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

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35 **Running Title:** Species range shifts-trait associations

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60 **ABSTRACT**

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

82

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

## 85        **1. INTRODUCTION**

86 Contemporary climate change has triggered the largest redistribution of life on Earth in the last  
87 tens of thousands of years (Chen et al., 2011; Lenoir et al., 2020; Parmesan, 2006). Yet,  
88 attributing the variation observed among range shifts to specific mechanisms governing these  
89 range shift processes remains unresolved. Paralleling the rise of trait-based approaches to  
90 understand community assembly (McGill et al., 2006; Violle et al., 2007), the last two decades  
91 have witnessed increased interest in the role of species traits – namely the behavioral,  
92 morphological, physiological or life history properties of organisms – in mediating species  
93 redistribution (Estrada et al., 2016; Madsen-Hepp et al., 2023; Miller et al., 2023; Williams et al.,  
94 2008). Theory suggests that various (and often different) traits can explain range shift processes  
95 at the leading (i.e., expanding) and trailing (i.e., contracting) edges of species distributions, thus  
96 providing testable hypotheses to understand causal mechanisms (e.g., Bates et al., 2014; Buckley  
97 & Kingsolver, 2012; Thurman et al., 2020). Uncovering relationships between species' traits and  
98 range dynamics may also allow for the identification of priority species and guide adaptive  
99 management strategies under climate change (Beever et al., 2016; Foden et al., 2019).

100

101 Although there are case studies successfully linking species traits to species range shifts (e.g.,  
102 warming tolerance and life history strategy for freshwater fishes: Comte et al., 2014; life forms  
103 and elevation ranges for plants: Lenoir et al., 2008; resource capture in plants; Madsen-Hepp et  
104 al., 2023; dispersal capacity in butterflies; Pöyry et al., 2009; mobility and range size in marine  
105 species: Sunday et al., 2015), other studies have found poor (Moritz et al., 2008; Pinsky et al.,  
106 2013) or counterintuitive (Tingley et al., 2012) associations. Hence, syntheses and meta-analyses  
107 tend to show weak or inconsistent effects of species traits on interspecific variation in rates of

108 range shifts (Angert et al., 2011; MacLean & Beissinger, 2017). Do these discrepancies between  
109 theory and empirical evidence suggest that trait-based approaches are not generalizable across  
110 species? Or, alternatively, have we as a research field been missing subtleties in trait-  
111 environment relationships (i.e., ecological processes) or not appropriately accounting for  
112 methodological factors (i.e., estimation processes) that affect detection and attribution of range  
113 shifts?

114

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

126

## 127 **2. Assess the mechanistic basis of traits**

128 Trait-based approaches offer clear conceptual foundations to understand the mechanisms  
129 underlying species range shifts (Box 2; Table 1). However, some major challenges remain for  
130 trait-based approaches to fulfill their potential. Among them, we first identify the need to clarify



131 the mechanistic basis of the set of species range shifts-trait associations in view of relevant  
132 ecological and evolutionary theories.

133

134 **(a) Account for interrelationships among traits**

135 Traits reflect complex patterns of co-adaptation, allocation trade-offs and by-products of  
136 selection – the so-called traits syndromes (Mauro & Ghalambor, 2020; Salguero-Gómez et al.,  
137 2016; Stevens et al., 2014) – such that covariations among traits can obscure the mechanisms  
138 underlying climate-induced range shifts. For example, body size is viewed as a master trait or the  
139 “Swiss army knife” trait that is integrative of a large number of physiological, life history and  
140 behavioral processes (Box 3; Fig. 2). Therefore, even if body size can be an efficient predictor of  
141 range shifts, it provides only weak mechanistic understanding owing to trait covariations  
142 (Visakorpi et al., 2023), especially as these trait syndromes may be inconsistent across  
143 taxonomic groups. For example, small-bodied species are usually associated with higher  
144 fecundity and shorter generation time among terrestrial animals (r-strategists) but not necessarily  
145 among aquatic animals (Winemiller & Rose, 1992). Trophic position increases with body size in  
146 fishes but not in mammals (Romanuk et al., 2011; Tucker & Rogers, 2014) and plants and  
147 animals appear to achieve demographic resilience through different combinations of life history  
148 traits (Capdevila et al., 2022). In this context, when pooling all taxonomic groups together, it is  
149 not entirely surprising that conflicting relationships between range shifts and these traits are  
150 frequently reported, sometimes in opposition with prevailing hypotheses (MacLean &  
151 Beissinger, 2017).

152

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

166

#### 167 **(b) Test stage-specific range shifts-trait associations**

168 Range shifts are by essence temporally dynamic and can be conceptualized as consecutive but  
169 interrelated stages, composed at the trailing edge of (i) decline in performance, (ii) population  
170 decrease and (iii) local extirpation; while at the leading edge, it can be composed of (i) dispersal  
171 (including both passive and decision-mediated active dispersal), (ii) population growth and (iii)  
172 persistence (Bates et al., 2014; Estrada et al., 2016). This suggests that developing and testing  
173 stage-specific range shifts-trait association expectations could improve our ability to develop a  
174 mechanistic understanding of the drivers of range shifts that explicitly consider both the spatial  
175 and temporal components of range shift processes. For instance, different facets of ecological

176 generalism or specialism may capture different stages of the range shift process, which may lead  
177 to conflicting hypotheses (and weak cross-study inferences) if the temporal dynamic of the range  
178 shift is ignored. Ecological generalism is often correlated with range size, and thus expected to  
179 be intrinsically linked with the evolution of dispersal ability over long time scales (Alzate &  
180 Onstein, 2022; Lancaster, 2022). Conversely, specialist species may have evolved better habitat-  
181 selection abilities (Jacob et al., 2018) and may therefore better track climatic conditions over  
182 short time scales; a hypothesis that has recently gained traction in contemporary climate-driven  
183 range shifting moths, butterflies and birds at their leading edge (Hällfors et al., 2023). Examining  
184 coral-reef fish species, Monaco et al. (2020) also demonstrated that dispersal capacity  
185 contributed to range expansions only in the dispersal stage of redistribution (stage i above),  
186 whereas resource-use breadth was more important during the growth and establishment stages  
187 (stages ii and iii above). As such, thermal specialists may display a higher dispersal propensity  
188 but being a generalist along other niche dimensions (e.g., tolerance to drought or generalist diet)  
189 may still be expected to facilitate dispersal and successful establishment. Understanding range  
190 shifts through the lens of traits might therefore benefit from looking at how traits act sequentially  
191 along the range shift pathway, and potentially interact beyond what might be expected from their  
192 additive effects (e.g., ‘extinction-promoting traits’; Davies et al., 2004).

193

#### 194 **(c) Consider non-linear range shifts-trait associations**

195 Finally, it is important to note that many associations between traits and ecological processes are  
196 intrinsically non-linear. In the context of species redistribution, the unimodal allometric scaling  
197 of dispersal and maximum speed with body size (Hirt et al., 2017; Stevens et al., 2014), or the  
198 fact that even species with moderate dispersal abilities may be able to keep up with the velocity

199 of isotherm shifts (Schloss et al., 2012; Urban et al., 2013) could translate into an asymptotic  
200 relationship between range expansion and body size. Likewise, given that the thresholds leading  
201 to extirpations are not expected to be reached for all species (e.g., Pinsky et al., 2019), range  
202 contractions might only be expected when temperatures greatly exceed thermal tolerance limits.  
203 Yet, hitherto, most studies have used linear responses to capture relationships between range  
204 shifts and species traits. Using models carefully informed by theory may therefore represent new  
205 opportunities to reveal the contribution of species traits to range shifts (Beissinger & Riddell,  
206 2021; Stenseth & Mysterud, 2002).

