Bringing traits back in the equation: A roadmap to understand species redistribution

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Running Title: Species range shifts-trait associations

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ABSTRACT

Ecological and evolutionary theories have proposed that species traits should be important in mediating species responses to contemporary climate change; yet empirical evidence has so far provided mixed evidence for the role of behavioral, life history or ecological characteristics in facilitating or hindering species range shifts. As such, the utility of trait-based approaches to predict species redistribution under climate change has been called into question. We develop the perspective, supported by evidence, that trait variation, if used carefully can have high potential utility, but that past analyses have in many cases failed to identify an explanatory value for traits by not fully embracing the complexity of species range shifts. First, we discuss the relevant theory linking species traits to range shift processes at the leading (expansion) and trailing (contraction) edges of species distributions, and highlight the need to clarify the mechanistic basis of traits-based approaches. Second, we provide a brief overview of range shifts-trait studies and identify new opportunities for trait integration that consider range-specific processes and intraspecific variability. Third, we explore the circumstances under which environmental and biotic context dependencies are likely to affect our ability to identify the contribution of species traits to range shift processes. Finally, we propose that revealing the role of traits in shaping species redistribution may likely require accounting for methodological variation arising from the range shift estimation process as well as addressing existing functional, geographical and phylogenetic biases. We provide a series of considerations for more effectively integrating traits as well as extrinsic and methodological factors into species redistribution research. Together, these analytical approaches promise stronger mechanistic and predictive understanding that can help society mitigate and adapt to the effects of climate change on biodiversity.

Keywords | Species range shift; Climate change; Trailing edge; Leading edge; Trait-based approach; Mechanism; Research bias

1. INTRODUCTION

Contemporary climate change has triggered the largest redistribution of life on Earth in the last tens of thousands of years (Chen et al., 2011; Lenoir et al., 2020; Parmesan, 2006). Yet, attributing the variation observed among range shifts to specific mechanisms governing these range shift processes remains unresolved. Paralleling the rise of trait-based approaches to understand community assembly (McGill et al., 2006; Violle et al., 2007), the last two decades have witnessed increased interest in the role of species traits – namely the behavioral, morphological, physiological or life history properties of organisms – in mediating species redistribution (Estrada et al., 2016; Madsen-Hepp et al., 2023; Miller et al., 2023; Williams et al., 2008). Theory suggests that various (and often different) traits can explain range shift processes at the leading (i.e., expanding) and trailing (i.e., contracting) edges of species distributions, thus providing testable hypotheses to understand causal mechanisms (e.g., Bates et al., 2014; Buckley & Kingsolver, 2012; Thurman et al., 2020). Uncovering relationships between species' traits and range dynamics may also allow for the identification of priority species and guide adaptive management strategies under climate change (Beever et al., 2016; Foden et al., 2019).

Although there are case studies successfully linking species traits to species range shifts (e.g., warming tolerance and life history strategy for freshwater fishes: Comte et al., 2014; life forms and elevation ranges for plants: Lenoir et al., 2008; resource capture in plants; Madsen-Hepp et al., 2023; dispersal capacity in butterflies; Pöyry et al., 2009; mobility and range size in marine species: Sunday et al., 2015), other studies have found poor (Moritz et al., 2008; Pinsky et al., 2013) or counterintuitive (Tingley et al., 2012) associations. Hence, syntheses and meta-analyses tend to show weak or inconsistent effects of species traits on interspecific variation in rates of range shifts (Angert et al., 2011; MacLean & Beissinger, 2017). Do these discrepancies between theory and empirical evidence suggest that trait-based approaches are not generalizable across species? Or, alternatively, have we as a research field been missing subtleties in trait-environment relationships (i.e., ecological processes) or not appropriately accounting for methodological factors (i.e., estimation processes) that affect detection and attribution of range shifts?

Here we propose that integrative approaches accounting for both ecological and estimation processes are needed to fully understand range shifts-trait associations (see Box 1). First, we provide a brief synthesis of the relevant theories and empirical studies linking species traits to contemporary range shifts. Next, supported by simulations, we discuss the extent to which range shifts-trait associations are mediated by abiotic and biotic factors, thereby blurring the perceived predictive power of traits. Finally, we explore the influence of methodology and research biases (i.e., functional, geographical, and phylogenetic) on our ability to understand range shifts. We conclude that it is premature to discard trait-based approaches for having low utility in species redistribution research. Rather, we posit that improved analytical approaches show substantial promise for combining traits with environmental and methodological data to accurately predict ongoing and future range shifts.

2. Assess the mechanistic basis of traits

Trait-based approaches offer clear conceptual foundations to understand the mechanisms underlying species range shifts (Box 2; Table 1). However, some major challenges remain for trait-based approaches to fulfill their potential. Among them, we first identify the need to clarify the mechanistic basis of the set of species range shifts-trait associations in view of relevant ecological and evolutionary theories.

(a) Account for interrelationships among traits

Traits reflect complex patterns of co-adaptation, allocation trade-offs and by-products of selection – the so-called traits syndromes (Mauro & Ghalambor, 2020; Salguero-Gómez et al., 2016; Stevens et al., 2014) – such that covariations among traits can obscure the mechanisms underlying climate-induced range shifts. For example, body size is viewed as a master trait or the “Swiss army knife" trait that is integrative of a large number of physiological, life history and behavioral processes (Box 3; Fig. 2). Therefore, even if body size can be an efficient predictor of range shifts, it provides only weak mechanistic understanding owing to trait covariations (Visakorpi et al., 2023), especially as these trait syndromes may be inconsistent across taxonomic groups. For example, small-bodied species are usually associated with higher fecundity and shorter generation time among terrestrial animals (r-strategists) but not necessarily among aquatic animals (Winemiller & Rose, 1992). Trophic position increases with body size in fishes but not in mammals (Romanuk et al., 2011; Tucker & Rogers, 2014) and plants and animals appear to achieve demographic resilience through different combinations of life history traits (Capdevila et al., 2022). In this context, when pooling all taxonomic groups together, it is not entirely surprising that conflicting relationships between range shifts and these traits are frequently reported, sometimes in opposition with prevailing hypotheses (MacLean & Beissinger, 2017).

These results caution against using a single trait to clarify the mechanisms of range shifts, especially across diverse taxonomic groups. Instead, detailed hypotheses and methods about range shifts-trait associations must be specified. First, it is important to implement a systematic and ecologically defensible approach of trait selection with clear links to range shift processes. Second, formal tests of hypotheses would benefit from being developed within a methodological framework addressing the interrelationships among traits. For example, advanced multivariate regression techniques (e.g., partial least square regression [PLS], geographically weighted regression [GWR], hierarchical partitioning [HP], and structural equation modeling [SEM]) lend themselves to understanding the complex relationships among a (very) large number of traits and their effects on ecological processes that can also take latent and non-stationary variables into consideration (Carrascal et al., 2009; Graham, 2003), thus providing useful tools to identify the potential mechanisms underlying range shifts (e.g., Bertrand, 2019; Bertrand et al., 2016; Pöyry et al., 2009).

(b) Test stage-specific range shifts-trait associations

Range shifts are by essence temporally dynamic and can be conceptualized as consecutive but interrelated stages, composed at the trailing edge of (i) decline in performance, (ii) population decrease and (iii) local extirpation; while at the leading edge, it can be composed of (i) dispersal (including both passive and decision-mediated active dispersal), (ii) population growth and (iii) persistence (Bates et al., 2014; Estrada et al., 2016). This suggests that developing and testing stage-specific range shifts-trait association expectations could improve our ability to develop a mechanistic understanding of the drivers of range shifts that explicitly consider both the spatial and temporal components of range shift processes. For instance, different facets of ecological generalism or specialism may capture different stages of the range shift process, which may lead to conflicting hypotheses (and weak cross-study inferences) if the temporal dynamic of the range shift is ignored. Ecological generalism is often correlated with range size, and thus expected to be intrinsically linked with the evolution of dispersal ability over long time scales (Alzate & Onstein, 2022; Lancaster, 2022). Conversely, specialist species may have evolved better habitat-selection abilities (Jacob et al., 2018) and may therefore better track climatic conditions over short time scales; a hypothesis that has recently gained traction in contemporary climate-driven range shifting moths, butterflies and birds at their leading edge (Hällfors et al., 2023). Examining coral-reef fish species, Monaco et al. (2020) also demonstrated that dispersal capacity contributed to range expansions only in the dispersal stage of redistribution (stage i above), whereas resource-use breadth was more important during the growth and establishment stages (stages ii and iii above). As such, thermal specialists may display a higher dispersal propensity but being a generalist along other niche dimensions (e.g., tolerance to drought or generalist diet) may still be expected to facilitate dispersal and successful establishment. Understanding range shifts through the lens of traits might therefore benefit from looking at how traits act sequentially along the range shift pathway, and potentially interact beyond what might be expected from their additive effects (e.g., ‘extinction-promoting traits’; Davies et al., 2004).

