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Why Are Species' Traits Weak Predictors of Range Shifts?

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Abstract

We examine the evidence linking species' traits to contemporary range shifts and find they are poor predictors of range shifts that have occurred over decades to a century. We then discuss reasons for the poor performance of traits for describing interspecific variation in range shifts from two perspectives: (*a*) factors associated with species' traits that degrade range-shift signals stemming from the measures used for species' traits, traits that are typically not analyzed, and the influence of phylogeny on range-shift potential and (*b*) issues in quantifying range shifts and relating them to species' traits due to imperfect detection of species, differences in the responses of altitudinal and latitudinal ranges, and emphasis on testing linear relationships between traits and range shifts instead of nonlinear responses. Improving trait-based approaches requires a recognition that traits within individuals interact in unexpected ways and that different combinations of traits may be functionally equivalent.

1. INTRODUCTION

With climate change accelerating and its associated impacts eroding biodiversity (Urban 2015), there is an immediate and urgent need to predict how geographic ranges of species will shift in the future. This requires new understanding of the ecological and evolutionary mechanisms that govern changes to the margins of species' ranges (Angert et al. 2020, Sexton et al. 2009, Sutherland et al. 2013). While there has been a globally coherent shift poleward and upward in elevation (Parmesan & Yohe 2003), geographic ranges of many species have not shifted, and others have moved in directions opposing expectations (Chen et al. 2011, Rapacciuolo et al. 2014).

Species' traits are promising candidates for explaining variation among species in geographical range shifts. Traits are measurable characteristics of organisms, such as morphological, physiological, behavioral, and life history attributes. Since Darwin, species' traits have been recognized as being both products and drivers of ecological and evolutionary processes. Evidence for the importance of traits in ecology is plentiful, including results from studies of competition (Kunstler et al. 2016), metacommunity assembly (Leibold & Chase 2018), ecosystem function (Cardinale et al. 2012), and life history (Adler et al. 2014). Enthusiasm has extended to building a trait-based functional biogeography to understand the spatial distribution of forms and functions (Violle et al. 2014). Trait databases and trait-based science are rapidly expanding areas of research (Gallagher et al. 2020).

Coupling traits to expansions and contractions at the edges of species' ranges would seem to be a natural extension and could provide a mechanistic understanding of the processes driving changes in latitudinal and altitudinal distributions (Buckley & Kingsolver 2012). The addition of traits to species distribution models could improve prediction success (Kearney & Porter 2009) and inform the construction of future assemblages (van Bodegom et al. 2014). For these reasons, species' traits have already been incorporated into recommendations and conservation prioritization schemes of major conservation organizations (Butt & Gallagher 2018, Foden et al. 2013).

Yet, species' traits have performed poorly as predictors of contemporary range shifts that have taken place over decades to a century (Angert et al. 2011, MacLean & Beissinger 2017). Why should this be the case? In this review, we first examine the evidence linking species' traits to range shifts. We then discuss reasons for the poor performance of traits for describing interspecific variation in range shifts from two perspectives: (*a*) factors associated with species' traits that degrade range-shift signals and (*b*) issues in quantifying range shifts and relating them to species' traits. We conclude by considering where to go from here, given that the processes leading to range shifts involve many different components of an organism's biology. Improving trait-based approaches requires a recognition that traits within individuals interact in unexpected ways and that different combinations of traits may be functionally equivalent.

2. SPECIES' TRAITS HAVE LOW SUCCESS AT PREDICTING RANGE SHIFTS

In this section, we review evidence that species' traits can predict range shifts. We concentrate on the commonly studied traits of organisms that have been linked by theory to the processes governing range shifts and for which independent studies have been replicated sufficiently to quantify effects. Due to lack of replication, our criteria excluded some traits associated with range shifts in a few studies of specific taxa, like brain size, diet composition (e.g., nitrogen-rich foods), and habitat niches (MacLean & Beissinger 2017). We follow Estrada et al. (2016) in defining a range shift as an expansion of one part of a range margin that may or may not be accompanied by a contraction in another part of the range.

We do not consider externalities like geographic range size, geographic position within the range, climatic conditions of the range (e.g., climate velocity), abundance, and phylogeny to be species' traits. They are not evolved properties, characteristics, or attributes of organisms per se. Instead, these externalities represent emergent phenomena related to environmental, ecological, biogeographical, or evolutionary patterns associated with the mechanisms driving range shifts. Nevertheless, these externalities are often strongly related to the probability that a species has shifted its geographic range and are often better predictors of range shifts than species' traits (MacLean & Beissinger 2017, Pacifici et al. 2020, Pinsky et al. 2013).

Expectations for how species' traits should affect range shifts are based on theory from invasion biology (Estrada et al. 2016), niche theory (Sexton et al. 2009), and population biology (Angert et al. 2011, Hampe & Petit 2005). Range expansions through colonization of new locations should be more likely to occur in species that are mobile (Berg et al. 2010) and are ecological generalists that exhibit greater diet and habitat breadth, since they should be more likely to find suitable resources (Buckley & Kingsolver 2012). Greater mobility and habitat breadth should also occur in migratory species, since they must adjust to different environments at either end of their journey (Tingley et al. 2012). Individuals that have dispersed to new areas are more likely to become established if they exhibit what is known as a fast lifestyle, with high fecundity and low longevity (Angert et al. 2011, Perry et al. 2005) and broad physiological tolerances (Diamond 2018). These traits should also be positively associated with persistence at range margins, with the exception that slow-lifestyle, long-lived species may be better able to persist at warm range margins than fast-lifestyle, short-lived species (Hampe & Jump 2011). Body size, however, could produce contrasting effects. Small body size is likely to be associated with a fast lifestyle, but dispersal ability is often positively associated with large body size (MacLean & Beissinger 2017).

These predicted relationships between species' traits and range shifts are tempered by the recognition that spatial changes in geographic ranges do not occur in a vacuum. They are influenced by environmental factors (e.g., climate), biotic interactions (e.g., competition, disease, and predation), human impacts (e.g., climate and land-use change), and nonequilibrium dynamics (e.g., time lags in species' responses to climate change). Moreover, species may reduce or even alleviate the need to shift ranges through phenological shifts (Socolar et al. 2017), phenotypic plasticity (Riddell et al. 2018), and evolutionary change (Angert et al. 2020), which may or may not be mediated by traits.

