size. Among grassland species in Sweden, they found support for a hump-shaped relationship between seed size and local abundance, but the relationship did not scale up to predict range size after phylogenetic correction. For herbs in central Europe, van der Veken *et al.* (2007) found that seed production, a proxy for propagule pressure, predicted range size, while seed mass predicted latitudinal range position, which the authors hypothesized to reflect postglacial recolonization speed of small-seeded species.

Niche breadth The *niche breadth hypothesis* posits that species that can maintain stable or growing populations across a broad range of environments or resources should be able to occupy a larger geographic area than species with narrow niches (Brown, 1984). A species may achieve a broad niche via generalist populations and/or general-purpose genotypes, locally adapted populations and/or specialized genotypes, or both (Fig. 2a; Slatyer *et al.*, 2013). Hence, local adaptation (in the case of specialized populations) and phenotypic plasticity (in the case of general-purpose genotypes) may play an important role in shaping the relationship between species-level niche breadth and range size (Fig. 2b,c; Dostál *et al.*, 2016; Hirst *et al.*, 2017). If a species' niche breadth is shaped by general purpose genotypes that perform well across a broad range of environments, then species with more plastic genotypes may have larger geographic ranges. However, testing this hypothesis is often challenging because niche breadth quantifies the width of the fitness curve and can be characterized for genotypes, populations, species, and clades, whereas phenotypic plasticity quantifies the degree to which a trait (e.g. flowering time, specific leaf area) varies across environments at the genotypic level (Sexton *et al.*, 2017). This may explain the lack of strong support for a positive relationship between phenotypic plasticity and range size, especially since

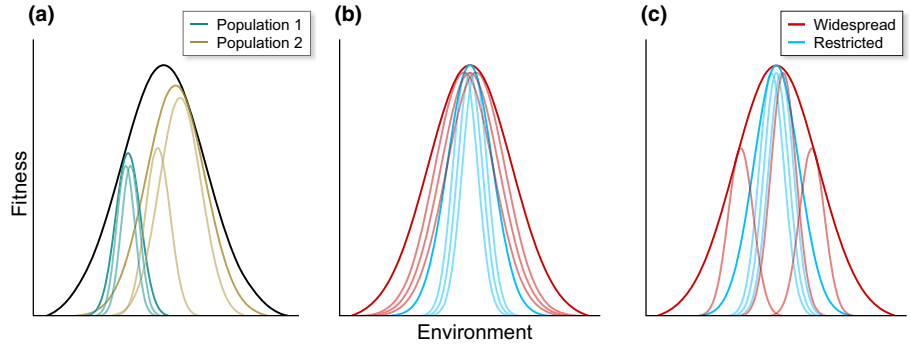

Fig. 2 Hypotheses about how variation in niche breadth (i.e. width of the fitness curve) among populations or genotypes can lead to variation in range size among species. (a) Species-level niche breadth (black curve) is accrued via niche breadths of individual populations across the species' range (bold hues), which in turn are accrued via the niche breadths of individual genotypes within each population (muted hues). (b) Hypothesis that geographically widespread species (bold hues) have populations or genotypes (muted hues) with broader niches than geographically restricted species. (c) Hypothesis that widespread species (bold hues) have populations that are more locally adapted and/or genotypes (muted hues) that are more specialized than restricted species.

studies differ drastically in focal traits used for quantifying plasticity (e.g., Sheth & Angert, 2014; Lovell & McKay, 2015; Hirst *et al.*, 2017) and are often unable to determine whether plasticity is adaptive (Dostál *et al.*, 2016).

Niche breadth has been quantified across a broad range of spatial scales, for many abiotic (e.g. edaphic properties, climatic variables, habitat types) and biotic (e.g. pollinator specificity, dispersal vector, competitive interactions, and mutualistic or pathogenic microbes) dimensions, and with a number of different metrics (reviewed in Sexton *et al.*, 2017). Most studies testing the *niche breadth hypothesis* in plants focus on range size and niche breadth estimates at regional, rather than global scales (summarized in Kambach *et al.*, 2018, who found that regional niche breadth is a poor predictor of global range size in a large dataset of European plant species). Given the n-dimensional nature of species' niches, support for the *niche breadth hypothesis* may be complicated if specialization is not correlated across multiple niche axes (Emery *et al.*, 2012). However, a recent meta-analysis showed consistent support for the *niche breadth hypothesis*, independent of taxonomic group or spatial scale, especially when niche breadth was quantified as environmental tolerance (Slatyer *et al.*, 2013).

Though biotic dimensions are thought to vary across finer spatial scales than other dimensions of niche breadth such as climate (Pearson & Dawson, 2003), biotic interactions may play an important role in shaping patterns of range size among species (Pigot & Tobias, 2013). Furthermore, biotic interactions may enhance or impede a plant species' tolerance to abiotic stress, thereby influencing its abiotic niche breadth and range size. For example, the California grass *Bromus laevipes* tolerated drier conditions in the presence of fungal leaf endophytes (Afkhami *et al.*, 2014). In addition, the presence of a competitor, herbivore, or disease may constrain abiotic niche breadth and hence range size (Bullock *et al.*, 2000; Svenning & Sandel, 2013). For example, lower competition pressure has been hypothesized to explain larger range sizes in areas of relatively low species richness such as high latitudes (cf. Stevens, 1996), though there is little theoretical rationale for this hypothesis (Gaston *et al.*, 1998). On the other hand, the presence of effective dispersal vectors can help species achieve larger range sizes. Megafauna such as elephants spread seeds of fruit trees across much longer distances than other animals (Blake *et al.*, 2009). In addition, reliance on pollinators vs having the ability to reproduce autonomously can impact species' abilities to colonize new areas (Box 2).

