UC Santa Cruz
UC Santa Cruz Previously Published Works

Title

Mechanisms, detection and impacts of species redistributions under climate change

Permalink

https://escholarship.org/uc/item/0fg9x8qt

Journal

Nature Reviews Earth & Environment, 5(5)

ISSN

Authors

Lawlor, Jake A

Comte, Lise

Grenouillet, Gaël

et al.

Publication Date

2024-05-01

DOI

Copyright Information

Peer reviewed

Mechanisms, detection and impacts of species redistributions under climate change

Jake A. Lawlor[1†], Lise Comte[2], Gaël Grenouillet[3], Jonathan Lenoir[4], J. Alex Baecher[5], R.M.W.J. Bandara[6], Romain Bertrand[3], I-Ching Chen[7], Sarah E. Diamond[8], Lesley T. Lancaster[9], Nikki Moore[1], Jerome Murienne[3], Brunno F. Oliveira[10], Gretta T Pecl[11,12], Malin L. Pinsky[13,14], Jonathan Rolland[3], Madeleine Rubenstein[15], Brett Scheffers[16], Laura M. Thompson[17], Brit van Amerom[18,19], Fabricio Villalobos[20], Sarah R. Weiskopf[15], Jennifer Sunday[1]

[1]Department of Biology, McGill University, Montreal, QC, Canada.
[2]School of Biological Sciences, Illinois State University, Normal, IL, USA.
[3]Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), UMR5300 Université Toulouse, CNRS, IRD, Toulouse INP, Université Toulouse 3 – Paul Sabatier (UT3), Toulouse, France
[4]UMR CNRS 7058, Ecologie et Dynamique des Systèmes Anthropisés (EDYSAN), Université de Picardie Jules Verne, 1 Rue des Louvels, 80000 Amiens, France.
[5]School of Natural Resources and Environment, University of Florida, Gainesville, FL, USA.
[6]Graduate Program in Ecology and Evolution, School of Environmental and Biological Sciences, Rutgers, The State University of New Jersey, 14 College Farm Road,New Brunswick, NJ, USA.
[7]Department of Life Sciences, National Cheng Kung University, Tainan, Taiwan.
[8]Department of Biology, Case Western Reserve University, Cleveland, Ohio, USA.
[9]School of Biological Sciences, University of Aberdeen, Aberdeen, UK.
[10]Fondation pour la Recherche sur la Biodiversité (FRB), Centre de Synthèse et d'Analyse sur la Biodiversité (CESAB), Montpellier, France.
[11]Centre for Marine Socioecology, University of Tasmania, Hobart, TAS, Australia.
[12]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS, Australia.
[13]Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ, USA.
[14]Department of Ecology & Evolutionary Biology, University of California Santa Cruz, Santa Cruz, CA, USA.
[15]U.S. Geological Survey National Climate Adaptation Science Center, Reston, VA, USA.
[16]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA.
[17]U.S. Geological Survey National Climate Adaptation Science Center, Knoxville, TN, USA.
[18]School of Construction and the Environment, British Columbia Institute of Technology, Burnaby, BC, Canada.
[19]Faculty of Environment, Simon Fraser University, Burnaby, BC, Canada.
[20]Red de Biología Evolutiva, Instituto de Ecología A.C., Xalapa, Mexico.

39   [†]e-mail: jake.lawlor@mail.mcgill.ca
40
41
42

Abstract

Shifts in species distributions are a common ecological response to climate change, and global temperature rise is often hypothesized as the primary driver. However, the directions and rates of distribution shifts are highly variable across species, systems and studies, complicating efforts to manage and anticipate biodiversity responses to anthropogenic change. In this Review, we summarize approaches to documenting species range shifts, discuss why observed range shifts often do not match our expectations, and explore the impacts of species range shifts on nature and society. The majority (59%) of documented range shifts are directionally consistent with climate change, based on the BioShifts database of range shift observations. However, many observed species have not shifted, or have shifted in directions opposite to temperature-based expectations. These lagging or expectation-contrary shifts might be explained by additional biotic or abiotic factors driving range shifts, including additional non-temperature climatic drivers, habitat characteristics and species interactions, which are not normally considered in range shift documentations. Understanding and managing range shifts will require increasing and connecting observational biological data, generalizing range shift patterns across systems and predicting shifts at management-relevant timescales.

[H1] Introduction

The varied geographic ranges of species are dynamic expressions of multiple factors. Abiotic conditions, such as temperature and light, are considered to set the bounds of a species' 'potential range': the set of areas where abiotic conditions do not exceed the physiological limits of population sustainability[1]. Dispersal limitations, habitat availability, and biotic factors can further limit potential ranges into 'realized ranges': subsets of environmentally suitable areas in which a species actually lives[2–4]. Although species ranges are often illustrated as single units, additional insight can be gained by conceptualizing them as disparate populations distributed across space that experience varying levels of climatic stress[5]. Because temperature conditions broadly exhibit a large-scale gradient across the globe, species' ranges typically span from a 'warm edge' (normally equatorward, downslope in elevation or shallower in water) to a 'cold edge' (normally poleward, upslope or deeper in water), between which conditions experienced by populations can vastly differ (Box 1). Although species ranges might not be directly limited by temperature at either edge and might not be at equilibrium with their environments, populations within a species' range experience different levels of temperature stress and can therefore have different or contrasting responses to temperature change[6,7].

Anthropogenic climate change is causing global temperatures to warm on average, shifting temperature isolines, or isotherms, across Earth's surface, and altering conditions that organisms experience[8]. At warm edges of species ranges, where individuals are already living near their upper range-wide temperatures, climate warming is expected to diminish populations by exceeding thermal limits for population growth or reproduction, thus contracting the range edge towards the center. By contrast, at cold edges, where individuals are living near thermal minima, climate warming can relax constraints on organisms, for example, by increasing temperatures enough for early life development[9], enabling increased survival and persistence of populations and facilitating expansion of the range edge away from the center[7,10] (Box 1). Together, these changes suggest that species will shift their distributions towards previously cooler regions as global temperatures warm, in general, occupying higher absolute latitudes, higher elevations in mountains, and deeper waters in oceans[11,12].

88

89   'Range shifts' are now recognized as common climate-driven phenomena that have varying

90   impacts on ecosystems, economies, and people[13,14], yet immense variation exists in the rates

91   and directions of range shifts observed globally[12,15–19]. Although range-shifting a mechanism by

92   which species (and biodiversity) can persist through climate change, an increasingly unstable

93   distribution of life challenges how we interact with, plan to manage, and conserve natural

94   systems. Anticipating range shifts in species of particular ecological, economic or health

95   concern will be key to successfully adapting to climate change. Moreover, species

96   redistributions and the human responses to them have been linked to a range of social equity

97   imbalances[20,21], underscoring that understanding species shifts is an important goal for a

98   sustainable future. Improved mechanistic understanding of processes driving and limiting range

99   shifts will increase our ability to respond to and learn from these changes.

100

101 In this Review, we draw together knowledge of species redistribution processes, summarize the

102 history and methods of detecting species' range shifts, and review mechanisms thought to

103 underlie variation in observed rates and directions — from ecological and evolutionary factors

104 to detection methods. We use BioShifts[22], a global database including over 26,000 empirical

105 estimates of latitudinal and elevational range shifts compiled from published literature, to

106 demonstrate general trends, knowledge gaps and observation biases in range shift

107 documentations to date. We briefly summarize the effects of range shifts on natural and

108 human systems as an update to a previous review[13]. Finally, we end by discussing areas for

109 improvement in range shift detections and three exciting avenues for future research.

110

111 **[H1] Observations of Climate-Driven Range Shifts**

112 Connections between climate and species distributions have long been documented in the

113 scientific literature[23]. Classic works by van Humboldt and Merriam hypothesized temperature

114 as a primary driver for setting and maintaining species ranges[23,24], and between 1900 and the

115 1970s, changes in species ranges in association with local periods of warming and cooling or

116 extreme weather events were frequently observed[25]. These early observations of range

117   changes shed light on when and where specific factors limit species ranges[26]. Decades later, the

118   onset of increasingly rapid and consistent global warming (for example, at increased rates

119   beginning in the early 1980s) provided a large-scale — if pseudo-replicated across Earth —

120   experiment in which to test the effects of climate conditions on species distributions in natural

121   environments[27].

122

123   The first contemporary observations of climate-driven range shifts were probably made in a

124   non-scientific context; for example, by fur trappers, fishers, or people with close economic or

125   cultural connections to species. In some cases, information from these sources, such as fur

126   trade figures and traditional ecological knowledge, has been used to reconstruct species'

127   historical ranges in large-scale biogeography studies[28–30]. Range shifts attributed to

128   anthropogenic climate change were first widely documented in the 1990s. These observations

129   included changes in species distributions near range edges, shifts in thermal affinities among

130   community members at static locations, inferences based on changing biogeographic

131   patterns[29,31,32], and eventually whole ranges shifting in response to climate change[11]. Since

132   then, range shifts have been observed across many taxa and environments[15,19,22,27], emerging as

133   a widespread ecological response to climate change.

134

135   **[H2] Measuring climate-driven range shifts**

136   Estimating species range shifts in response to climate change over time is difficult, because

137   observing these changes requires knowledge of species' current and historical distributions as

138   well as, ideally, climate variables over the relevant time period. In some exceptionally data-rich

139   taxa and regions, range shifts can be estimated with relative precision by analyzing

140   systematically monitored data of species occurrences and/or abundances from sources such as

141   National Oceanic and Atmospheric Administration fish trawls[33,34], Breeding Bird Surveys [35], and

142   the UK Butterfly Monitoring Scheme[36]. However, observational data of species distributions at

143   large spatial and temporal scales are not always available.

144

145 In the absence of high-resolution time series data, other methods can be used to infer species

146 range movements. When survey data are available for the present but not in the past, natural

147 history records and museum collections can be used to reconstruct past species ranges to

148 estimate distributional shifts[37,38]. When species range survey data are available for the past

149 only, conducting targeted re-surveys in the same regions years to decades later is a relatively

150 common method for assessing distribution changes[39,40]. For cases in which data are available

151 over broad temporal, but not spatial scales, assessing change in biogeographic communities at

152 fixed locations can show relative abundance changes as 'cross-sections' of shifting species

153 ranges[31,41]. Conversely, when data are available at broad spatial, but not temporal scales,

154 comparing distributions of life stages of organisms at one point in time (for example, seedlings

155 versus adult trees[42–44]) can reveal distributional changes in new versus old growth. Finally,

156 emerging techniques such as telemetry[45] and citizen science observations provide new

157 methods to help to detect range shifts[46,47]. These various methods have enabled rapid

158 documentation of biogeographic change across regions and systems and together have

159 identified range shifts as a relatively ubiquitous 'fingerprint' of climate change[12,48], however,

160 variation among methods has caused difficulty in synthesizing and comparing studies globally.

161

162 **[H2] Locations of range shift study**

163 Although range shifts have been documented across continents and ecosystems, reported

164 observations are highly geographically skewed towards Europe and North America[15,49]. Indeed,

165 among the over 26,000 latitudinal and elevational range shift estimates collated in the BioShifts

166 database[22], more studies have been conducted and more species' ranges assessed per study in

167 Europe and North America than in other continents (Fig. 1a,b), although the focus of this

168 database on English-language papers could contribute to this bias[50,51]. Observations are also

169 biased taxonomically, as most range shift observations are documented among terrestrial

170 arthropods (including freshwater), vascular plants, and birds (Fig. 1a). Of all latitudinal and

171 elevational range shifts included in the database, 84% are from these three taxonomic groups

172 and are measured in Europe or North America (Fig. 1a), lending a disproportionate amount of

173 our knowledge of range shift directions and speeds to a limited set of species and locations.

174

175   Range shifts are most often assessed over latitudinal gradients on land, latitudinal gradients in

176   the ocean, or elevation gradients in montane systems, but estimation effort has been unequal

177   across these three groups. The vast majority of estimates have been made in terrestrial systems

178   — fewer than 5% of all shifts estimated in the BioShifts database are in marine systems, while

179   terrestrial shifts across latitude and elevation are more well-represented (44% and 51% of all

180   estimates in BioShifts, respectively) (Fig 1b, 2). Because species in these three ecological

181   gradients interact differently with their environments, insight gained by synthesizing shifts

182   within these groups likely has limited applicability to generalizing between them. Furthermore,

183   freshwater species could respond differently to climate change than their fully terrestrial

184   counterparts; however, the distinguishing between terrestrial and freshwater species can be

185   difficult since many terrestrial species rely on freshwater environments for certain life stages or

186   behaviors but are not necessarily bound to them for movement. For this reason, all species that

187   live all or part of their life cycle in freshwater are considered terrestrial in the BioShifts

188   database and throughout this review, but further distinguishing freshwater from terrestrial

189   species could be beneficial in future research.

190

191   Within species ranges, range shift estimates are made far more rarely at warm range edges

192   than at cold edges or range centers (11%, 41%, and 48% of all shift estimates, respectively) (Fig

193   2). This bias might limit our understanding of mechanisms, since the processes driving range

194   changes are expected to differ between sections of a range[7]. Assessments of range shifts

195   encompassing both range edges within single studies are exceptionally rare — for example,

196   accounting for only 2% of range shift estimates in Australia[52] — and the vast majority of our

197   observations capture only glimpses of full-range responses to climate change.

198

199   **[H2] General findings on range shifts**

200   The directions of collated latitudinal and elevational range shift estimates in the BioShifts

201   database are remarkably variable. Within the database, most range shift estimates (59% of all

202   estimates) are in the direction expected based on local temperature change (here defined as

203   the direction of isotherm shifts over time in the study region). However, a high proportion of

204   shift estimates (35%) are in the opposite direction to expected (opposite to the direction of

205   local isotherm shifts; Fig. 2), and a portion (6%) of species were not found to shift at all. These

206   tallies of raw change in range position over time do not take into account uncertainty or

207   distance of range shifts, and make null shifts methodologically unlikely to detect; nevertheless,

208   even in this coarse tally, the proportion of estimates matching the direction of temperature

209   change is greater than those opposing temperature change in all gradients and range sections

210   (Fig. 2).

211

212   Along both latitudinal and elevational gradients, shifts at the cold edge and range center are

213   more often directionally consistent with climate expectations than shifts at the warm edge (Fig.

214   2). Although fewer shift estimates have been made at warm edges in general (Fig 2), and

215   extinction processes are more difficult to detect than range expansion[53], the greater

216   inconsistency of range shifts with temperature shifts at warm edges compared to cold edges

217   could indicate that extirpation processes adhere less closely to temperature change than range

218   expansion processes perhaps owing to factors including long life histories or compensatory

219   processes[54,55], although empirical evidence has not yet been able to support this hypothesis[56].