2.1. Approaches to Evaluate the Strength of Evidence for Traits as Predictors of Range Shift

There are two general approaches to evaluating the strength of evidence for traits as predictors of recent range shifts (MacLean & Beissinger 2017). One method is to conduct a meta-analysis of primary data that are compiled from existing studies of range shifts of individual species and their corresponding traits. Meta-analysis of primary data is often championed, but valid applications need to address problems of comparability among studies due to methodological heterogeneity. Assembling a comprehensive and comparable data set with all the relevant information can be difficult, costly, and time-consuming (Mengersen et al. 2013a). A resource called BioShifts, which contains >30,000 range shifts from >12,000 plant and animal species (Comte et al. 2020), was recently made available, representing the first step in this process.

The second method is to conduct a formal meta-analysis of aggregated results derived from different published studies that compared changes in geographic distributions of assemblages composed of taxonomically related species that occurred together in space and were sampled across two or more time periods. These analyses tested whether species' traits accounted for heterogeneity in range shifts. Meta-analyses of aggregated data use a set of rigorous statistical techniques to synthesize evidence and have been employed for over three decades in ecology (Koricheva et al. 2013). Vote-counting of the number of studies supporting or refuting a pattern is a rudimentary form of aggregated meta-analysis. A stronger method for inference is to calculate the mean effect size across multiple studies after weighting the strength of a relationship by its standard error; studies with bigger effects and smaller standard errors receive more weight. This approach can also account for ecological and methodological heterogeneity among studies using covariates (MacLean & Beissinger 2017).

2.2. Results from Meta-Analyses of the Strength of Traits to Predict Range Shifts

There is now a sufficient number of primary studies and formal meta-analyses to draw some conclusions about the ability of traits to account for contractions and expansions of species' ranges. Although studies varied in their objectives, most were conducted with the goal of determining whether species' traits could explain interspecific differences in range shifts in response to climate change. To this end, assemblages sampled in the same set of locations were compared over intervals between decades and a century or more. These studies offer the advantage of quantifying long-term changes in species' ranges rather than short-lived expansions and contractions. They typically examined changes to latitudinal or elevational margins of ranges, rather than turnover within the geographic range of species (i.e., range filling and thinning).

There have been four meta-analyses of the strength of traits to predict range shifts that compared responses of multiple taxa (Angert et al. 2011, Buckley & Kingsolver 2012, Estrada et al. 2016, MacLean & Beissinger 2017). The number of species' range responses tended to expand, as each study subsequently incorporated many of the data sets that were previously analyzed as well as adding new studies.

Angert et al. (2011) investigated how well traits accounted for range shifts at the leading (poleward or upward) edge in 254 species of North American birds, 24 species of European Odonata, 133 species of Swiss alpine plants, and 28 small mammal species in montane California, for a total of 439 species responses. Each taxon was analyzed separately using linear models with and without phylogenetic autocorrelation. Traits included body size, movement behaviors (e.g., migration, flight ability, and dispersal mode), reproduction (e.g., seed mass, flowering duration, and clutch size), habitat affinities and breadth, and diet breadth. While traits explained variation consistent with invasion models and life history, they had very low explanatory power and none had significant model-averaged regression coefficients. Generally, there was an absence of significant phylogenetic signal. Moreover, the results were idiosyncratic for different taxa. For example, range shifts of British Odonata were modestly predicted by egg-laying habit, while the duration of seed dispersal was a marginally significant predictor of elevation shifts in Swiss alpine plants. Angert et al. (2011) concluded that species' traits are unlikely to be of predictive utility for conservation and management.

Buckley & Kingsolver (2012) compared the performance of traits and phylogenies as predictors of range shifts attributed to recent climate change for 882 species. Their data set included species analyzed by Angert et al. (2011) and added assemblages of European plants and butterflies, Peruvian birds, and North Sea fish. Buckley & Kingsolver (2012) reported that traits explained a significant but very modest amount of variation in range shifts (mean $R^2 = 0.16$) and found few individual traits that were significant predictors. Phylogenetic effects on range shifts were generally not significant and were much weaker than effects on phenological shifts.

Estrada et al. (2016) also found equivocal results for traits as predictors of recent range shifts. Their evaluation was limited to vote-counting of the results of responses (supporting, refuting, or nonsignificant) from nine selected studies of range shifts, representing 811 species, which included many of the same studies analyzed earlier in this section. Traits were not treated specifically but instead were combined into categories related to site fidelity, movement, ecological generalization, reproduction, and competitive ability. None of the trait categories were clearly associated with range shifts. The few trends that did emerge were associated with range filling. Estrada et al. (2016) suggested the lack of support for traits as predictors of range shifts occurred for multiple reasons: the drivers of range shifts are complex, few studies had been published because of the requirement for multispecies surveys conducted over multiple time periods, a sufficient period of time had not elapsed for species to have responded with range shifts, and the studies had not considered the exposure of species to climate change, which affects whether new regions had become climatically suitable for colonization.

MacLean & Beissinger (2017) produced the most extensive meta-analysis of the role of traits as predictors of range shift. They expanded the number of studies documenting latitudinal or altitudinal range shifts to 42 assemblages and 8,653 species responses. This sample was used for vote-counting of range responses with seven commonly reported traits: body size, migratory strategy, movement ability (including seed dispersal mode, flight behavior, or dispersal distance), fecundity, longevity, diet breadth, and habitat breadth.

We updated the vote-counting results of MacLean & Beissinger (2017) to create **Figure 1** (see **Supplemental Appendix 1** for details on the studies added and search methods). The patterns exhibited now represent 50 assemblages and 12,094 trait-range responses. As in MacLean & Beissinger (2017), none of the seven traits showed strong effects on range shifts, and relationships appear to be highly study specific. Predicted relationships between traits and range shifts were supported in half the studies for habitat breadth and less frequently for movement ability (35%), fecundity (25%), diet breadth (25%), longevity (20%), body size (18%), and migratory strategy (9%). These traits exhibited a mixture of significant positive and negative relationships, as well as many nonsignificant results.