One criticism of studies supporting the *niche breadth hypothesis*, particularly when niche breadth is quantified as realized environmental tolerance or habitat specificity, is that niche estimations may be truncated due to missing values in climatic space. For instance, tropical lowland species may have fundamental thermal niches that are broader than their realized niches, simply because there are no places that are hotter under the current climate (Feeley & Silman, 2010). Another key criticism is the failure to account for different levels of sampling effort for widespread versus restricted species (Burgman, 1989). Although early studies suggested that correcting for sampling effort weakens the positive relationship between niche breadth and range size (e.g. Burgman, 1989), a meta-analysis recently showed that this relationship persists even after correction (Slatyer *et al.*, 2013). Further, by encompassing a greater geographic area, widespread species may span a greater range of environments simply by chance due to spatial autocorrelation in climate across landscapes (Boucher-Lalonde & Currie, 2016). In the formulation of this hypothesis, Brown (1984) explicitly proposed that spatial autocorrelation in environmental variables would lead to a positive relationship between local abundance and range size across closely related species (Blackburn *et al.*, 2006), which were assumed to differ across very few niche dimensions. Nonetheless, using the same spatial occurrence dataset to estimate niche breadth and range size has been viewed as problematic by some authors who maintain that spatial autocorrelation hinders our ability to estimate niche breath for species whose ranges are limited by dispersal or biotic interactions (e.g. Moore *et al.*, 2018; Cardillo *et al.*, 2019). In other words, if two species have the same niche breadth but one is dispersal-limited, its niche breadth is likely to be underestimated due to spatial autocorrelation compared to the other species whose range has grown to fill its niche. On the other hand, a primary effect of spatial autocorrelation could be that species with larger ranges encounter a greater range of selective

Box 2 Mating system and range size

Plants can reproduce autonomously through asexual (e.g. bulbil production, apomixis, or vegetative clones) or sexual reproduction (e.g. self-pollination). Autonomous reproduction can enhance colonization and establishment in new areas by providing reproductive assurance in the absence of pollinators or mates (Baker, 1955; Kalisz & Vogler, 2003). Species that self-pollinate should thus have larger geographic ranges than outcrossing species, a pattern robustly supported by a study of hundreds of angiosperm species (Grossenbacher *et al.*, 2015). Auxiliary support is lent by similar niche breadths between selfers and outcrossers (Randle *et al.*, 2009; Johnson *et al.*, 2014; Park *et al.*, 2018), suggesting that selfing increases range size via colonization of areas that are already abiotically suitable, rather than abiotic niche evolution (but see Espeland & Emam, 2011). Given that species with broader niches often have larger ranges (Slatyer *et al.*, 2013), it is surprising that selfers have larger geographic ranges, but not broader climatic niches than outcrossers.

Other hypotheses about the effects of reproductive mode on range size focus on effective population size (Wright *et al.*, 2013), which impacts fitness and evolvability. First, low genetic variation associated with autonomous reproduction could constrain the evolution of niche breadth and range size. If so, then species with autonomous reproduction should have narrower niches and smaller geographic ranges than outcrossers, yet, to our knowledge only one study supports this hypothesis (Lowry & Lester, 2006). The second consequence of low effective population size is the accumulation of deleterious mutations (Wright *et al.*, 2013). Functionally asexual *Oenothera* species on average had 72% larger geographic ranges than sexually reproducing species, although the difference was not statistically significant (Johnson *et al.*, 2010). Thus, asexuality may aid in initial colonization and expansion, but ranges subsequently decrease in size as deleterious mutations accumulate.

environments, leading to the evolution of greater niche breadth, which does not necessitate correction. Until we have a better understanding of the relative importance of niche evolution and dispersal for promoting range expansion, we caution that studies that adjust for spatial autocorrelation may underestimate true and biologically meaningful differences in niche breadth.

Some plant studies have addressed the issue of spatial autocorrelation by independently estimating niche breadth from experiments, and several of these studies have documented support for the *niche breadth hypothesis* even when estimates of niche breadth and range size are independent (e.g. Lloyd *et al.*, 2003; Sheth & Angert, 2014). Though experiments can only quantify niche breadth for a relatively small number of species and niche axes, they are a potentially powerful complement to verify tests of the *niche breadth hypothesis* based on correlative methods for a large number of species. For example, a study of western North American monkeyflowers found strong support for the climatic *niche breadth hypothesis* when using herbarium records to quantify both niche breadth and range size for 72 species (Sheth *et al.*, 2014), and weaker support (possibly due to small sample sizes) when quantifying niche breadth experimentally with thermal performance curves for 10 of those species (Sheth & Angert, 2014).

3. Evolutionary constraints to range expansion

Although the above hypotheses explain current (ecological) reasons for equilibrial differences in range size, they cannot explain why factors such as dispersal ability or niche breadth do not continually evolve to permit ranges to grow 'like the rings of a tree' (Mayr, 1963). Models of the evolutionary stasis of range limits assume that populations are under strong selection for adaptation to environments at and beyond the range edge, but are ultimately unable to respond to that selection for a variety of reasons. To extend these models to equilibrial differences in range size, the mechanisms that limit response to selection on range-limiting traits should take effect more rapidly along environmental gradients for restricted vs widespread species. In the following section we describe key theoretical models of range-limit evolution and attempt to translate their lessons to understanding evolutionary constraints on range size.