207

### 208 **3. Assess opportunities for new trait integration**

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

213

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

215 Although in some circumstances the same suite of traits may be useful to predict both range  
216 contractions and expansions (although often in the opposite direction), the assumption that range  
217 expansions and contractions are simply the two sides of the same coin is likely to be an  
218 oversimplification (Table 1). Yet, many of the same traits have been used with the same  
219 frequency in range shifts-trait studies, irrespective of the range position (trailing edge, center or  
220 leading edge; Box 2, Table 1). For example, studies remain dominated by traits related to range  
221 size, habitat specialization and preference, whose underlying mechanisms might be sometimes

222 difficult to interpret (as discussed above for body size; Box 3). In comparison, behavioral and  
223 physiological traits have been less explored. This reflects the scarcity of databases compiling  
224 organismal traits (measured on individuals) over distribution-based traits (estimated from species  
225 distributions), and highlights opportunities for new trait integration as data on physiological,  
226 dispersal and behavioral traits become increasingly available (e.g., Bennett et al., 2018;  
227 Herberstein et al., 2022; Lososová et al., 2023). This coupled with new methodological  
228 approaches for trait imputation to fill in data gaps (e.g., Thorson et al., 2023), as well as  
229 transcriptome databases to detect significant gene-trait associations (e.g., Primmer et al., 2013),  
230 may help researchers to integrate traits that have been less explored but that are more likely to  
231 capture the mechanisms underlying range shifts.

232

233 Studies also often used markedly different proxies or estimates per trait, which may make  
234 findings on the importance of traits incomparable across studies. For instance, habitat breadth  
235 has been estimated using many different indices, including the number of habitat types (e.g.,  
236 Powney et al., 2015), the coefficient of variation across habitat classes (e.g., Platts et al., 2019),  
237 and multivariate indices based on continuous environmental gradients (e.g., Comte et al., 2014).  
238 Yet, it is unclear whether these indices, estimated from a variety of variables and across different  
239 spatial resolutions, are inter-comparable and approximate the same hypothesized process, which  
240 complicates subsequent meta-analyses that seek to test how traits relate to observed variation in  
241 range shifts across studies. Furthermore, most studies conduct cross-species comparisons using  
242 only adult traits, despite the fact that traits can vary across a species' lifespan and life-history  
243 stages (e.g., ontogenetic niche shifts); this in turn can have direct consequences on our ability to  
244 test the role of traits. For example, the fact that thermal tolerances and plasticity can vary through

245 ontogeny (e.g., plants: Caron et al. 2021; fishes: Dahlke et al. 2020; insects: Weaving et al. 2022)  
246 suggests that traits measured on non-adult life stages may be complementary and thus necessary  
247 to explain the rates of species redistribution. Likewise, traits can vary across species ranges for a  
248 variety of reasons (e.g., predation risk can alter the temperature dependence of life-history traits;  
249 Luhring et al. 2018), and trailing edge populations that are often small and isolated often display  
250 unique intraspecific phenotypic adaptations to local conditions that can increase their resilience  
251 to climate change (Hampe & Petit, 2005). Linking range shifts to traits measured at specific  
252 range positions represents a promising path of inquiry. Although widely available and easier-to-  
253 get traits may prove sufficient for certain conservation applications (Gallagher et al., 2021),  
254 supporting a more mechanistic and predictive science of range shifts will likely require spending  
255 more time on difficult-to-get and time-consuming traits, including renewed considerations for  
256 cross-studies standardization and incorporation of intraspecific variability (e.g., across life stages  
257 or at different range positions). However, we note that there is no such dichotomy between “bad”  
258 and “good” traits; instead, trait selection must be informed by strong a priori hypotheses based  
259 on the taxonomic and geographic scope of the study and the subsequent analytical framework  
260 developed using informed models accounting for (co)variation among traits.

261

#### 262 **(b) Consider evolutionary potential alongside traits**

263 An additional consideration is that species trait means and variances are not fixed, but instead  
264 can change through evolutionary adaptation (Diamond, 2018; Donelson et al., 2019; Hoffmann  
265 & Sgrò, 2011). While recognizing that evolutionary potential can hardly be classified as a ‘trait’,  
266 by facilitating adaptive responses to climate change, trait evolution can strongly influence  
267 species’ range shifts and could thus be more often considered alongside traits. A classic example

268 is the evolution of dispersal ability at expanding range limits due to spatial sorting of the most  
269 dispersive individuals (Phillips et al., 2008; Travis et al., 2013). Climatic niche shifts have also  
270 been documented during range expansion, which may explain why some species have shifted  
271 faster than expected (Lustenhouwer & Parker, 2022). Providing accurate estimates of  
272 evolutionary potential remains challenging (Forester et al., 2022; Hoffmann & Sgrò, 2011),  
273 particularly as many factors such as population size, phenotypic plasticity, life history traits,  
274 genetic correlations or spatial connectivity may either facilitate or hinder evolutionary responses  
275 to selection (Martin et al., 2023). Genetic diversity indices (e.g., allelic richness, heterozygosity)  
276 and effective population size or genetic markers identified through genotype-environment  
277 associations or adaptive landscape modeling may be effective proxies for evolutionary potential,  
278 but are difficult to gather across multiple taxa and at large spatial extents (Capblancq et al., 2020;  
279 Hoban et al., 2022; Razgour et al., 2019; see also Thompson et al., 2023). A complementary  
280 approach is to assess the degree to which species niches and underlying traits are conserved  
281 through evolutionary time (Bennett et al., 2021; Diamond, 2018; Lavergne et al., 2013). While  
282 macroecological approaches may not provide great precision, they could nonetheless help in  
283 providing a benchmark to estimate evolutionary potential (Diniz-Filho et al., 2019). Testing  
284 whether lineages that have experienced faster niche evolution in the past display a higher  
285 potential for evolutionary rescue that prevents range contraction in response to contemporary  
286 selective pressures remains an exciting and under-explored research question.

287

#### 288 **4. Assess the abiotic and biotic context of traits**

289 To illuminate the role of species traits in explaining range shifts, it is important to recognize that  
290 range shifts result from complex interactions between species' intrinsic features and the abiotic

291 and biotic context in which these shifts occur. It follows that examining *solely* species traits  
292 (even if these traits have a strong mechanistic basis and fine resolution) may fail at uncovering  
293 the mechanisms at play, particularly in cross-study comparisons where climate change exposure,  
294 habitat characteristics, and biotic dependencies can drastically vary.

295

296 **(a) Account for interactions between traits and climate exposure**

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



314 99.5%; Fig. 4e,f). Consistent with theoretical expectations (see Table 1), we found that species  
315 with short lifespans and high dispersal abilities shift their distribution limits faster at the trailing  
316 and leading edges, respectively, and especially so when the exposure to climate change is higher.  
317 At the trailing edge, the velocity of range contraction is negatively associated with lifespan and  
318 displays an interaction with climate velocity, such that range contractions are hastened when  
319 lifespan is short and climate exposure is high, indicating that climate impacts are more readily  
320 detectable in short-lived species (Fig. 4c). At the leading edge, the velocity of range expansion is  
321 positively associated with maximum dispersal distance through an asymptotic relationship whose  
322 slope becomes steeper when the velocity of isotherm shifts increases, indicating that the  
323 expansion process is likely limited by dispersal ability (Fig. 4d).

324

325 Interestingly, even if the individual effects of species traits can be weaker predictors of species  
326 range shifts than the individual effect of isotherm shift velocity, it is the interaction effect that  
327 captures most of the observed variation in species range shifts. Empirical studies in marine  
328 systems, where climate velocities are up to seven times higher than on land and where ocean  
329 currents strongly influence redistribution, also suggest that traits may be comparatively less  
330 important than extrinsic factors to explain variation in biotic velocity among species (García  
331 Molinos et al., 2022; Pinsky et al., 2013). Nonetheless, in accordance with our simulations,  
332 Sunday et al. (2015) demonstrated that considering the interactions between climate exposure  
333 and species traits (including mobility) more than doubled the percentage of explained variance in  
334 range expansion of marine fish and invertebrate species compared to a model accounting only for  
335 climate expectations. Hence, incorporating these complex interactions may help reveal the  
336 contributions of species traits to explain the observed variation in range shift patterns,

337 particularly when the trait effect is weaker (e.g., such as when considering the effect of lifespan  
338 alone on range contraction). Obviously, species climatic niches are by essence multidimensional  
339 and considering only changes in temperature might also misrepresent range shift expectations  
340 (Tingley et al., 2012). Similarly, accounting for extreme events in addition to long-term climatic  
341 changes (e.g., heat waves as opposed to mean annual temperature trends) may better capture  
342 climate exposure and subsequent impacts on the distribution of populations and species (Auth et  
343 al., 2018). In this context, considering multiple climate axes simultaneously (Crimmins et al.,  
344 2011; Dobrowski et al., 2013), using model-based bioclimatic velocities (VanderWal et al.,  
345 2013) or accounting for both climatic presses and pulses (Harris et al., 2018) could help refine  
346 range shift expectations based on the multifaceted effects of climate change, thereby providing a  
347 stronger conceptual framework to understand the contribution of species traits to range shifts.