(c) Consider non-linear range shifts-trait associations

Finally, it is important to note that many associations between traits and ecological processes are intrinsically non-linear. In the context of species redistribution, the unimodal allometric scaling of dispersal and maximum speed with body size (Hirt et al., 2017; Stevens et al., 2014), or the fact that even species with moderate dispersal abilities may be able to keep up with the velocity of isotherm shifts (Schloss et al., 2012; Urban et al., 2013) could translate into an asymptotic relationship between range expansion and body size. Likewise, given that the thresholds leading to extirpations are not expected to be reached for all species (e.g., Pinsky et al., 2019), range contractions might only be expected when temperatures greatly exceed thermal tolerance limits. Yet, hitherto, most studies have used linear responses to capture relationships between range shifts and species traits. Using models carefully informed by theory may therefore represent new opportunities to reveal the contribution of species traits to range shifts (Beissinger & Riddell, 2021; Stenseth & Mysterud, 2002).

3. Assess opportunities for new trait integration

The complexity of the mechanisms underlying range shifts is reflected by the wide suite of traits that have been used and tested in cross-species comparisons of range shifts (Fig. 3). Still, this synthesis of the species’ range shifts-trait associations also reveals opportunities for new trait integration that would support a more mechanistic understanding of the drivers of range shifts.

(a) Integrate traits that capture the mechanisms of range shifts

Although in some circumstances the same suite of traits may be useful to predict both range contractions and expansions (although often in the opposite direction), the assumption that range expansions and contractions are simply the two sides of the same coin is likely to be an oversimplification (Table 1). Yet, many of the same traits have been used with the same frequency in range shifts-trait studies, irrespective of the range position (trailing edge, center or leading edge; Box 2, Table 1). For example, studies remain dominated by traits related to range size, habitat specialization and preference, whose underlying mechanisms might be sometimes difficult to interpret (as discussed above for body size; Box 3). In comparison, behavioral and physiological traits have been less explored. This reflects the scarcity of databases compiling organismal traits (measured on individuals) over distribution-based traits (estimated from species distributions), and highlights opportunities for new trait integration as data on physiological, dispersal and behavioral traits become increasingly available (e.g., Bennett et al., 2018; Herberstein et al., 2022; Lososová et al., 2023). This coupled with new methodological approaches for trait imputation to fill in data gaps (e.g., Thorson et al., 2023), as well as transcriptome databases to detect significant gene-trait associations (e.g., Primmer et al., 2013), may help researchers to integrate traits that have been less explored but that are more likely to capture the mechanisms underlying range shifts.

Studies also often used markedly different proxies or estimates per trait, which may make findings on the importance of traits incomparable across studies. For instance, habitat breadth has been estimated using many different indices, including the number of habitat types (e.g., Powney et al., 2015), the coefficient of variation across habitat classes (e.g., Platts et al., 2019), and multivariate indices based on continuous environmental gradients (e.g., Comte et al., 2014). Yet, it is unclear whether these indices, estimated from a variety of variables and across different spatial resolutions, are inter-comparable and approximate the same hypothesized process, which complicates subsequent meta-analyses that seek to test how traits relate to observed variation in range shifts across studies. Furthermore, most studies conduct cross-species comparisons using only adult traits, despite the fact that traits can vary across a species' lifespan and life-history stages (e.g., ontogenetic niche shifts); this in turn can have direct consequences on our ability to test the role of traits. For example, the fact that thermal tolerances and plasticity can vary through ontogeny (e.g., plants: Caron et al. 2021; fishes: Dahlke et al. 2020; insects: Weaving et al. 2022) suggests that traits measured on non-adult life stages may be complementary and thus necessary to explain the rates of species redistribution. Likewise, traits can vary across species ranges for a variety of reasons (e.g., predation risk can alter the temperature dependence of life-history traits; Luhring et al. 2018), and trailing edge populations that are often small and isolated often display unique intraspecific phenotypic adaptations to local conditions that can increase their resilience to climate change (Hampe & Petit, 2005). Linking range shifts to traits measured at specific range positions represents a promising path of inquiry. Although widely available and easier-to-get traits may prove sufficient for certain conservation applications (Gallagher et al., 2021), supporting a more mechanistic and predictive science of range shifts will likely require spending more time on difficult-to-get and time-consuming traits, including renewed considerations for cross-studies standardization and incorporation of intraspecific variability (e.g., across life stages or at different range positions). However, we note that there is no such dichotomy between "bad" and "good" traits; instead, trait selection must be informed by strong a priori hypotheses based on the taxonomic and geographic scope of the study and the subsequent analytical framework developed using informed models accounting for (co)variation among traits.

(b) Consider evolutionary potential alongside traits

An additional consideration is that species trait means and variances are not fixed, but instead can change through evolutionary adaptation (Diamond, 2018; Donelson et al., 2019; Hoffmann & Sgrò, 2011). While recognizing that evolutionary potential can hardly be classified as a 'trait', by facilitating adaptive responses to climate change, trait evolution can strongly influence species' range shifts and could thus be more often considered alongside traits. A classic example is the evolution of dispersal ability at expanding range limits due to spatial sorting of the most dispersive individuals (Phillips et al., 2008; Travis et al., 2013). Climatic niche shifts have also been documented during range expansion, which may explain why some species have shifted faster than expected (Lustenhouwer & Parker, 2022). Providing accurate estimates of evolutionary potential remains challenging (Forester et al., 2022; Hoffmann & Sgrò, 2011), particularly as many factors such as population size, phenotypic plasticity, life history traits, genetic correlations or spatial connectivity may either facilitate or hinder evolutionary responses to selection (Martin et al., 2023). Genetic diversity indices (e.g., allelic richness, heterozygosity) and effective population size or genetic markers identified through genotype-environment associations or adaptive landscape modeling may be effective proxies for evolutionary potential, but are difficult to gather across multiple taxa and at large spatial extents (Capblancq et al., 2020; Hoban et al., 2022; Razgour et al., 2019; see also Thompson et al., 2023). A complementary approach is to assess the degree to which species niches and underlying traits are conserved through evolutionary time (Bennett et al., 2021; Diamond, 2018; Lavergne et al., 2013). While macroecological approaches may not provide great precision, they could nonetheless help in providing a benchmark to estimate evolutionary potential (Diniz-Filho et al., 2019). Testing whether lineages that have experienced faster niche evolution in the past display a higher potential for evolutionary rescue that prevents range contraction in response to contemporary selective pressures remains an exciting and under-explored research question.

4. Assess the abiotic and biotic context of traits

To illuminate the role of species traits in explaining range shifts, it is important to recognize that range shifts result from complex interactions between species' intrinsic features and the abiotic and biotic context in which these shifts occur. It follows that examining *solely* species traits (even if these traits have a strong mechanistic basis and fine resolution) may fail at uncovering the mechanisms at play, particularly in cross-study comparisons where climate change exposure, habitat characteristics, and biotic dependencies can drastically vary.

(a) Account for interactions between traits and climate exposure

One obvious extrinsic factor likely to influence species' range shifts-trait associations is climate exposure. At the simplest level, without any changes in climatic conditions, species would not be expected to show any range shifts despite displaying very different traits; conversely the same species would be expected to display different directions and speed of range shifts because of variability in climate exposure alone. More complex interactions between species traits and climate exposure are also likely to arise, yet they have not received the same level of attention compared with the individual effects of climate change exposure or species traits. For instance, using a process-based model to simulate, under a set of different climate change scenarios, the redistribution of virtual animal species with different dispersal abilities and lifespans (simRShift; see Supplementary Material Appendix S2; Bertrand, 2012), we show that the velocity of range shifts at the trailing and leading edges are, at first glance, poorly correlated with species traits (Fig. 4a,b). Indeed, lifespan and dispersal abilities alone explain 7.5% and 33.8%, respectively, of the simulated range shifts at the trailing and leading edges. However, once we illuminate the plots with information on the velocity at which isotherms are shifting (expressed in terms of shifts in mean annual temperature along a hypothetical latitudinal gradient), interactions between climate change exposure and species traits appear (Fig. 4c,d). Accounting for these trait-environmental change interactions drastically increases the explanatory power of traits (up to

99.5%; Fig. 4e,f). Consistent with theoretical expectations (see Table 1), we found that species with short lifespans and high dispersal abilities shift their distribution limits faster at the trailing and leading edges, respectively, and especially so when the exposure to climate change is higher. At the trailing edge, the velocity of range contraction is negatively associated with lifespan and displays an interaction with climate velocity, such that range contractions are hastened when lifespan is short and climate exposure is high, indicating that climate impacts are more readily detectable in short-lived species (Fig. 4c). At the leading edge, the velocity of range expansion is positively associated with maximum dispersal distance through an asymptotic relationship whose slope becomes steeper when the velocity of isotherm shifts increases, indicating that the expansion process is likely limited by dispersal ability (Fig. 4d).