220

221   The magnitudes of range shifts display further consistencies with climate warming. Despite

222   wide variation between individual range shift magnitudes, in general, range shifts have

223   occurred faster in regions with higher rates of climate warming than in regions with lower

224   rates[16,17,57]. Although a basic tabulation indicates that marine species range shifts show less

225   directional consistency with climate change than terrestrial species (Fig 2), an analysis of range

226   shift velocities that accounted for methodological variation and non-random taxonomic

227   sampling found that marine species adhere to isotherm shifts more closely than terrestrial

228   species, and shift more than five times faster on average in the poleward direction (5.9 ± 0.9

229   km.yr^{-1} for marine vs 1.1 ± 1.0 km.yr^{-1} for terrestrial)[15]. These patterns might be related to the

230   tighter thermal niche 'filling' of marine organisms[58], the relative unavailability of microclimate

231   refugia in marine habitats[59], the relative lack of human-created barriers in the ocean[60] and the

232 faster climate velocities in marine habitats than on land[8], and suggest climate and non-climatic

233 mechanisms for slower or delayed range shifts on land.

234

235 Despite these generalized global patterns of species redistributions showing consistency with

236 climate warming, a substantial portion of range shift estimations do not match the rate or even

237 direction expected from temperature shifts alone[15,18,49,61]. The proportion of estimates

238 consistent with the direction of temperature change across all realms is not overwhelmingly

239 high (59%) (Fig 2), and some range shift estimates vary in rate by an order of magnitude from

240 their corresponding temperature shifts[16,19]. Although some of these inconsistencies could result

241 from methodological limitations or random variation[18], others might be due to ecological

242 processes that affect species ranges over and above temperature. Identifying these non-

243 intuitive responses could be especially valuable to improving our understanding of factors that

244 limit and alter species distributions.

245

246 **[H1] Why observations deviate from expectations**

247 Several potential mechanisms could explain why species ranges don't keep pace with changing

248 isotherms, and why 'naïve' isotherm-tracking hypotheses might be insufficient for

249 understanding and predicting species redistributions. These mechanisms can be classified into

250 three categories: climate drivers other than (average) temperature; non-climatic drivers of

251 species ranges; and low signal to noise in range shift detections.

252

253 **[H2] Climate drivers other than (average) temperature**

254 There are multiple approaches to deriving climate-based expectations of the direction and

255 velocity of species shifts, and mismatches in scale between predictions and observations can be

256 influential. In some cases, range shift expectations are derived from broad hypotheses based on

257 global-scale temperature patterns, in which species are expected to move towards higher

258 latitudes, higher elevations and deeper waters without explicit consideration of the actual

259 climate gradient in the study region[27,48]. These global-scale expectations can misrepresent local-

260 scale changes experienced by organisms, since microclimates and climate refugia can misalign

261 local gradients with global gradients; in other words, local isotherms might not be shifting

262 polewards or upslope[17,62,63]. Omission of local processes in favor of global-scale expectations

263 can increase the proportion of detections that appear to defy expectations[49]. However,

264 methods for including micro-scale changes are being developed[64,65] and data to do so are

265 increasingly available[62,66,67]. These advances can even allow for *a posteriori* reassessment of

266 range shift studies[68]; for example, when local isotherm velocities were calculated for range

267 shifts in the BioShifts database[15] following methods for calculating climate velocity from [8],

268 isotherm velocities in approximately 2% of elevational study areas and 5% of latitudinal study

269 areas were in directions opposite to global gradients (that is, downslope or equatorwards). If

270 species perfectly tracked temperature changes and only global gradients were used to form

271 expectations, situations like these would manifest as expectation-contrary shifts.

272

273 Even at relevant spatial scales, temperature is not the only climatic variable limiting species

274 ranges. Because different climate variables can show contrasting patterns of change through

275 time[69], a species might show shifts contrary to temperature-based expectations if it is

276 responding to changes in an abiotic dimension other than temperature. For example, some

277 species shifts have more closely tracked changes in precipitation or water balance than

278 temperature, even when those environmental changes are directionally misaligned with

279 temperature shifts[70,71]. In other cases, species range shifts have been more closely correlated

280 with niche-tracking (over multiple abiotic dimensions) than isotherm-tracking alone[72,73]. Still,

281 non-temperature variables are rarely incorporated when forming expectations of climate-

282 driven range shifts, and likely explain a portion of the temperature-contrary shifts seen in global

283 estimates. Moreover, constraints imposed by abiotic gradients that are not changing with

284 climate change can be important[74]. For example, day length can constrain photosynthetic

285 processes of plants and corals from shifting across latitudes[75,76], and atmospheric pressure and

286 oxygen availability can constrain animals from shifting up elevations[74,77]. Interactions between

287 variables and warming might also lead to expectation-contrary shifts, such as the link between

288 temperature and oxygen demand driving oxygen-supply limitations downslope on warming

289 mountains[77] or offshore in marine coastal systems[78].

290

291 Even for cases in which temperature is the primary driver of species' responses and the variable

292 forming expectations, the chosen metric of temperature (for example, annual mean, annual

293 max or number of days over temperature threshold) might not best represent the limiting

294 factor for the species. Temperature extremes, growing degree days, duration of summer, or

295 temperature-related landscape variables such as spring snow cover can variably be more direct

296 drivers of ecological responses to climate change than long-term averages[79–81]. Any of these

297 variables can affect species differently throughout their life histories, rendering average

298 temperature a coarse predictor of species responses[82]. Temperature anomalies that are not

299 resolutely captured by average trends can also acutely affect species over and above long-term

300 changes. For instance, marine heatwaves over the past decade have exacerbated poleward

301 range shifts in shallow reef species in addition to gradual change through time[83]. Long-term

302 temperature averages might therefore serve as a useful proxy to capture species responses to

303 many correlated temperature variables in large-scale studies, but might not drive responses of

304 individual species.

305

306 **[H2] Non-climatic drivers of species ranges**

307 Species can be excluded from portions of their climatically suitable niches for many reasons,

308 and the extent to which species' ranges are in equilibrium with their environments can affect

309 the predictability of their responses to climate change[58,84]. Limitations indirectly or completely

310 unrelated to climate change can pose constraints on species' realized ranges (Fig 3) and result

311 in ranges tat display inertia or climate-change-contrary shifts. Non-climatic range-limiting

312 factors can be classified into four categories — habitat limitations, dispersal constraints, biotic

313 interactions, and contemporary evolution — and each can alter leading or trailing range shift

314 rates against temperature-based expectations.

315

316 *[H3] Habitat Limitations*

317 Habitat limitations caused by fragmentation, geographic barriers and human activity can either

318 prevent or facilitate range shifts. Geographic barriers such as mountain ranges, valleys and

319 coastlines can present obstacles for range-shifting species, regardless of climatic suitability

320 beyond these barriers[39]. For species that are bound to geographically constrained habitats such

321 as rivers, coastlines, or alpine environments (i.e. 'sky islands'), landscape connectivity can be far

322 more influential than climate in determining distribution ranges[85]. Constrained species ranges

323 can result in overall range reductions in response to climate change if ranges are able to

324 contract at one edge but cannot expand past geographic barriers at the other[39]. When habitat

325 availability does not align with latitudes, elevations, or climatic gradients over which range

326 shifts are expected, species might be unable to keep pace with shifting isotherms (for example,

327 fish in an east-to-west river are unable to migrate north)[86] and thus might exhibit little or no

328 range shifts in the directions expected as a result of climate change.

329

330 Even when a habitat generally extends in the direction of climate velocity, habitat

331 fragmentation and land use change can inhibit range expansions at the cold edge or amplify

332 range contractions at the warm edge[87–89] (Fig. 3b). Human activity such as forest clearing can

333 change the overall permeability of landscapes, which can slow or stop range shifts of forest

334 species through cleared areas[90,91]; landscapes with higher conductance are more quickly shifted

335 across than fragmented landscapes[92]. Alternatively, conserving habitat through establishing

336 protected areas can facilitate species range shifts compared with surrounding areas[93] (Fig. 3b).

337 By contrast, for species that specialize in human-modified landscapes (such as, farmland-

338 associated birds or mussels on man-made offshore structures), human modifications might

339 represent increased connectivity and actually facilitate range shifts[94,95]. Some projections of

340 climate-driven range shifts account for geographic barriers by including landscape connectivity

341 in models or projecting range-shift corridors[96,97], but such considerations are normally not

342 addressed in range shift detections and might present as unexplained lags or advances with

343 climate tracking.

344

345 *[H3] Dispersal Constraints*

346 Climatically suitable areas unobstructed by physical barriers can remain inaccessible to species

347 that lack a mode of dispersal to reach them, thus slowing range shifts from temperature-based

348   expectations. Dispersal of sessile or slow-moving species such as benthic marine invertebrates

349   and wind-dispersing plants relies on external directional forces (ocean currents or prevailing

350   wind directions), and these forces can be misaligned with the direction of isotherm shifts (Fig.

351   3b). Misaligned dispersal processes can impede species from tracking changing environments,

352   particularly at the leading edge[98,99]. Animal-assisted dispersal can also impede range shifts of

353   seed-bearing plants as animal vectors do not always disperse in the direction of climate

354   shifts[100,101]. Among actively dispersing organisms, such as most terrestrial vertebrates, dispersal

355   abilities can vastly differ, in some cases limiting species' ability to track environmental change[91].

356   In addition, when few dispersers exist, Allee effects and inbreeding depression can limit the

357   success of early arrivals, leading to lags between species responses and climate shifts[102].

358

359   The role of dispersal ability is typically assessed using various proximal traits such as body size

360   and reproductive mode[103–106]. Although strong relationships between these traits and range

361   shift rates are not commonly found, these expectation-contrary results could be a greater

362   reflection of inadequate estimates of dispersal ability (in which proxies can perform poorly)

363   than a true absence of effect[107]. Dispersal and species traits and their relation to range shifts

364   are reviewed in further detail elsewhere[105,107].

365

366   *[H3] Biotic interactions*

367   Biotic interactions can affect a species' ability to redistribute under climate change, causing lags

368   or unexpected range shifts relative to climate expectations. Species interactions are expected

369   to affect leading and trailing range edges differently according to whether they are positive

370   (such as food, mutualism or commensalism) or antagonistic (such as predation, parasitism or

371   competition)[108].

372

373   Positive interactions can result in reduced or delayed range shifts at either range edge. At the

374   leading edge, a species might be unable to shift in response to climate change if its distribution

375   is bound through an obligate positive interaction with another species (for example, a specific

376   habitat, host, or food resource species) that cannot expand at the same pace. Such limitations

13

377 have been demonstrated in butterflies shifting up mountain slopes being limited by

378 distributions of host plants which are shifting at a slower rate[109,110]. At the trailing edge,

379 positive interactions such as fungal mutualists on plant roots can broaden the environmental

380 tolerance of the interacting species such that populations with mutualists contract more slowly

381 than populations without mutualists in response to environmental change[111,112]. Positive

382 interactions can also manifest as a direct alteration of climate conditions, such as when desert

383 plants create microclimates for associated species; these can appear to alter the rate of climate

384 responses, particularly when expectations are built on macro-level climate patterns that don't

385 capture the microclimate conditions experienced by organisms.

386

387 Antagonistic interactions can lead to slower range shifts than expected. If a species has a

388 trailing edge limited by antagonistic interactions (but not by climate), the trailing edge shift of

389 the focal species could be driven by the speed of the leading edge shift of the antagonistic

390 species, which, depending on the climate-tracking ability of the antagonistic species and the

391 time-course of the interaction, might be slower than that expected as a result of climate

392 change[29,113–115]. The reverse is also possible, in which a species' leading edge is limited by an

393 antagonistic species' trailing edge that is not (or is slowly) responding to climate change. This

394 phenomenon has been observed in intertidal habitats in which mussels and barnacles shifting

395 towards deeper, cooler waters have their leading edge (the deeper edge) limited by the

396 presence of sea star predators[116]. In this scenario, the sea stars' trailing edge (the shallower

397 edge) is determined by a non-temperature constraint (high-tide desiccation stress), which is not

398 responding to warming, and therefore the edge remains stable in response to warming while

399 mussels and barnacles attempt to shift.

400

401 In some cases, climate-consistent shifts of one species could lead to climate-contrary shifts of

402 an interacting species. For example, if two competing species had overlapping ranges, but only

403 one was sensitive and responded to temperature change, warming could lead to an expected

404 range shift in one species and an increase in abundance near the warm range edge of the other

405 species (where the competitor vacated)[117]. This scenario, and many of those previously

406 mentioned, hinges on differences in the climate responsiveness of interacting species, the

407 frequency of which is plausibly high but generally unknown. Methods to model distributions of

408 interacting species are becoming increasingly common and might be able to disentangle some

409 of these nuances[118–120].

410

411 Although mechanisms by which biotic interactions alter range shift rates compared to climate

412 expectations have been theorized[121], they are difficult to observe. In these examples, species-

413 interaction-driven range shifts (or lack thereof) were identified through careful natural history

414 observations and/or directed research. However, most large-scale range shift studies assess

415 many species' ranges at once and typically lack the context of species-specific climate

416 tolerances or community interaction webs. Without independent knowledge of species'

417 interactions, these examples could have presented as species responding in unexpected ways

418 to climate change driven by unrecognized underlying mechanisms. Thus, unidentified biotic

419 mechanisms are likely responsible for a portion of the expectation-contrary shifts that have

420 been documented.

421

422 *[H3] Contemporary evolution*

423 Contemporary evolution can affect the rate of species range shifts in response to climate

424 change[122–124], although a full summary of the theoretical directions and mechanisms is beyond

425 the scope of this review. Briefly, evolution of dispersal ability can increase the rate of range

426 expansions if previously unsuitable areas become suitable beyond the species range[125,126], just

427 as evolution of any trait that alters the role of range-limiting factors (desiccation resistance,

428 species interactions, heat tolerance) can affect the response of ranges away from

429 expectations[127,128]. The challenge of invoking trait or niche evolution during range shifts is

430 explaining why these traits would evolve more readily during a range shift when they could

431 have been under selection in previous climatically-stable periods[129], that is, ultimately

432 understanding the limits to niche width evolution at all range edges.

433

434 **[H2] Low signal to noise in range shift detections**

435 Methodological differences can greatly influence estimates of range shifts from empirical data.

436 Two separate syntheses of species range shifts have made similar conclusions that

437 methodological factors are better predictors of estimated range shift rates than ecological traits

438 or climate variables[15,18]. As range shift detections often rely on sparse or opportunistically

439 collected data, researchers often have little choice in methodology applied within individual

440 studies. This range of methodologies adds noise that can impede our ability to detect

441 meaningful signals of change or draw synthetic conclusions between systems[18]. As species

442 ranges are naturally variable from year to year[7], and are themselves observed imperfectly[53,130],

443 low sampling frequency or spatial coverage can result in estimates that misrepresent or are

444 even contrary to long-term trends[33].

445

446 High noise in range shift estimates can be expected when the temporal extent of a study is

447 small (that is, a short total duration of observations). Even if the pace of climate change has

448 been fast within this time frame, life-history constraints and stochasticity likely affect range

449 edges in the short term. Therefore, time can be required for robust changes to be detected at

450 range edges. Indeed, both latitudinal and elevational shifts of range edges from the BioShifts

451 database show patterns of high variability around the temperature-based expectation in short-

452 duration studies. Variability around temperature-based expectations diminishes towards zero

453 (matching expectations) as study duration increases (Fig. 4), suggesting that, at least among

454 long-term studies, temperature is a main direct or indirect driver of range shifts. This trend is

455 promising but unfortunate, as reconstructing high-resolution biogeography information for the

456 past to increase study duration is difficult, leaving few avenues for long-term studies except the

457 continued monitoring of biodiversity into the future. Nevertheless, these findings lend support

458 to the value of reassessing documented range shifts in cases where sampling can be continued

459 after an initial study is completed.