Models of range-limit evolution Some models demonstrate that range expansion might be prevented by gene swamping from central populations because of feedback between adaptation and population density (Haldane, 1956; Kirkpatrick & Barton, 1997). More individuals at the range center than the range edge cause edge populations to become 'swamped' with alleles adapted to central environments. Because local population density is coupled to the degree of adaptation, gene swamping depresses population growth and prevents further range expansion. This model emphasizes the costs of migration, a compound parameter reflecting the fitness costs of dispersing across environmental gradients due to the interplay of environmental gradient steepness and stabilizing selection around a local optimum (inversely proportional to niche breadth). Environmental gradients in this model can be biotic or abiotic; for example, negative species interactions simply steepen the costs of migration (Polechová & Barton, 2015). Because range limits evolve where environmental gradients are steep, or suddenly steepen, these models lend theoretical support for the hypothesis that ranges of narrowly distributed taxa are positioned in areas with steeper environmental gradients than their widespread relatives (Cook *et al.*, 2015; Section II.1). Narrower niches also increase the fitness cost of dispersing, so this intrinsic property can steepen the effective environmental gradient and yield smaller ranges (Section II.2). Contrary to the expectation that greater dispersal leads to larger ranges, this model suggests that high dispersal could lead to maladaptive gene swamping that limits range expansion.

While the Kirkpatrick and Barton model assumed fixed genetic variance and no stochasticity, more recent models let variance evolve and incorporate demographic and genetic stochasticity (i.e. genetic drift; Polechová & Barton, 2015; Polechova, 2018). These models reveal that genetic drift can preclude adaptation in edge populations when it reduces the efficacy of selection along environmental gradients. Whether range expansion continues or stalls depends on the costs of migration (as initially emphasized by Kirkpatrick and Barton), but relative to the genetic neighborhood size; adaptation fails when the effective environmental gradient is steeper than the efficacy of selection relative to genetic drift. These models provide the theoretical foundation for the *genetic variation*

hypothesis (discussed in the next section), with the implication for range size that genetic drift hinders response to selection more in narrow compared to wide-ranging species. Newer models of the evolution of ranges advocate comparing the fitness costs of movement along environmental gradients (i.e. via field transplants) to genetic neighborhood size (i.e. via molecular markers; Polechová & Barton, 2015). We are unaware of any work that has done this explicitly for one species, let alone for species with differing range sizes. It remains an open question whether the fitness cost of migration along environmental gradients is higher, or the efficacy of selection relative to genetic drift is lower, for range-restricted compared to widespread species.

Evidence for genetic variation and multivariate constraints Several empirical studies have tested the *genetic variation hypothesis*, which predicts a positive relationship between range size and genetic variation in traits related to niche breadth across closely related species. A study of 10 *Drosophila* (fruit fly) species with contrasting range sizes found that species restricted to the tropics had lower additive genetic variances for cold and desiccation resistance compared to geographically widespread species (Kellermann *et al.*, 2009). Similarly, a study of five pairs of monkeyflower species with contrasting range sizes showed that widespread species with broader thermal performance curves had greater genetic variation for thermal reaction norms (Sheth & Angert, 2014). Although additive genetic variance for traits associated with niche or dispersal evolution is required for evolution of ranges by natural selection, several studies have compared neutral genetic variation among plant species with contrasting range sizes (e.g. Gitzendanner & Soltis, 2000; Cole, 2003). Overall, studies of neutral genetic variation show mixed support for the prediction of lower genetic variation in geographically restricted species, and there are several examples of restricted species with high genetic variation and widespread species with low genetic variation (Stebbins, 1980; Gitzendanner & Soltis, 2000).

There are several challenges that hinder testing the *genetic variation hypothesis*. First, in comparative studies, it has not been possible to disentangle whether low genetic variation is a cause or a consequence of small range size. Second, quantifying additive genetic variances for multiple species is labor-intensive and often restricted to a small number of traits in short-lived, tractable organisms amenable to quantitative genetic study. Thus, most studies that have compared quantitative genetic variation in widespread and restricted species have had limited sample sizes for making robust inferences, often 1–2 species pairs with contrasting range sizes (e.g. Lovell & McKay, 2015), and we are unaware of any study involving more than 10 species (Kellermann *et al.*, 2009; Sheth & Angert, 2014). Third, genetic variation may change across space (Pujol & Pannell, 2008) and time (Leigh *et al.*, 2019), so including multiple populations per species at multiple time points would further increase the sample sizes needed to test this hypothesis. Finally, even if species have sufficient genetic variation in single traits, they might lack appropriate genetic variation in multiple traits to respond to natural selection at range edges. Thus, species with smaller ranges may experience stronger multivariate constraints resulting from genetic correlations antagonistic to the direction of selection (Antonovics, 1976). To test this idea, estimates of selection gradients for multiple traits, along with genetic variance–covariance matrices, would be needed for multiple species differing in range size. We are unaware of any study that has compared such matrices or multivariate responses to selection among species varying in range size.

III. Non-equilibrial limits: variation in ranges that change through time

1. Extrinsic factors

Changes over time in extrinsic factors such as biotic interactions, the existence and placement of barriers to dispersal, climate, and human influence provide opportunities for species' ranges to expand or contract. Biotic factors such as the loss of dispersers can lead to reductions in range size (e.g. in large-seeded trees following megafauna extinctions in South America; Doughty *et al.*, 2016), and contribute to extinctions (e.g. in palms; Onstein *et al.*, 2018). The loss of a barrier can drive changes in the range sizes of previously restricted species. An example is the closure of the Isthmus of Panama, leading to interchanges of the terrestrial biota between North and South America. The southward expansions of *Quercus* and *Alnus* across the Isthmus exemplify the interaction between extrinsic and intrinsic factors, with animal-dispersed *Quercus* only reaching northern Colombia and wind-dispersed *Alnus* spreading all the way to Chile (Hooghiemstra, 2006).