348

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

350 Beyond climate exposure, a myriad of abiotic and biotic factors likely influences the ability of  
351 species to track shifting climate conditions at a variety of temporal and spatial scales, as  
352 mediated through their traits. Although these context-dependencies must be considered on a  
353 case-by-case basis, here we discuss a few examples to illustrate the importance of considering  
354 environment-trait interactions to explain range shifts. Habitats differ in terms of spatio-temporal  
355 heterogeneity and human pressures, which will determine opportunities for dispersal and  
356 persistence under climate change (Pinsky et al., 2022). These variations in habitat characteristics  
357 may explain the faster rates of redistribution in the ocean than on land (Lenoir et al., 2020), but  
358 the importance of habitat characteristics to range shift processes will ultimately depend on the  
359 interactions with species traits. On land, landscape fragmentation (both natural and

360 anthropogenic) is likely to represent a major constraint on species redistribution but its influence  
361 is expected to vary with species-specific habitat requirements, such that habitat generalists may  
362 be less constrained by habitat availability than more specialized species (Platts et al., 2019). In  
363 the ocean, the opportunities offered by habitat verticality in 3-D habitats can mediate the rate of  
364 latitudinal range shifts by allowing species to locally exploit deeper ocean layers (Brito-Morales  
365 et al., 2020), yet the rates of depth shifts likely depend on both the niche characteristics and  
366 fishing pressure exerted on the shifting species (Dahms & Killen, 2023).

367

368 Biotic factors may also affect the associations between species traits and range shifts. For  
369 example, in polyphagous insects, the ability to exploit alternative hosts may confer a  
370 survivorship advantage and decrease contraction at the trailing edge, but these benefits rely upon  
371 host plant availability now and in the future (Hellmann, 2002). Conversely, although in general  
372 the higher mobility of animals compared to plants a priori suggests that plants should not be  
373 limited by dispersal limitations of their animal vectors to keep up with climate change at their  
374 leading edge, defaunation of seed-dispersing birds and mammals may drastically reduce the  
375 ability of plants to shift their ranges (Fricke et al., 2022). This highlights the importance of  
376 examining realized as opposed to fundamental adaptive capacity when testing the relationships  
377 between species traits and range shifts (through trait-environment interactions) – an analogy with  
378 the duality between realized and fundamental ecological niches intended to capture the extent to  
379 which extrinsic factors constrain the expression of the intrinsic determinants of the range shifts  
380 processes (Beever et al., 2016). The characteristics of the range shifting species with respect to  
381 the recipient communities can also influence range expansions via biotic resistance and niche  
382 opportunities as in the case of biological invasions (Shea & Chesson, 2002), although such

383 hypotheses have so far received mixed support (Alexander et al., 2015; Miller et al., 2023).  
384 There is still much to be learned by developing a trait-based framework that explicitly considers  
385 the biotic community context (Gilman et al., 2010; Lavergne et al., 2010; Schleuning et al.,  
386 2020), as well as capitalizing on the decades-old field of invasion biology to better apprehend the  
387 mechanisms underlying range shifts (Pauchard et al., 2016; Wallingford et al., 2020).

388

## 389 **5. Assess the effects of the estimation process and research biases**

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

395

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

397 The distribution and abundance patterns of species within their range limits are not static but  
398 fluctuate due to demographic and environmental stochasticity and can result in gaps and  
399 fragmented areas, particularly at range limits (Brown et al., 1996; Hampe & Petit, 2005).  
400 Estimating species range shifts, especially at the edges, may thus be particularly sensitive to the  
401 sampling method, number and consistency of studied locations, temporal coverage, spatial grain,  
402 as well as the analytical methods used (Loehle, 2020; Shoo et al., 2006). Noteworthy, beyond the  
403 noise introduced by the different methods used in the scientific literature, the traits and the  
404 estimation process can interact. For instance, species detectability can vary as a function of  
405 species morphological and behavioral characteristics (e.g., Sólymos et al., 2018), and the

406 influence of the temporal resolution on perceived range shifts will likely depend on the pace of  
407 life of the organisms under study. Therefore, carefully accounting for methodological differences  
408 in cross-studies comparisons may greatly improve our ability to detect ecologically meaningful  
409 relationships with species traits and thus our power to explain species redistribution.

410

#### 411 **(b) Reduce functional biases in species redistribution research**

412 Biases with respect to the trait coverage of the species for which range shifts have been  
413 documented may also lead to misrepresentations of the strength and direction of the relationships  
414 between range shifts and species traits, particularly if these relationships are non-linear  
415 ('functional biases'; Fig. 5a-c). Yet, a comparison of the degree of morphological trait space  
416 covered by BioShifts, a range shift database compiled from the scientific literature (Comte et al.,  
417 2020), for two widely studied taxonomic groups – birds and fishes – reveals that these functional  
418 biases may be prevalent (Fig. 5d-e). For instance, among terrestrial birds, range shift detections  
419 of functionally unique species such as flightless (e.g., ostrich, emu, kiwi) or lightweight (e.g.,  
420 hummingbirds) birds remain understudied. Similarly, a bias against small-bodied fishes  
421 displaying a high caudal peduncle depth is evident in both marine and freshwater species, with  
422 these attributes being strongly related to swimming ability (Fisher & Hogan, 2007; Radinger &  
423 Wolter, 2014). Although the consequences of these functional biases on our ability to detect  
424 meaningful relationships between range shifts and species traits remain to be formally  
425 investigated, to fully understand range shift processes, both functionally common and unique  
426 species would benefit from being studied in a shared framework. Functional uniqueness may  
427 represent adaptations to specific environmental conditions (e.g., reduced physical capacity for  
428 dispersal for flightless birds on islands due to the island syndrome; Wright et al., 2016), distinct

429 alternative phenotypic adaptations to the same environmental challenges (e.g., active dispersal  
430 versus in situ drought resistance forms in aquatic invertebrates; Osakabe et al., 2014) or  
431 competition-driven specialization (e.g., morphological and foraging microhabitat specialization  
432 in coral reef fishes; Brandl et al., 2015), and may thus hold key insights to contextualize the  
433 functions and evolutionary trajectories of trait syndromes (Munoz et al., 2023), including in the  
434 context of species redistribution.

435

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

437 In addition, geographic and phylogenetic biases in research effort may impair our ability to  
438 comprehend the importance of the intrinsic and extrinsic factors relevant to range shifts (Feeley  
439 et al., 2017; Lenoir et al., 2020). Overrepresentation of temperate species may, for instance,  
440 underestimate the vulnerability of tropical species that display particular combinations of  
441 behavioral and physiological adaptations, such as narrower thermal tolerances and lower  
442 dispersal abilities (Feeley et al., 2017; Tewksbury et al., 2008). Indeed, from an evolutionary  
443 perspective, climatic variations (from long-term geological to annual seasonality or daily  
444 fluctuations) in the tropics are very different from the ones in the temperate zone or at higher  
445 latitudes, with important implications for shaping the current distribution, traits, and genetic  
446 diversity of species and populations (De Kort et al., 2021; Hampe & Petit, 2005). These  
447 variations can influence their sensitivity and adaptive capacity to climate change (Chan et al.,  
448 2016; Steele et al., 2019). These types of bias call for more balanced comparative approaches  
449 across the tree of life and globe, leveraging differences across a variety of taxa and regions  
450 (including less researched taxa and areas as well as between mainland and islands), to better  
451 tease apart the relative contribution of intrinsic species traits and extrinsic factors to explain

452 species redistribution (Pinsky et al., 2022). Recognizing that all the challenges cannot all be  
453 resolved at once, we also emphasize the opportunities for carefully targeted laboratory and  
454 mesocosm studies that can more directly focus on the mechanisms at play and improve our  
455 ability to tease apart the context-dependencies of range shifts-trait associations (e.g., Luhring et  
456 al., 2018).