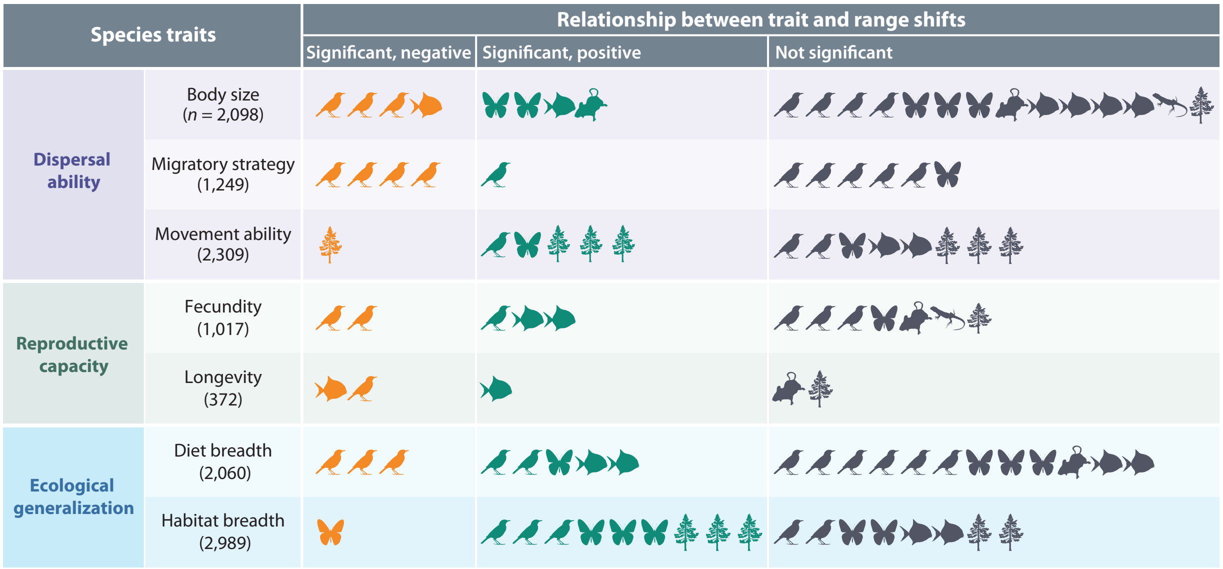

Figure 1

The relationship between the traits of species comprising assemblages and shifts in their latitudinal or altitudinal range limits. Each icon represents a single study of small mammal, bird, reptile, fish, invertebrate, or plant assemblages. The total number of species-range responses for each trait is given by *n*. See **Supplemental Materials** for details on the studies, assemblages, and traits. Figure adapted from MacLean & Beissinger (2017). Silhouettes of organisms reproduced from **http://phylopic.org** (CC BY 1.0).

MacLean & Beissinger (2017) also produced the first estimates of effect sizes from data gleaned across studies for body size, reproductive effort, diet breadth, and habitat breadth for 3,123 species responses in 26 assemblages, which were the only studies and traits with sufficient data for such an analysis. Mean effect sizes did not differ from zero for any of the traits, indicating that they did not have a significant overall effect on range shifts across studies. MacLean & Beissinger (2017) probed the ecological and methodological covariates that account for heterogeneity in effect sizes. Results for all traits were unaffected by the number of years that elapsed between surveys and whether a study controlled for phylogeny. Other results were highly trait specific and did not necessarily match what would be expected from theory. For example, range shifts increased as body size decreased for mobile taxa (birds and marine fishes), while body size explained little variation for less mobile organisms. Effect sizes of diet breadth were negative for altitudinal range shifts and positive for latitudinal range shifts. In addition, effect size of habitat breadth increased with the size of the study region.

In summary, the picture that emerges from these meta-analyses is that ecological and life-history traits have limited success in accounting for variation among species in range shifts over the past century. Adding more studies and taxa improves our understanding but seems unlikely to change the general conclusions. Predicted relationships between traits and range shifts received low levels of support or were inconsistently supported (**Figure 1**). Thus, we conclude that, while traits may show effects in individual studies, overall their effects and importance are inconsistent across studies, making them problematic indicators of species' range responses to future climate change.

The inconsistent relationships between species' traits and range shifts may explain why authors can arrive at conflicting conclusions about the role of traits in assemblages of similar species and in similar ecosystems. For example, Pinsky et al. (2013) and Schuetz et al. (2019) concluded that traits representing dispersal, trophic level, and reproductive capacity had little power to explain the distribution shifts of 126 species of marine invertebrates and 199 species of fish relative to climate velocities off North American coasts. Yet, Sunday et al. (2015) found the inclusion of mobility, trophic level, and ecological specialization improved range-shift prediction success compared to climate velocity alone for 50 species of marine fish and 54 invertebrates off the coast of Australia. We next consider some perspectives on why traits have performed so inconsistently.

3. FACTORS THAT DECOUPLE TRAITS FROM RANGE SHIFTS

The poor performance of traits for describing interspecific variation in range shifts could partly stem from the measures used for species' traits, traits that typically are not included in meta-analyses, and the influence of phylogeny on range-shift potential.

3.1. Average Values for Species' Traits Can be Problematic

Most analyses treat species' traits as fixed entities, yet many traits vary over time, space, or both. This applies to many morphological, physiological, life history, and behavioral traits. In the following sections, we discuss three important processes associated with trait variation.