Climatic changes and the spread and waning of ice sheets during glaciation cycles of the Pleistocene drove changes in species' range sizes, especially in the northern hemisphere (Svenning & Skov, 2007). Yet hypotheses about the legacies of such climatic changes on current ranges yield contrasting predictions about how range size has changed over time. The *climatic relict hypothesis* posits that mountain areas are refugia for cool-adapted, narrow-ranged species that were formerly widespread during the cooler climate conditions of the Pleistocene (Willis & Whittaker, 2000; Ohlemüller *et al.*, 2008). This hypothesis predicts a clustering of small-ranged species with similar climate niches in mountains, limited by currently rare climatic conditions. By contrast, the *post-glacial migrational lag hypothesis* posits that species are still spreading from their Last Glacial Maximum (LGM) refugia 21 000 yr ago, and species' ranges are smaller than their potential due to dispersal limitation rather than current climate (Svenning *et al.*, 2008). Several lines of evidence favor the *post-glacial migrational lag hypothesis*. For instance, in the European Alps, accessibility to refugia explained patterns of endemic vascular plant and invertebrate richness (Essl *et al.*, 2011). Environmental niche modelling also supports the view that many European and North American plant species display limited filling of their potential ranges and are thus not in equilibrium with current interglacial climate conditions. Dispersal lags since the LGM are species-specific, with a stronger imprint of historical legacies on small-ranged species richness (Svenning & Skov, 2007) possibly explaining a lower congruence of hotspots of endemism across plants and other taxonomic groups (Essl *et al.*, 2011). Across the northern hemisphere, species and phylogenetic

endemism is skewed towards areas of higher climatic stability since the LGM (Feng *et al.*, 2019). However, even widespread species exhibit moderate to strong dispersal limitations from former glacial refugia (e.g. for majority of European forest species in Svenning *et al.*, 2008). Transplant experiments and naturalizations north of current distributions (Svenning *et al.*, 2008; Van der Veken *et al.*, 2012) support this hypothesis. The effects of past ice sheets are also discernible in North America. Here, in regions glaciated during the LGM, the mean range size for plants is significantly larger than in the rest of the Americas, likely reflecting selection for generalist species and good dispersers (Morueta-Holme *et al.*, 2013).

An increasingly recognized predictor of range size is human influence, which is studied primarily in animals (e.g. Marco & Santini, 2015). On the one hand, unintended dispersal of propagules by humans plays a major role in the spread and establishment of nonindigenous species (Mack *et al.*, 2000), and the spread of species used for food has increased the range size of large-fruited trees in the Americas (Zonneveld *et al.*, 2018). On the other hand, habitat fragmentation poses new barriers to plant migrations and reduces habitat for establishment. For instance, simulations predict that fragmentation may reduce climate-change driven range expansions in understory forest plants to 25–70% of the migration rate expected in a continuous forest landscape (Dullinger *et al.*, 2015). Empirical studies are scarce in plants though, and the role of rare long-distance dispersal in alleviating the negative impacts of fragmentation is hard to quantify. Together, these examples show that extrinsic changes may be faster than species can track, and create historical legacies in current range sizes. Again, the impacts on individual species interact with their intrinsic traits such as dispersal syndromes.

2. Models of changes in range size over time

The waxing and waning of a species' range size over its lifetime has been compared to the life cycle of a single organism (Ricklefs & Cox, 1972). Several models have been proposed for change in range size of lineages over time (i.e. along branches of a phylogenetic tree; Fig. 2). Ranges at equilibrium with extrinsic and intrinsic limiting factors should remain stable over long periods of time (Fig. 3a; Gaston, 1998). Alternatively, ranges subject to changing extrinsic factors may change in size idiosyncratically, rather than predictably, over time (Fig. 3b; Gaston, 1998). The *stasis post-expansion hypothesis* suggests that if a species is born with a smaller range than its potential (e.g. in a glacial refugia scenario), then range size may rapidly increase post-speciation, and then remain stable over time (Fig. 3c; Jablonski, 1987). There is considerable empirical evidence for this model, both in the fossil record (mollusks; Jablonski, 1987) and extant taxa (bats; de Moraes Weber *et al.*, 2014). In plants, a study of *Fragaria* (strawberries, Rosaceae) is consistent with the stasis post-expansion model, but the relationship is relatively weak and appears to be largely driven by a small number of taxa (Johnson *et al.*, 2014). The *taxon cycle hypothesis* proposes that new species rapidly fill their potential ranges, after which their ranges begin declining due to fragmentation driven by local extinctions (Fig. 3d; Ricklefs & Cox, 1972). This model predicts a hump-shaped relationship between species' age and realized range size or range