460

461 Related to the role of time, estimates made from too few observations can carry both process

462 and sampling error, affecting their accuracy. Range edges are particularly prone to low-accuracy

463   shift estimates based on the likelihood of both types of error. Process error can greatly

464   influence range edge identifications when stochastic events and idiosyncratic biological

465   processes vary their positions from year to year (for example, higher than normal wind

466   dispersal in some years). Moreover, as edges normally contain lower population densities of

467   focal species[131], position estimates can be substantially affected by sampling effort such that

468   low sampling can add noise to already variable range edges[130]. Although studies with many

469   observations of range edge positions through time might be able to cut through this error to

470   detect biological signal, those with sparse data will likely be confounded by these issues to

471   some extent.

472

473   Statistical limitations can further complicate range shift detections and are often unaddressed

474   in range shift detection studies[132]. For example, when range edge estimates are expected to be

475   variable across observations (either because of natural range edge variability or observer error),

476   the 'regression towards the mean' effect can lead to an apparent range shift in which an

477   estimated range edge is shifted towards the location of the true range edge (the expected

478   sample mean), even in the absence of a true biological change[133,134]. In addition, because

479   sampling of species range position occurs over a finite sampling domain (for example, transects

480   up mountains or across latitudes), range shifts that surpass the domain will necessarily be

481   underestimated. Unless removed from the study, these 'observation domain crossers' will lead

482   to predictable correlations between the starting range edge relative to the domain edge and

483   the magnitude of the detected shift[133]. Despite these potential sources of error, fewer than 2%

484   of range shift detections are tested against null models[132], resulting in an inability to distinguish

485   whether range shift detections differ from range shifts due to chance alone.

486

487   Detecting range edge shifts based on the furthest occurrence of a species at only two points in

488   time without comparison to a null model is one situation in which noise might particularly

489   outweigh biological signal. Yet due to understandable limitations in data availability, such

490   scenarios are quite common; of the latitudinal range shifts in the BioShifts database, 10% of

491   cold edge and 20% of warm edge estimates used furthest-occurrence detections to establish

492   range edge positions (see Box 2), and two syntheses of range shift estimates reported that 38%

493   and 85% of range shift estimates were made using two time-point data[18,22]. Various approaches

494   can be taken to reduce the influence of these sources of noise when comparing range positions

495   between few time periods or with sparse data[38,135]. Common strategies include aggregating

496   observations across multiple years to reduce the influence of natural variation and observer

497   bias, accounting for sampling effort and detectability in occupancy models, and aggregating

498   error-prone shifts across multiple species to form an understanding of community shift rate

499   among noisy individual estimates. Future work should consider estimating error in range edge

500   detections, including meta-analytic methods and null models that account for variation in

501   precision among studies.

502

503   **[H1] Impacts on natural and human systems**

504   Range shifts and their cascading effects will lead to both positive and negative outcomes for

505   species, ecosystems, and people. Range-shifting towards suitable habitats is an adaptation that

506   enables persistence in the face of ongoing climate change. Therefore, climate-driven leading-

507   edge shifts have broadly positive effects for individual species and for maintaining biodiversity

508   at large. Yet, rapid changes in species ranges have led to corresponding needs for adaptation in

509   natural and human systems that were established under previously stable conditions. Among

510   social–ecological coupled systems, range shifts are expected to have an increased impact on

511   those that lack the financial or political capacity to quickly adapt[20,21], creating possible equity

512   imbalances that should be addressed in future research.

513

514   Species shifting into new areas at their leading edges occupy a unique position in science, policy

515   and management. Although climate-induced shifts of species' 'native' ranges fundamentally

516   differ from the spread of invasive alien species, existing policies are not consistently or

517   decidedly equipped to manage them. Owing to the vast potential impacts of newly arriving

518   species, understanding and predicting range shifts has been increasingly prioritized by

519   governmental research agencies[136–138] and the perception of these species by resource

520   managers has varied from new exploitable resources to dangerous invaders[139,140]. Range-

521   shifting species have already had major cascading effects on ecosystems and people[13] although

522   future projections of their impacts is beyond the focus of this review.

523

524   **[H2] Impacts on Natural Ecosystems**

525   Redistributions of species can lead to changes in community composition and dynamics or

526   otherwise alter natural ecosystems, and leading edge shifts, wherein species enter new

527   environments, can have effects akin to those caused by non-native biological invasions[14,115].

528   Range shifts of multiple species in a region can result in cold-adapted species being replaced by

529   warm-adapted species, referred to as 'thermophilization', thus altering the historical structure

530   and function of the community[141–145]. Despite changes in distributions of individual species, the

531   ecosystem as a whole might maintain function if species lost due to range shifts are functionally

532   replaced by species entering, or if species change their functional contributions as communities

533   change[146]. Range shifts can also lead to loss of specialist species in favor of generalists,

534   potentially reducing biodiversity at regional scales[147,148]. The magnitude and rate of

535   thermophilization can vary between taxonomic groups, biogeographic contexts, or species

536   traits related to persistence and mobility[145], but changes in thermal affinities of communities

537   tend to lag behind climate warming in general[41,149], possibly leading to changes in the stability

538   of communities as they become increasingly out of sync with their environments.

539

540   Some species range shifts can have disproportionate impacts on natural ecosystems, such as

541   changes in habitat-forming foundation species or species that interact with them. For example,

542   the barren-forming urchin, *Centrostephanus rodgersii*, has exhibited a poleward expansion

543   along the south-eastern coast of Australia in the past 4-5 decades, leading to overgrazing of

544   large areas of kelp forests and removing key habitat for kelp-associated species including those

545   comprising major fisheries exports of the region[150–153]. Alternatively, global mangrove species

546   have exhibited poleward shifts between historical distributions (1950-1990) and present

547   distributions (1991-2019)[154] that could disproportionately change the composition of

548   communities in areas in which they have established, given that mangroves provide essential

549   habitat for a wide range of species[155]. Shifts of species that shape their environments can open

550   niche spaces and promote shifts of other species, resulting in increased species richness or

551   phase changes to new ecological communities[144,156].

552

553   **[H2] Impacts on Humans**

554   Climate-mediated shifts in species distributions can have direct consequences for human

555   communities, affecting the economic and cultural systems with which they are connected.

556   Shifting ranges of food species can lead to positive or negative outcomes for human

557   communities, and require adaptation in order to begin harvesting and managing newly-arrived

558   species or transition away from reliance on outward-bound species. For example, distributional

559   shifts of commercially important fisheries species have created opportunities to open

560   commercial and recreational fisheries as new species arrive in some locations[157], but have

561   reduced fishing employment[158] and necessitated increased travel for harvesting as target

562   species shift in other locations[159]. Similarly, crop harvest areas have shifted ranges since the

563   1970s[160], leading to economic opportunities in areas that have become more favorable and

564   necessity for adaptation in places that have become less favorable; crop pests and pathogens

565   have also shifted, changing the spatial distribution of some food security threats[161].

566

567   The effects of species redistributions on human cultural systems can be considerable. For

568   indigenous communities, species range shifts can threaten the abundance of culturally

569   important resources[157], access to traditional foods[162], and traditional knowledge systems built

570   around natural ecosystems[20,162]. Range shifts can also occur in species emblematic of the places

571   where they were historically found[163], potentially altering societal connections with local

572   ecosystems.

573

574   Species range shifts can also present threats for human health. Documented range shifts of

575   disease-vector species owing to climate change have resulted in spatial changes to health risks

576   for human communities. Malaria-vector mosquitoes in Africa have shifted upslope by

577   approximately 6.5 m per year and poleward by about 4.7 km per year since the late 1800s[164].

578   Similar shifts of mosquitos and other disease-bearing species such as ticks and bats have been

579   documented around the world[165–167] and are expected to continue in the future[168,169]. Ciguatera

580   poisoning, caused by eating certain types of reef fish found typically in warm tropical water, has

581   expanded geographically since 2000 as warm-water fish shift polewards along the east

582   Australian coast[170]. Public-health-relevant range shifts have direct implications for human

583   wellbeing, introducing regions and human populations to risks for which they are historically

584   not prepared and requiring preparation from healthcare systems to manage these risks.

585   Meanwhile, range shifts of disease-bearing species could theoretically relieve human

586   populations from diseases that have historically been prevalent as trailing edges of their ranges

587   contract upslope or away from the equator. Some such cases have been observed[171], and

588   others are predicted in coming decades[168,172]. In addition to direct range shifts of diseases and

589   their established vectors, novel species interactions from range shifts are one factor leading to

590   an increase in risk of zoonotic spillover of pandemic-causing viruses, and a majority of these

591   novel interactions to come in the next century might have already occurred[173].

592

593   **[H2] Impacts on resource management and conservation**

594   Most conservation decision-making processes have been built around assumptions of relative

595   stationarity – that is, assuming current ranges will persist into the future[139]. The global

596   redistribution of species in response to climate change breaks this assumption, and

597   management actions (including land acquisition, habitat management and direct population

598   management) will need to incorporate projected impacts of range shifts in order to achieve

599   optimal or workable outcomes. Protected areas, for example, have been useful tools for

600   preserving biodiversity, abundance and assemblage structure[174], but risk losing their

601   effectiveness (depending on their stated goals) when species shift away and new species

602   enter[175,176]. In anticipation of species range shifts, conservation managers have needed to re-

603   evaluate their goals and adapt their strategies to preserve biodiversity into the future.

604

605   One approach to conservation management that aims to address anticipated range shifts

606   involves supplementing permanent protective measures with temporary efforts as needed,

607   effectively increasing connectivity where existing protective networks are insufficient[177]. This

608 strategy has been implemented in marine environments by adding temporary protective

609 measures to increase connectivity between permanent sites or to protect new marginal

610 populations[178], adapting protected areas to shift over time in accordance with gradual shifting

611 of species[179], designing protected areas as stepping stones across climatic gradients[180], and

612 streaming low-latency ("real-time") data to project species distributions and guide harvesting

613 and management[181,182]. Although less common in terrestrial settings, similar dynamic

614 conservation goals have been achieved by implementing short-term conservation areas for

615 migratory species through 'rentals' of private land[183,184]. Despite the stated fundamental

616 objectives of most conservation programs appearing to be at odds with time-limited protected

617 status, combining temporary conservation areas with traditional permanent protected areas

618 might help to maximize conservation benefit with limited funds.

619

620 A related strategy is targeting establishment of new protective measures within 'climate

621 corridors' in which species range shifts are likely to occur. For example, The Nature

622 Conservancy (USA) implemented the Cumberland Forest Project in 2019[185] — one of its largest

623 land acquisition projects to date — specifically intended to protect key 'climate escape routes'

624 for range-shifting species. Priority for range-shift corridors has also already been integrated in

625 the biodiversity guidelines of the US Department of Agriculture's National Agroforestry

626 Center[186].

627

628 Climate-driven range shifts have also spurred novel strategies in biodiversity conservation. In

629 light of shifting climatic suitability, assisted migration has emerged as a conservation strategy

630 wherein individuals are transplanted either within or outside of their current geographic range

631 with the intention of situating them in locations to which they are more climatically adapted[187].

632 Although controversial[188], some assisted range migration efforts have already begun[189–192]. To

633 facilitate persistence at the warm edge, conservation efforts that protect genotypes pre-

634 adapted to future conditions are particularly effective[193]. These efforts facilitate evolutionary

635 rescue, a process likely to be particularly important to maintain biodiversity in the tropics[194],

636 but raise ethical considerations regarding where and for which species such efforts should be

637 applied.

638

639 Given their importance to human systems, range shift projections have highlighted the need for

640 transboundary management strategies as species shift across political or jurisdictional

641 borders[195]. Transboundary conflicts have already arisen when commercially important species

642 have shifted to neighboring jurisdictions[196], and have been addressed as a priority in

643 international resource management in the Anthropocene[139,197]. The need for proper

644 transboundary strategies will only increase, given that models predict vast swaths of future

645 habitat for many species to emerge across jurisdictional borders, in many cases to countries

646 where those species are not currently found[198–200], and many of these changes will

647 disproportionately impact countries with high reliance on resource species and low capacity to

648 adapt[20]. Without proactive management and transboundary agreements in place, species

649 shifting from one historical jurisdiction to another might result in an incentivized depletion of

650 the resource by the country the species is shifting away from that stands to lose future

651 access[201].

652

653 **[H1] Summary and Future Perspectives**

654 Species' range shifts are a ubiquitous response to climate warming. Despite considerable

655 advances in understanding mechanisms by which species redistribute in response to climate

656 change, vast room for progress in the field remains. Here we outline three key priority areas to

657 advance how we understand and predict biodiversity redistribution and improve our ability to

658 make sound management decisions about shifting species and their associated impacts.

659

660 **[H2] Increased effort in monitoring and harnessing of data**

661 Existing monitoring programs have contributed greatly to observations of climate-driven range

662 shifts, but are often limited to specific ecosystems, geographical areas, or taxa. Although

663 funding agencies can be hesitant to prioritize monitoring programs as their benefits largely

664 accrue over longer time frames, increased support for these efforts will improve our ability to

665   observe, attribute, and anticipate species responses to climate change[202]. Increased monitoring

666   could be particularly valuable for establishing baselines in systems or locations where current

667   data are limited, or for testing and improving model prediction skill in areas in which species

668   ranges are already predicted to shift[57,203]. Furthermore, efforts to integrate disparate existing

669   monitoring programs and introduce comparable and pertinent indicators of biodiversity change

670   (such as Essential Biodiversity Variables[204]), can help up-scale existing monitoring investments

671   for inference at larger scales, such as whole-range biogeographical shifts[205].

672

673   When systematically surveyed 'gold standard' datasets aren't available, range shift research

674   could benefit from increased use of publicly available citizen and community science data. Such

675   volunteer-driven data are collected around the world and already account for over half of

676   biodiversity occurrence records in the Global Biodiversity Information Facility (GBIF)

677   database[206]. These records have already shown applications in biogeography research[52,207–209],

678   and ongoing citizen science monitoring programs having contributed greatly to our

679   observations of range shifts within systems (for example, the Christmas Bird Count, used

680   in[35,210–212]). Outstanding barriers to further integrating citizen science data into climate change

681   biogeography research include the strong spatial and temporal biases of data collections, the

682   statistical measures needed to account for unstructured data collection (although efforts are

683   being made to address these statistical challenges[213]), and the validation of data from non-

684   expert contributors (although robust post-hoc verification measures are possible[207]). Further

685   research into how to control for these variables to best apply public data sources will open

686   research pathways in the field.

687

688   **[H2] Understanding mechanisms to increase generalizability**

689   Synthesis of range shift studies has offered valuable insight into general trends and variability in

690   observed species range shifts, but better understanding of the sources of variability between

691   studies and the influence of data biases are needed to make generalizations. Identifying

692   organism-specific or environment-specific factors that make range shifts likely will improve our

693   ability to anticipate them in cases where observational data is limited.