3.1.1. Intraspecific variation in traits across space. Intraspecific trait variation poses substantial challenges because species' traits often vary across geographic ranges, complicating the appropriate trait value to use in an analysis. Moreover, geographic variation in traits can be directly related to the processes driving range shifts. Individuals that inhabit the leading edge of a geographic range often exhibit trait values that depart from the species' mean due to unique selective pressures at the range edge (Chuang & Peterson 2016). At range margins, individuals with a certain behavior, body size, or life history strategy can have a higher propensity for dispersal relative to other individuals within the same population (Clobert et al. 2009). In fish, birds, and insects, the body sizes of individuals that live on the leading edge of the population tend to be larger, possibly due to size-dependent dispersal capacity (Gunnarsson et al. 2012, Hill et al. 1999, Lopez et al. 2012). Reduced competition at the expanding range edge can also select for strategies that maximize reproduction, whereas individuals in the core may invest more in competitive ability due to greater population density (Chuang & Peterson 2016).

Geographic variation in traits related to range-shift capacity is not isolated to animals. Many plant species exhibit similar patterns, with seeds on the range edge having traits that maximize dispersal distance (Huang et al. 2015). Surprisingly, intraspecific variation in these traits can arise quite rapidly. Geographic variation in plume loading of seeds emerged only 30 years after the introduction of an invasive vine (Huang et al. 2015). Thus, trait values that originate from less recent studies or studies that focus only on a single population may not capture the trait values responsible for driving range shifts.

3.1.2. Phenotypic plasticity changes trait values over an organism's lifetime. Traits that contribute to range shifts can vary over an organism's lifetime (Kingsolver & Huey 1998). In some cases, plasticity is irreversible, with trait values determined early in development, and in other cases, it can be reversible over an organism's lifetime. These phenotypic changes are rarely considered in trait-based analyses of range shifts. Phenotypic plasticity describes the environmentally sensitive expression of a particular phenotype. Organisms exhibit plasticity in many of the morphological, physiological, life history, and behavioral traits predicted to influence range-shift capacity (Gunderson & Stillman 2015, Simmons & Thomas 2004), potentially allowing organisms to tolerate a large breadth of environmental conditions caused by climate change. For instance, some invertebrate species show strong plasticity in heat tolerance in response to warm temperatures, and this plasticity can promote the same degree of persistence as strong natural selection over many generations (Palumbi et al. 2014). Physiological and morphological traits can also vary seasonally over an individual's life span or across generations (Gunderson & Stillman 2015, Kingsolver & Huey 1998). Seasonal changes in traits have important implications for range contractions under climate-warming scenarios (Riddell et al. 2018).

Range-shift responses are facilitated by certain combinations of traits, each of which may exhibit their own degree of plasticity. For instance, species with greater plasticity in thermal tolerance should exhibit a limited range shift in response to warming because they are capable of tolerating hotter conditions within their current range (Comte et al. 2014, Estrada et al. 2016). This prediction is generally supported in a recent meta-analysis (Diamond 2018), but low plasticity in physiological tolerance does not necessarily translate into a large range-shift response. Such a response would require a combination of low physiological plasticity and high movement capacity. Perhaps unsurprisingly, a high degree of plasticity in one trait does not necessarily confer a high degree of plasticity in another (Fischer et al. 2016). Thus, trait-based analyses of range shifts require independent estimates of plasticity among categorically different traits that enhance a species' capacity to shift its range.

3.1.3. Adaptation leaves parental phenotypes and traits behind. Despite the rapid pace of contemporary climate change, evolutionary responses across generations appear strong enough to influence some species' traits that affect range shift capacity. Traits are known to evolve during range expansions when individuals with a greater capacity to migrate reproduce together in newly established territory (Chuang & Peterson 2016). If heritability is high for these traits, then reproduction among colonizers generates a positive feedback loop driving further evolution in a process termed the Olympic Village effect (Phillips et al. 2008). Similar adaptive responses have also been found in insects. Selection on the enhancement of morphological traits such as leg length, thorax size, or wing length may be indicative of adaptive evolution during invasions and range expansions (Laparie et al. 2013, Simmons & Thomas 2004). In contrast, climate change has not systematically affected morphological traits in birds but has advanced the phenology of nesting, although the response appears incomplete and unable to keep pace with the changing environment (Radchuk et al. 2019).

Genetic variation is not considered a species' trait, but it can constrain or promote evolution in traits that influence contemporary range shifts. The abundant center model predicts that a species is generally more abundant in the center of their geographic range, leading to more isolated populations at the range edge (Lawton 1993). As a consequence, genetic diversity within populations is predicted to decline from the center of the geographic range to the edge. Similarly, populations should also become more genetically differentiated at the range edge. Empirical evidence for these two patterns has been generally supported across both plant and animal systems (Eckert et al. 2008). The lack of genetic variation may constitute a significant barrier to evolutionary responses that enhance range-shift capacity as climate warming accelerates (Pauls et al. 2013). Moreover, the increased genetic differentiation of locally adapted populations is likely to produce highly region-specific range shifts under contemporary climate change (Sork et al. 2010). Evolutionary responses such as these indicate that trait-based analyses might incorporate the adaptive potential of relevant traits while also accounting for relatedness, particularly for populations at range edges.

3.2. What's Missing from Many Trait-Based Analyses?

Traits used for describing interspecific variation in range shifts in meta-analyses represent a small sample of the potential traits that could be important. In the following sections, we discuss three kinds of traits and one process associated with trait variation that could be valuable to include in future analyses.

3.2.1. Species' traits related to exposure need better consideration. Traits may poorly describe range shifts because species in the same location vary in their exposure to climate change. Exposure is defined by the magnitude of climate change at a location and the capacity of the species to use microhabitat buffering to avoid the direct effects of climate change (Williams et al. 2008). A species may experience low exposure because the climate has remained relatively stable at a location or the species exhibits behaviors that buffer individuals from climate change. Without exposure to an environmental change, species are not expected to exhibit a geographic range shift, regardless of whether they exhibit traits associated with a high capacity to shift their range. Consequently, range shifts in response to contemporary climate change may be weakly related to traits involving movement, dispersal, or reproductive strategy and more strongly related to the factors that influence exposure, be they species' traits or environmental characteristics, such as microhabitat variation. The effect of microhabitat buffering on exposure depends primarily on the use and availability of microhabitats. To complicate matters, exposure can vary substantially among similar taxa inhabiting the same geographic region and experiencing the same magnitude of climate change (Riddell et al. 2021).