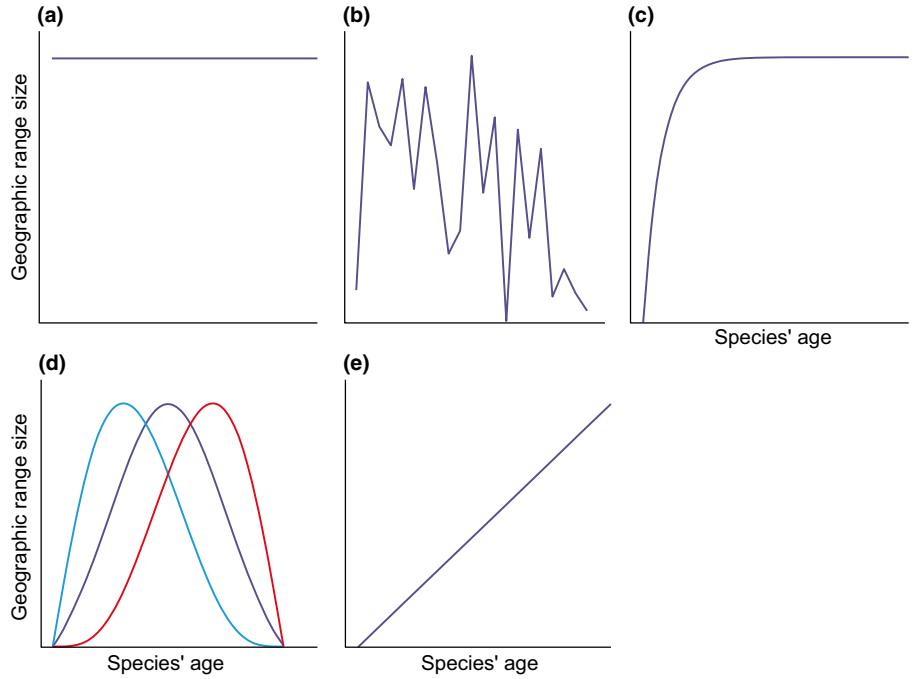

Fig. 3 Hypothesized relationships between species' age and range size. (a) Range size remains stable over time (i.e. the *stasis hypothesis*); (b) range size varies idiosyncratically over a species' lifespan; (c) range size rapidly expands after speciation and then remains stable over time (*stasis post-expansion hypothesis*); (d) range size increases after speciation, and then decreases until extinction (i.e. the *taxon-cycle hypothesis*); note this can be symmetric (black line), the rate of expansion can be greater than the rate of decline (blue line), or the rate of decline can be more rapid than the rate of expansion (purple line); (e) range size increases over time (e.g. the *age-and-area hypothesis*).

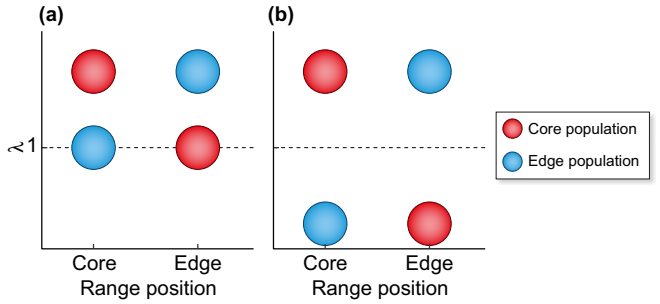

Fig. 4 Hypothetical results from a reciprocal transplant experiment of two populations (red and blue circles) originating from the core and edge of the species' range, designed to distinguish time-for-dispersal and time-for-adaptation as alternative mechanisms underlying a positive association between species' age and range size. (a) If range expansion follows the *time-for-dispersal hypothesis*, then core (ancestral) genotypes will be able to persist in more recently colonized edge sites (absolute fitness expressed as population growth rate, $\lambda \geq 1$), even if edge populations have a relative fitness advantage. (b) If adaptations must accumulate before range expansion can proceed (supporting the *time-for-adaptation hypothesis*), then ancestral genotypes from the range core will be unable to persist in more recently colonized edge sites.

filling (Fig. 3d; Liow & Stenseth, 2007). While there is some support for a hump-shaped relationship between age and range size for marine fossils (e.g. Liow & Stenseth, 2007) and extant birds (e.g. Pepke *et al.*, 2019), we are unaware of any plant studies that empirically support this model.

Given the role of dispersal in facilitating range expansions, species that have had more time to disperse may have larger geographic ranges than species that have formed more recently. If so, then there may be a positive correlation between species age and range size (Fig. 3e). This was initially coined as the *age-and-area hypothesis* by Willis (1922), and it assumes that, first, speciation results in geographically restricted species whose realized ranges are smaller than their potential ranges and, second, range size is negatively correlated with extinction risk, such that the prevalence of old species with small ranges is rare. Another prediction derived from this hypothesis is that older species have had more time to fill their potential ranges and thus occupy a larger fraction of suitable niche space relative to younger species (Svenning & Skov, 2004). Studies in the angiosperm genera *Piper* and *Psychotria* supported this hypothesis (Paul & Tonsor, 2008; Paul *et al.*, 2009), but in *Psychotria* results were sensitive to metrics of range size and filling. A major criticism of the *age-and-area hypothesis* is the prevalence of paleo-endemics (Stebbins & Major, 1965). Comparing fits of models with and without quadratic terms for species age is essential for distinguishing support for the *age-and-area hypothesis* from other models of range size evolution (de Moraes Weber *et al.*, 2014).

The same positive relationship between age and range size predicted by the *age-and-area hypothesis* could appear with greater time for adaptation, if range expansion proceeds via evolutionary adaptations to novel environments rather than solely via dispersal. Recent meta-analyses of transplant experiments suggest that most species' ranges coincide with niche limits, rather than falling short of niche limits as predicted by dispersal limitation (Hargreaves *et al.*, 2014; Lee-Yaw *et al.*, 2016). Once species have filled their potential ranges and reached niche limits, niche evolution is necessary for range expansion (Section II.3). Thus, older species should have had more time to acquire mutations that expand their niche. Though time-for-dispersal and time-for-adaptation both predict positive relationships between age and range size, they do make unique predictions (Fig. 4). In its simplest formulation, the *time for dispersal hypothesis* assumes a fixed species-level niche breadth, and that a species simply needs time to colonize sites that are within its niche limits. By contrast, *time for adaptation* assumes that niche breadth is not an inherent species-level trait, but rather that niche breadth accumulates from sequential adaptation among populations across the range. However, time for dispersal is not incompatible with local adaptation across the range or a positive relationship between niche breadth and range size. Rather, the key distinction is whether or not adaptation is required to boost absolute fitness above the persistence threshold upon colonization of a new site (Fig. 4).

Studies to date have not fully teased apart whether range expansion is more likely to proceed via dispersal or evolutionary adaptation. Further, whether widespread species exhibit greater local adaptation among populations than restricted species remains unknown. Reciprocal transplants that quantify absolute fitness instead of relative fitness could help tease apart the *time for dispersal* vs *time for adaptation* hypotheses by assessing whether core genotypes could populate the range edge. If they can, then any local adaptation that has happened was not strictly necessary for range expansion, even if it has increased fitness and abundance at the edge (Fig. 4a). If not, then adaptation was necessary to expand the range past the niche of core populations (Fig. 4b).