694

695   Assessing the influence of species traits on range shifts, for example, should help to generalize

696   the types of species most likely to shift at their leading and trailing edges. Intrinsic factors such

697   as a species' ability to move, its level of generalism or its lifespan could influence its ability to

698   shift in response to climate change, and theory suggests varying mechanisms by which these

699   factors should explain range shift rates[10,107,214–216]. Yet, evidence to date suggests fairly weak or

700   variable explanatory power of traits in relation to observed range shift patterns[107], suggesting

701   the methods and perhaps quality of data used to assess their influence have been lacking[107].

702   Further research into intrinsic sources of variation could benefit from simulations and

703   theoretical models to understand the influence that traits might have on range shifts within

704   biological communities[217], combined with data synthesis to test theories against empirical data.

705

706   Another promising direction is generalizing how the spatial pathways of species shifts interact

707   with properties of the landscape. For instance, global climate velocities can be used to identify

708   regions where range shifts might be expected[218], global ocean and wind currents can identify

709   areas where these forces will facilitate or impede shifts of passively dispersing species[98,99], and

710   landscape quality maps can estimate potential routes through which range shifts have an

711   increased likelihood of occurring[219]. Such area-based approaches could aid in management

712   efforts to facilitate climate-driven range shifts even in systems where species-specific data are

713   unavailable.

714

715   Once mechanisms have been identified that can explain variation in species' range shifts, a

716   promising avenue will be to integrate these into mechanistic or process-based models that

717   simulate the eco-evolutionary response of species to climate change[220–222]. Integrating variables

718   such as dispersal, evolutionary potential, or demographic processes into models can improve

719   model fits and extrapolations over correlative approaches[223,224], and have the advantage of

720   flexibility as key parameters can be estimated or imputed when species-specific data is

721   unavailable[225]. Reliance on underlying mechanisms (such as species traits or landscape habitats)

722   makes models of this type transferable to systems where statistical models might be limited by

723 data scarcity. Moreover, mechanistic models can be used in simulation experiments to better

724 identify specific drivers of range shifts when other factors are held constant. Process-based

725 simulations can control for intrinsic and extrinsic factors affecting range shifts, as well as natural

726 variation and detection error to assess the effects of potential drivers of range shifts[194,226], and

727 can even be used to assess effects of management interventions on species distributions[227].

728 The theoretical relationships that arise from simulations experiments can then inform data

729 collection needs, which can circularly aid in improving *in situ* range shift observations.

730

731 **[H2] Improving range shift predictions at usable scales**

732 Although observing and detecting impacts of climate change is a necessary step in

733 understanding processes, projections of range shifts into the future are necessary to inform

734 mediation and management strategies to avoid or adapt to severe ecological impacts of climate

735 change. In range shift research, projections are often made in the long-term (for example, up to

736 2100) using tools such as species distribution models or other correlative models of range

737 position based on environmental variables, rather than predicting range shifts in near-term,

738 management-relevant timescales. This dearth of near-term predictions is one barrier to

739 implementation of effective management strategies for species redistributions, since

740 management strategies more often operate on seasonal-to-decadal scales than to long-term

741 trends.

742

743 Near-term forecasting has grown in popularity and priority in the past decade across subfields

744 in ecology[228,229]. In some data-rich systems with direct applications, near-term forecasts of

745 species distributions have already been implemented to support dynamic management

746 strategies[230–234]. However, in most systems, such efforts have not been implemented. We

747 suggest predictive efforts focus on systems in which predictions can occur in tandem with

748 ongoing monitoring systems to ensure that near-term predictions can be tested, falsified

749 and/or validated, and improved as monitoring continues[228]. Focus on statistical tools that can

750 accurately characterize and project uncertainty, as well as those that can integrate multiple

751   processes from environmental suitability to landscape connectivity will be an important step in

752   improving the predictive power of the field.

753

754   **[H1] Conclusion**

755   Despite substantial strides in our understanding of climate-driven species redistributions since

756   the 19990s, much remains to be understood and discovered in the field. Since the field began,

757   observations of climate-driven range shifts have been made around the world[22], revealing both

758   clear trends in observed responses and high variation due to observational, methodological and

759   biological factors[15,18,132]. Given the growth of the field of climate change biogeography in the

760   last 3 decades and the urgency to predict climate change responses globally, projections,

761   models, and theory seem to have outpaced empirical observations and our collective

762   knowledge and prediction abilities stand to benefit from further efforts to augment empirical

763   data for testing and validation. Expanding research efforts to increase monitoring, deepen our

764   understanding of mechanisms underlying range shifts, and improve near-term predictions will

765   help identify range shifts in the present, anticipate range shifts in the future, and use this

766   knowledge to inform strategies for preserving biodiversity through climate change.

767

768

769

References

771

1. Grinnell, J. Field Tests of Theories Concerning Distributional Control. *Am. Nat.* **51**, 115–128 (1917).

2. Colwell, R. K. & Rangel, T. F. Hutchinson's duality: The once and future niche. *Proc. Natl. Acad. Sci.* **106**, 19651–19658 (2009).

3. Soberón, J. Grinnellian and Eltonian niches and geographic distributions of species. *Ecol. Lett.* **10**, 1115–1123 (2007).

4. Soberón, J. & Nakamura, M. Niches and distributional areas: Concepts, methods, and assumptions. *Proc. Natl. Acad. Sci.* **106**, 19644–19650 (2009).

5. Brown, J. H., Stevens, G. C. & Kaufman, D. M. The Geographic Range: Size, Shape, Boundaries, and Internal Structure. *Annu. Rev. Ecol. Syst.* **27**, 597–623 (1996).

6. Anderson, B. j *et al.* Dynamics of range margins for metapopulations under climate change. *Proc. R. Soc. B Biol. Sci.* **276**, 1415–1420 (2009).

7. Lenoir, J. & Svenning, J.-C. Latitudinal and Elevational Range Shifts under Contemporary Climate Change. in *Encyclopedia of Biodiversity* 599–611 (Elsevier, 2013). doi:10.1016/B978-0-12-384719-5.00375-0.

8. Burrows, M. T. *et al.* The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. *Science* **334**, 652–655 (2011).

9. Ling, S. D., Johnson, C. R., Ridgway, K., Hobday, A. J. & Haddon, M. Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. *Glob. Change Biol.* **15**, 719–731 (2009).

792   10.   Bates, A. E. *et al.* Defining and observing stages of climate-mediated range shifts in marine

793   systems. *Glob. Environ. Change* **26**, 27–38 (2014).

794   11.   Parmesan, C. Climate and species' range. *Nature* **382**, 765–766 (1996).

795   12.   Parmesan, C. & Yohe, G. A globally coherent fingerprint of climate change impacts across

796   natural systems. *Nature* **421**, 37–42 (2003).

797   13.   Pecl, G. T. *et al.* Biodiversity redistribution under climate change: Impacts on ecosystems

798   and human well-being. *Science* **355**, eaai9214 (2017).

799   14.   Sorte, C. J. B., Williams, S. L. & Carlton, J. T. Marine range shifts and species introductions:

800   comparative spread rates and community impacts: Range shifts and non-native species

801   introductions. *Glob. Ecol. Biogeogr.* **19**, 303–316 (2010).

802   15.   Lenoir, J. *et al.* Species better track climate warming in the oceans than on land. *Nat. Ecol.*

803   *Evol.* **4**, 1044–1059 (2020).

804   16.   Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid Range Shifts of

805   Species Associated with High Levels of Climate Warming. *Science* **333**, 1024–1026 (2011).

806   17.   Pinsky, M. L., Worm, B., Fogarty, M. J., Sarmiento, J. L. & Levin, S. A. Marine Taxa Track

807   Local Climate Velocities. *Science* **341**, 1239–1242 (2013).

808   18.   Brown, C. J. *et al.* Ecological and methodological drivers of species' distribution and

809   phenology responses to climate change. *Glob. Change Biol.* **22**, 1548–1560 (2016).

810   19.   Poloczanska, E. S. *et al.* Global imprint of climate change on marine life. *Nat. Clim. Change*

811   **3**, 919–925 (2013).

812   20.   Melbourne-Thomas, J. *et al.* Poleward bound: adapting to climate-driven species

813   redistribution. *Rev. Fish Biol. Fish.* **32**, 231–251 (2022).

814   21.   Alexander, K. A. *et al.* Equity of our future oceans: practices and outcomes in marine

815   science research. *Rev. Fish Biol. Fish.* **32**, 297–311 (2022).

816   22.   Comte, L. *et al.* BioShifts: a global geodatabase of climate-induced species redistribution

817   over land and sea. 5238495 Bytes (2020) doi:10.6084/M9.FIGSHARE.7413365.V1.

818   23.   Humboldt, A. von & Bonpland, A. *Essai sur la géographie des plantes :accompagné d'un*

819   *tableau physique des régions équinoxiales, fondé sur des mesures exécutées, depuis le*

820   *dixième degré de latitude boréale jusqu'au dixième degré de latitude australe, pendant les*

821   *années 1799, 1800, 1801, 1802 et 1803 /par Al. de Humdboldt et A. Bonpland ; rédigée par*

822   *Al. de Humboldt.* (Chez Levrault, Schoell et compagnie, libraires, 1805).

823   doi:10.5962/bhl.title.9309.

824   24.   Merriam, C. H. *Laws of Temperature Control of the Geographic Distribution of Terrestrial*

825   *Animals and Plants*. (1894).

826   25.   Parmesan, C. Ecological and Evolutionary Responses to Recent Climate Change. *Annu. Rev.*

827   *Ecol. Evol. Syst.* **37**, 637–669 (2006).

828   26.   Odum, E. P. The Concept of the Biome as Applied to the Distribution of North American

829   Birds. *Wilson Bull.* **57**, 191–201 (1945).

830   27.   Thomas, C. D. Climate, climate change and range boundaries. *Divers. Distrib.* **16**, 488–495

831   (2010).

832   28.   Gonzalez, P. Desertification and a shift of forest species in the West African Sahel. *Clim.*

833   *Res.* **17**, 217–228 (2001).

834   29. Hersteinsson, P. & MacDonald, D. W. Interspecific Competition and the Geographical

835   Distribution of Red and Arctic Foxes *Vulpes Vulpes* and *Alopex lagopus*. *Oikos* **64**, 505

836   (1992).

837   30. Service, C. N. *et al.* Indigenous Knowledge and Science Unite to Reveal Spatial and

838   Temporal Dimensions of Distributional Shift in Wildlife of Conservation Concern. *PLoS ONE*

839   **9**, e101595 (2014).

840   31. Barry, J. P., Baxter, C. H., Sagarin, R. D. & Gilman, S. E. Climate-Related, Long-Term Faunal

841   Changes in a California Rocky Intertidal Community. *Science* **267**, 672–675 (1995).

842   32. Grabherr, G., Gottfried, M. & Pauli, H. Climate effects on mountain plants. *Nature* **369**,

843   448–448 (1994).

844   33. Fredston-Hermann, A., Selden, R., Pinsky, M., Gaines, S. D. & Halpern, B. S. Cold range

845   edges of marine fishes track climate change better than warm edges. *Glob. Change Biol.*

846   **26**, 2908–2922 (2020).

847   34. Nye, J., Link, J., Hare, J. & Overholtz, W. Changing spatial distribution of fish stocks in

848   relation to climate and population size on the Northeast United States continental shelf.

849   *Mar. Ecol. Prog. Ser.* **393**, 111–129 (2009).

850   35. La Sorte, F. A. & Thompson III, F. R. POLEWARD SHIFTS IN WINTER RANGES OF NORTH

851   AMERICAN BIRDS. *Ecology* **88**, 1803–1812 (2007).

852   36. Diamond, S. E., Frame, A. M., Martin, R. A. & Buckley, L. B. Species' traits predict

853   phenological responses to climate change in butterflies. *Ecology* **92**, 1005–1012 (2011).

854   37. Shaffer, H. B., Fisher, R. N. & Davidson, C. The role of natural history collections in

855   documenting species declines. *Trends Ecol. Evol.* **13**, 27–30 (1998).

856 38. Tingley, M. W. & Beissinger, S. R. Detecting range shifts from historical species

857 occurrences: new perspectives on old data. *Trends Ecol. Evol.* **24**, 625–633 (2009).

858 39. Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V. & Fitzpatrick, J. W. Climate change

859 causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proc.*

860 *Natl. Acad. Sci.* **115**, 11982–11987 (2018).

861 40. Poloczanska, E. S. *et al.* Little change in the distribution of rocky shore faunal communities

862 on the Australian east coast after 50 years of rapid warming. *J. Exp. Mar. Biol. Ecol.* **400**,

863 145–154 (2011).

864 41. Devictor, V. *et al.* Differences in the climatic debts of birds and butterflies at a continental

865 scale. *Nat. Clim. Change* **2**, 121–124 (2012).

866 42. Lenoir, J., Gégout, J.-C., Pierrat, J.-C., Bontemps, J.-D. & Dhôte, J.-F. Differences between

867 tree species seedling and adult altitudinal distribution in mountain forests during the

868 recent warm period (1986–2006). *Ecography* **32**, 765–777 (2009).

869 43. Zhu, K., Woodall, C. W. & Clark, J. S. Failure to migrate: lack of tree range expansion in

870 response to climate change. *Glob. Change Biol.* **18**, 1042–1052 (2012).

871 44. Monleon, V. J. & Lintz, H. E. Evidence of tree species' range shifts in a complex landscape.

872 *PloS One* **10**, e0118069 (2015).

873 45. Hammerschlag, N. *et al.* Ocean warming alters the distributional range, migratory timing,

874 and spatial protections of an apex predator, the tiger shark (Galeocerdo cuvier). *Glob.*

875 *Change Biol.* **28**, 1990–2005 (2022).

876 46. Robinson, L. M. *et al.* Rapid assessment of an ocean warming hotspot reveals "high"

877 confidence in potential species' range extensions. *Glob. Environ. Change* **31**, 28–37 (2015).

878   47. García Molinos, J. *et al.* Climate, currents and species traits contribute to early stages of

879   marine species redistribution. *Commun. Biol.* **5**, 1–10 (2022).

880   48. Root, T. L. *et al.* Fingerprints of global warming on wild animals and plants. *Nature* **421**,

881   57–60 (2003).

882   49. Rubenstein, M. A. *et al.* Climate change and the global redistribution of biodiversity:

883   substantial variation in empirical support for expected range shifts. *Environ. Evid.* **12**, 7

884   (2023).

885   50. Amano, T. *et al.* Tapping into non-English-language science for the conservation of global

886   biodiversity. *PLOS Biol.* **19**, e3001296 (2021).

887   51. Konno, K. *et al.* Ignoring non-English-language studies may bias ecological meta-analyses.

888   *Ecol. Evol.* **10**, 6373–6384 (2020).

889   52. Gervais, C. R., Champion, C. & Pecl, G. T. Species on the move around the Australian

890   coastline: A continental-scale review of climate-driven species redistribution in marine

891   systems. *Glob. Change Biol.* **27**, 3200–3217 (2021).

892   53. Thomas, C. D., Franco, A. M. A. & Hill, J. K. Range retractions and extinction in the face of

893   climate warming. *Trends Ecol. Evol.* **21**, 415–416 (2006).

894   54. Doak, D. F. & Morris, W. F. Demographic compensation and tipping points in climate-

895   induced range shifts. *Nature* **467**, 959–962 (2010).