Many organisms rely on behavioral buffering to minimize their exposure to the environment. For example, activity patterns and habitat preferences play a major role in how species experience the direct effects of warming (Kearney et al. 2009). Small mammals exhibit a high degree of fossoriality and nocturnality and have also exhibited a high degree of interspecific variation in elevational range shifts from climate change over the last century (Moritz et al. 2008, Rowe et al. 2014). Indeed, trait-based analyses revealed that movement ability and reproductive strategies failed to explain interspecific differences in range shifts (Angert et al. 2011, Moritz et al. 2008). Activity pattern (diurnal versus nocturnal) was also unable to explain variation in range shifts, counter to expectation based on the fact that diurnal rodents are more exposed to the direct effects of warmer conditions. However, exposure can be similar for diurnal and nocturnal rodents because both have easy access to cool microhabitats below ground (Riddell et al. 2021).

Even traits seemingly unrelated to microhabitat use, such as morphology, can influence exposure to climate change and the propensity of species to shift geographic ranges by influencing exposure. Traits related to heat balance, such as coloration, influence the rate of heat exchange and total heat loads such that some species experience substantially warmer conditions than others, all else held equal (Kearney & Porter 2009). For instance, animals with darker plumage or pelage experience greater heat loads due to more absorption of solar radiation compared to species with lighter plumage or pelage in the same environment (Walsberg & Wolf 1995). Differences in heat loads due to morphological traits that superficially appear to be unrelated to range shifts, like color, may translate into differences among species in exposure to climatic conditions. As evidence, simulations of heat flux for a desert bird community indicated that species-specific exposure to climate was associated with site-level persistence and climate-driven declines in the Mojave Desert over the last century (Riddell et al. 2019a).

In reality, a great variety of morphological and behavioral traits interact to affect exposure to heat loads. For birds, body size, body shape, and plumage properties (e.g., absorptance, length, density, and depth) interact to determine the amount of heat that each species experienced from climate change over the last century (Riddell et al. 2019a). For rodents, similar traits, like the thermal conductance of the pelage, influence exposure to climate change, but reliance on subterranean burrows greatly diminishes the exposure of small mammals to climate change, resulting in long-term community stability over the last century (Riddell et al. 2021). Plants also have traits that influence exposure in ways yet to be fully explored by trait-based analyses. For example, plant species that specialize in microhabitats (Zellweger et al. 2020) or exhibit efficient cooling capacities through enhanced transpiration (Crawford et al. 2012) might reduce their exposure to climate change.

Thus, traits related to exposure might cast new light on the processes that drive range shifts, but doing so requires approaches that integrate across traits to understand their combined influence on the exposure of organisms. One method is to use biophysical simulations. To date, heat flux models have proved effective at explaining endotherm energetics, climate vulnerability, and geographic variation in body size (Kearney et al. 2016, Medina et al. 2018, Riddell et al. 2019a) but have yet to be applied to investigate whether interspecific differences affect range-shift capacity. In addition, these models can address the time-dependent effects of exposure to temperature variability and extremes on physiological responses (Kingsolver & Buckley 2017). Heat flux simulations may be useful for identifying species or different combinations of traits that are most likely to experience the greatest pressure for a range shift based on exposure to climate change.

3.2.2. Species' traits related to hygric niches are understudied. Range shifts of many species have responded more strongly to long-term changes in precipitation than temperature (Fei et al. 2017, Tingley et al. 2012). Like thermal niches, hygric niches provide a framework for linking performance of species to distributional limits (Boyle et al. 2020). Indeed, species distribution models have demonstrated the potential for hygric traits to determine the limits of geographic ranges (Riddell et al. 2017). If there are hygric niches, are there species' traits related to them that have not been considered to date in analyzing the relationship between traits and range shifts?

Few species' traits directly related to the hygric niche have been considered in past meta-analyses of traits and range shifts (Angert et al. 2011, Buckley & Kingsolver 2012, Estrada et al. 2016, MacLean & Beissinger 2017). Yet, some traits related to hygric niches have been studied across a large number of taxa, including rates of water loss (e.g., Riddell et al. 2017), effects of dehydration on performance, and rates of evaporative cooling (e.g., Song & Beissinger 2020). Rates of water loss describe how quickly an organism loses water to its environment; however, these estimates are often biased by experimental conditions (Riddell et al. 2017). Trait-based analyses might benefit from focusing on resistance to water loss as a less-biased trait to compare across species because it incorporates environmental factors that often confound metrics of water loss. Dehydration reduces the performance of traits related to range-shift capacities, particularly locomotor performance, and the sensitivity of performance to dehydration also correlates with climatic conditions across the species' geographic range (Titon & Gomes 2015). In mammals, the relative medullary thickness of the kidney is a good indicator of the ability to concentrate urine and species' persistence under arid conditions (Kohli & Rowe 2019). Desiccation and inundation resistance are thought to be important species' traits for invertebrates (Moretti et al. 2017). Too much water can be a problem for endotherms too, and endotherms in humid environments are less efficient at evaporative cooling to maintain homeothermy (McKechnie & Wolf 2019).

Hygric traits related to water transport and desiccation resistance are equally relevant to range shift responses in plants. For example, climate change threatens to increase mortality in trees by disrupting water-transport pathways (Choat et al. 2018). To predict which species are most vulnerable to drought, trait-based approaches have integrated combinations of characteristics related to water use (Blackman et al. 2019). Species' traits, such as stomatal closure points and leaf hydraulic vulnerability, have proved effective in predicting the risk of desiccation in certain plants and may provide promising avenues for trait-based analyses of range shifts.