Tests of hypotheses about how range size changes over time can be complicated by stochasticity and observer bias. If species with large ranges have lower extinction risk, then they are more likely to be present in a phylogeny of extant taxa. By contrast, species with small ranges may be less likely to be present due to extinction (Saupe *et al.*, 2015). Thus, age-and-area relationships may be detected even in the absence of any directional change in range size over time (Pigot *et al.*, 2012). In summary, there is substantial evidence that range size can vary predictably with age, but the shape of such relationships varies across taxa and timescales (birds; Webb & Gaston, 2000).

3. Range dynamics upon speciation

Range size evolution is intimately related to the geography of speciation, as daughter species must either inherit a portion of the ancestral range or colonize a new area. In turn, the geographic mode of speciation can affect the range size and placement of sister species. In traditional allopatric speciation, the ancestral range becomes divided by a barrier into two portions of variable size; daughter species could have small or large ranges, of equal or asymmetric size, depending on the exact location of the barrier. By contrast, the 'budding' mode of speciation predicts that speciation consistently results in highly asymmetric range sizes between sister species, with one daughter originating with a small range that is

either peripheral to (Mayr, 1954) or embedded within (Mayr, 1982) the larger range of the persistent progenitor. By this logic, determining the predominant geographic mode of speciation across many clades could help explain the origin of narrowly distributed species. Skeels & Cardillo (2019) hypothesize that vicariant barriers within established populations arise much less often than stochastic but repeated long-distance dispersal events that can create isolated, peripheral populations. Although divergence of budded populations within the range of a progenitor species was traditionally thought to be unlikely in the face of gene flow, case studies of the ecological divergence of regionally sympatric narrow endemics from their widespread progenitors suggest that successful divergence often involves adaptation to a novel habitat, such as serpentine soils (Baldwin, 2005), rock outcrops (Ferris *et al.*, 2014), or tidal estuaries (Heydel *et al.*, 2017). Strong divergent selection on traits that promote adaptation to novel habitats could contribute to reproductive isolation and facilitate ecological speciation. In turn, mechanisms that promote reproductive isolation in sympatry, such as self-fertilization (Box 2) and polyploidy (Box 3), can promote rapid ecological divergence. Thus, the budding mode of speciation might be particularly likely for habitat specialists, especially in plants (Davies *et al.*, 2011; Grossenbacher *et al.*, 2014; Anacker & Strauss, 2014). Consistent with *age-and-area* and *stasis post-expansion hypotheses*, newly-formed species resulting from budding speciation will start small and grow their ranges over time if they do not go extinct, but it would be difficult to detect support for either hypothesis since the other sister species will be widespread.

Although not explicitly about the geography of speciation, Raia *et al.* (2016) also weave together ecological specialization, narrow range sizes, and speciation to propose the *weak directionality hypothesis*, for which they found support in the fossil record of 21 extinct animal clades. The *weak directionality hypothesis* posits that density dependence at the level of the clade ultimately creates an evolutionary trap: as more species accumulate, sympatry increases, driving increased specialization and decreased range size, hence extinction rates rise (Raia *et al.*, 2016).

Box 3 Ploidy and range size

The hypothesis that polyploidy is positively related to range size (reviewed in Weiss-Schneeweiss *et al.*, 2013) is based on two mechanisms. First, by increasing genetic variation, polyploidy may facilitate niche evolution, allowing species to expand their geographic ranges (Otto & Whitton, 2000). Allopolyploids that form via hybridization between two species often exhibit asexual reproduction, and are thereby triply poised to have broader environmental tolerances via reproductive assurance, greater adaptive potential due to mutations, and greater adaptive potential due to the joining of two parental genomes. Further, allopolyploids that reproduce asexually via apomictic seeds represent fixed heterozygotes, and may either behave as general-purpose genotypes with broad phenotypic plasticity and environmental tolerance, or specialized lineages that collectively confer broad tolerance to the polyploid taxon as a whole (Coughlan *et al.*, 2017). Second, larger genome and cell sizes associated with polyploidy may lead to instantaneous shifts in physiological tolerances and trait values (Levin, 2002). Polyploids may thus exhibit niche divergence from diploids, because polyploids may be better at exploiting extreme environments where competition with the parent species is relaxed (Weiss-Schneeweiss *et al.*, 2013). However, it is less clear whether this effect would result in broader niches or merely shifted niche positions in polyploids.

Studies of polyploid complexes represent a first step to dissecting the relationships among different types of ploidy and their interactions with mating system, niche breadth, dispersal ability and range size. Although one key study in western North American *Clarkia* supported the hypothesis that polyploids have larger geographic ranges than their diploid relatives (Lowry & Lester, 2006), other studies have found no differences in range size between polyploids and diploids (Hijmans *et al.*, 2007; Martin & Husband, 2009). In the *Alyssum montanum* species complex, allopolyploids had higher rates of climatic niche evolution and expanded into unique climates not occupied by their diploid ancestors, while autopolyploids had slower rates of niche evolution and their niches more closely resembled those of their diploid progenitors (Arrigo *et al.*, 2016). In hawthorns (genus *Crataegus)*, allopolyploids had larger geographic ranges and ecological niches than diploids or autopolyploids, and this difference in range size was related to increased resource allocation to dispersal traits such as larger quantities of fruit pulp and smaller seed size trading off with reduced allocation to competitive traits (Coughlan *et al.*, 2017, 2014). Further, many hybrid clones occurred in several habitat types, supporting the hypothesis that polyploidization results in general-purpose genotypes (Coughlan *et al.*, 2017). Transplant experiments of diploid and polyploid cytotypes (i.e. from the same taxonomic complex) within and beyond the total geographic range are a powerful approach for assessing whether polyploids confer fitness advantages in extreme environments lacking diploids (e.g., Ramsey, 2011; McIntyre & Strauss, 2017). Additional studies are needed to determine whether observed differences between cytotypes of different ploidy levels arise immediately as a result of polyploidization or have evolved over time since the genome duplication event (Ramsey, 2011; Husband *et al.*, 2016).