Interestingly, even if the individual effects of species traits can be weaker predictors of species range shifts than the individual effect of isotherm shift velocity, it is the interaction effect that captures most of the observed variation in species range shifts. Empirical studies in marine systems, where climate velocities are up to seven times higher than on land and where ocean currents strongly influence redistribution, also suggest that traits may be comparatively less important than extrinsic factors to explain variation in biotic velocity among species (García Molinos et al., 2022; Pinsky et al., 2013). Nonetheless, in accordance with our simulations, Sunday et al. (2015) demonstrated that considering the interactions between climate exposure and species traits (including mobility) more than doubled the percentage of explained variance in range expansion of marine fish and invertebrate species compared to a model accounting only for climate expectations. Hence, incorporating these complex interactions may help reveal the contributions of species traits to explain the observed variation in range shift patterns, particularly when the trait effect is weaker (e.g., such as when considering the effect of lifespan alone on range contraction). Obviously, species climatic niches are by essence multidimensional and considering only changes in temperature might also misrepresent range shift expectations (Tingley et al., 2012). Similarly, accounting for extreme events in addition to long-term climatic changes (e.g., heat waves as opposed to mean annual temperature trends) may better capture climate exposure and subsequent impacts on the distribution of populations and species (Auth et al., 2018). In this context, considering multiple climate axes simultaneously (Crimmins et al., 2011; Dobrowski et al., 2013), using model-based bioclimatic velocities (VanderWal et al., 2013) or accounting for both climatic presses and pulses (Harris et al., 2018) could help refine range shift expectations based on the multifaceted effects of climate change, thereby providing a stronger conceptual framework to understand the contribution of species traits to range shifts.

(b) Account for interactions between traits and other abiotic and biotic conditions

Beyond climate exposure, a myriad of abiotic and biotic factors likely influences the ability of species to track shifting climate conditions at a variety of temporal and spatial scales, as mediated through their traits. Although these context-dependencies must be considered on a case-by-case basis, here we discuss a few examples to illustrate the importance of considering environment-trait interactions to explain range shifts. Habitats differ in terms of spatio-temporal heterogeneity and human pressures, which will determine opportunities for dispersal and persistence under climate change (Pinsky et al., 2022). These variations in habitat characteristics may explain the faster rates of redistribution in the ocean than on land (Lenoir et al., 2020), but the importance of habitat characteristics to range shift processes will ultimately depend on the interactions with species traits. On land, landscape fragmentation (both natural and anthropogenic) is likely to represent a major constraint on species redistribution but its influence is expected to vary with species-specific habitat requirements, such that habitat generalists may be less constrained by habitat availability than more specialized species (Platts et al., 2019). In the ocean, the opportunities offered by habitat verticality in 3-D habitats can mediate the rate of latitudinal range shifts by allowing species to locally exploit deeper ocean layers (Brito-Morales et al., 2020), yet the rates of depth shifts likely depend on both the niche characteristics and fishing pressure exerted on the shifting species (Dahms & Killen, 2023).

Biotic factors may also affect the associations between species traits and range shifts. For example, in polyphagous insects, the ability to exploit alternative hosts may confer a survivorship advantage and decrease contraction at the trailing edge, but these benefits rely upon host plant availability now and in the future (Hellmann, 2002). Conversely, although in general the higher mobility of animals compared to plants a priori suggests that plants should not be limited by dispersal limitations of their animal vectors to keep up with climate change at their leading edge, defaunation of seed-dispersing birds and mammals may drastically reduce the ability of plants to shift their ranges (Fricke et al., 2022). This highlights the importance of examining realized as opposed to fundamental adaptive capacity when testing the relationships between species traits and range shifts (through trait-environment interactions) – an analogy with the duality between realized and fundamental ecological niches intended to capture the extent to which extrinsic factors constrain the expression of the intrinsic determinants of the range shifts processes (Beever et al., 2016). The characteristics of the range shifting species with respect to the recipient communities can also influence range expansions via biotic resistance and niche opportunities as in the case of biological invasions (Shea & Chesson, 2002), although such hypotheses have so far received mixed support (Alexander et al., 2015; Miller et al., 2023). There is still much to be learned by developing a trait-based framework that explicitly considers the biotic community context (Gilman et al., 2010; Lavergne et al., 2010; Schleuning et al., 2020), as well as capitalizing on the decades-old field of invasion biology to better apprehend the mechanisms underlying range shifts (Pauchard et al., 2016; Wallingford et al., 2020).

5. Assess the effects of the estimation process and research biases

The methods used to document range shifts influence the range shift estimates and our ability to detect meaningful relationships with species traits (Brown et al., 2016; Dahms & Killen, 2023; Lenoir et al., 2020). Similarly, research biases may not only result in an incomplete picture of which species and areas are vulnerable to climate change but may also alter our comprehension of the underlying drivers of range shifts (Feeley et al., 2017; Lenoir et al., 2020).

(a) Account for methodological differences in cross-study comparisons

The distribution and abundance patterns of species within their range limits are not static but fluctuate due to demographic and environmental stochasticity and can result in gaps and fragmented areas, particularly at range limits (Brown et al., 1996; Hampe & Petit, 2005). Estimating species range shifts, especially at the edges, may thus be particularly sensitive to the sampling method, number and consistency of studied locations, temporal coverage, spatial grain, as well as the analytical methods used (Loehle, 2020; Shoo et al., 2006). Noteworthy, beyond the noise introduced by the different methods used in the scientific literature, the traits and the estimation process can interact. For instance, species detectability can vary as a function of species morphological and behavioral characteristics (e.g., Sólymos et al., 2018), and the influence of the temporal resolution on perceived range shifts will likely depend on the pace of life of the organisms under study. Therefore, carefully accounting for methodological differences in cross-studies comparisons may greatly improve our ability to detect ecologically meaningful relationships with species traits and thus our power to explain species redistribution.

(b) Reduce functional biases in species redistribution research

Biases with respect to the trait coverage of the species for which range shifts have been documented may also lead to misrepresentations of the strength and direction of the relationships between range shifts and species traits, particularly if these relationships are non-linear (‘functional biases’; Fig. 5a-c). Yet, a comparison of the degree of morphological trait space covered by BioShifts, a range shift database compiled from the scientific literature (Comte et al., 2020), for two widely studied taxonomic groups – birds and fishes – reveals that these functional biases may be prevalent (Fig. 5d-e). For instance, among terrestrial birds, range shift detections of functionally unique species such as flightless (e.g., ostrich, emu, kiwi) or lightweight (e.g., hummingbirds) birds remain understudied. Similarly, a bias against small-bodied fishes displaying a high caudal peduncle depth is evident in both marine and freshwater species, with these attributes being strongly related to swimming ability (Fisher & Hogan, 2007; Radinger & Wolter, 2014). Although the consequences of these functional biases on our ability to detect meaningful relationships between range shifts and species traits remain to be formally investigated, to fully understand range shift processes, both functionally common and unique species would benefit from being studied in a shared framework. Functional uniqueness may represent adaptations to specific environmental conditions (e.g., reduced physical capacity for dispersal for flightless birds on islands due to the island syndrome; Wright et al., 2016), distinct alternative phenotypic adaptations to the same environmental challenges (e.g., active dispersal versus in situ drought resistance forms in aquatic invertebrates; Osakabe et al., 2014) or competition-driven specialization (e.g., morphological and foraging microhabitat specialization in coral reef fishes; Brandl et al., 2015), and may thus hold key insights to contextualize the functions and evolutionary trajectories of trait syndromes (Munoz et al., 2023), including in the context of species redistribution.

(c) Leverage differences across a variety of taxa and regions

In addition, geographic and phylogenetic biases in research effort may impair our ability to comprehend the importance of the intrinsic and extrinsic factors relevant to range shifts (Feeley et al., 2017; Lenoir et al., 2020). Overrepresentation of temperate species may, for instance, underestimate the vulnerability of tropical species that display particular combinations of behavioral and physiological adaptations, such as narrower thermal tolerances and lower dispersal abilities (Feeley et al., 2017; Tewksbury et al., 2008). Indeed, from an evolutionary perspective, climatic variations (from long-term geological to annual seasonality or daily fluctuations) in the tropics are very different from the ones in the temperate zone or at higher latitudes, with important implications for shaping the current distribution, traits, and genetic diversity of species and populations (De Kort et al., 2021; Hampe & Petit, 2005). These variations can influence their sensitivity and adaptive capacity to climate change (Chan et al., 2016; Steele et al., 2019). These types of bias call for more balanced comparative approaches across the tree of life and globe, leveraging differences across a variety of taxa and regions (including less researched taxa and areas as well as between mainland and islands), to better tease apart the relative contribution of intrinsic species traits and extrinsic factors to explain species redistribution (Pinsky et al., 2022). Recognizing that all the challenges cannot all be resolved at once, we also emphasize the opportunities for carefully targeted laboratory and mesocosm studies that can more directly focus on the mechanisms at play and improve our ability to tease apart the context-dependencies of range shifts-trait associations (e.g., Luhring et al., 2018).