3.2.3. Competitive ability is a key trait but can be difficult to measure. Competitive ability ranks highly among species' traits with the potential to explain range shifts, yet measures of competitive ability are lacking from most primary and meta-analyses of range shifts. The behavioral, morphological, and physiological traits that make a species more or less competitive are often not well understood or measured in a standardized manner across taxa (Estrada et al. 2016). The problem is particularly acute for animals, for which competitive ability is indirectly inferred from abundance, population growth rates, body size, or brain size, and the importance of these traits seems to vary greatly among analyses. Lacking are direct observations of competitive interactions and their outcomes. Competitive ability in plants is often inferred by relating species' traits, such as leaf dimensions and plant height, to growth rates or densities. For example, three species' traits—wood density, specific leaf area, and maximum height—influence competitive interactions in a global analysis of tree community assembly (Kunstler et al. 2016). Missing from this perspective are the belowground processes, including interactions with the soil bacterial community, which can also mediate competition among plants (Casper & Jackson 1997, Hortal et al. 2017).

Using traits to predict range-shift responses, however, requires the incorporation of additional factors because competitive ability is often context dependent, even in plants (Kimball et al. 2016). For instance, cooccurring species may exhibit negative interactions within and near the lower limit of their elevational range, but at the upper range limits these interactions can become facultative, facilitating establishment by creating microhabitat conditions that minimize climatic stress (Ettinger & HilleRisLambers 2017). Similarly, competitive ability cannot be assumed to remain constant during range shifts. Changes in diet, which may occur as species disperse into novel habitats, can quickly cascade into the evolution of reduced competitive ability (Messina 2004). The context dependence of competitive ability complicates the efficacy of trait-based analyses, yet it may explain why traits can appear to be good predictors in some situations and weak predictors in others (Sandel et al. 2010).

3.2.4. Phylogeny creates mixed signals for relationships between traits and range shifts.

Studies of range shifts often focus on particular clades or larger nonmonophyletic taxonomic groups (McCain & King 2014, Rapacciuolo et al. 2014). Regardless of the taxonomic scope, a trait-based analysis can suffer from statistical nonindependence if it does not correct for the lack of phylogenetic independence (Felsenstein 1985). Yet, relatively few primary studies have incorporated phylogenetic inference into trait-based analyses of range shifts (Diamond 2018).

Phylogeny can affect range-shift capacity in several ways. If range-shift responses are conserved, like environmental niches sometimes are (Wiens et al. 2010), then shared evolutionary history or phylogenetic relatedness might enhance or retard range shifts because closely related species would respond similarly (Buckley & Kingsolver 2012). When a phylogenetic signal is consistently small, range shifts may be labile compared to cases where there is mixed evidence of small and large phylogenetic signals (Diamond 2018). With many traits and other externalities (e.g., geographic position, range size, and climate velocity) potentially capable of contributing to range-shift capacity, the notion that range shifts would be phylogenetically constrained seems less plausible.

Accounting for phylogenetic relatedness in some manner has often been part of meta-analyses. Angert et al. (2011) found little evidence of a significant phylogenetic signal across North American birds, European Odonata, Swiss alpine plants, and small mammal species in the Sierra Nevada. Likewise, Buckley & Kingsolver (2012) found weak evidence for a phylogenetic signal on range shifts, especially compared to phenological shifts. There are no formal methods for incorporating phylogenetic relatedness in effect-size calculations in formal meta-analyses of aggregated results, and taxa are so diverse that combining phylogenies would be difficult (Mengersen et al. 2013b). As a result, MacLean & Beissinger (2017) used a binary indicator to distinguish studies by whether they controlled for phylogeny. They found no differences in effect sizes between studies that did and did not control for phylogenetic relatedness.

Diamond (2018) presented the most comprehensive meta-analysis of phylogenetic signals, producing 27 estimates for seven taxa (bees, birds, butterflies, fishes, mammals, odonates, and plants). She found highly variable phylogenetic signals for range-shift capacity. Although range-shift capacity appeared to be evolutionarily constrained in some taxa, range-shift capacity generally appeared to be highly labile, likely owing to the complex suite of traits and processes that may contribute to a successful shift in a geographic range (Diamond 2018). Evolutionary lability suggested trait-based approaches may be more likely to explain range shifts than phylogenetic relatedness, but it also suggested that constraints related to range-shift ability can be shared in closely related species.

In conclusion, there is conflicting evidence for and against a phylogenetic signal affecting range-shift capacity, and it remains an area for future study. The variation in phylogenetic signals observed across taxa and the potential for rapid evolution of traits underlying range-shift capacity indicates that evolutionary responses and relationships remain critical aspects of predicting shifts in geographic ranges. Phylogenetic signal has the potential to serve as both a control for and an alternative to trait-based analysis of range shifts.

4. ISSUES IN QUANTIFYING RANGE SHIFTS AND RELATING THEM TO TRAITS

The weak ability of species' traits to describe interspecific variation in range shifts could partly stem from the challenges and uncertainties in quantifying range shifts over time and space, differences in the responses of altitudinal and latitudinal ranges, and an emphasis on testing linear relationships between traits and range shifts. In the following three sections, we discuss how each of these aspects can contribute to variability in the relationship between species' traits and range shifts.

4.1. Range-Shift Estimates Suffer from Ignoring Imperfect Detection

Evidence for a range shift comes from survey data on occupancy that have inherent uncertainties due to imperfect detection (Tingley & Beissinger 2009). Here, we emphasize how imperfect detection affects estimates of site occupancy and range shifts, but the same issues befall measures of change in centers of abundance (Dénes et al. 2015), which are sometimes used as a surrogate for range boundary shifts. The issues we discuss apply to all measures of range change—expansion, contraction, and filling—and to the use of contemporary as well as historic survey or occurrence data (Tingley & Beissinger 2009).

A range shift depends on the absence of evidence—evidence that a species did not occur at a location at some period of time—as well as confidence that the evidence is not erroneous. Occurrence data are likely to include both false absences (where a species is undetected in surveys at sites but was present) and, depending on the sampling and detection process, false presences (where a species was mistakenly detected but, in reality, was not present). Both forms of imperfect detection bias range estimation (Guillera-Arroita 2017, Miller et al. 2011, Tingley & Beissinger 2009). Imperfect detection is not just an issue for animal surveys; even sessile plant surveys imperfectly detect species (Chen et al. 2013) and individuals (Shefferson et al. 2001). False absences are likely the most prevalent form of detection error, but false presences also occur (Royle & Link 2006) and may be common with surveys using aural detection (Miller et al. 2012) and environmental DNA (Schmidt et al. 2013). Species misidentifications resulting in false presences are an important source of error in citizen science data (Kosmala et al. 2016).