IV. Meta-analysis of the relative importance of hypothesized determinants of range size

In the previous sections we highlighted key studies that test various hypotheses for variation in range size among species, but these examples cannot reveal which hypotheses are most often supported or which have the largest effects on range size. In this section, we conduct a systematic, quantitative meta-analysis of the effect sizes of various intrinsic and extrinsic predictors of the range sizes of plants. Due to the limited number of suitable studies, this analysis highlights important research gaps rather than conclusively revealing the relative importance of hypothesized determinants of range size.

1. Overview of meta-analysis methods

We required studies to estimate native range size as a continuous, species-level response variable for three or more plant species. On 23 May 2019, we searched the Web of Science database for articles containing *geographic** and '*range size**' and *plant** in all fields; this returned 412 articles. After screening and data extraction (Supporting Information Methods S1), we retained 24 studies for analysis (Appendix A1). We required the ability to extract (or convert to) the univariate correlation coefficient, Pearson's *r*,

between range size and each predictor variable, which was then transformed to Fisher's *z*, a metric of standardized effect size for correlations (Koricheva *et al.*, 2013; Methods S1). The final dataset included 123 estimates of *z* across five categories of intrinsic predictors (dispersal ability, mating system, ploidy, niche breadth, species' age), three categories of extrinsic predictors (range position, environmental heterogeneity, and niche availability), and three categories of range size metrics as responses (area, extent, or filling; Methods S1). We collapsed observations to one per study per predictor category (regardless of range size metric) by either taking the mean *z* (if all estimates had the same sample size) or by selecting the *z* with the lowest variance (if estimates differed in sample size). To conduct a meta-analysis assessing the relative importance of each hypothesized predictor of range size, we used the METAFOR v.2.1-0 package (Viechtbauer, 2010) in R v.3.6.1 (R Core Team, 2019). In our meta-analytical model, mean standardized effect size was the response variable, predictor category was a fixed effect, and study was a random effect.

2. Meta-analysis results and discussion

Of eight general predictors of range size, two intrinsic and two extrinsic predictors were estimated to have consistently strong, positive effects on range size: niche breadth, species' age, niche availability, and range position (Figs 5, S1–S3). Mating system (coded as selfing ability), ploidy, environmental heterogeneity, and dispersal ability were not consistently associated with range size (Figs 5, S1), but all of these except dispersal ability had very low sample sizes, making any conclusions about their effects premature. Though three out of four studies of mating system reported positive effects of selfing ability on range size (Fig. S1; Table S1), the confidence interval for this category encompassed 0. By contrast, dispersal ability had larger sample sizes, but this broad predictor category encompassed substantial heterogeneity in specific estimates, from proxies for movement distance such as plant height and propagule size to correlates of propagule pressure such as reproductive frequency. Though we do not have sufficient sample sizes for formal tests, propagule size tended to have the weakest associations with range size (e.g. Sonkoly *et al.*, 2017), while effect sizes incorporating proxies for propagule pressure tended to be larger (e.g. Svenning & Skov, 2004; Fig. S1; Table S1). Realized dispersal is notoriously hard to measure well, and coarse proxies may miss true signal. Alternatively, the *gene swamping hypothesis* (Section II.3) posits that high dispersal prevents niche evolution and range expansion. The category of niche breadth also contained diverse estimates based on habitat usage and climatic tolerance, measured via observations and experiments. Though again we do not have sufficient sample sizes for formal tests, the two experimental assessments of niche breadth based on performance across treatments (e.g. Lloyd *et al.*, 2003; Luna & Moreno, 2010) had among the smallest effect sizes, while those based on distributional observations tended to be larger (e.g. Sheth *et al.*, 2014; Kambach *et al.*, 2018; Fig. S1).

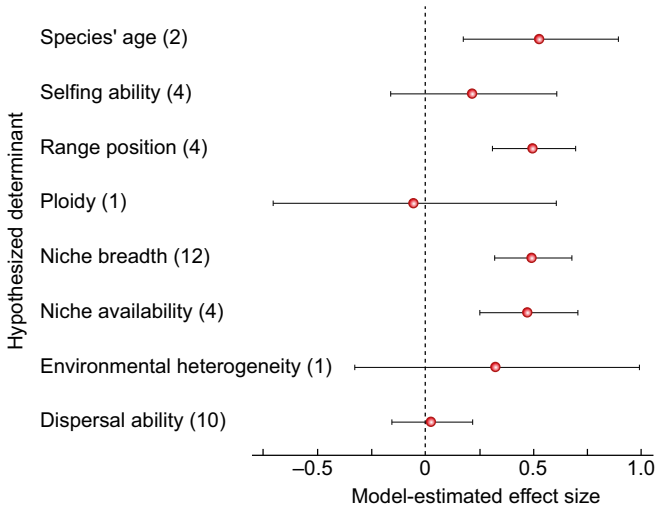

Fig. 5 Relative influence, expressed as model-estimated effect size, of each of eight general categories of hypothesized predictors of range size in plants. Mean effect size and 95% confidence intervals for each predictor are based on a meta-analytic model including predictor as a moderator (QM = 264.95; df = 8; $P < 0.0001$) and study as a random effect. A total of 24 studies were included in the meta-analysis, and the number of studies included for each predictor variable is reported parenthetically.