6. A path to move forward

As the scientific community grapples to understand the mechanisms behind range shifts, we demonstrate that the increasing availability of organismal trait databases together with fine scale environmental data can pave the way for new insights into climate-driven range shifts. To support this endeavor, we identified a set of four key considerations for future species range shifts-trait studies.

- *Clarifying the mechanistic basis of trait-based approaches*. Traits selected based on theory-driven links to range limit-specific shifts (e.g., Visakorpi et al., 2023) as opposed to traits with vague or conflicting connections with range shifts have more potential to resolve the underlying mechanisms of range shifts. As the field of species redistribution research matures, opportunities emerge to refine our conceptualization of the range shift processes for example by exploring the stage-dependent processes during range expansions and contractions (e.g., Monaco et al., 2020). If appropriate, the methodology should be suitable for syndrome-based hypothesis testing (e.g., using partial least squares regression; Carrascal et al., 2009) and be adapted to account for potential non-linear responses (Stenseth & Mysterud, 2002).

- *Fill gaps in trait databases for key categories*. The most important traits to explain species responses to climate change may not always match with the restrictive suite of traits available in large trait databases (Green et al., 2022; Kühn et al., 2021). Recent efforts to address this limitation include standardized metabolic traits across animal groups (AnimalTraits: Herberstein et al., 2022), temperature tolerance limits across ectotherms (e.g., GlobTherm: Bennett et al., 2018; but see Clusella-Trullas et al., 2021 for a discussion on the limitation of thermal sensitivity indices), dispersal traits for vascular plants (Lososová et al., 2023) and standardized diet and morphological information for birds (Hurlbert et al., 2021; Tobias et al., 2022). To the extent possible, accounting for sources of intraspecific variation (particularly considering ontogenetic shifts) and ensuring that traits are being measured at the correct scale and geographic position with respect to the observed range shifts may improve the predictive power of traits to explain range shifts. Emerging advances in genomics also hold promise to understand the role of evolution in facilitating or hindering range shifts (e.g., Capblancq et al., 2020; Razgour et al., 2019), and could be used alongside trait-based approaches.

- *Identifying interactions between intrinsic species traits and extrinsic factors*. Identifying the general determinants of range shifts that transcend any context-dependencies requires careful integration of a series of abiotic and biotic factors (both natural and anthropogenic) in analytical frameworks that explicitly include interactions with species traits (e.g., Bertrand et al., 2016; García Molinos et al., 2022; Platts et al., 2019). This can be further improved by simulation experiments conducted from mechanistic models (e.g., as done above or in Henry et al., 2014). In addition, there is much to be learnt by studying range shifts in a community context (Lavergne et al., 2010), including through the lens of invasion biology by exploring the role of biotic resistance based on key functional traits (e.g., Miller et al., 2023).

- *Accounting for the effects of different methods used to assess range shifts and reducing research biases*. The influence of the estimation process on range shift detection is increasingly recognized and would benefit from being explicitly accounted for when trying to make inference on the role of species traits in large cross-taxa analyses (e.g., Brown et al., 2016; Dahms & Killen, 2023; Lenoir et al., 2020). This is especially true as the choice and effect of methodological factors may covary with species traits (e.g., when species detectability varies with life history or behavioral traits), ultimately decreasing our power to explain range shifts. Last but not least, reducing functional, phylogenetic, and geographic research biases will provide the ability to draw more definitive conclusions regarding the shape and direction of range shifts-trait associations.

By implementing these considerations in future research, we expect that the importance of traits will become clearer for explaining the ongoing redistribution of life on Earth in different places and situations. Trait-based approaches could then provide a powerful basis for generalizing knowledge and predictions far beyond the relatively small fraction of species for which observations exist and for developing effective strategies that support biodiversity conservation under climate change.

Acknowledgments

This research is a product of the BIOSHIFTS working group funded by the synthesis center (CESAB) of the French Foundation for Research on Biodiversity (FRB; www.fondationbiodiversite.fr) and the project FRAGSHIFTS funded by the Ministry of Ecological Transition (MTE), French Office for Biodiversity (OFB), and the French Foundation for Research on Biodiversity (FRB). We thank Holly Embke and two reviewers (including Tom Luhring) for their time and constructive comments that have improved the initial submission.

Author Contributions Statement

Conceptualization: all authors; Methodology: L.C., R.B., M.L.P., J.L.; Formal analysis: L.C., R.B.; Data curation: L.C.; Writing - Original Draft: L.C., R.B., S.D., L.T.L., M.L.P., B.R.S., J.L.; Writing - Review & Editing: all authors; Visualization: L.C., R.B., S.D., L.T.L., B.F.O., S.W., J.L.; Project administration: L.C., J.L.; Funding acquisition: L.C., J.L.

Data availability

The data that support the findings of this study are available in FigShare at 10.6084/m9.figshare.25467664. The data were derived from the following resources available in the public domain: https://doi.org/10.1146/annurev-ecolsys-012021-092849, https://doi.org/10.1111/gcb.13736, https://doi.org/10.6084/m9.figshare.7413365.v1, https://figshare.com/s/b990722d72a26b5bfead.

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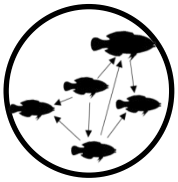
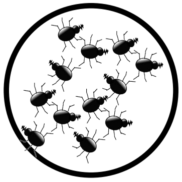
Table 1. Mechanisms by which species traits are expected to mediate range shifts and selected trait examples. Multiple traits influence species distribution limits and range dynamics in response to climate change. Species-level traits can be organized into major categories of mechanisms that may vary in their degree of intraspecific variation expressed in nature. Furthermore, traits exhibit varying degrees of phenotypic plasticity or additive genetic variation upon which selection can act to compensate for the effects of environmental change (as exemplified in the 'Moderator of traits' column). The directionality of the expected range shifts-trait relationship is given with respect to high trait values but opposite effects can be expected for lower trait values. TE = trailing edge; LE = leading edge. See Box 2.

Category of mechanism	**Trait**	**Example (expressed rel. to higher values of each trait)**	**Temperature-driven range shifts-trait expectation**	**Moderators of traits (plasticity and evolutionary potential)**
Physiology 	High temperature physiology	Heat tolerance (as compared to experienced temperature)	Hinders TE contraction (decrease sensitivity to heat waves)	*Thermal plasticity and niche shifts* Cold/heat tolerance acclimation; Facilitates LE expansion & hinders TE contraction (lower sensitivity to temperature fluctuations)
Behavior & phenology 	Behavioral thermoregulation	Selection of shaded microhabitats	Hinders TE contraction (avoids overheating)	*Phenological plasticity* Shift in emergence timing; Hinders LE expansion & TE contraction (tracks shifting climate conditions in time) or facilitates LE expansion (improves fitness in new environments)
	Types of phenological cues as information of future climates	Whether organisms use temperature or light as a phenological cue	Facilitates LE expansion (temperature-dependence of cues enable faster phenological responsiveness)	
Biotic interactions	Interaction specialization	Resource-use breadth	Facilitates LE expansion (facilitates en route	*Morphological plasticity* Induction of

			fueling and establishment in new communities) & hinders TE contraction driven by indirect biotic effects (by enabling food switching)	morphological defenses; Facilitates LE expansion (protection from novel predators)
	Competitive ability	Resource exploitation capacity	Facilitates LE expansion (reduces biotic resistance) & hinders TE contraction (if competition is or become the dominant factor)	
Dispersal 	Dispersal mode	Whether organisms disperse via: passive, crawling, swimming, or flying mode	Facilitates LE expansion (higher dispersal distances)	*Evolution of dispersal capability* Increase in maximum dispersal distance; Facilitates LE expansion (via spatial sorting of alleles during range expansion and release from intraspecific competition)
	Migratory tendency	Whether organisms are: resident, irregular migrant, regular migrant	Facilitates LE expansion (better navigatory skills)	
Pace of life 	Life history	Life history components (age at maturity, fecundity, generation time, longevity) capturing slower to faster pace of life	Facilitates LE expansion (more propagule production events and numbers in fast-lived species). Either hinders (higher demographic compensation and shorter recovery times in fast-lived species) or facilitate (extinction debt paid faster in short-lived species) TE contraction	*Developmental plasticity* Development time; Facilitates LE expansion (longer development times improves fecundity)
Ecological generalism	Abiotic niche breadth	Degree of tolerance to a diversity of abiotic factors	Facilitate LE expansion (larger range of environment tolerated during dispersal and	*Physiological plasticity* Drought acclimation; Hinders TE contraction (lower sensitivity to

		(pH, O2, drought, light)	establishment)	drought)
	Cognitive flexibility	Relative brain size	Hinders TE contraction (adjust behavior to changing conditions)	

Box captions

Box 1. Embracing the complexity of species range shifts

Documented range shifts (i.e., general directions and speed of species range shifts) are typically estimated at the *leading edge* of species distribution (expanding or cold edge), usually located at high latitude, high elevation on land or at deeper depths in the oceans in the context of current climate warming, and at the *trailing edge* of species distribution (contracting or warm edge), usually located at low latitude, low elevation on land or at shallower depths in the oceans (Fig. 1). These documented range shifts at the cold (e.g., upper elevation) and warm (e.g., lower elevation) edges along spatial gradients are frequently equated to the dynamics of range expansion and contraction, although we note that each edge can either expand or contract.