The possibility of false absences and false presences complicates the interpretation of data used to quantify range shifts (**Table 1**). Sites surveyed over two time periods (t_1, t_2) can have four possible states of naive range dynamics: unoccupied (not detected in t_1 and t_2), persistence (detected in both t_1 and t_2), colonization (detected only in t_2), or extinction (detected only in t_1). Confidence in the true range dynamic that a pair of surveys represents can be calculated from the site-level probabilities in one or both time periods of detecting a species (D) and that the detection was not a false presence ($1 - F$). For example, while naive persistence is unaffected by a false absence, the chance of a false-positive detection in both time periods results in a probability that, in addition to a persistence, the site could represent a colonization or an extinction or could always have been unoccupied (**Table 1**). A naive colonization could represent a persistence due to a false absence in t_1 or an unoccupied site due to a false-positive detection in t_2. Similarly, a

Table 1 How imperfect detection affects confidence in range-shift dynamics[a]

Bias caused by imperfect detection	Naive range change		Probabilities associated with true range dynamic			
	Naive site dynamic	**Naive site occupancy**	**Persistence (1,1)**	**Colonization (0,1)**	**Extinction (1,0)**	**Unoccupied (0,0)**
False absence	**Persistence**	1,1	1	0	0	0
	Colonization	0,1	$1 - D_1$	D_1	0	0
	Extinction	1,0	$1 - D_2$	0	D_2	0
	Unoccupied	0,0	$(1 - D_1)\cdot(1 - D_2)$	$D_1\cdot(1 - D_2)$	$(1 - D_1)\cdot D_2$	$D_1\cdot D_2$
False presence	**Persistence**	1,1	$(1 - F_1)\cdot(1 - F_2)$	$F_1\cdot(1 - F_2)$	$(1 - F_1)\cdot F_2$	$F_1\cdot F_2$
	Colonization	0,1	0	$1 - F_2$	0	F_2
	Extinction	1,0	0	0	$1 - F_1$	F_1
	Unoccupied	0,0	0	0	0	0

[a] For a given naive site occupancy history (1 = species present, 0 = species absent) sampled over two time periods (t_1, t_2), the probability associated with the true range dynamic depends on the site-level probability of a false-negative detection (D), assuming no false-positive detections, or on the site-level probability of a false-positive detection (F), assuming no false negatives.

naive extinction could represent a persistence due to a false absence in t_2 or an unoccupied site due to a false presence in t_1. Additionally, while an unoccupied site is unaffected by the probability of false-positive detections, false absences in both time periods result in a chance that the site represents a persistence, a colonization, or an extinction, in addition to being unoccupied (**Table 1**). Occupancy models couple these possible states with detection histories for estimation of key probabilities.

Imperfect detection is rarely accounted for when making inferences about range shifts in terrestrial (Tingley & Beissinger 2009) and marine systems (Monk 2014) and had been generally ignored in ecology until recently (Kellner & Swihart 2014). Yet, disregarding detection error can lead to severe bias and mislead inference about species distributions (Kery et al. 2010, Smith et al. 2013), community dynamics across elevational gradients (Tingley & Beissinger 2013), diversity metrics (Iknayan et al. 2014, Jarzyna & Jetz 2016), phenological timing (Strebel et al. 2014), and abundance estimation (Clare et al. 2021).

A number of recent advancements in statistical modeling make it more feasible to address shortcomings caused by imperfect detection when estimating range shifts. Imperfect detection can be incorporated directly into species distribution models (Guillera-Arroita 2017, Kery et al. 2010). A promising trend is the development of models that combine multiple sources of occurrences—data from citizen science programs, atlases, museums, and planned surveys—through integrative modeling using weighted-joint likelihoods (Fletcher et al. 2019). Simulation approaches have been proposed to distinguish geographic range shifts from artifacts of detectability and sampling effort for marine species (Bates et al. 2015). General model-based solutions are available to account for false presences (Clare et al. 2021). Statistical modeling of species distributions is an area of rapid methodological advancement.

Nearly all studies quantifying the relationships between traits and range shifts used estimates of range shift that did not account for imperfect detection (MacLean & Beissinger 2017). Thus, it seems likely that the range-shift results we have come to depend on include a mix of false shifts that did not occur and shifts that occurred but were not detected. Correcting for these biases requires reanalyzing the original data when it is possible and controlling for methodological differences in studies going forward.

4.2. Are Different Traits Associated with Latitudinal and Elevational Range Shifts?

Inferences from studies relating traits to range shifts typically treat elevational and latitudinal shifts as equivalents. For example, MacLean & Beissinger (2017) combined a similar number of elevational and latitudinal range shifts to estimate effect sizes. They found no significant differences for any trait between elevational and latitudinal range responses. Yet, there are some key abiotic differences between latitudinal and elevational gradients that could cause different species' traits to be associated with latitudinal versus elevational range shifts. If so, this would contribute to the weak relationship between species' traits and range-shift capability.

While many temperature-related characteristics change in similar ways along elevational and latitudinal gradients, other factors do not, including day length, UV radiation, light intensity, air pressure, and daily variability in temperature extremes (Halbritter et al. 2013, Körner 2007, Spence & Tingley 2020). Moreover, the distance required for species to move in order to remain in their climatic niche is much shorter for altitudinal than latitudinal shifts (Jump et al. 2009). In general, a 1°C increase in mean annual temperature results in a range change of ∼167 m in altitude but requires a 145-km change in latitude (Jump et al. 2009). This results in altitudinal compression of climates. For example, a horizontal distance of a few kilometers in the Swiss Alps might be associated with an increase in elevation of 2,500 m and a decline in mean annual temperature of

10°C, while along a latitudinal gradient the same temperature decline would occur over 1,800 km (Halbritter et al. 2013).