896   55. Boisvert-Marsh, L., Périé, C. & de Blois, S. Shifting with climate? Evidence for recent

897   changes in tree species distribution at high latitudes. *Ecosphere* **5**, art83 (2014).

898   56.   Freeman, B. G., Lee-Yaw, J. A., Sunday, J. M. & Hargreaves, A. L. Expanding, shifting and

899   shrinking: The impact of global warming on species' elevational distributions. *Glob. Ecol.*

900   *Biogeogr.* **27**, 1268–1276 (2018).

901   57.   Comte, L., Buisson, L., Daufresne, M. & Grenouillet, G. Climate-induced changes in the

902   distribution of freshwater fish: observed and predicted trends: *Climate change and*

903   *freshwater fish*. *Freshw. Biol.* **58**, 625–639 (2013).

904   58.   Sunday, J. M., Bates, A. E. & Dulvy, N. K. Thermal tolerance and the global redistribution of

905   animals. *Nat. Clim. Change* **2**, 686–690 (2012).

906   59.   Pinsky, M. L., Eikeset, A. M., McCauley, D. J., Payne, J. L. & Sunday, J. M. Greater

907   vulnerability to warming of marine versus terrestrial ectotherms. *Nature* **569**, 108–111

908   (2019).

909   60.   Myers, A. A. Biogeographic Barriers and the Development of Marine Biodiversity. *Estuar.*

910   *Coast. Shelf Sci.* **44**, 241–248 (1997).

911   61.   Huang, Q. *et al.* Modeled distribution shifts of North American birds over four decades

912   based on suitable climate alone do not predict observed shifts. *Sci. Total Environ.* **857**,

913   159603 (2023).

914   62.   Lembrechts, J. J. & Lenoir, J. Microclimatic conditions anywhere at any time! *Glob. Change*

915   *Biol.* **26**, 337–339 (2020).

916   63.   Lenoir, J., Hattab, T. & Pierre, G. Climatic microrefugia under anthropogenic climate

917   change: implications for species redistribution. *Ecography* **40**, 253–266 (2017).

918   64.   Maclean, I. M. D. Predicting future climate at high spatial and temporal resolution. *Glob.*

919   *Change Biol.* **26**, 1003–1011 (2020).

920 65. Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D. & Coomes, D. Advances in Microclimate

921   Ecology Arising from Remote Sensing. *Trends Ecol. Evol.* **34**, 327–341 (2019).

922 66. Haesen, S. *et al.* ForestTemp – Sub-canopy microclimate temperatures of European

923   forests. *Glob. Change Biol.* **27**, 6307–6319 (2021).

924 67. Lembrechts, J. J. *et al.* Global maps of soil temperature. *Glob. Change Biol.* **28**, 3110–3144

925   (2022).

926 68. Maclean, I. M. D. & Early, R. Macroclimate data overestimate range shifts of plants in

927   response to climate change. *Nat. Clim. Change* (2023) doi:10.1038/s41558-023-01650-3.

928 69. Dobrowski, S. Z. *et al.* The climate velocity of the contiguous United States during the 20th

929   century. *Glob. Change Biol.* **19**, 241–251 (2013).

930 70. Crimmins, S. M., Dobrowski, S. Z., Greenberg, J. A., Abatzoglou, J. T. & Mynsberge, A. R.

931   Changes in Climatic Water Balance Drive Downhill Shifts in Plant Species' Optimum

932   Elevations. *Science* **331**, 324–327 (2011).

933 71. Hordley, L. A., Fox, R., Suggitt, A. J. & Bourn, N. A. D. Precipitation buffers temperature-

934   driven local extinctions of moths at warm range margins. *Ecol. Lett.* **00**, 1–11 (2023).

935 72. Tingley, M. W., Monahan, W. B., Beissinger, S. R. & Moritz, C. Birds track their Grinnellian

936   niche through a century of climate change. *Proc. Natl. Acad. Sci.* **106**, 19637–19643 (2009).

937 73. McHenry, J., Welch, H., Lester, S. E. & Saba, V. Projecting marine species range shifts from

938   only temperature can mask climate vulnerability. *Glob. Change Biol.* **25**, 4208–4221

939   (2019).

940 74. Spence, A. R. & Tingley, M. W. The challenge of novel abiotic conditions for species

941   undergoing climate-induced range shifts. *Ecography* **43**, 1571–1590 (2020).

942   75.   Huffeldt, N. P. Photic Barriers to Poleward Range-shifts. *Trends Ecol. Evol.* **35**, 652–655

943   (2020).

944   76.   Muir, P. R., Wallace, C. C., Done, T. & Aguirre, J. D. Limited scope for latitudinal extension

945   of reef corals. *Science* **348**, 1135–1138 (2015).

946   77.   Jacobsen, D. The dilemma of altitudinal shifts: caught between high temperature and low

947   oxygen. *Front. Ecol. Environ.* **18**, 211–218 (2020).

948   78.   Sunday, J. M. *et al.* Biological sensitivities to high-resolution climate change projections in

949   the California current marine ecosystem. *Glob. Change Biol.* **28**, 5726–5740 (2022).

950   79.   Harris, R. M. B. *et al.* Biological responses to the press and pulse of climate trends and

951   extreme events. *Nat. Clim. Change* **8**, 579–587 (2018).

952   80.   Smith, M. D. An ecological perspective on extreme climatic events: a synthetic definition

953   and framework to guide future research. *J. Ecol.* **99**, 656–663 (2011).

954   81.   Zong, S. *et al.* Upward range shift of a dominant alpine shrub related to 50 years of snow

955   cover change. *Remote Sens. Environ.* **268**, 112773 (2022).

956   82.   Twiname, S. *et al.* Mismatch of thermal optima between performance measures, life

957   stages and species of spiny lobster. *Sci. Rep.* **10**, 21235 (2020).

958   83.   Edgar, G. J. *et al.* Continent-wide declines in shallow reef life over a decade of ocean

959   warming. *Nature* **615**, 858–865 (2023).

960   84.   Dullinger, S. *et al.* Post-glacial migration lag restricts range filling of plants in the European

961   Alps. *Glob. Ecol. Biogeogr.* **21**, 829–840 (2012).

962   85.   Carvajal-Quintero, J. *et al.* Drainage network position and historical connectivity explain

963   global patterns in freshwater fishes' range size. *Proc. Natl. Acad. Sci.* **116**, 13434–13439

964   (2019).

965   86.   Matthews, W. J. & Zimmerman, E. G. Potential Effects of Global Warming on Native Fishes

966   of the Southern Great Plains and the Southwest. *Fisheries* **15**, 26–32 (1990).

967   87.   Guo, F., Lenoir, J. & Bonebrake, T. C. Land-use change interacts with climate to determine

968   elevational species redistribution. *Nat. Commun.* **9**, 1315 (2018).

969   88.   Hill, J. K., Thomas, C. D. & Huntley, B. Climate and habitat availability determine 20th

970   century changes in a butterfly's range margin. *Proc. R. Soc. Lond. B Biol. Sci.* **266**, 1197–

971   1206 (1999).

972   89.   Morelli, T. L. *et al.* Anthropogenic refugia ameliorate the severe climate-related decline of

973   a montane mammal along its trailing edge. *Proc. R. Soc. B Biol. Sci.* **279**, 4279–4286 (2012).

974   90.   Fischer, J. & Lindenmayer, D. B. Landscape modification and habitat fragmentation: a

975   synthesis. *Glob. Ecol. Biogeogr.* **16**, 265–280 (2007).

976   91.   Schloss, C. A., Nuñez, T. A. & Lawler, J. J. Dispersal will limit ability of mammals to track

977   climate change in the Western Hemisphere. *Proc. Natl. Acad. Sci.* **109**, 8606–8611 (2012).

978   92.   Hodgson, J. A., Randle, Z., Shortall, C. R. & Oliver, T. H. Where and why are species' range

979   shifts hampered by unsuitable landscapes? *Glob. Change Biol.* **28**, 4765–4774 (2022).

980   93.   Thomas, C. D. *et al.* Protected areas facilitate species' range expansions. *Proc. Natl. Acad.*

981   *Sci.* **109**, 14063–14068 (2012).

982   94.   Coolen, J. W. P. *et al.* Marine stepping-stones: Connectivity of Mytilus edulis populations

983   between offshore energy installations. *Mol. Ecol.* **29**, 686–703 (2020).

984   95. Reino, L. *et al.* Modelling landscape constraints on farmland bird species range shifts under

985   climate change. *Sci. Total Environ.* **625**, 1596–1605 (2018).

986   96. Lawler, J. J., Ruesch, A. S., Olden, J. D. & McRae, B. H. Projected climate-driven faunal

987   movement routes. *Ecol. Lett.* **16**, 1014–1022 (2013).

988   97. Littlefield, C. E., Krosby, M., Michalak, J. L. & Lawler, J. J. Connectivity for species on the

989   move: supporting climate-driven range shifts. *Front. Ecol. Environ.* **17**, 270–278 (2019).

990   98. García Molinos, J., Burrows, M. T. & Poloczanska, E. S. Ocean currents modify the coupling

991   between climate change and biogeographical shifts. *Sci. Rep.* **7**, 1332 (2017).

992   99. Kling, M. M. & Ackerly, D. D. Global wind patterns and the vulnerability of wind-dispersed

993   species to climate change. *Nat. Clim. Change* **10**, 868–875 (2020).

994 100. Copeland, S. M., Bradford, J. B., Duniway, M. C. & Butterfield, B. J. Life history

995   characteristics may be as important as climate projections for defining range shifts: An

996   example for common tree species in the intermountain western US. *Divers. Distrib.* **24**,

997   1844–1859 (2018).

998 101. Naoe, S. *et al.* Downhill seed dispersal by temperate mammals: a potential threat to plant

999   escape from global warming. *Sci. Rep.* **9**, 14932 (2019).

1000 102. Ramos, J. E. *et al.* Population genetic signatures of a climate change driven marine range

1001   extension. *Sci. Rep.* **8**, 9558 (2018).

1002 103. MacLean, S. A. & Beissinger, S. R. Species' traits as predictors of range shifts under

1003   contemporary climate change: A review and meta-analysis. *Glob. Change Biol.* **23**, 4094–

1004   4105 (2017).

1005   104. Sunday, J. M. *et al.* Species traits and climate velocity explain geographic range shifts in an

1006   ocean-warming hotspot. *Ecol. Lett.* **18**, 944–953 (2015).

1007   105. Angert, A. L. *et al.* Do species' traits predict recent shifts at expanding range edges?: Traits

1008   and range shifts. *Ecol. Lett.* **14**, 677–689 (2011).

1009   106. Alofs, K. M., Jackson, D. A. & Lester, N. P. Ontario freshwater fishes demonstrate differing

1010   range-boundary shifts in a warming climate. *Divers. Distrib.* **20**, 123–136 (2014).

1011   107. Beissinger, S. R. & Riddell, E. A. Why Are Species' Traits Weak Predictors of Range Shifts?

1012   *Annu. Rev. Ecol. Evol. Syst.* **52**, 47–66 (2021).

1013   108. HilleRisLambers, J., Harsch, M. A., Ettinger, A. K., Ford, K. R. & Theobald, E. J. How will

1014   biotic interactions influence climate change–induced range shifts? *Ann. N. Y. Acad. Sci.*

1015   **1297**, 112–125 (2013).

1016   109. Kerner, J. M., Krauss, J., Maihoff, F., Bofinger, L. & Classen, A. Alpine butterflies want to fly

1017   high: Species and communities shift upwards faster than their host plants. *Ecology* **104**,

1018   e3848 (2023).

1019   110. Merrill, R. M. *et al.* Combined effects of climate and biotic interactions on the elevational

1020   range of a phytophagous insect. *J. Anim. Ecol.* **77**, 145–155 (2008).

1021   111. Afkhami, M. E., McIntyre, P. J. & Strauss, S. Y. Mutualist-mediated effects on species' range

1022   limits across large geographic scales. *Ecol. Lett.* **17**, 1265–1273 (2014).

1023   112. Lankau, R. A., Zhu, K. & Ordonez, A. Mycorrhizal strategies of tree species correlate with

1024   trailing range edge responses to current and past climate change. *Ecology* **96**, 1451–1458

1025   (2015).

1026   113. Elmhagen, B. *et al.* Homage to Hersteinsson and Macdonald: climate warming and

1027   resource subsidies cause red fox range expansion and Arctic fox decline. *Polar Res.* **36**,

1028   (2017).

1029   114. Pokallus, J. W. & Pauli, J. . N. Population dynamics of a northern-adapted mammal:

1030   disentangling the influence of predation and climate change. *Ecol. Appl.* **25**, 1546–1556

1031   (2015).

1032   115. Wallingford, P. D. *et al.* Adjusting the lens of invasion biology to focus on the impacts of

1033   climate-driven range shifts. *Nat. Clim. Change* **10**, 398–405 (2020).

1034   116. Harley, C. D. G. Climate Change, Keystone Predation, and Biodiversity Loss. *Science* **334**,

1035   1124–1127 (2011).

1036   117. Lenoir, J. *et al.* Going against the flow: potential mechanisms for unexpected downslope

1037   range shifts in a warming climate. *Ecography* **33**, 295–303 (2010).

1038   118. Pollock, L. J. *et al.* Understanding co-occurrence by modelling species simultaneously with

1039   a Joint Species Distribution Model (JSDM). *Methods Ecol. Evol.* **5**, 397–406 (2014).

1040   119. Devarajan, K., Morelli, T. L. & Tenan, S. Multi-species occupancy models: review, roadmap,

1041   and recommendations. *Ecography* **43**, 1612–1624 (2020).

1042   120. Zhang, C., Chen, Y., Xu, B., Xue, Y. & Ren, Y. Improving prediction of rare species'

1043   distribution from community data. *Sci. Rep.* **10**, 12230 (2020).

1044   121. Wisz, M. S. *et al.* The role of biotic interactions in shaping distributions and realised

1045   assemblages of species: implications for species distribution modelling. *Biol. Rev.* **88**, 15–

1046   30 (2013).

1047 122. Diamond, S. E. Contemporary climate-driven range shifts: Putting evolution back on the

1048   table. *Funct. Ecol.* **32**, 1652–1665 (2018).

1049 123. Bridle, J. R. & Vines, T. H. Limits to evolution at range margins: when and why does

1050   adaptation fail? *Trends Ecol. Evol.* **22**, 140–147 (2007).

1051 124. Nadeau, C. P. & Urban, M. C. Eco-evolution on the edge during climate change. *Ecography*

1052   **42**, 1280–1297 (2019).

1053 125. Dudaniec, R. Y. *et al.* Latitudinal clines in sexual selection, sexual size dimorphism and sex-

1054   specific genetic dispersal during a poleward range expansion. *J. Anim. Ecol.* **91**, 1104–1118

1055   (2022).

1056 126. Krause, J. S. *et al.* Breeding on the leading edge of a northward range expansion:

1057   differences in morphology and the stress response in the arctic Gambel's white-crowned

1058   sparrow. *Oecologia* **180**, 33–44 (2016).

1059 127. Campbell-Staton, S. C. *et al.* Parallel selection on thermal physiology facilitates repeated

1060   adaptation of city lizards to urban heat islands. *Nat. Ecol. Evol.* **4**, 652–658 (2020).