The quantitative estimates from the meta-analysis, though based on a systematic literature search and standardized effect sizes that adjust for differences among studies in precision and power, potentially suffer from biases in publication and reporting. Though residuals are symmetrically distributed around 0 and show no evidence that small studies were biased towards positive residuals (Fig. S4), weak associations were frequently reported incompletely (e.g. '$P > 0.05$' or 'results not shown'), precluding their quantitative incorporation. Thus, the estimates here are potentially inflated towards those that meet the threshold for statistical significance. Additionally, the meta-analytic framework we used could not incorporate estimates from phylogenetically corrected, non-parametric, or multivariate analyses. These problems were particularly prevalent in the dispersal ability category (Table S1), making any conclusions about its effect on plant range size even more tenuous.

More than providing conclusive evidence for the importance of particular hypotheses, the results from our meta-analysis point to a strong need for more studies that evaluate multiple hypothesized determinants simultaneously, report all findings regardless of statistical significance thresholds, and include interdependencies (i.e. via path analysis; Sheth *et al.*, 2014). As hypotheses about range size have been tested for plants and other taxa, it has become increasingly clear that no single hypothesis can explain variation in range size among species or across space. Although identifying the most important drivers of range size across all spaces or regions may seem unlikely, general patterns may emerge with the proper inclusion of sufficient taxa, geographic regions, and explanatory variables. Often, conflicting conclusions across studies stem from methodological differences and the difficulties of defining range size (reviewed in Gaston *et al.*, 1998). Extrinsic factors interact with one another and often vary in importance across regions of the world. For instance, Morueta-Holme *et al.* (2013) showed that both habitat availability and climatic stability were important predictors of the distribution of mean and variation of range size of vascular plants in the Americas, but distinct drivers dominated in

different regions. Ultimately, what constitutes a boundary for a species – and the temporal scales at which it is relevant – is the result of the interaction between extrinsic and intrinsic factors.

V. Conclusions

Despite the multitude of studies of geographic range size in plants, we still lack a unified understanding of the relative importance of the hypothesized determinants described here, particularly for predictor variables that are largely unique to plants, such as mating system and ploidy. We also need additional studies that merge approaches from macroecology and evolutionary ecology to understand how adaptation and dispersal interact to facilitate niche evolution and range expansion. Although geographic range size is often negatively related to extinction risk (Leão *et al.*, 2014), small-ranged species may have evolved the ability to tolerate threats (Waldron, 2010), so whether small geographic range size is an evolutionary dead end remains unknown. In the face of ongoing anthropogenic global change, narrow-ranged species have decreased, while widespread species have increased in abundance in habitats with human disturbance (Newbold *et al.*, 2018). Gaining insights into the drivers of geographic range size among species and across space informs our understanding of species endemism and rarity, hotspots of biodiversity, and invasibility. Ultimately, our knowledge of geographic range size relies on natural history observations and collections coupled with well-supported taxonomic and phylogenetic hypotheses. As these data continue to accumulate for plants, we hope to gain a more comprehensive understanding of the processes that govern range size variation among taxa and across space for this large branch of the tree of life.

VI. Future directions

(**1**) Although spatial variation in range size has been studied at the continental scale and below, mapping global mean and other moments of range size distributions in plants is the first step needed towards quantifying the relative importance of hypotheses to explain geographic variation in range size worldwide.
(**2**) To further grasp how intrinsic factors shape variation in range size, future studies need to consider intra-specific variation in and interactions between dispersal ability and niche breadth. Given the strong global support for the *niche breadth hypothesis*, studies that examine how species-level niche breadth is partitioned among populations and genotypes would be valuable for understanding the roles of individual- and population-level niche breadth in driving patterns of range size.
(**3**) There is a paucity of work on the role of biotic interactions, particularly positive interactions, in expanding species' niche breadths and thus range sizes (Stanton-Geddes & Anderson, 2011; Afkhami *et al.*, 2014). A largely untested hypothesis, especially in plants, is that narrowly distributed species are more sensitive to negative interactions or mutualisms (e.g. sparrows: Herrera-Alsina & Villegas-Patraca, 2014). When it comes to pollination or other mutualisms, the degree of specialization (e.g. the number of pollinator species on which a plant species relies) is one often overlooked dimension of niche breadth that could be related to a species' ability to expand its geographic range (Karron, 1987).
(**4**) To disentangle cause and effect of the correlation between genetic variation and range size, simulations or microcosms – where starting populations vary in initial genetic variation and range expansion can be followed in real time – are particularly powerful approaches (e.g. beetles: Szűcs *et al.*, 2017; Williams *et al.*, 2019).
(**5**) It has been hypothesized that trade-offs constrain niche evolution and range expansion (Futuyma & Moreno, 1988). If so, then small-ranged species should have steeper fitness trade-offs between core vs edge environments, yet to our knowledge, these predictions have not yet been tested.
(**6**) Phylogenetic reconstruction methods that explicitly incorporate geography (e.g. BioGeoBEARS; Matzke, 2013) are a promising way forward in terms of modelling patterns of range change through time and testing whether most range change happens upon cladogenesis or afterwards.

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ORCID

Amy L. Angert https://orcid.org/0000-0003-3082-0133
Naia Morueta-Holme https://orcid.org/0000-0002-0776-4092
Seema Nayan Sheth https://orcid.org/0000-0001-8284-7608

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Appendix A1

Citations included in meta-analysis and Supporting Information Table S1

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Summary of effect sizes from studies included in meta-analysis.

Fig. S2 Sensitivity analysis with underrepresented categories omitted.

Fig. S3 Sensitivity analyses with underrepresented categories pooled.

Fig. S4 Funnel plot inspecting possible publication bias in meta-analysis.

Methods S1 Detailed methods for meta-analysis.

Table S1 Summary of studies included in meta-analysis.

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