Thus, it seems likely that some heterogeneity among trait responses could be due to differences between the traits that are important for elevational versus latitudinal shifts. For example, traits related to movement ability and dispersal might be less informative along elevational than latitudinal range shifts. Siefert et al. (2015) found strong positive relationships between latitudinal and climatic limits for 28 common tree species. However, some species with poor dispersal ability failed to grow as far north as expected based on their elevational limits, suggesting dispersal limited latitudinal but not altitudinal limits. Conversely, there are many examples of interspecific competition limiting elevational distributions (Cahill et al. 2014), reducing dispersal and range expansion potential for some high-elevation species.

4.3. Nonlinear Relationships Between Traits and Range Shifts

Most studies test for linear relationships between continuous species' traits and the magnitude or speed of range shifts. We suspect most relationships in ecology probably work on the Goldilocks Principle, i.e., nonlinear responses of density, fitness, suitability, traits, etc. to environmental conditions that are considered too warm and too cold, too wet and too dry, too big and too small, too dense and too sparse, etc. Even seemingly straightforward linear relationships can exhibit nonlinear trends. In theory, the dispersal capacity of wind-dispersed seeds should decline with greater mass and increase with greater surface area–to-mass ratio. However, seeds of intermediate mass and surface area–to-mass ratios can exhibit the greatest dispersal distance during range expansions (Huang et al. 2015). Other examples of nonlinear relationships that influence responses of traits to climate include (*a*) the thermal sensitivity of performance (e.g., sprint speed, endurance, and metabolic rate) in ectotherms (Kearney & Porter 2009) and (*b*) the risk of desiccation, which also increases exponentially with warming temperatures (Riddell et al. 2019b).

The ability to detect nonlinear relationships depends not only on fitting alternative forms of relationships but also on the degree to which a particular study captures the full (or nearly so) range of environmental conditions a species or set of species is exposed to in order to see nonlinear responses. Otherwise, linear responses may perform nearly as well.

5. WHERE TO GO FROM HERE?

The field of ecology has lagged behind other fields in understanding complex phenomena (Houlahan et al. 2017), but this has occurred for a good reason. The physical sciences can assume that one hydrogen atom behaves the same as another hydrogen atom. In ecology, however, individuals of the same species exhibit different phenotypes that drive important ecological patterns, such as geographic range shifts. Moreover, traits within individuals can interact in unexpected ways that complicate how they respond to environmental changes and interact with conspecifics and other species.

Individually, the traits associated with invasion have a weak ability to explain differences in range shifts (MacLean & Beissinger 2017) (**Figure 1**). As a result, in virtually every analysis, externalities like geographic position, measures of climate or land-use change, climate velocity, etc. are usually much stronger predictors of range shifts than are species' traits. The effects of species' traits are inconsistent across studies, and support is so weak that species' traits should probably not be used in conservation planning for climate change vulnerability analyses—if such efforts are based on evidence rather than theory. Thus, it is not surprising that trait-based assessments of climate change vulnerability performed poorly in a validation study (Wheatley et al. 2017). So, where does that leave us?

Perhaps traits would be better predictors of range shifts if a number of analytical shortcomings identified in Sections 3 and 4 were addressed. Among the key advances to consider are improvements in how traits are used in analyses by incorporating variation in the traits. This might include using Bayesian approaches that model intraspecific and interspecific trait variation, weighting trait means by the inverse of their variance, or exploring trait variances. In addition, analyses should incorporate traits that have rarely been evaluated, such as those related to exposure, hygric niches, and competitive interactions. At the same time, analyses must use valid measures of range shifts. To date, the vast majority of estimates for the distances that species have shifted have ignored imperfect detection and sampling biases. Yet, there are well-established methods to correct for detectability, which should be expected to differ among species, taxa, sampling periods, and observers. Analyses relating species' traits to range shifts should also explore both linear and nonlinear relationships and account for phylogenetic dependencies. Alternatively, it may be time explore other approaches.

Trait-based analyses of changes in species' ranges might leverage new perspectives from macroecology and the biogeography of functional traits (Violle et al. 2014). Shifting from a biogeography of species to a biogeography of traits is intended to identify the ecological and evolutionary underpinnings of gradients in species, functional, and phylogenetic diversities. For instance, species often exhibit predictable variation in thermal tolerances across latitudes, which can be used to predict the range shifts and extinction risk across a variety of terrestrial and marine taxa (Pinsky et al. 2019, Sunday et al. 2012). To date, however, few biogeographic analyses relate spatial patterns of traits directly to past range shifts. Moreover, species are not always distributed where they perform the best, leading to mismatches between traits, their performance, and species' occurrence (Bohner & Diez 2020). While a biogeography of functional traits might indicate which traits are more likely to be suited to a changing environment, additional inference is needed to determine which of the species that possess key traits are likely to shift their geographic ranges.

The failure of traits to strongly describe metacommunity assembly contributed to the development of the neutral theory of biogeography (Hubbell 2001, Leibold & Chase 2018), which recognizes the functional equivalence of species and the role of stochasticity in the dispersal and establishment processes. Perhaps it is time to recognize that there may be a similar functional equivalency of trait combinations that individuals and species possess that may predispose them to become successful colonists and enable range shifts or to persist at the harsh edges of their ranges. Certainly not all trait combinations are equally likely to offer distinct advantages. But the successful trait combinations are likely to be many and fluid, due to ecological contingency and stochasticity.

The way forward here would be to assess interactions and covariation among traits in a search for functional equivalencies to identify the suites of traits that promote range shifts. For example, experimenting with gene flow at the warm range limit of the plant *Mimulus laciniatus*, Sexton et al. (2011) found that reproduction between plants located in different regions of their range produced different combinations of traits (seedling emergence and development time) that resulted in similar fitness. Functional equivalencies could easily be produced by different trait combinations that differentially facilitate the stages of range-shift processes (emigration, movement, establishment, and proliferation) (Estrada et al. 2016).

Replacing the single-trait approach that has characterized the field to date with analyses to identify taxa-specific trait suites of functional equivalencies should advance trait-based analyses for predicting range shifts. The processes at range limits that lead to range expansions and contractions are multifaceted and complex, involving many different components of an organism's biology. So too are the likely combinations of traits that predispose or retard range shifts.

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