Documented range shifts are underpinned by complex ecological processes, among which species' traits are expected to be key – but not the sole – underlying drivers. Here, we define a trait as any intrinsic morphological, physiological or phenological feature measurable at the individual level that influences species ecological performance, without consideration to the extrinsic environment or other levels of biological organization (Violle et al., 2007). It follows that the ecological processes underlying range shifts are likely to arise from the interaction between species' traits (or the set of intrinsic factors such as thermal tolerance and dispersal ability) and its abiotic and biotic context (or set of extrinsic factors such as climate change exposure, biotic dependencies, and habitat characteristics).

The documented range shifts are additionally influenced by the estimation processes, as the direction and speed of species range shifts cannot be observed directly but instead are dependent on the set of methodological factors used, including the underlying data types (e.g., species abundance, presence-absence), spatial (e.g., grain and extent) and temporal (e.g., number of time periods) resolution of available datasets, and the statistical methods (e.g., quantile regression, species distribution models). Given the variation caused by circumstances of individual shifts and the methods used to detect them, analytical methods that consider both are necessary for properly attributing shifts to associated mechanisms when synthesizing data across studies. We note that species traits (and to some extent the set of extrinsic factors) are also prone to measurement errors and are themselves dependent on the estimation process such as the inclusion of intraspecific variability, or choice of the upper endpoint of the thermal performance curve (e.g., lethality versus loss of motor control), among others.

Box 2. Theoretical expectations for range shifts-trait associations

Physiology: From a fundamental point of view, species distribution limits and responses to climate change chiefly depend on the thermal (and other climate) sensitivity of species physiological performance as well as the level and temporal patterns of exposure, which together affect population persistence at the trailing edge and opportunities for leading edge expansion (Angilletta et al., 2003; Huey et al., 2012; Kingsolver et al., 2013) (Table 1). To buffer themselves against sublethal or lethal thermal stress, organisms have evolved strategies enabling them to adjust physiological responses over the short to long term (days to years). Examples include active transpiration in plants (De Frenne et al., 2021) and thermal acclimation in ectotherms (Gunderson & Stillman, 2015; Seebacher et al., 2015; Weaving et al., 2022). Evolution of physiological traits such as heat or cold tolerance can also facilitate expansion or slow down contraction (Martin et al., 2023), but these effects are unlikely to be universal. Physiological plasticity can initially facilitate entry into and persistence within novel environments but can impede long-term evolutionary adaptation when it acts in the same direction as selection (e.g., Leonard & Lancaster, 2020).

Behavior & phenology: Behavioral thermoregulation in mobile ectotherms allows individuals to exploit local heterogeneity in microclimates by shifting the time (e.g., diurnal, circadian cycles) and place (e.g., burrowing, nesting) of activity (Kearney et al., 2009; Sunday et al., 2014), which may slow range contraction at the trailing edge (Table 1). Likewise, in endotherms, behaviors such as torpor and hibernation can allow regulation of body temperature to survive adverse conditions (Geiser & Turbill, 2009). Phenological adjustments can also hinder range contractions by enabling plants and animals to track climatic changes in time (instead of space) via shifts in seasonal life history events (e.g., emergence, development and reproduction), as well as promote range expansion at their leading edge by improving survival after establishment (Socolar et al., 2017; Vitasse et al., 2021; Zettlemoyer & Peterson, 2021).

Biotic interactions: Species can be indirectly affected by climate change through altered biotic interactions, as mediated through their traits (Gunderson et al., 2017; Schleuning et al., 2020; Urban et al., 2013) (Table 1). For instance, species engaged in highly specialized interactions (e.g., for reproduction via pollinator dependency, for dispersal through zoochory) may be more sensitive due to mismatches in climatic sensitivities or dispersal ability with their obligate species. These indirect sensitivities can precipitate range contraction or slow range expansion (Cahill et al., 2013; Gilman et al., 2010; Schleuning et al., 2020). Conversely, better competitors may be less susceptible to biotic resistance from recipient communities at their leading edges (wherein the resident communities exert negative effects on the range shifting species, usually through predation or competition) and competitive exclusion at their trailing edges, including from novel range shifting competitors (Alexander et al., 2015; Sanczuk et al., 2022).

Dispersal: As climate change opens new suitable habitats, dispersal is expected to be a key mechanism by which species track climate shifts through space, especially at the leading edge (Corlett & Westcott, 2013; Schloss et al., 2012) (Table 1). For instance, movement costs for active dispersers can be lower in large-bodied species with enhanced locomotion efficiency, species displaying specific dispersal structures (e.g., wing size in insects and birds or aspect ratio of the caudal fin in fish), species with better navigational skills, or species displaying collective dispersal behaviors (Berdahl et al., 2018; Sambilay, 1990; Stevens et al., 2014). Among passive dispersers, investment in seed dispersal structures or longer duration of dispersal phase also leads to greater dispersal opportunities (Thomson et al., 2018). In addition, human-mediated dispersal (i.e., species translocation and assisted migration in general) may play a key role in facilitating range expansions of species of commercial or recreational interest (e.g., Alofs et al., 2014).

Pace of life: Fast life history attributes can confer a higher demographic potential to rapidly establish new founding populations at the leading edge (Table 1). High propagule pressure (i.e., the number and frequency of dispersing individuals) reduces the effects of genetic, environmental and demographic stochasticity, and high population growth rates reduce genetic bottlenecks and Allee effects that may precipitate extinction in small populations (Roman & Darling, 2007; Taylor & Hastings, 2005). Higher fecundity and shorter generation times are also expected to promote faster demographic compensation and shorter recovery times after mortality events (Capdevila et al., 2022), and thus slow down range contractions at the trailing edge in the short term. Nonetheless, demographic collapses and range contractions may be slower to detect in long-lived species, where older individuals may be indicative of past conditions (extinction debt; Boisvert-Marsh et al., 2014; Pacifici et al., 2017), resulting in a negative association between range shifts and lifespan.

Ecological generalism: Ecological generalism is expected to allow propagules to establish faster and farther at expanding limits and further improve persistence after dispersal due to the wider diversity of environments tolerated (Stevens et al., 2014) (Table 1). For example, tolerance to light availability towards high latitudes and oxygen depletion towards high elevations (Jacobsen, 2020; Ljungström et al., 2021; Spence & Tingley, 2020) or acclimation to hypoxia in aquatic systems (Souchet et al., 2020; Storz et al., 2010) may be particularly important to enable climate-induced range expansions. Species that display a greater potential for cognitive or behavioral flexibility may also be able to better cope with changing environmental conditions through local shifts in microhabitat or diet, resulting in slower trailing edge contractions (‘cognitive buffer hypothesis’; Baldwin et al., 2022).

Box 3. Body size, the Swiss army knife of all traits.

Being both large and small can confer various – albeit sometimes opposite – benefits in the context of species redistribution (Fig. 2). Large-bodied species often display higher dispersal capacities (‘allometric scaling of dispersal’; Stevens et al., 2014) and greater competitive abilities (Goldberg, 1996), and small-bodied species higher fecundity and shorter generation times (‘fast species’; Capdevila et al., 2022) – attributes that are all expected to promote range expansion at the leading (cold) edge under environmental change. Large-bodied species can persist longer after habitat quality change due to their longer longevity (‘extinction debt’; Boisvert-Marsh et al., 2014), and small-bodied species typically display a lower sensitivity to heat that likely arises from metabolic constraints (Peralta-Maraver & Rezende, 2021) and higher opportunities for behavioral thermoregulation (von May et al., 2019) or wider range of microclimatic refugia use (Pincebourde et al., 2021) – attributes that are all expected to hinder contraction at the trailing (warm) edge under environmental change.