457

## 458 **6. A path to move forward**

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

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

- 474 • *Fill gaps in trait databases for key categories.* The most important traits to explain  
475 species responses to climate change may not always match with the restrictive suite of  
476 traits available in large trait databases (Green et al., 2022; Kühn et al., 2021). Recent  
477 efforts to address this limitation include standardized metabolic traits across animal  
478 groups (AnimalTraits: Herberstein et al., 2022), temperature tolerance limits across  
479 ectotherms (e.g., GlobTherm: Bennett et al., 2018; but see Clusella-Trullas et al., 2021  
480 for a discussion on the limitation of thermal sensitivity indices), dispersal traits for  
481 vascular plants (Lososová et al., 2023) and standardized diet and morphological  
482 information for birds (Hurlbert et al., 2021; Tobias et al., 2022). To the extent possible,  
483 accounting for sources of intraspecific variation (particularly considering ontogenetic  
484 shifts) and ensuring that traits are being measured at the correct scale and geographic  
485 position with respect to the observed range shifts may improve the predictive power of  
486 traits to explain range shifts. Emerging advances in genomics also hold promise to  
487 understand the role of evolution in facilitating or hindering range shifts (e.g., Capblancq  
488 et al., 2020; Razgour et al., 2019), and could be used alongside trait-based approaches.  
489
- 490 • *Identifying interactions between intrinsic species traits and extrinsic factors.* Identifying  
491 the general determinants of range shifts that transcend any context-dependencies requires  
492 careful integration of a series of abiotic and biotic factors (both natural and  
493 anthropogenic) in analytical frameworks that explicitly include interactions with species  
494 traits (e.g., Bertrand et al., 2016; García Molinos et al., 2022; Platts et al., 2019). This can  
495 be further improved by simulation experiments conducted from mechanistic models (e.g.,  
496 as done above or in Henry et al., 2014). In addition, there is much to be learnt by studying



497 range shifts in a community context (Lavergne et al., 2010), including through the lens of  
498 invasion biology by exploring the role of biotic resistance based on key functional traits  
499 (e.g., Miller et al., 2023).

500

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

511

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

518

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526

### 527 **Author Contributions Statement**

528 Conceptualization: all authors; Methodology: L.C., R.B., M.L.P., J.L.; Formal analysis: L.C.,  
529 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.;  
530 Writing - Review & Editing: all authors; Visualization: L.C., R.B., S.D., L.T.L., B.F.O., S.W.,  
531 J.L.; Project administration: L.C., J.L.; Funding acquisition: L.C., J.L.

532

### 533 **Data availability**

534 The data that support the findings of this study are available in FigShare at  
535 10.6084/m9.figshare.25467664. The data were derived from the following resources available in  
536 the public domain: <https://doi.org/10.1146/annurev-ecolsys-012021-092849>,  
537 <https://doi.org/10.1111/gcb.13736>, <https://doi.org/10.6084/m9.figshare.7413365.v1>,  
538 <https://figshare.com/s/b990722d72a26b5bfead>.

539

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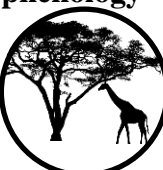
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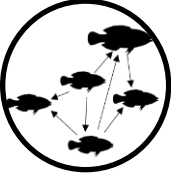

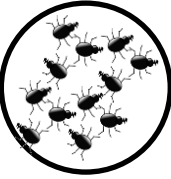
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1080

1081 **Table 1. Mechanisms by which species traits are expected to mediate range shifts and**  
 1082 **selected trait examples.** Multiple traits influence species distribution limits and range dynamics  
 1083 in response to climate change. Species-level traits can be organized into major categories of  
 1084 mechanisms that may vary in their degree of intraspecific variation expressed in nature.  
 1085 Furthermore, traits exhibit varying degrees of phenotypic plasticity or additive genetic variation  
 1086 upon which selection can act to compensate for the effects of environmental change (as  
 1087 exemplified in the ‘Moderator of traits’ column). The directionality of the expected range shifts-  
 1088 trait relationship is given with respect to high trait values but opposite effects can be expected for  
 1089 lower trait values. TE = trailing edge; LE = leading edge. See Box 2.

<b>Category of mechanism</b>	<b>Trait</b>	<b>Example (expressed rel. to higher values of each trait)</b>	<b>Temperature-driven range shifts-trait expectation</b>	<b>Moderators of traits (plasticity and evolutionary potential)</b>
<b>Physiology</b> 	High temperature physiology	Heat tolerance (as compared to experienced temperature)	Hinders TE contraction (decrease sensitivity to heat waves)	<i>Thermal plasticity and niche shifts</i> Cold/heat tolerance acclimation; Facilitates LE expansion & hinders TE contraction (lower sensitivity to temperature fluctuations)
<b>Behavior &amp; phenology</b> 	Behavioral thermoregulation  Types of phenological cues as information of future climates	Selection of shaded microhabitats  Whether organisms use temperature or light as a phenological cue	Hinders TE contraction (avoids overheating)  Facilitates LE expansion (temperature-dependence of cues enable faster phenological responsiveness)	<i>Phenological plasticity</i> Shift in emergence timing; Hinders LE expansion & TE contraction (tracks shifting climate conditions in time) or facilitates LE expansion (improves fitness in new environments)
<b>Biotic interactions</b>	Interaction specialization	Resource-use breadth	Facilitates LE expansion (facilitates en route	<i>Morphological plasticity</i> 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)	
<b>Dispersal</b>	Dispersal mode	Whether organisms disperse via: passive, crawling, swimming, or flying mode	Facilitates LE expansion (higher dispersal distances)	<i>Evolution of dispersal capability</i> 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)	
<b>Pace of life</b>	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	<i>Developmental plasticity</i> Development time; Facilitates LE expansion (longer development times improves fecundity)
	<b>Ecological generalism</b>	Abiotic niche breadth	Degree of tolerance to a diversity of abiotic factors	Facilitate LE expansion (larger range of environment tolerated during dispersal and
				<i>Physiological plasticity</i> Drought acclimation; Hinders TE contraction (lower sensitivity to



Cognitive flexibility

(pH, O<sub>2</sub>, drought, light)

Relative brain size

establishment)

drought)

Hinders TE contraction (adjust behavior to changing conditions)

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1090

1091 **Box captions**

1092 **Box 1. Embracing the complexity of species range shifts**

1093 *Documented range shifts* (i.e., general directions and speed of species range shifts) are typically  
1094 estimated at the *leading edge* of species distribution (expanding or cold edge), usually located at  
1095 high latitude, high elevation on land or at deeper depths in the oceans in the context of current  
1096 climate warming, and at the *trailing edge* of species distribution (contracting or warm edge),  
1097 usually located at low latitude, low elevation on land or at shallower depths in the oceans (Fig.  
1098 1). These documented range shifts at the cold (e.g., upper elevation) and warm (e.g., lower  
1099 elevation) edges along spatial gradients are frequently equated to the dynamics of range  
1100 expansion and contraction, although we note that each edge can either expand or contract.

1101

1102 Documented range shifts are underpinned by complex ecological processes, among which  
1103 species' traits are expected to be key – but not the sole – underlying drivers. Here, we define a  
1104 trait as any intrinsic morphological, physiological or phenological feature measurable at the  
1105 individual level that influences species ecological performance, without consideration to the  
1106 extrinsic environment or other levels of biological organization (Violle et al., 2007). It follows  
1107 that the ecological processes underlying range shifts are likely to arise from the interaction  
1108 between species' traits (or the set of intrinsic factors such as thermal tolerance and dispersal  
1109 ability) and its abiotic and biotic context (or set of extrinsic factors such as climate change  
1110 exposure, biotic dependencies, and habitat characteristics).