1061 128. Diamond, S. E., Chick, L., Perez, A., Strickler, S. A. & Martin, R. A. Rapid evolution of ant

1062   thermal tolerance across an urban-rural temperature cline. *Biol. J. Linn. Soc.* **121**, 248–257

1063   (2017).

1064 129. Donelson, J. M. *et al.* Understanding interactions between plasticity, adaptation and range

1065   shifts in response to marine environmental change. *Philos. Trans. R. Soc. B Biol. Sci.* **374**,

1066   20180186 (2019).

1067 130. Shoo, L. P., Williams, S. E. & Hero, J.-M. Detecting climate change induced range shifts:

1068   Where and how should we be looking? *Austral Ecol.* **31**, 22–29 (2006).

1069   131. Guo, Q., Taper, M., Schoenberger, M. & Brandle, J. Spatial-Temporal Population Dynamics

1070   across Species Range: From Centre to Margin. *Oikos* **108**, 47–57 (2005).

1071   132. Taheri, S., Naimi, B., Rahbek, C. & Araújo, M. B. Improvements in reports of species

1072   redistribution under climate change are required. *Sci. Adv.* **7**, eabe1110 (2021).

1073   133. Iseli, E. *et al.* Rapid upwards spread of non-native plants in mountains across continents.

1074   *Nat. Ecol. Evol.* **7**, 405–413 (2023).

1075   134. Mazalla, L. & Diekmann, M. Regression to the mean in vegetation science. *J. Veg. Sci.* **33**,

1076   e13117 (2022).

1077   135. Bates, A. E. *et al.* Distinguishing geographical range shifts from artefacts of detectability

1078   and sampling effort. *Divers. Distrib.* **21**, 13–22 (2015).

1079   136. Davis, A. *et al. Tools for predicting wildlife species distribution response to ecological shifts*.

1080   https://hdl.handle.net/11681/33482 (2019) doi:10.21079/11681/33482.

1081   137. Lindsay, K. *Wildlife conservation, protected areas and climate change in Canada:*

1082   *implications of projected species range shifts*. (Canadian Council on Ecological Areas,

1083   2016).

1084   138. Weiskopf, S. R. *et al.* Climate change effects on biodiversity, ecosystems, ecosystem

1085   services, and natural resource management in the United States. *Sci. Total Environ.* **733**,

1086   137782 (2020).

1087   139. Pinsky, M. L. *et al.* Preparing ocean governance for species on the move. *Science* **360**,

1088   1189–1191 (2018).

1089   140. Scheffers, B. R. & Pecl, G. Persecuting, protecting or ignoring biodiversity under climate

1090   change. *Nat. Clim. Change* **9**, 581–586 (2019).

1091   141. Bowler, D. E. *et al.* Cross-realm assessment of climate change impacts on species'

1092   abundance trends. *Nat. Ecol. Evol.* **1**, 1–7 (2017).

1093   142. Feeley, K. J., Bravo-Avila, C., Fadrique, B., Perez, T. M. & Zuleta, D. Climate-driven changes

1094   in the composition of New World plant communities. *Nat. Clim. Change* **10**, 965–970

1095   (2020).

1096   143. Kuhn, E. & Gégout, J.-C. Highlighting declines of cold-demanding plant species in lowlands

1097   under climate warming. *Ecography* **42**, 36–44 (2019).

1098   144. Kumagai, N. H. *et al.* Ocean currents and herbivory drive macroalgae-to-coral community

1099   shift under climate warming. *Proc. Natl. Acad. Sci.* **115**, 8990–8995 (2018).

1100   145. Zarzyczny, K. M., Rius, M., Williams, S. T. & Fenberg, P. B. The ecological and evolutionary

1101   consequences of tropicalisation. *Trends Ecol. Evol.* S0169534723002732 (2023)

1102   doi:10.1016/j.tree.2023.10.006.

1103   146. Balik, J. A., Greig, H. S., Taylor, B. W. & Wissinger, S. A. Consequences of climate-induced

1104   range expansions on multiple ecosystem functions. *Commun. Biol.* **6**, 390 (2023).

1105   147. Cauvy-Fraunié, S. & Dangles, O. A global synthesis of biodiversity responses to glacier

1106   retreat. *Nat. Ecol. Evol.* **3**, 1675–1685 (2019).

1107   148. Stuart-Smith, R. D., Mellin, C., Bates, A. E. & Edgar, G. J. Habitat loss and range shifts

1108   contribute to ecological generalization among reef fishes. *Nat. Ecol. Evol.* **5**, 656–662

1109   (2021).

1110   149. Bertrand, R. *et al.* Changes in plant community composition lag behind climate warming in

1111   lowland forests. *Nature* **479**, 517–520 (2011).

1112 150. Davis, T. R., Knott, N. A., Champion, C. & Przeslawski, R. Impacts of Climate Change on

1113   Densities of the Urchin Centrostephanus rodgersii Vary among Marine Regions in Eastern

1114   Australia. *Diversity* **15**, 419 (2023).

1115 151. Ling, S. D. Range expansion of a habitat-modifying species leads to loss of taxonomic

1116   diversity: a new and impoverished reef state. *Oecologia* **156**, 883–894 (2008).

1117 152. Ling, S. & Johnson, C. Population dynamics of an ecologically important range-extender:

1118   kelp beds versus sea urchin barrens. *Mar. Ecol. Prog. Ser.* **374**, 113–125 (2009).

1119 153. Johnson, C., Ling, S., Ross, J., Shepherd, S. & Miller, K. *Establishment of the Long-Spined*

1120   *Sea Urchin Centrostephanus rodgersii in Tasmania: First Assessment of Potential Threats to*

1121   *Fisheries*. (2005).

1122 154. Fazlioglu, F., Wan, J. S. H. & Chen, L. Latitudinal shifts in mangrove species worldwide:

1123   evidence from historical occurrence records. *Hydrobiologia* **847**, 4111–4123 (2020).

1124 155. Nagelkerken, I. *et al.* The habitat function of mangroves for terrestrial and marine fauna: A

1125   review. *Aquat. Bot.* **89**, 155–185 (2008).

1126 156. Descombes, P. *et al.* Novel trophic interactions under climate change promote alpine plant

1127   coexistence. *Science* **370**, 1469–1473 (2020).

1128 157. Pecl, G. T. *et al.* Autonomous adaptation to climate-driven change in marine biodiversity in

1129   a global marine hotspot. *Ambio* **48**, 1498–1515 (2019).

1130 158. Oremus, K. L. Climate variability reduces employment in New England fisheries. *Proc. Natl.*

1131   *Acad. Sci.* **116**, 26444–26449 (2019).

1132 159. Young, T. *et al.* Adaptation strategies of coastal fishing communities as species shift

1133   poleward. *ICES J. Mar. Sci.* **76**, 93–103 (2019).

1134   160. Sloat, L. L. *et al.* Climate adaptation by crop migration. *Nat. Commun.* **11**, 1243 (2020).

1135   161. Bebber, D. P., Ramotowski, M. A. T. & Gurr, S. J. Crop pests and pathogens move

1136   polewards in a warming world. *Nat. Clim. Change* **3**, 985–988 (2013).

1137   162. Blackfeet Nation. Blackfeet climate change adaptation plan. (2018).

1138   163. Sweet, L. C. *et al.* Congruence between future distribution models and empirical data for

1139   an iconic species at Joshua Tree National Park. *Ecosphere* **10**, e02763 (2019).

1140   164. Carlson, C. J., Bannon, E., Mendenhall, E., Newfield, T. & Bansal, S. Rapid range shifts in

1141   African Anopheles mosquitoes over the last century. *Biol. Lett.* **19**, 20220365 (2023).

1142   165. Clow, K. M. *et al.* Northward range expansion of Ixodes scapularis evident over a short

1143   timescale in Ontario, Canada. *PLOS ONE* **12**, e0189393 (2017).

1144   166. McCracken, G. F. *et al.* Rapid range expansion of the Brazilian free-tailed bat in the

1145   southeastern United States, 2008–2016. *J. Mammal.* **99**, 312–320 (2018).

1146   167. Siraj, A. S. *et al.* Altitudinal changes in malaria incidence in highlands of Ethiopia and

1147   Colombia. *Science* **343**, 1154–1158 (2014).

1148   168. Alkishe, A., Raghavan, R. K. & Peterson, A. T. Likely Geographic Distributional Shifts among

1149   Medically Important Tick Species and Tick-Associated Diseases under Climate Change in

1150   North America: A Review. *Insects* **12**, 225 (2021).

1151   169. Ryan, S. J. *et al.* Warming temperatures could expose more than 1.3 billion new people to

1152   Zika virus risk by 2050. *Glob. Change Biol.* **27**, 84–93 (2021).

1153   170. Chinain, M., Gatti, C. M. i., Darius, H. T., Quod, J.-P. & Tester, P. A. Ciguatera poisonings: A

1154   global review of occurrences and trends. *Harmful Algae* **102**, 101873 (2021).

1155   171. Kulkarni, M. A. *et al.* 10 Years of Environmental Change on the Slopes of Mount

1156   Kilimanjaro and Its Associated Shift in Malaria Vector Distributions. *Front. Public Health* **4**,

1157   (2016).

1158   172. Ryan, S. J., Carlson, C. J., Mordecai, E. A. & Johnson, L. R. Global expansion and

1159   redistribution of Aedes-borne virus transmission risk with climate change. *PLoS Negl. Trop.*

1160   *Dis.* **13**, e0007213 (2019).

1161   173. Carlson, C. J. *et al.* Climate change increases cross-species viral transmission risk. *Nature*

1162   **607**, 555–562 (2022).

1163   174. Gray, C. L. *et al.* Local biodiversity is higher inside than outside terrestrial protected areas

1164   worldwide. *Nat. Commun.* **7**, 12306 (2016).

1165   175. Bruno, J. F. *et al.* Climate change threatens the world's marine protected areas. *Nat. Clim.*

1166   *Change* **8**, 499–503 (2018).

1167   176. Lewis, S. A., Stortini, C. H., Boyce, D. G. & Stanley, R. R. E. Climate change, species thermal

1168   emergence, and conservation design: a case study in the Canadian Northwest Atlantic.

1169   *FACETS* **8**, 1–16 (2023).

1170   177. Parks, S. A., Holsinger, L. M., Abatzoglou, J. T., Littlefield, C. E. & Zeller, K. A. Protected

1171   areas not likely to serve as steppingstones for species undergoing climate-induced range

1172   shifts. *Glob. Change Biol.* **00**, 1–16 (2023).

1173   178. D'Aloia, C. C. *et al.* Coupled Networks of Permanent Protected Areas and Dynamic

1174   Conservation Areas for Biodiversity Conservation Under Climate Change. *Front. Ecol. Evol.*

1175   **7**, (2019).

1176   179. Cashion, T. *et al.* Shifting seas, shifting boundaries: Dynamic marine protected area designs

1177   for a changing climate. *PLOS ONE* **15**, e0241771 (2020).

1178   180. Pinsky, M. L., Rogers, L. A., Morley, J. W. & Frölicher, T. L. Ocean planning for species on

1179   the move provides substantial benefits and requires few trade-offs. *Sci. Adv.* **6**, eabb8428

1180   (2020).

1181   181. Lewison, R. *et al.* Dynamic Ocean Management: Identifying the Critical Ingredients of

1182   Dynamic Approaches to Ocean Resource Management. *BioScience* **65**, 486–498 (2015).

1183   182. Maxwell, S. M. *et al.* Dynamic ocean management: Defining and conceptualizing real-time

1184   management of the ocean. *Mar. Policy* **58**, 42–50 (2015).

1185   183. Golet, G. H. *et al.* Using ricelands to provide temporary shorebird habitat during migration.

1186   *Ecol. Appl.* **28**, 409–426 (2018).

1187   184. Reynolds, M. D. *et al.* Dynamic conservation for migratory species. *Sci. Adv.* **3**, e1700707

1188   (2017).

1189   185. Bloom, A. The Cumberland Forest Project: 253,000 Acres of Preserved Land.

1190   https://www.nature.org/en-us/what-we-do/our-priorities/protect-water-and-land/land-

1191   and-water-stories/cumberland-forest-project (2019).

1192   186. Bentrup, G. *Conservation Buffers—Design guidelines for buffers, corridors, and greenways*.

1193   SRS-GTR-109 https://www.fs.usda.gov/treesearch/pubs/33522 (2008) doi:10.2737/SRS-

1194   GTR-109.

1195   187. Handler, S., Pike, C., St. Clair, B., Abbotts, H. & Janowiak, M. Assisted Migration. USDA

1196   Forest Service Climate Change Resource Center.

1197   https://www.fs.usda.gov/ccrc/topics/assisted-migration (2018).

1198   188. Ricciardi, A. & Simberloff, D. Assisted colonization is not a viable conservation strategy.

1199   *Trends Ecol. Evol.* **24**, 248–253 (2009).

1200   189. Carbajal-Navarro, A. *et al.* Ecological Restoration of Abies religiosa Forests Using Nurse

1201   Plants and Assisted Migration in the Monarch Butterfly Biosphere Reserve, Mexico. *Front.*

1202   *Ecol. Evol.* **7**, 421 (2019).

1203   190. Widhalm, T., Fourcade, Y., Frank, T. & Öckinger, E. Population dynamics of the butterfly

1204   Pyrgus armoricanus after translocation beyond its northern range margin. *Insect Conserv.*

1205   *Divers.* **13**, 617–629 (2020).

1206   191. Liu, H. *et al.* Overcoming extreme weather challenges: Successful but variable assisted

1207   colonization of wild orchids in southwestern China. *Biol. Conserv.* **150**, 68–75 (2012).

1208   192. Twardek, W. M. *et al.* The application of assisted migration as a climate change adaptation

1209   tactic: An evidence map and synthesis. *Biol. Conserv.* **280**, 109932 (2023).

1210   193. Walsworth, T. E. *et al.* Management for network diversity speeds evolutionary adaptation

1211   to climate change. *Nat. Clim. Change* **9**, 632–636 (2019).

1212   194. Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. A. & Loeuille, N. Eco-evolutionary

1213   responses of biodiversity to climate change. *Nat. Clim. Change* **2**, 747–751 (2012).

1214   195. Palacios-Abrantes, J. *et al.* Quantifying fish range shifts across poorly defined management

1215   boundaries. *PLOS ONE* **18**, e0279025 (2023).

1216   196. Spijkers, J. & Boonstra, W. J. Environmental change and social conflict: the northeast

1217   Atlantic mackerel dispute. *Reg. Environ. Change* **17**, 1835–1851 (2017).

1218   197. Parks, S. A. *et al.* Efficacy of the global protected area network is threatened by

1219   disappearing climates and potential transboundary range shifts. *Environ. Res. Lett.* **17**,

1220   054016 (2022).

1221   198. Palacios-Abrantes, J. *et al.* Timing and magnitude of climate-driven range shifts in

1222   transboundary fish stocks challenge their management. *Glob. Change Biol.* **28**, 2312–2326

1223   (2022).

1224   199. Titley, M. A., Butchart, S. H. M., Jones, V. R., Whittingham, M. J. & Willis, S. G. Global

1225   inequities and political borders challenge nature conservation under climate change. *Proc.*

1226   *Natl. Acad. Sci.* **118**, e2011204118 (2021).