Figure captions

Figure 1. Set of factors and interactions that may influence the documented patterns of range shifts and suggested steps to model range shifts-trait associations. Documented patterns of range shifts at the trailing (i.e., range contraction) and leading (i.e., range expansion) edges of species distributions are typically documented in response to anthropogenic climate change along spatial gradients such as latitude, elevation (on land), and depth (in the oceans) and reflect both (a) the ecological processes (left panel) and the (b) estimation processes (right panel), which involve a set of intrinsic, extrinsic and methodological factors (see Box 1). Ecological processes may involve complex interaction terms between species traits and either the abiotic or biotic context such that it suggests complex context dependencies. Numbers illustrate a set of suggestions to improve our ability to decipher the mechanisms of range shifts.

Figure 2. Benefits of large versus small body size in the context of climate change-related range shifts. See Box 3 for more context and Table S1 for image attribution.

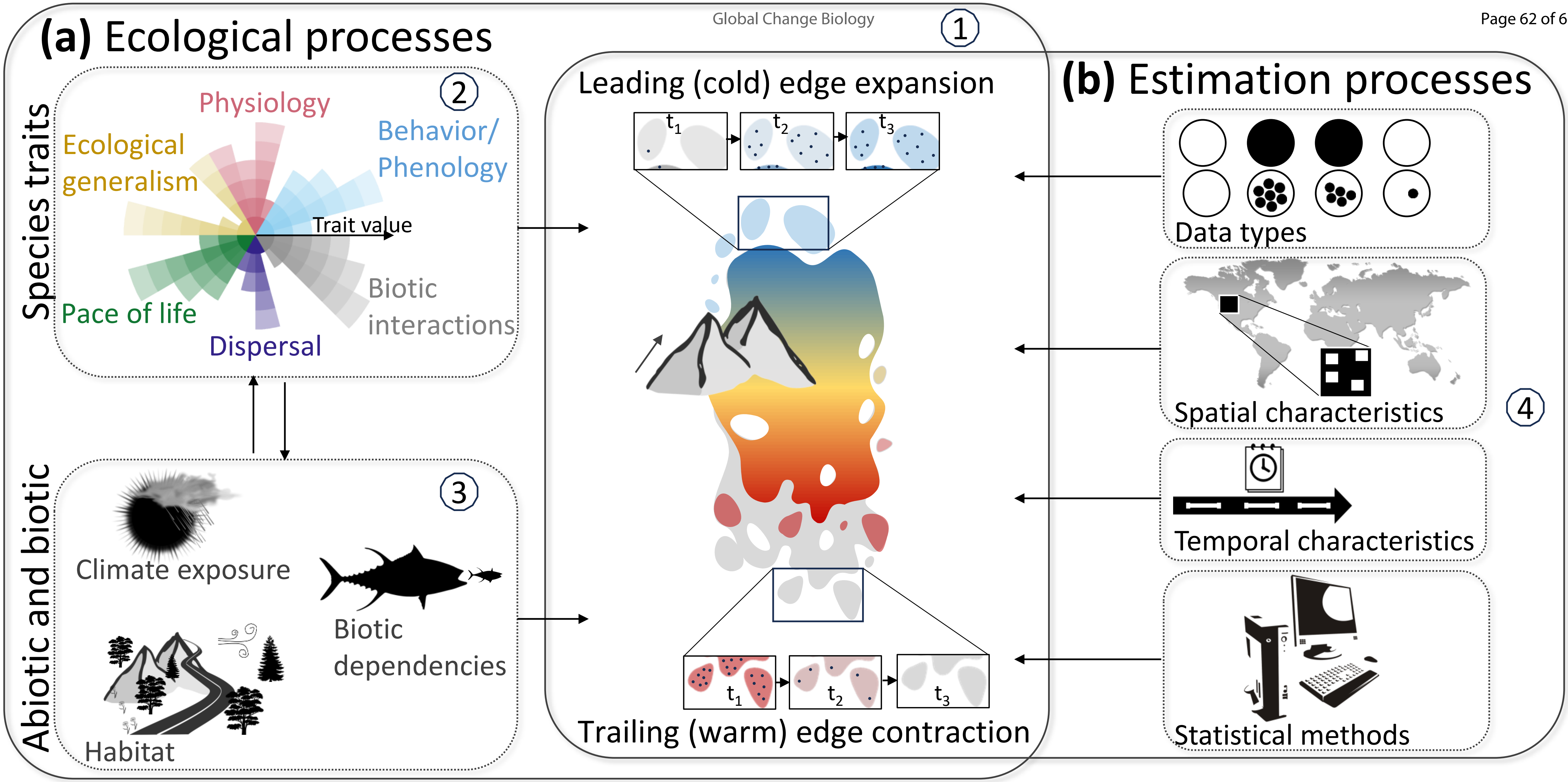
Figure 3. Synthesis of the scientific literature testing for relationships between traits and range shifts. Traits (bottom) that have been used in the scientific literature to explain the documented patterns and rates of species redistribution at different range parameters (top) ($N_{articles}$ = 44; $N_{species}$ = 9788). Traits have been coded into different subcategories and classified (colors) based on the hypothesized mechanisms that were studied (see Table 1). The category ‘Other’ indicates traits used to capture the effect of extrinsic factors (e.g., exposure to climate change or other drivers of change) or unclear mechanisms. The thickness of the arrows denotes

the number of studies that tested a particular link, where one trait can appear more than once (for clarity only traits that have been reported in more than one study are labeled). The list of scientific publications was identified based on the literature review performed by Beissinger & Ridell (2021) and MacLean & Beissinger (2017). Only quantitative shifts at the species-level were kept for this figure (i.e., range expansion or contraction at the leading and trailing edges or center of the distribution). See Supplementary Material (Appendix S1) for plots pertaining to kingdoms (plants vs. animals) and realms (marine, terrestrial, freshwater).

Figure 4. Revealing the explanatory power of species traits on the velocity of range shifts through interaction effects between species traits and climate exposure: (a,c,e) trailing edge contraction and (b,d,f) leading edge expansion. Dots in panels a-d are the outputs of a process-based model used to simulate the distribution of virtual animal species defined by different combinations of lifespan (x-axis in panels a and c) and maximal dispersal distance (x-axis in panels b and d) under different climate warming scenarios. The curves in panels a-b are from models fitted between the velocity of range shifts (i.e., the response variable) and species traits (dispersal ability or lifespan) without considering the velocity of isotherm shifts, while in panels c-d they are from models that consider the interaction between species traits and the velocity of isotherm shifts. The color scale in panels c-d indicates the velocity of isotherm shifts used in the simulations, with the vertical colored bars next to it illustrating the range of climate velocities reported for different climate change Representative Concentration Pathways (purple: RCP 2.6 and brown: RCP 4.5) in the marine (light colors) and terrestrial (dark colors) realms, where the triangles indicate the median values (according to Asamoah et al., 2021; Brito-Morales et al., 2020; Trisos et al., 2018). The animal silhouettes in panels c-d illustrate examples of lifespans

[AnAge database: De Magalhães & Costa, 2009] and maximum dispersal distances [butterfly: Sekar, 2012, frog: Smith & Green, 2005, common brushtail possum, horn shark and pinnated grouse: Jenkins et al., 2007] reported in the scientific literature. (e-f) Venn diagrams decomposing the proportion of explained variance (R^2) between the single and interactive effects of species traits and the velocity of isotherm shifts on the velocity of range shifts.

Figure 5. Consequences of coverage biases within the functional trait space on our understanding of the relationships between range shifts and species traits. (a-c) Hypothetical relationships between range shifts and species traits illustrating the potential consequences of using a truncated trait space on our understanding of the shape of these relationships. Blue and red dashed boxes: using only a subset of species displaying extreme functional characteristics; orange dashed box: using a subset of species with intermediate functional characteristics. (d-e) Examples of functional trait space coverage for bird and fish species estimated based on the first two components (PC) of a principal component analysis using morphological traits from the (d) AVONET (Nbird = 11,109; Tobias et al., 2022) and (e) FISHLIFE (N_{fish} = 26,622; Thorson et al., 2023) databases where the selection of species included in BioShifts (a database of range shift estimates) are highlighted in blue (N_{bird} = 973, N_{fish} = 431; Comte et al., 2020). The functional trait spaces are illustrated by the convex hulls encompassing all the species, wherein each dot represents a species and the solid squares represent the centroids of the respective convex hulls. The interpretation of the functional trait spaces is represented by the correlation circles showing the covariation among the morphological traits, with pictures illustrating the position of some selected species (see Table S1 for image attribution and Supplementary Material Appendix S3 for details on the analysis).