1111

1112 The documented range shifts are additionally influenced by the estimation processes, as the  
1113 direction and speed of species range shifts cannot be observed directly but instead are dependent

1114 on the set of methodological factors used, including the underlying data types (e.g., species  
1115 abundance, presence-absence), spatial (e.g., grain and extent) and temporal (e.g., number of time  
1116 periods) resolution of available datasets, and the statistical methods (e.g., quantile regression,  
1117 species distribution models). Given the variation caused by circumstances of individual shifts  
1118 and the methods used to detect them, analytical methods that consider both are necessary for  
1119 properly attributing shifts to associated mechanisms when synthesizing data across studies. We  
1120 note that species traits (and to some extent the set of extrinsic factors) are also prone to  
1121 measurement errors and are themselves dependent on the estimation process such as the  
1122 inclusion of intraspecific variability, or choice of the upper endpoint of the thermal performance  
1123 curve (e.g., lethality versus loss of motor control), among others.

1124

1125

1126 **Box 2. Theoretical expectations for range shifts-trait associations**

1127 *Physiology*: From a fundamental point of view, species distribution limits and responses to  
1128 climate change chiefly depend on the thermal (and other climate) sensitivity of species  
1129 physiological performance as well as the level and temporal patterns of exposure, which together  
1130 affect population persistence at the trailing edge and opportunities for leading edge expansion  
1131 (Angilletta et al., 2003; Huey et al., 2012; Kingsolver et al., 2013) (Table 1). To buffer  
1132 themselves against sublethal or lethal thermal stress, organisms have evolved strategies enabling  
1133 them to adjust physiological responses over the short to long term (days to years). Examples  
1134 include active transpiration in plants (De Frenne et al., 2021) and thermal acclimation in  
1135 ectotherms (Gunderson & Stillman, 2015; Seebacher et al., 2015; Weaving et al., 2022).  
1136 Evolution of physiological traits such as heat or cold tolerance can also facilitate expansion or  
1137 slow down contraction (Martin et al., 2023), but these effects are unlikely to be universal.  
1138 Physiological plasticity can initially facilitate entry into and persistence within novel  
1139 environments but can impede long-term evolutionary adaptation when it acts in the same  
1140 direction as selection (e.g., Leonard & Lancaster, 2020).

1141

1142 *Behavior & phenology*: Behavioral thermoregulation in mobile ectotherms allows individuals to  
1143 exploit local heterogeneity in microclimates by shifting the time (e.g., diurnal, circadian cycles)  
1144 and place (e.g., burrowing, nesting) of activity (Kearney et al., 2009; Sunday et al., 2014), which  
1145 may slow range contraction at the trailing edge (Table 1). Likewise, in endotherms, behaviors  
1146 such as torpor and hibernation can allow regulation of body temperature to survive adverse  
1147 conditions (Geiser & Turbill, 2009). Phenological adjustments can also hinder range contractions  
1148 by enabling plants and animals to track climatic changes in time (instead of space) via shifts in



1149 seasonal life history events (e.g., emergence, development and reproduction), as well as promote  
1150 range expansion at their leading edge by improving survival after establishment (Socolar et al.,  
1151 2017; Vitasse et al., 2021; Zettlemyer & Peterson, 2021).

1152

1153 *Biotic interactions:* Species can be indirectly affected by climate change through altered biotic  
1154 interactions, as mediated through their traits (Gunderson et al., 2017; Schleuning et al., 2020;  
1155 Urban et al., 2013) (Table 1). For instance, species engaged in highly specialized interactions  
1156 (e.g., for reproduction via pollinator dependency, for dispersal through zoochory) may be more  
1157 sensitive due to mismatches in climatic sensitivities or dispersal ability with their obligate  
1158 species. These indirect sensitivities can precipitate range contraction or slow range expansion  
1159 (Cahill et al., 2013; Gilman et al., 2010; Schleuning et al., 2020). Conversely, better competitors  
1160 may be less susceptible to biotic resistance from recipient communities at their leading edges  
1161 (wherein the resident communities exert negative effects on the range shifting species, usually  
1162 through predation or competition) and competitive exclusion at their trailing edges, including  
1163 from novel range shifting competitors (Alexander et al., 2015; Sanczuk et al., 2022).

1164

1165 *Dispersal:* As climate change opens new suitable habitats, dispersal is expected to be a key  
1166 mechanism by which species track climate shifts through space, especially at the leading edge  
1167 (Corlett & Westcott, 2013; Schloss et al., 2012) (Table 1). For instance, movement costs for  
1168 active dispersers can be lower in large-bodied species with enhanced locomotion efficiency,  
1169 species displaying specific dispersal structures (e.g., wing size in insects and birds or aspect ratio  
1170 of the caudal fin in fish), species with better navigational skills, or species displaying collective  
1171 dispersal behaviors (Berdahl et al., 2018; Sambilay, 1990; Stevens et al., 2014). Among passive

1172 dispersers, investment in seed dispersal structures or longer duration of dispersal phase also leads  
1173 to greater dispersal opportunities (Thomson et al., 2018). In addition, human-mediated dispersal  
1174 (i.e., species translocation and assisted migration in general) may play a key role in facilitating  
1175 range expansions of species of commercial or recreational interest (e.g., Alofs et al., 2014).

1176

1177 *Pace of life*: Fast life history attributes can confer a higher demographic potential to rapidly  
1178 establish new founding populations at the leading edge (Table 1). High propagule pressure (i.e.,  
1179 the number and frequency of dispersing individuals) reduces the effects of genetic,  
1180 environmental and demographic stochasticity, and high population growth rates reduce genetic  
1181 bottlenecks and Allee effects that may precipitate extinction in small populations (Roman &  
1182 Darling, 2007; Taylor & Hastings, 2005). Higher fecundity and shorter generation times are also  
1183 expected to promote faster demographic compensation and shorter recovery times after mortality  
1184 events (Capdevila et al., 2022), and thus slow down range contractions at the trailing edge in the  
1185 short term. Nonetheless, demographic collapses and range contractions may be slower to detect  
1186 in long-lived species, where older individuals may be indicative of past conditions (extinction  
1187 debt; Boisvert-Marsh et al., 2014; Pacifici et al., 2017), resulting in a negative association  
1188 between range shifts and lifespan.

1189

1190 *Ecological generalism*: Ecological generalism is expected to allow propagules to establish faster  
1191 and farther at expanding limits and further improve persistence after dispersal due to the wider  
1192 diversity of environments tolerated (Stevens et al., 2014) (Table 1). For example, tolerance to  
1193 light availability towards high latitudes and oxygen depletion towards high elevations (Jacobsen,  
1194 2020; Ljungström et al., 2021; Spence & Tingley, 2020) or acclimation to hypoxia in aquatic