1227   200. Velazco, S. J. E., Villalobos, F., Galvão, F. & De Marco Júnior, P. A dark scenario for Cerrado

1228   plant species: Effects of future climate, land use and protected areas ineffectiveness.

1229   *Divers. Distrib.* **25**, 660–673 (2019).

1230   201. Intergovernmental Panel On Climate Change (Ipcc). *Climate Change 2022 – Impacts,*

1231   *Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment*

1232   *Report of the Intergovernmental Panel on Climate Change*. (Cambridge University Press,

1233   2023). doi:10.1017/9781009325844.

1234   202. Lindenmayer, D. B., Lavery, T. & Scheele, B. C. Why We Need to Invest in Large-Scale,

1235   Long-Term Monitoring Programs in Landscape Ecology and Conservation Biology. *Curr.*

1236   *Landsc. Ecol. Rep.* **7**, 137–146 (2022).

1237   203. Maclean, I. M. D. & Wilson, R. J. Recent ecological responses to climate change support

1238   predictions of high extinction risk. *Proc. Natl. Acad. Sci.* **108**, 12337–12342 (2011).

1239   204. Kissling, W. D. *et al.* Building essential biodiversity variables (EBV s) of species distribution

1240   and abundance at a global scale. *Biol. Rev.* **93**, 600–625 (2018).

1241   205. Gonzalez, A. *et al.* A global biodiversity observing system to unite monitoring and guide

1242   action. *Nat. Ecol. Evol.* (2023) doi:10.1038/s41559-023-02171-0.

1243   206. Chandler, M. *et al.* Contribution of citizen science towards international biodiversity

1244   monitoring. *Biol. Conserv.* **213**, 280–294 (2017).

1245   207. Pecl, G. T. *et al.* Redmap Australia: Challenges and Successes With a Large-Scale Citizen

1246   Science-Based Approach to Ecological Monitoring and Community Engagement on Climate

1247   Change. *Front. Mar. Sci.* **6**, 349 (2019).

1248   208. Middleton, I. *et al.* Introduced alien, range extension or just visiting? Combining citizen

1249   science observations and expert knowledge to classify range dynamics of marine fishes.

1250   *Divers. Distrib.* **27**, 1278–1293 (2021).

1251   209. Fraisl, D. *et al.* Citizen science in environmental and ecological sciences. *Nat. Rev. Methods*

1252   *Primer* **2**, 64 (2022).

1253   210. Paprocki, N., Heath, J. A. & Novak, S. J. Regional Distribution Shifts Help Explain Local

1254   Changes in Wintering Raptor Abundance: Implications for Interpreting Population Trends.

1255   *PLOS ONE* **9**, 9 (2014).

1256   211. Wilson, S., Anderson, E. M., Wilson, A. S. G., Bertram, D. F. & Arcese, P. Citizen Science

1257   Reveals an Extensive Shift in the Winter Distribution of Migratory Western Grebes. *PLoS*

1258   *ONE* **8**, e65408 (2013).

1259   212. Kirchman, J. J. & Van Keuren, A. E. Altitudinal Range Shifts of Birds At the Southern

1260   Periphery of the Boreal Forest: 40 Years of Change In the Adirondack Mountains. *Wilson J.*

1261   *Ornithol.* **129**, 742–753 (2017).

1262   213. Bird, T. J. *et al.* Statistical solutions for error and bias in global citizen science datasets.

1263   *Biol. Conserv.* **173**, 144–154 (2014).

1264   214. Estrada, A., Morales-Castilla, I., Caplat, P. & Early, R. Usefulness of Species Traits in

1265   Predicting Range Shifts. *Trends Ecol. Evol.* **31**, 190–203 (2016).

1266   215. Green, S. J., Brookson, C. B., Hardy, N. A. & Crowder, L. B. Trait-based approaches to global

1267   change ecology: moving from description to prediction. *Proc. R. Soc. B Biol. Sci.* **289**,

1268   20220071 (2022).

1269   216. Couet, J. *et al.* Short-lived species move uphill faster under climate change. *Oecologia* **198**,

1270   877–888 (2022).

1271   217. Tekwa, E. W., Watson, J. R. & Pinsky, M. L. Body size and food–web interactions mediate

1272   species range shifts under warming. *Proc. R. Soc. B Biol. Sci.* **289**, 20212755 (2022).

1273   218. Brito-Morales, I. *et al.* Climate Velocity Can Inform Conservation in a Warming World.

1274   *Trends Ecol. Evol.* **33**, 441–457 (2018).

1275   219. McRae, B. H., Viral B. Shah & Edelman, A. Circuitscape: modeling landscape connectivity to

1276   promote conservation and human health. (2016) doi:10.13140/RG.2.1.4265.1126.

1277   220. Bocedi, G. *et al.* RangeShifter 2.0: an extended and enhanced platform for modelling

1278   spatial eco-evolutionary dynamics and species' responses to environmental changes.

1279   *Ecography* **44**, 1453–1462 (2021).

1280   221. Cotto, O., Schmid, M. & Guillaume, F. Nemo-age: Spatially explicit simulations of eco-

1281   evolutionary dynamics in stage-structured populations under changing environments.

1282   *Methods Ecol. Evol.* **11**, 1227–1236 (2020).

1283   222. Kearney, M. R. & Porter, W. P. NicheMapR – an R package for biophysical modelling: the

1284   ectotherm and Dynamic Energy Budget models. *Ecography* **43**, 85–96 (2020).

1285   223. Bush, A. *et al.* Incorporating evolutionary adaptation in species distribution modelling

1286   reduces projected vulnerability to climate change. *Ecol. Lett.* **19**, 1468–1478 (2016).

1287   224. Engler, R., Hordijk, W. & Guisan, A. The MIGCLIM R package – seamless integration of

1288   dispersal constraints into projections of species distribution models. *Ecography* **35**, 872–

1289   878 (2012).

1290   225. Evans, M. E. K., Merow, C., Record, S., McMahon, S. M. & Enquist, B. J. Towards Process-

1291   based Range Modeling of Many Species. *Trends Ecol. Evol.* **31**, 860–871 (2016).

1292   226. Urban, M. C., Tewksbury, J. J. & Sheldon, K. S. On a collision course: competition and

1293   dispersal differences create no-analogue communities and cause extinctions during

1294   climate change. *Proc. R. Soc. B Biol. Sci.* **279**, 2072–2080 (2012).

1295   227. Bleyhl, B. *et al.* Reducing persecution is more effective for restoring large carnivores than

1296   restoring their prey. *Ecol. Appl.* **31**, e02338 (2021).

1297   228. Dietze, M. C. *et al.* Iterative near-term ecological forecasting: Needs, opportunities, and

1298   challenges. *Proc. Natl. Acad. Sci.* **115**, 1424–1432 (2018).

1299   229. Halpern, B. S. *et al.* Priorities for synthesis research in ecology and environmental science.

1300   *Ecosphere* **14**, (2023).

1301   230. Eveson, J. P., Hobday, A. J., Hartog, J. R., Spillman, C. M. & Rough, K. M. Seasonal

1302   forecasting of tuna habitat in the Great Australian Bight. *Fish. Res.* **170**, 39–49 (2015).

1303   231. Howell, E. A. *et al.* Enhancing the TurtleWatch product for leatherback sea turtles, a

1304   dynamic habitat model for ecosystem-based management. *Fish. Oceanogr.* **24**, 57–68

1305   (2015).

1306   232. Hobday, A. J., Spillman, C. M., Paige Eveson, J. & Hartog, J. R. Seasonal forecasting for

1307   decision support in marine fisheries and aquaculture. *Fish. Oceanogr.* **25**, 45–56 (2016).

1308   233. Hobday, A. J., Hartog, J. R., Spillman, C. M. & Alves, O. Seasonal forecasting of tuna habitat

1309   for dynamic spatial management. *Can. J. Fish. Aquat. Sci.* **68**, 898–911 (2011).

1310   234. Horton, K. G., Van Doren, B. M., Albers, H. J., Farnsworth, A. & Sheldon, D. Near-term

1311   ecological forecasting for dynamic aeroconservation of migratory birds. *Conserv. Biol.* **35**,

1312   1777–1786 (2021).

1313   235. Brooks, T. M. *et al.* Measuring Terrestrial Area of Habitat (AOH) and Its Utility for the IUCN

1314   Red List. *Trends Ecol. Evol.* **34**, 977–986 (2019).

1315   236. Fortin, M.-J. *et al.* Species' geographic ranges and distributional limits: pattern analysis and

1316   statistical issues. *Oikos* **108**, 7–17 (2005).

1317   237. Gaston, K. J. & Fuller, R. A. The sizes of species' geographic ranges. *J. Appl. Ecol.* **46**, 1–9

1318   (2009).

1319   238. Gaston, K. J. *The Structure and Dynamics of Geographic Ranges*. (Oxford University Press,

1320   2003).

1321   239. Yalcin, S. & Leroux, S. J. Diversity and suitability of existing methods and metrics for

1322   quantifying species range shifts: Yalcin and Leroux. *Glob. Ecol. Biogeogr.* **26**, 609–624

1323   (2017).

1324   240. Xu, C., Kohler, T. A., Lenton, T. M., Svenning, J.-C. & Scheffer, M. Future of the human

1325   climate niche. *Proc. Natl. Acad. Sci.* **117**, 11350–11355 (2020).

1326   241. Lenton, T. M. *et al.* Quantifying the human cost of global warming. *Nat. Sustain.* (2023)

1327   doi:10.1038/s41893-023-01132-6.

1328   242. Moat, J. *et al.* Resilience potential of the Ethiopian coffee sector under climate change.

1329   *Nat. Plants* **3**, 1–14 (2017).

1330   243. Pham, Y., Reardon-Smith, K., Mushtaq, S. & Cockfield, G. The impact of climate change and

1331   variability on coffee production: a systematic review. *Clim. Change* **156**, 609–630 (2019).

1332   244. Swartz, W., Sala, E., Tracey, S., Watson, R. & Pauly, D. The Spatial Expansion and Ecological

1333   Footprint of Fisheries (1950 to Present). *PLOS ONE* **5**, e15143 (2010).

1334   245. Cao, Y. *et al.* Trans-Arctic shipping routes expanding faster than the model projections.

1335   *Glob. Environ. Change* **73**, 102488 (2022).

1336   246. Paglia, E. A higher level of civilisation? The transformation of Ny-Ålesund from Arctic

1337   coalmining settlement in Svalbard to global environmental knowledge center at 79° North.

1338   *Polar Rec.* **56**, e15 (2020).

1339   247. Sokolickova, Z., Meyer, A. & Vlakhov, A. V. Changing Svalbard: Tracing interrelated socio-

1340   economic and environmental change in remote Arctic settlements. *Polar Rec.* **58**, e23

1341   (2022).

1342 248. OECD. *Climate Change in the European Alps: Adapting Winter Tourism and Natural*

1343 *Hazards Management*. (Organisation for Economic Co-operation and Development, 2007).

1344 249. Ma, S., Craig, C. A. & Feng, S. The Camping Climate Index (CCI): The development,

1345 validation, and application of a camping-sector tourism climate index. *Tour. Manag.* **80**,

1346 104105 (2020).

1347 250. Fisichelli, N. A., Schuurman, G. W., Monahan, W. B. & Ziesler, P. S. Protected Area Tourism

1348 in a Changing Climate: Will Visitation at US National Parks Warm Up or Overheat? *PLOS*

1349 *ONE* **10**, e0128226 (2015).

1350 251. Grillakis, M. G., Koutroulis, A. G., Seiradakis, K. D. & Tsanis, I. K. Implications of 2 °C global

1351 warming in European summer tourism. *Clim. Serv.* **1**, 30–38 (2016).

1352 252. World Tourism Organization, U. N. E. P. Climate Change and Tourism: Responding to

1353 Global Challenges. (2008).

1354 253. Coffel, E. D., Horton, R. M. & De Sherbinin, A. Temperature and humidity based

1355 projections of a rapid rise in global heat stress exposure during the 21st century. *Environ.*

1356 *Res. Lett.* **13**, 014001 (2018).

1357

1358

1359

1366   **Author contributions**

1367   J.A.L., L.C., G.G., J.L., B.v.A. and J.S. researched data for the article. J.A.L., L.C., G.G., J.L., J.A.B.,

1368   R.M.W.J.B., R.B., I.-C.C., S.E.D., L.T.L., N.M., J.M., B.F.O., G.T.P., M.L.P., J.R., M.R., B.S., L.M.T.,

1369   F.V., S.R.W., B.v.A., J.S. made a substantial contribution to discussion of content. All authors

1370   contributed to writing the article, and J.A.L. and J.S. reviewed the manuscript before

1371   submission.

1372

1373   **Competing interests**

1374   The authors declare no competing interests.

1375

1376   **Peer review information**

1377   *Nature Reviews Earth & Environment* thanks Janet Franklin and the other anonymous

1378   reviewer(s) for their contribution to the peer review of this work

1379

1380 **Figure legends**

1381

1382 Figure 1. Geographical and taxonomic biases in range shift detections. a) Taxonomic and

1383 geographical breakdown of latitudinal and elevational range shift estimates in the BioShifts

1384 database[22]. Each tile represents 10 empirically estimated range shifts of a given taxonomic

1385 group, always rounded up. b) Geographic bias of range shift studies in the BioShifts database.

1386 Each circle represents one range shift estimation study; circle sizes and inset numbers

1387 represent the number of species ranges assessed in each study, and color represents the type

1388 of shift estimated (marine latitudinal, terrestrial latitudinal and terrestrial elevational shifts).

1389 Note that one species might appear multiple times in a study if the study assesses multiple

1390 parts of the species range, or estimates shifts over multiple time periods, and a study might be

1391 represented in multiple continents.

1392

1393 Figure 2. Proportion of elevational (a) and latitudinal (terrestrial and marine) (b) range shift

1394 estimates consistent with temperature-based expectations (that is, direction of isotherm shifts)

1395 in the BioShifts database. Green and orange arrows signify range shift observations (raw

1396 changes in range positions over time) in agreement and opposition (respectively) to the

1397 direction of isotherm shifts in the study area, and tan segments show number of observations

1398 that estimated no range shift. Bars (excluding arrow heads) are sized by the total number of

1399 detections in each group. Note that only agreement between biological and climate shifts, but

1400 not the direction of the shift, are shown; (for example, in some cases climate change yields a

1401 downslope expectation for elevational shifts, but are portrayed as part of the upward arrow

1402 here if the detected biological shift matches the isotherm shift).

1403

1404 For new Fig 3 including numbered annotations:

1405 Figure 3. Factors driving range shifts. Solid and dotted outlines show the thermally-suitable

1406 habitat ('potential range') of a species in T1 and T2; blue and red shapes show the areas where

1407 the species is present ('realized range'). A) If temperature is the only driver of range shifts, a

1408 species' range is expected to shift from T1 (blue) to T2 (red), expanding at the cool edge and

1409   contracting at the warm edge owing to temperature-driven changes in performance of

1410   populations (inset graphs). B) Additional factors can deviate and/or diverge range shifts and

1411   range shift estimates from temperature-based expectations, including climate drivers other

1412   than temperature (1), non-climatic factors (2-5), and imperfect detection methods (6).