① Develop strong a priori hypotheses and account for trait (co)variations

→ *What are the expectations regarding the range shifts-trait relationships (shape and direction)?*

② Identify new opportunities for trait integration

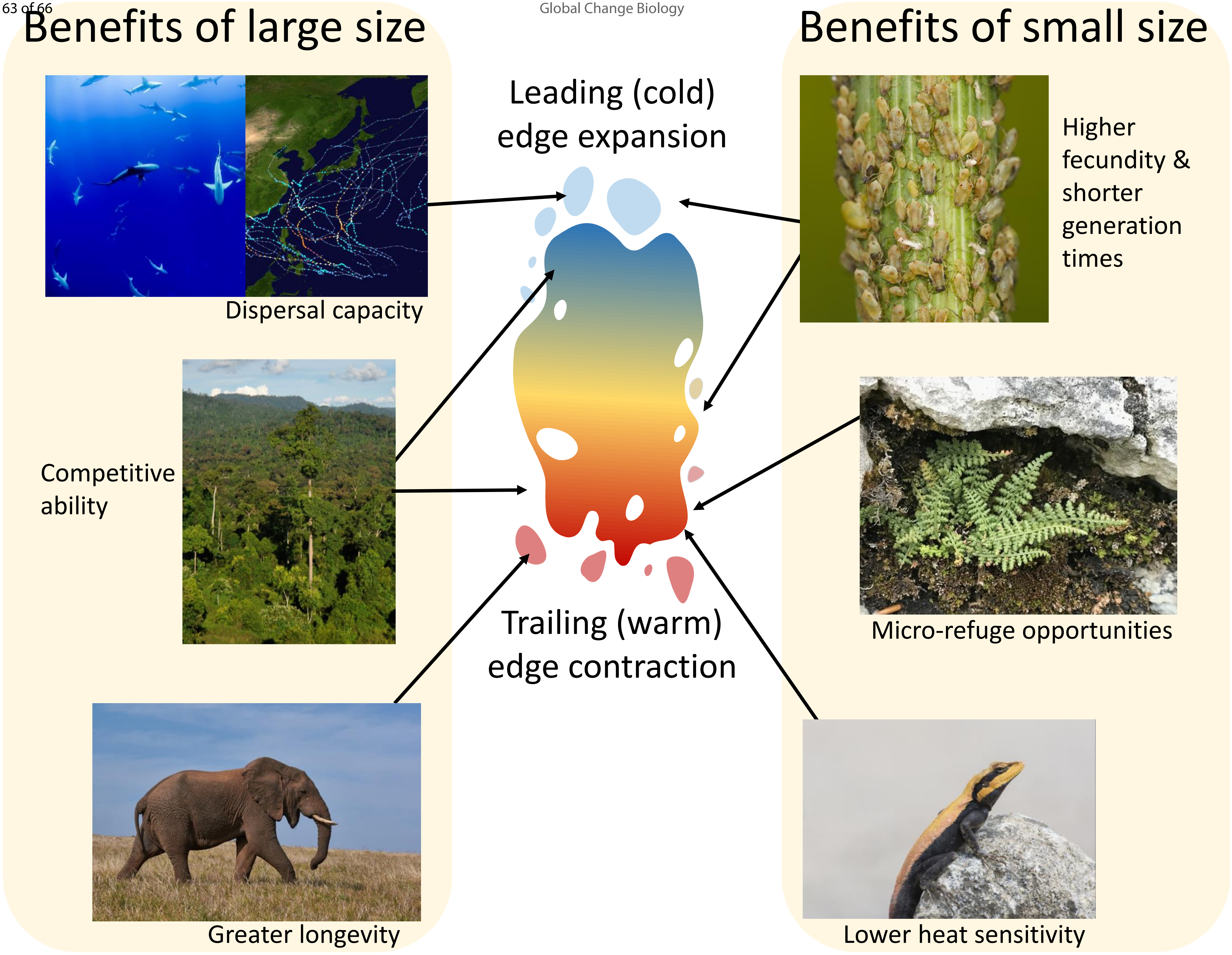
→ *Are the key mechanisms captured by the available traits?*

③ Account for abiotic and biotic context dependencies

→ *Is the influence of species traits likely to vary according to the local context?*

④ Account for estimation processes & research biases

→ *How are the underlying datasets and statical methods influencing the detected range shifts and ability to detect range shifts-trait associations?*