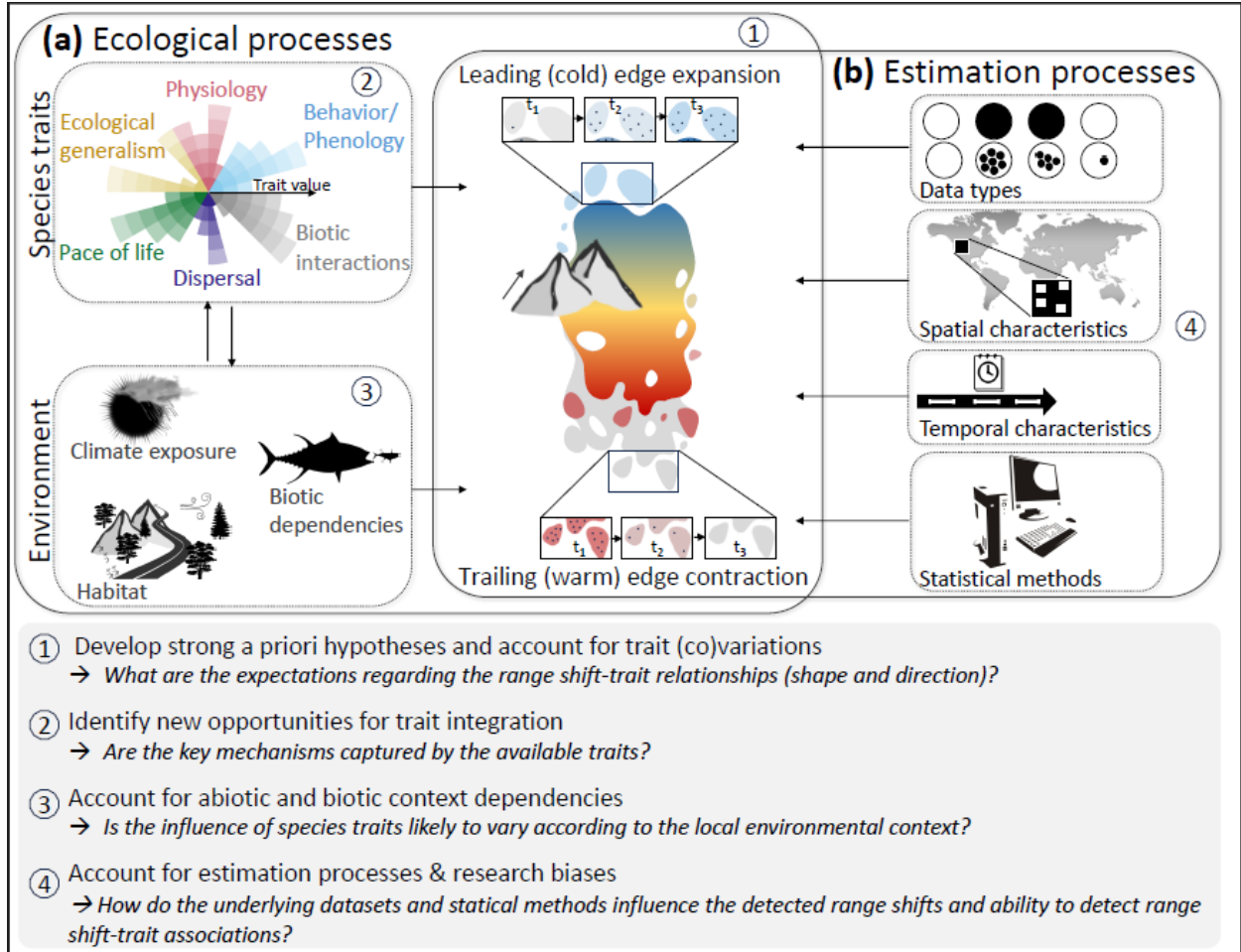
1195 systems (Souchet et al., 2020; Storz et al., 2010) may be particularly important to enable climate-  
1196 induced range expansions. Species that display a greater potential for cognitive or behavioral  
1197 flexibility may also be able to better cope with changing environmental conditions through local  
1198 shifts in microhabitat or diet, resulting in slower trailing edge contractions ('cognitive buffer  
1199 hypothesis'; Baldwin et al., 2022).

1200 **Box 3. Body size, the Swiss army knife of all traits.**

1201 Being both large and small can confer various – albeit sometimes opposite – benefits in the  
1202 context of species redistribution (Fig. 2). Large-bodied species often display higher dispersal  
1203 capacities ('allometric scaling of dispersal'; Stevens et al., 2014) and greater competitive abilities  
1204 (Goldberg, 1996), and small-bodied species higher fecundity and shorter generation times ('fast  
1205 species'; Capdevila et al., 2022) – attributes that are all expected to promote range expansion at  
1206 the leading (cold) edge under environmental change. Large-bodied species can persist longer  
1207 after habitat quality change due to their longer longevity ('extinction debt'; Boisvert-Marsh et  
1208 al., 2014), and small-bodied species typically display a lower sensitivity to heat that likely arises  
1209 from metabolic constraints (Peralta-Maraver & Rezende, 2021) and higher opportunities for  
1210 behavioral thermoregulation (von May et al., 2019) or wider range of microclimatic refugia use  
1211 (Pincebourde et al., 2021) – attributes that are all expected to hinder contraction at the trailing  
1212 (warm) edge under environmental change.

1213

1214 **Figure captions**



1215

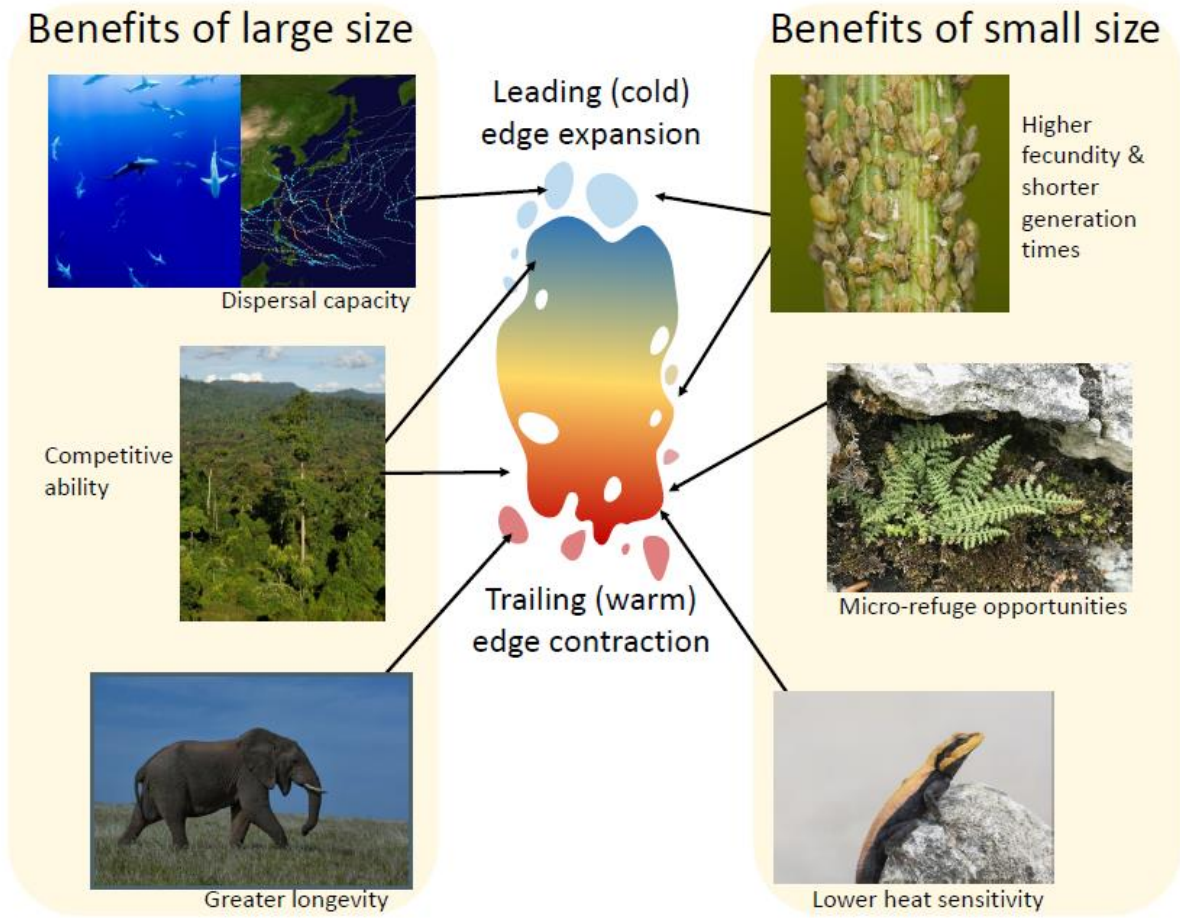
1216 **Figure 1. Set of factors and interactions that may influence the documented patterns of**  
 1217 **range shifts and suggested steps to model range shifts-trait associations.** Documented  
 1218 patterns of range shifts at the trailing (i.e., range contraction) and leading (i.e., range expansion)  
 1219 edges of species distributions are typically documented in response to anthropogenic climate  
 1220 change along spatial gradients such as latitude, elevation (on land), and depth (in the oceans) and  
 1221 reflect both (a) the ecological processes (left panel) and the (b) estimation processes (right  
 1222 panel), which involve a set of intrinsic, extrinsic and methodological factors (see Box 1).

1223 Ecological processes may involve complex interaction terms between species traits and either the

1224 abiotic or biotic context such that it suggests complex context dependencies. Numbers illustrate a  
1225 set of suggestions to improve our ability to decipher the mechanisms of range shifts.