1413

1414   For new Fig 3 including in-figure text boxes and side legend:

1415   Figure 3. Factors driving range shifts. A) If temperature is the only driver of range shifts, a

1416   species' range is expected to shift from T1 (blue) to T2 (red), expanding at the cool edge and

1417   contracting at the warm edge owing to temperature-driven changes in performance of

1418   populations (inset graphs). B) Additional factors can deviate and/or diverge range shifts and

1419   range shift estimates from temperature-based expectations, including climate drivers other

1420   than temperature, non-climatic factors, and imperfect detection methods.

1421

1422   Figure 4. Lag between isotherm shifts and range shifts across study durations in the BioShifts

1423   database. Lag is calculated as shift velocity minus isotherm velocity; a perfectly isotherm-

1424   tracking shift would have a lag of zero. Purple dots signify range shifts estimates of trailing

1425   edges, green of leading edges for both elevational and latitudinal range shifts. Dashed lines

1426   show the 5th and 95th quantile regressions of all points in each plot.

1427
1428
1429   **Boxes**

1430   **Box 1. Key terms**

1431   [bH1] Isotherm

1432   Isolines connecting areas of equal temperature conditions across space, either at a given

1433   instance or as a summary of conditions over time (for example, annual mean temperature).

1434

1435   [bH1] Range edge

1436   Peripheries of a species' geographic distribution. Range edges (also called range margins, or

1437   limits) move across space in response to environmental change, and this process is termed

1438 range shifting. Range edges can be difficult to define in space (Box 2) and might not be set by

1439 current climate conditions, but denote the distributional limit for the species.

1440

1441 [bH1] Cold Edge

1442 The edge of a species distribution range located at the colder end of the temperature gradient,

1443 often the poleward or upslope edge.

1444

1445 [bH1] Warm Edge

1446 The edge of a species distribution range located at the warmer end of the temperature

1447 gradient, often the equatorward or downslope edge.

1448

1449 [bH1] Leading Edge

1450 Of a shifting range, the edge experiencing expansions, thus leading a range shift. Under climate

1451 change, this is normally expected to be the cold edge of the species range, where abiotic

1452 constraints will ease with warming.

1453

1454 [bH1] Trailing Edge

1455 Of a shifting range, the edge experiencing contractions, thus trailing a range shift. Under

1456 climate change, this usually refers to the warm edge of the species range, where warming

1457 makes regions of the past range increasingly unsuitable for the species.

1458

1459 [bH1] Range Expansion

1460 Dispersal and establishment of populations in areas where individuals were not consistently

1461 present. Climate change is expected to cause expansions when areas beyond the cold limit

1462 warm above the suitable threshold for the species. Also commonly termed range extension.

1463

1464 [bH1] Range Contraction

1465 Population declines or extirpations (that is, local extinction processes) at the edge of a species

1466 range, causing the edge to contract towards the center. In climate change scenarios,

1467 contractions are expected to occur; for example, when environments at the warm edge of a

1468 species range warm past the upper temperature threshold of the species such that populations

1469 are no longer viable.

1470

1471 Box 2.

1472 Range shift studies have taken a practical yet varied approach to defining range limits and

1473 centers despite an extensive literature on how species ranges could be defined[235–238], and these

1474 variations could influence downstream comparisons. Methods commonly used to define

1475 species ranges in biogeography research include mapping based on gridded occurrence records,

1476 creating convex polygons or linear extents along a transect from irregular observation points

1477 and using species distribution models to infer distributions based on environmental parameters

1478 when observational data are limited or disparate[239]. Each of these methods are further affected

1479 by the definition of viable occurrences which are used as input data. For example, depending

1480 on the resolution of the underlying data, the edge of a species range might be defined as the

1481 furthest straying individual at any life stage, the mean among multiple extreme individual

1482 observations, a high percentile among all observations, or the furthest known reproductively

1483 viable population (see figure). In addition, depending on the location and spatial extent of the

1484 study, the 'range edges' or 'range centers' defined within the study do not always represent the

1485 range edge or center of the global distribution. These varied definitions can cause problems

1486 when comparing findings between studies or even between sampling periods within studies,

1487 and can have a greater effect on range edges (that are defined by a lack of observations) than

1488 on range centers[130].

1489

1490 Practicality often calls for different definitions of range edges and centers for different data

1491 types. If a study relies on data from only a few sampling locations over a large timescale, a

1492 range edge defined as the furthest sampling location where the species is found might be

1493 appropriate. Alternatively, if a study uses high-resolution data such as regularly sampled grid

1494 cells over a continental scale, the authors might define the range edge as the average position

1495 of some percentile of occupied cells. In over 16,000 latitudinal range shift estimates included in

1496   the BioShifts database[22], a diversity of definitions have been used for each range section, and

1497   some tendency of consensual definitions across studies (see figure). Although consistency in

1498   the definition within taxa or studies can still provide estimates of shifts within studies (for

1499   example, the location of the 95% percentile of occurrences moved polewards), differences in

1500   definitions among studies can limit the interoperability of range shift data when combining

1501   them — for example, if some range definitions are more responsive to climate change than

1502   others.

1503

1504

1505   **Box 3. Human range shifts.**

1506   Shifting isotherms across Earth's surface are also changing climate conditions experienced by

1507   humans. Despite our great powers of niche construction and climate buffering compared with

1508   many other species, human distribution for centuries has clustered in a surprisingly narrow

1509   envelope of climatic conditions[240]. Anthropogenic climate change is shifting this climatic

1510   envelope away from existing human population centers, especially those in tropical climates,

1511   and creating novel challenges, opportunities, and ethical considerations regarding 'range shifts'

1512   of our own occupancy patterns and activities in a warming world[241].

1513

1514   Range shifts of human activities due to climate warming have already begun, both at

1515   contracting warm margins and expanding cold margins. Warming temperatures over the past 5

1516   decades have already led to poleward and upslope shifts of agricultural activities, including

1517   latitudinal shifts of 'breadbasket' and 'rice bowl' crops across continents[160] and upslope shifts

1518   of mountain crops such as coffee[242,243]. In the ocean, historical patterns of human ocean use

1519   have expanded concurrently with warming, as fishing fleets are shifting polewards by almost 1

1520   degree latitude per year[244] and trans-Arctic shipping routes have greatly expanded in

1521   navigability since the 1980s[245]. Warming conditions have also changed spatial patterns of

1522   scientific pursuit, resource extraction, and even recreation and tourism across latitude and

1523   elevation[246–252]. These changes to human behaviors might already be having downstream

1524   effects on natural environments, adding additional pressures to systems already facing stress

1525   from changing climates.

1526

1527   Whereas climate-driven range shifts of human activities have been documented, direct climate-

1528   related changes to human distributions are more difficult to attribute and predict because

1529   many factors, including politics, wealth distribution, infrastructure and cultural ties, influence

1530   people's decisions and ability to migrate. Shifting human climate envelopes underscore the

1531   need for robust adaptation strategies when climate-tracking migration is not possible. Models

1532   developed in the past 5-10 years predict large areas of extreme and unprecedented climates

1533   emerging as soon as 2030 that are projected to expand rapidly throughout the 21st

1534   century[240,241], even surpassing hypothesized human physiological tolerance thresholds by 2080

1535   in some scenarios[253]. Moreover, these trends call attention to the global ethical considerations

1536   of shifting climate regimes, as many regions at the warm margin of the shifting human niche

1537   are those contributing the least to global climate change[241].

1538

1539   **ToC blurb**

1540   Warming temperatures driven by climate change are causing species' geographic ranges to shift,

1541   but factors such as habitat characteristics and species interactions impact these changes. This

1542   Review examines empirical documentations of species' range shifts, the mechanisms by which

1543   shifts differ from temperature-based expectations, and the effects of range shifts on natural and

1544   human systems.

1545

Fig 1

a Taxonomic and geographic bias in range shift estimates
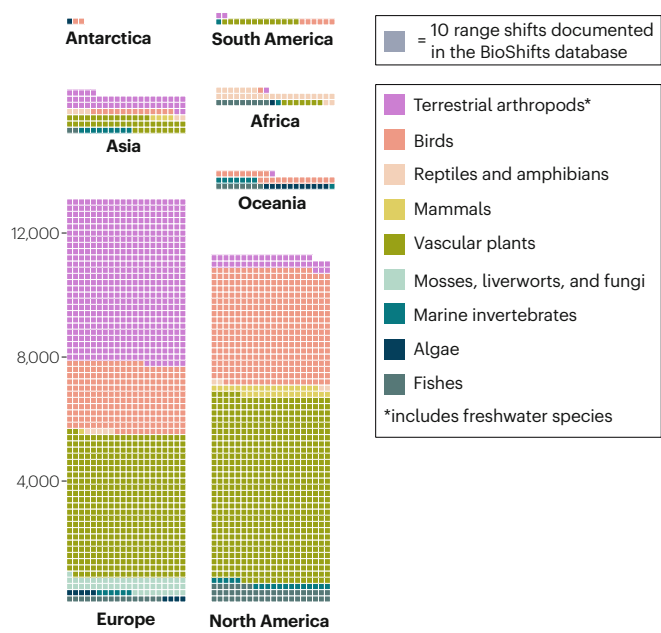
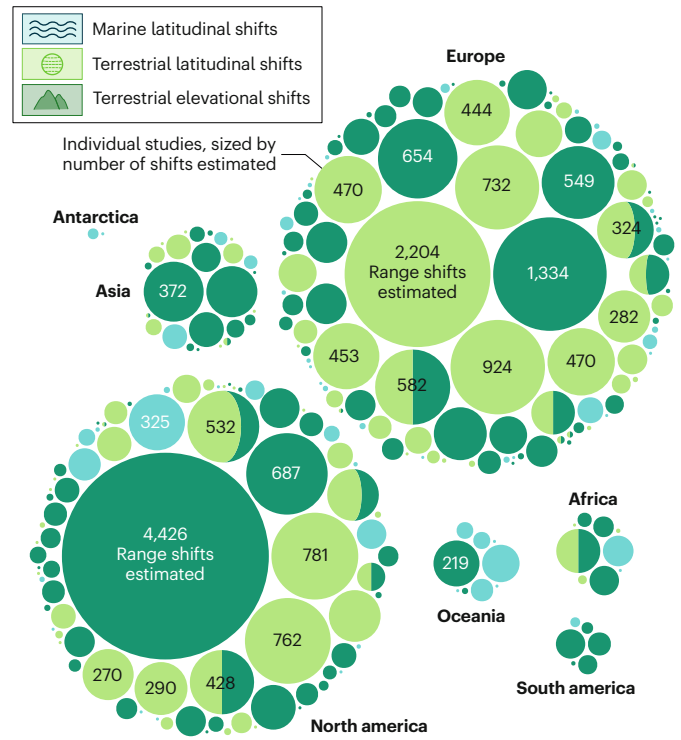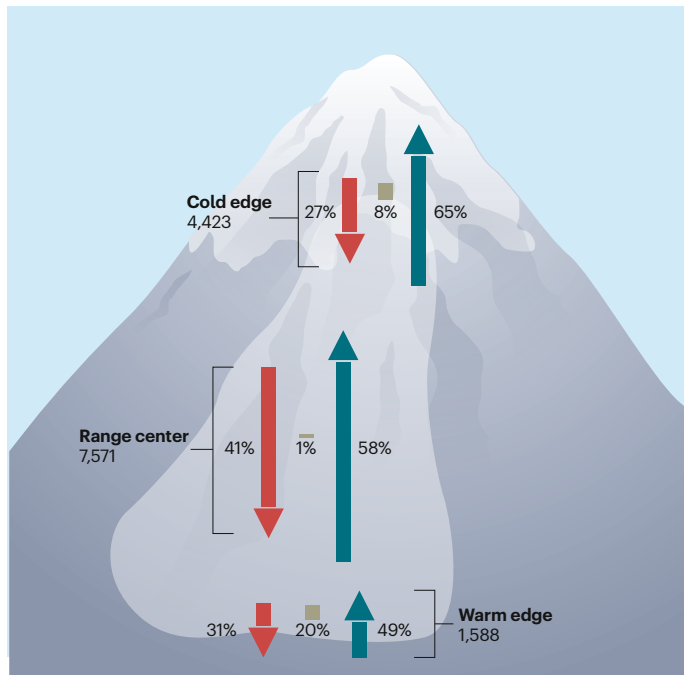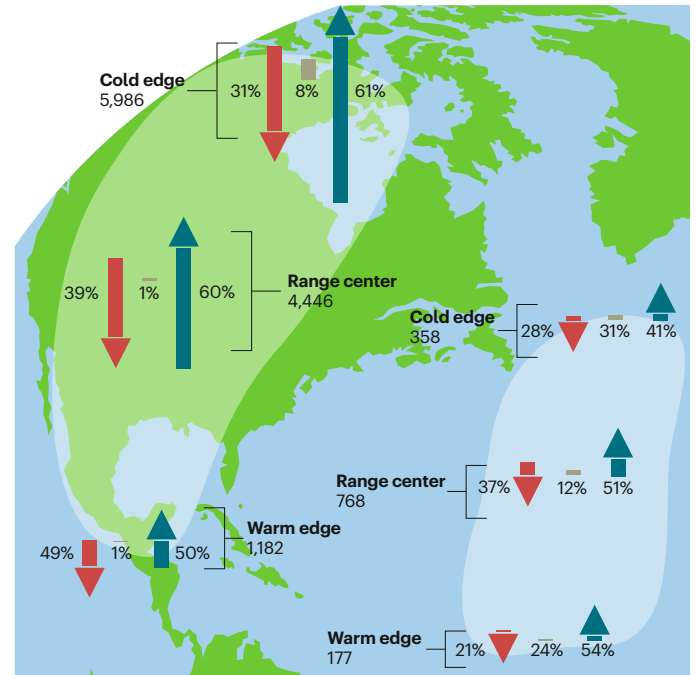**b** Geographic bias in range shift detection studies

Fig 2

a Elevational shifts

b Latitudinal shifts

Fig 3

a Range shifts driven solely by temperature shifts

Greater occurrence enabled by warming

Population persistence despite warming

Local extirpation caused by warming

Range expansions occur when populations disperse to newly climatically-available habitat at the leading edge.

Range contractions occur when temperature increases past the critical threshold, extirpating populations at the trailing edge.

T2 range — Area of expansion

T1 range — Area of range maintenance — Area of contraction

b Range shifts influenced by additional factors

Dispersal constraints can render newly-suitable area inaccessible to species, thus slowing shifts from temperature expectations.

Biotic interactions such as competing species' ranges can prevent shifts to otherwise suitable habitat.

Contemporary evolution or acclimation can broaden tolerance limits and allow persistence after climate conditions change.

Habitat limitations caused by human land use change or fragmented ecosystems can slow or stop range shifts from temperature-based expectations.

Detection methods and data resolution can skew observed shifts from true patterns.

Thermal niche underfilling can affect predictability of species responses to warming; ranges that are set by non-temperature factors during T1 are unlikely to track isotherms directly.

Climate drivers other than temperature can buffer or intensify temperature effects on range edges.

Fig 4

Elevational shifts   n = 6,010

Latitudinal shifts   n = 7,703

● Leading edge   ● Trailing edge

Box 1

Box 2