Benefits of large size

Dispersal capacity

Competitive ability

Greater longevity

Leading (cold) edge expansion

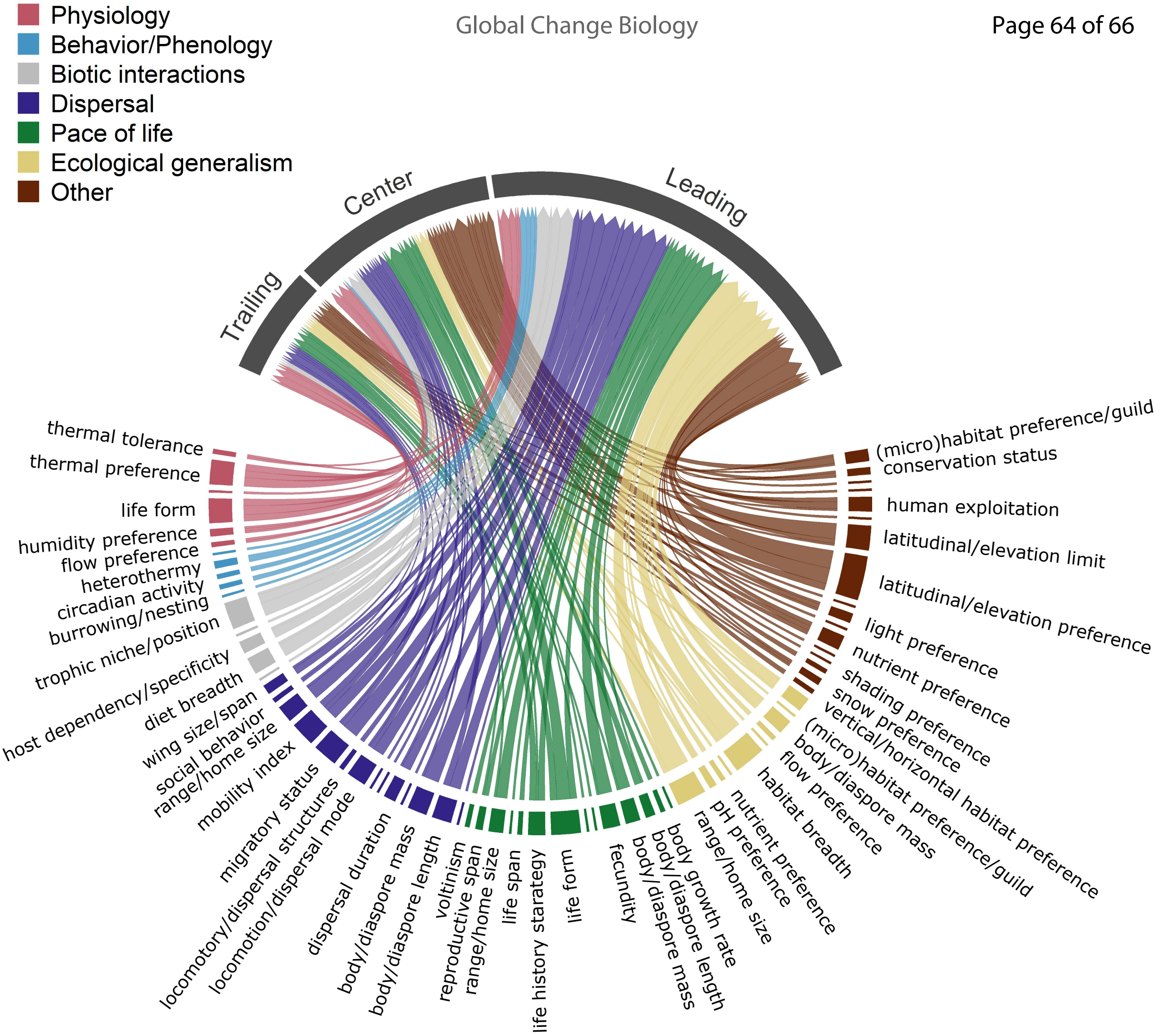
Trailing (warm) edge contraction

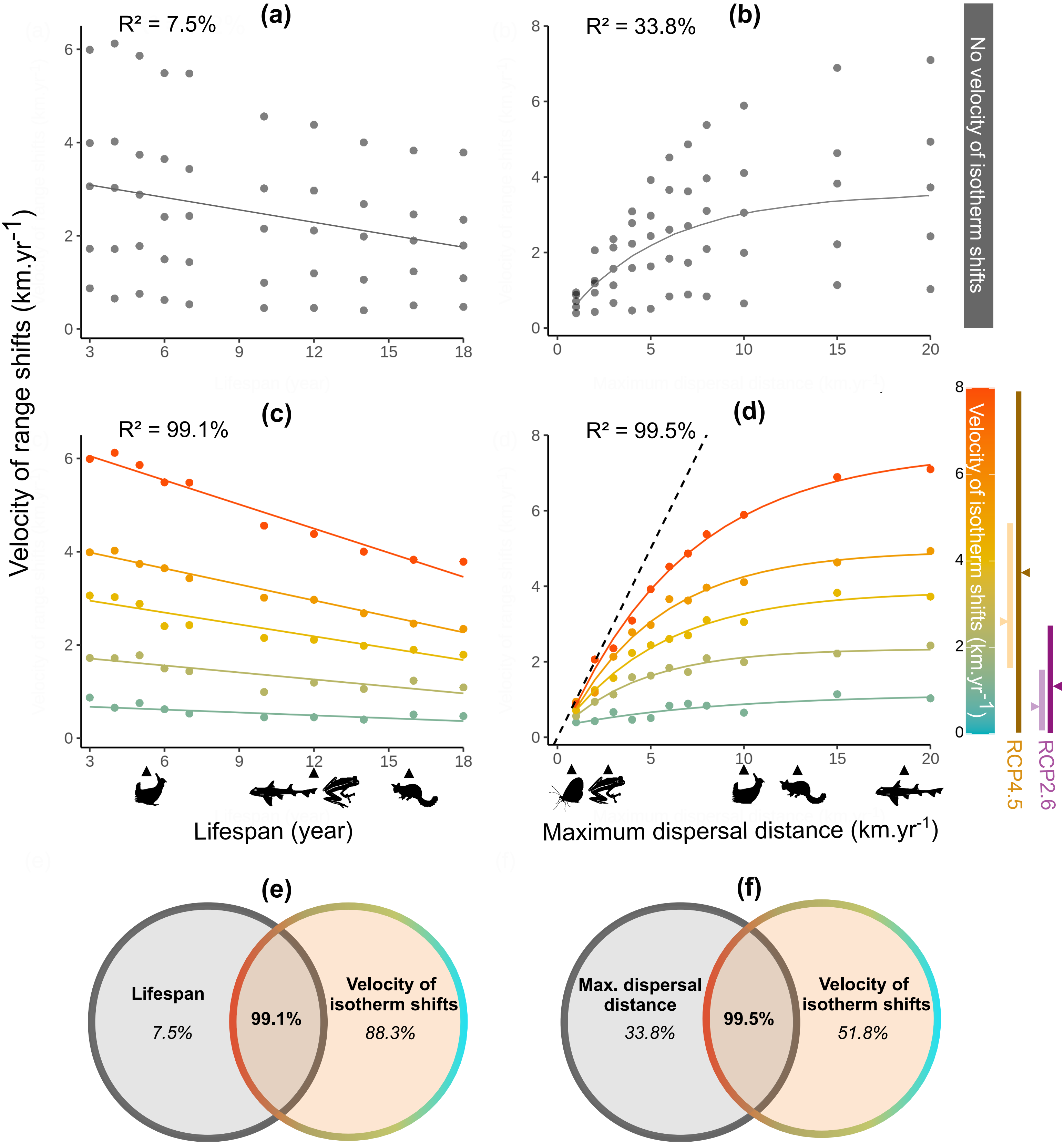
Benefits of small size

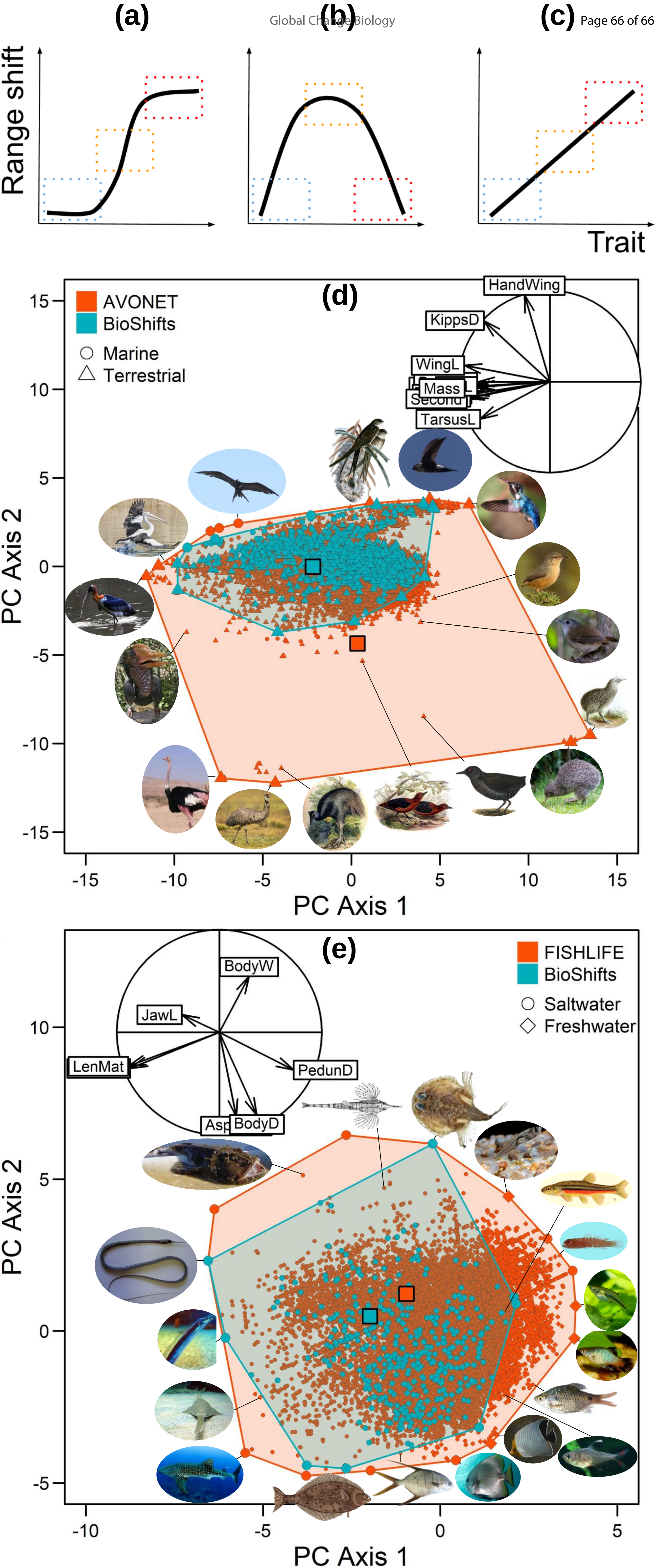
Higher fecundity & shorter generation times

Micro-refuge opportunities

Lower heat sensitivity


🟥 Physiology
🟦 Behavior/Phenology
⬜ Biotic interactions
🟪 Dispersal
🟩 Pace of life
🟨 Ecological generalism
🟫 Other
Trailing
Center
Leading
thermal tolerance
thermal preference
life form
humidity preference
flow preference
heterothermy
circadian activity
burrowing/nesting
trophic niche/position
host dependency/specificity
diet breadth
wing size/span
social behavior
range/home size
mobility index
migratory status
locomotory/dispersal structures
locomotion/dispersal mode
dispersal duration
body/diaspore mass
body/diaspore length
voltinism
reproductive span
range/home size
life span
life history starategy
life form
fecundity
body/diaspore mass
body/diaspore length
body growth rate
range/home size
pH preference
nutrient preference
habitat breadth
flow preference
body/diaspore mass
(micro)habitat preference/guild
vertical/horizontal habitat preference
snow preference
shading preference
nutrient preference
light preference
latitudinal/elevation preference
latitudinal/elevation limit
human exploitation
conservation status
(micro)habitat preference/guild


(a)
R² = 7.5%
(b)
R² = 33.8%
No velocity of isotherm shifts
Velocity of range shifts (km.yr^{-1})
0
2
4
6
8
3
6
9
12
15
18
0
5
10
15
20
(c)
R² = 99.1%
(d)
R² = 99.5%
Velocity of isotherm shifts (km.yr^{-1})
RCP4.5
RCP2.6
Lifespan (year)
Maximum dispersal distance (km.yr^{-1})
(e)
Lifespan
7.5%
99.1%
Velocity of isotherm shifts
88.3%
(f)
Max. dispersal distance
33.8%
99.5%
Velocity of isotherm shifts
51.8%


(a)
(b)
(c)
Range shift
Trait
(d)
AVONET
BioShifts
Marine
Terrestrial
HandWing
KippsD
WingL
Mass
Second
TarsusL
PC Axis 2
PC Axis 1
15
10
5
0
-5
-10
-15
(e)
FISHLIFE
BioShifts
Saltwater
Freshwater
BodyW
JawL
LenMat
PedunD
Asp
BodyD
PC Axis 2
PC Axis 1
-10
-5
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