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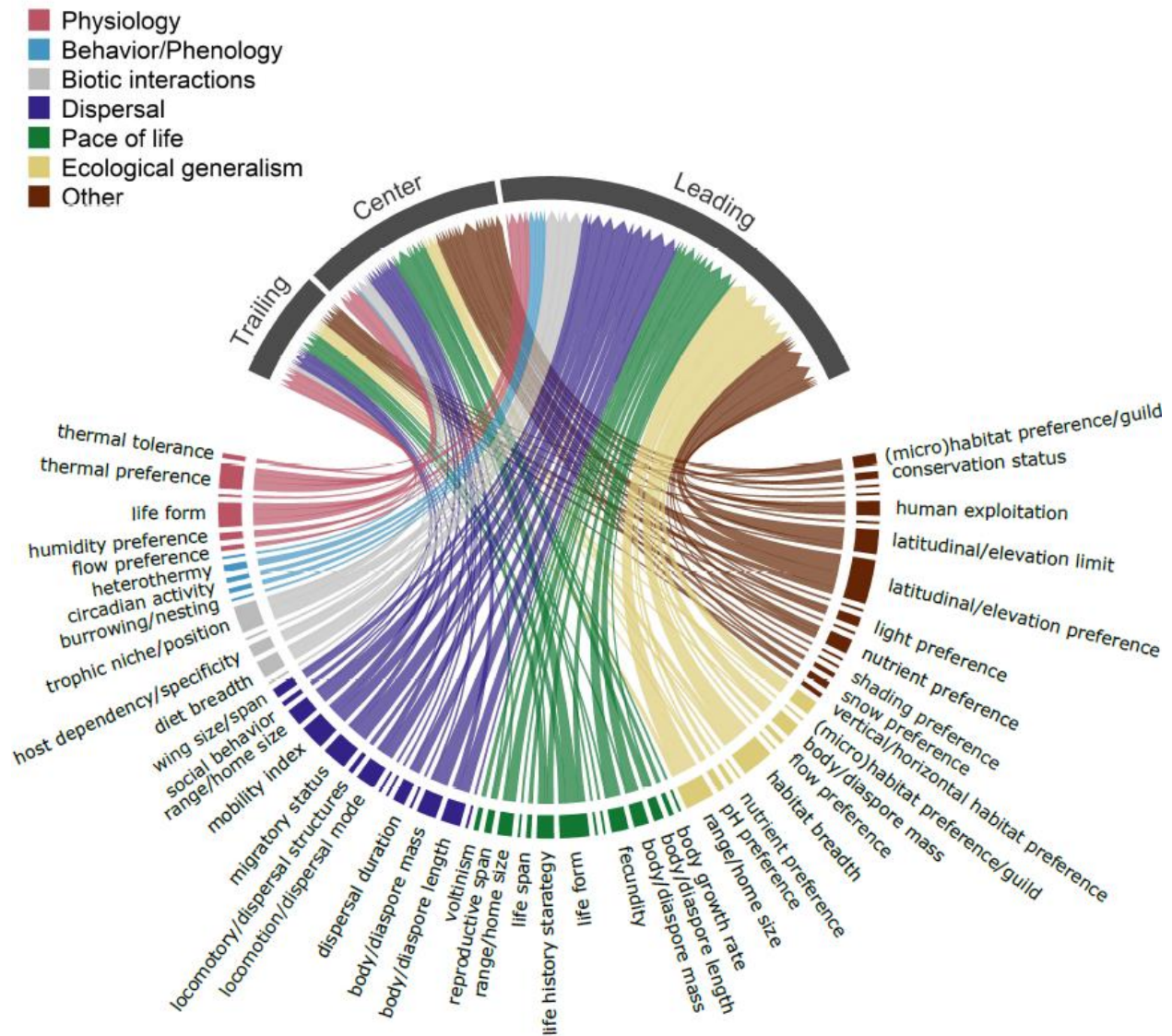
1228

1229 **Figure 2. Benefits of large versus small body size in the context of climate change-related**

1230 **range shifts.** See Box 3 for more context and Table S1 for image attribution.

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1234 **Figure 3. Synthesis of the scientific literature testing for relationships between traits and**

1235 **range shifts.** Traits (bottom) that have been used in the scientific literature to explain the

1236 documented patterns and rates of species redistribution at different range parameters (top)

1237 ( $N_{\text{articles}} = 44$ ;  $N_{\text{species}} = 9788$ ). Traits have been coded into different subcategories and classified

1238 (colors) based on the hypothesized mechanisms that were studied (see Table 1). The category

1239 ‘Other’ indicates traits used to capture the effect of extrinsic factors (e.g., exposure to climate

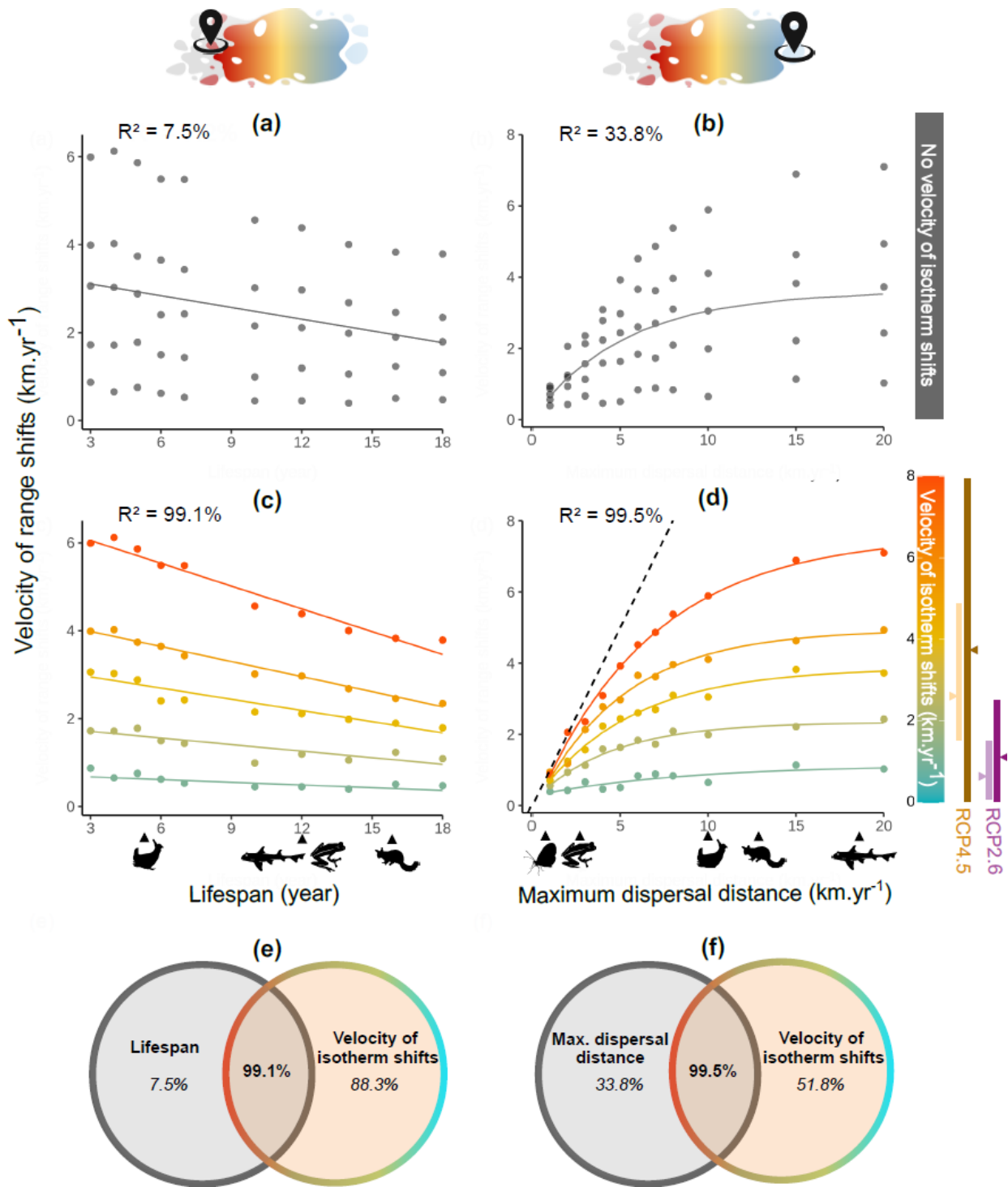
1240 change or other drivers of change) or unclear mechanisms. The thickness of the arrows denotes



1241 the number of studies that tested a particular link, where one trait can appear more than once (for  
1242 clarity only traits that have been reported in more than one study are labeled). The list of  
1243 scientific publications was identified based on the literature review performed by Beissinger &  
1244 Ridell (2021) and MacLean & Beissinger (2017). Only quantitative shifts at the species-level  
1245 were kept for this figure (i.e., range expansion or contraction at the leading and trailing edges or  
1246 center of the distribution). See Supplementary Material (Appendix S1) for plots pertaining to  
1247 kingdoms (plants vs. animals) and realms (marine, terrestrial, freshwater).

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1251 **Figure 4. Revealing the explanatory power of species traits on the velocity of range shifts**

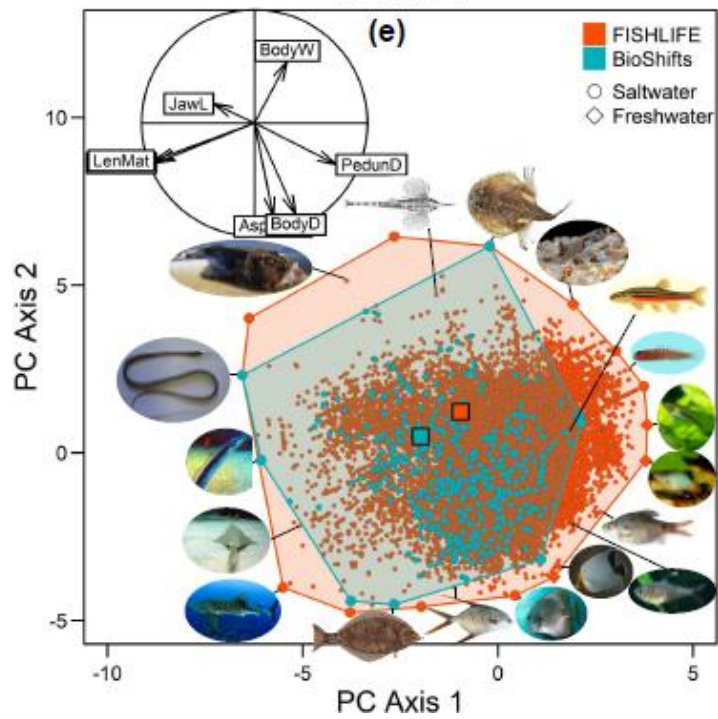
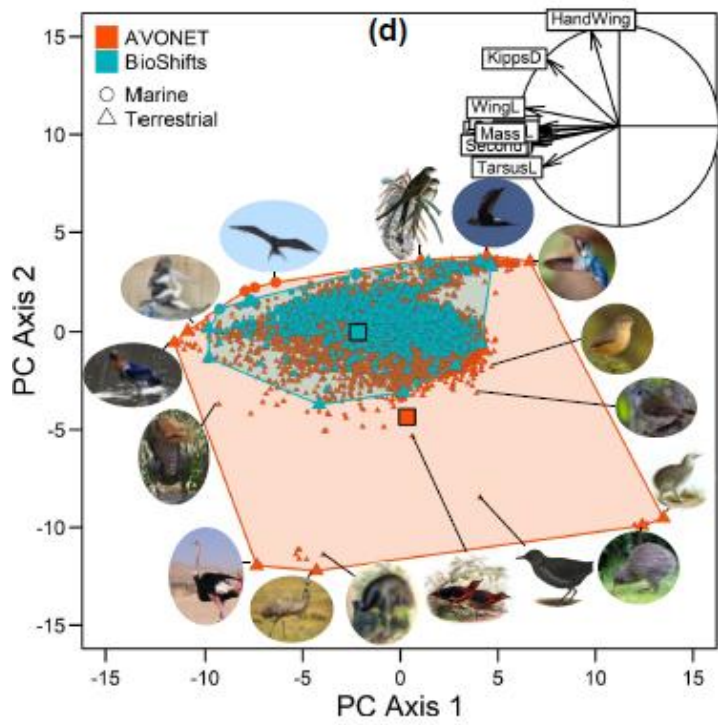
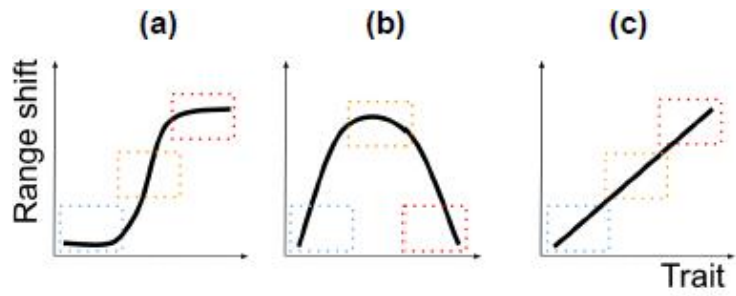
1252 **through interaction effects between species traits and climate exposure: (a,c,e) trailing edge**

1253 **contraction and (b,d,f) leading edge expansion. Dots in panels a-d are the outputs of a process-**

1254 based model used to simulate the distribution of virtual animal species defined by different  
1255 combinations of lifespan (x-axis in panels a and c) and maximal dispersal distance (x-axis in  
1256 panels b and d) under different climate warming scenarios. The curves in panels a-b are from  
1257 models fitted between the velocity of range shifts (i.e., the response variable) and species traits  
1258 (dispersal ability or lifespan) without considering the velocity of isotherm shifts, while in panels  
1259 c-d they are from models that consider the interaction between species traits and the velocity of  
1260 isotherm shifts. The color scale in panels c-d indicates the velocity of isotherm shifts used in the  
1261 simulations, with the vertical colored bars next to it illustrating the range of climate velocities  
1262 reported for different climate change Representative Concentration Pathways (purple: RCP 2.6  
1263 and brown: RCP 4.5) in the marine (light colors) and terrestrial (dark colors) realms, where the  
1264 triangles indicate the median values (according to Asamoah et al., 2021; Brito-Morales et al.,  
1265 2020; Trisos et al., 2018). The animal silhouettes in panels c-d illustrate examples of lifespans  
1266 [AnAge database: De Magalhães & Costa, 2009] and maximum dispersal distances [butterfly:  
1267 Sekar, 2012, frog: Smith & Green, 2005, common brushtail possum, horn shark and pinnated  
1268 grouse: Jenkins et al., 2007] reported in the scientific literature. (e-f) Venn diagrams  
1269 decomposing the proportion of explained variance ( $R^2$ ) between the single and interactive effects  
1270 of species traits and the velocity of isotherm shifts on the velocity of range shifts.

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1272



1274 **Figure 5. Consequences of coverage biases within the functional trait space on our**  
1275 **understanding of the relationships between range shifts and species traits.** (a-c) Hypothetical  
1276 relationships between range shifts and species traits illustrating the potential consequences of  
1277 using a truncated trait space on our understanding of the shape of these relationships. Blue and  
1278 red dashed boxes: using only a subset of species displaying extreme functional characteristics;  
1279 orange dashed box: using a subset of species with intermediate functional characteristics. (d-e)  
1280 Examples of functional trait space coverage for bird and fish species estimated based on the first  
1281 two components (PC) of a principal component analysis using morphological traits from the (d)  
1282 AVONET ( $N_{\text{bird}} = 11,109$ ; Tobias et al., 2022) and (e) FISHLIFE ( $N_{\text{fish}} = 26,622$ ; Thorson et  
1283 al., 2023) databases where the selection of species included in BioShifts (a database of range  
1284 shift estimates) are highlighted in blue ( $N_{\text{bird}} = 973$ ,  $N_{\text{fish}} = 431$ ; Comte et al., 2020). The  
1285 functional trait spaces are illustrated by the convex hulls encompassing all the species, wherein  
1286 each dot represents a species and the solid squares represent the centroids of the respective  
1287 convex hulls. The interpretation of the functional trait spaces is represented by the correlation  
1288 circles showing the covariation among the morphological traits, with pictures illustrating the  
1289 position of some selected species (see Table S1 for image attribution and Supplementary  
1290 Material Appendix S3 for details on the analysis).