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Title: Improving the forecast for biodiversity under climate change

One sentence summary:

We review the information needed to understand, anticipate, and reduce the impacts of climate change on biodiversity.

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(1-6) (References from expanded abstract)

41 **Abstract:** New biological models are incorporating the realistic processes underlying biological
42 responses to climate change and other human-caused disturbances. However, these more realistic
43 models require detailed information, which is lacking for most species on Earth. Current
44 monitoring efforts mainly document changes in biodiversity, rather than collect the mechanistic
45 data needed to predict future changes. Here, we describe and prioritize the biological information
46 needed to inform more realistic projections of species responses to climate change. We also
47 highlight how trait-based approaches and adaptive modeling can leverage sparse data to make
48 broader predictions. We outline a global effort to collect the data necessary to better understand,
49 anticipate, and reduce the damaging effects of climate change on biodiversity.

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55 **Main Text:**

56 **Introduction**

57 We need to predict how climate change will alter biodiversity in order to prevent serious damage
58 to the biosphere (7). Biologists develop predictive models to anticipate how environmental
59 changes might affect the future properties of species and ecosystems (8, 9). Many models have
60 been developed to understand climate change impacts (Fig. S1) (10), but biological responses
61 remain difficult to predict (11, 12). One reason is that most models forecasting biodiversity
62 change ignore underlying mechanisms such as demographic shifts, species interactions, and
63 evolution, and instead extrapolate correlations between current species' ranges and climate (Fig.
64 1) (10). These omissions are troubling because we know that these missing biological
65 mechanisms played key roles in mediating past and present biotic responses to climate change
66 (13-15). Moreover, models ignoring biological mechanisms often become unreliable when
67 extrapolated to novel conditions (16-19). As climates and ecological communities without
68 historical precedent become more common and correlations between current species distributions
69 and climate become uncoupled (16, 20, 21), we cannot rely on tools based on statistical
70 descriptions of the past. Given the essential role of biological processes in mediating species
71 responses to climate change, accurate forecasts of future biodiversity likely will require more
72 realistic models.

73 Emerging models incorporate fundamental biological mechanisms rather than rely solely
74 on statistical correlations (6, 22-24). Unlike correlative approaches, mechanistic models do not
75 assume that a species' range reflects its niche perfectly, has reached equilibrium with the
76 environment, or is independent of species interactions – all commonly violated assumptions (13,
77 19, 25, 26). Mechanistic models also can integrate multiple, interacting biological processes,

78 nonlinear and stochastic dynamics (Fig. 2) (6, 23, 27), and can better characterize uncertainty by
79 directly modeling error sources (8, 26, 28).

80 By incorporating realistic processes such as demography and dispersal, mechanistic
81 models commonly outperform correlative approaches in projecting climate change responses
82 (19, 25). For example, mechanistic models consistently predicted simulated species' range
83 dynamics over 75 years, whereas correlative models became increasingly inaccurate over this
84 same timeframe (25). Mechanistic models improve predictive accuracy especially when species
85 face strong biotic interactions, experience novel climates, or cannot disperse far (19, 25, 29).
86 Moreover, mechanistic models can inform predictive efforts by indicating processes (e.g., biotic
87 limits on ranges) hidden by current associations between environments and species distributions
88 (29). Although more work is needed to craft more sophisticated and accurate mechanistic models
89 that are customizable for individual species and ecosystems, the tools are already mature enough
90 to improve projections (8, 22, 24).

91 Mechanistic models, however, require high-quality data about how a species' unique
92 biology governs its responses to climate. Parameters provide this information. For example, a
93 parameter like population growth rate determines how population abundances change through
94 time. In contrast, model variables like population abundance describe emergent properties.
95 Differentiating between parameters and variables is important given the recent focus on
96 harmonizing efforts to collect variables that monitor the state of global biodiversity (30). We
97 believe that such endeavors should not focus solely on collecting variables that indicate the state
98 of biodiversity, but also on measuring mechanistic parameters critical for predicting future
99 responses.

100 Here we identify the mechanistic data needed to make substantial gains in predictive
101 modeling. Rather than focusing on one particular mechanism (21, 23, 27, 31, 32), we take a
102 comprehensive approach, assess data availability for each mechanism, prioritize data needs,
103 demonstrate how to leverage sparse data to make general predictions, and suggest how global
104 coordination could facilitate these efforts. By synthesizing this information in one framework,
105 we aim to inspire the future research agenda needed to develop the full predictive potential of
106 mechanistic models. Consistent with the Intergovernmental Panel on Climate Change (IPCC),
107 we use ‘projection’ to define all descriptions of the future and reserve ‘forecast’ for the most
108 likely projections.

109

110 **Crucial biological information**

111 In table 1, we identify six mechanisms that determine biological responses to climate change.
112 Based on these six mechanisms, we assess data availability for four well-studied species (Fig. 3).
113 We find that although information on the six key mechanisms partly exists for species with high
114 economic value, it is incomplete for even the best-studied species and absent for the vast
115 majority of Earth’s species. Consequently, the most realistic models usually rely on sparse data
116 or data extrapolated from non-representative populations, environments, or species.

117 We next describe each mechanism in further detail, highlighting key parameters and
118 discussing challenges with measurement, uncertainty, and sensitivity. Here, uncertainty
119 encompasses both limited knowledge and random outcomes. Sensitivity denotes how changes in
120 a parameter value influence model outcomes. After describing these mechanisms, we
121 recommend how to collect data efficiently and leverage imperfect data.

122 **Physiology** – Physiology mediates how climate conditions like temperature, growing degree-
123 days, water availability, and potential evapotranspiration influence survival, growth,
124 development, movement, and reproduction (23, 33, 34). Physiological parameters include critical
125 thermal minima or maxima (the low and high temperatures at which organisms cease organized
126 movement), evaporative water loss, photosynthetic rate, and metabolic rate. These individual
127 physiological responses often are used to inform higher-level processes such as population
128 persistence and range shifts (34). For example, the time a lizard remains active outside its
129 burrow, where it is thermally neutral, can help predict its extinction risk under future climates
130 (35).

131 Physiologists measure parameters from natural observations or experiments in climate-
132 controlled chambers (33). However, using natural observations risks confounding responses to
133 climate with other environmental factors (33). High-priority traits include responses to extreme
134 heat or dryness, where survival often declines steeply. Uncertainty about physiological responses
135 increases when we lack information on habitat heterogeneity, local adaptation, and physiological
136 impacts on overall fitness.

137

138 **Demography, life history, and phenology** – Demographic (birth, death, migration), life history
139 (schedule of life cycle events), and phenological (timing of life history events) traits play critical
140 roles in climate change responses (34, 36). Important parameters include birth and death rates,
141 age at maturity, development rate, and reproductive investment. Parameters are best collected on
142 marked individuals across representative populations spanning different densities and climates.
143 However, these efforts require long-term, costly commitments. Changes in population
144 abundances from short-term weather variation can provide proxies, but become unreliable over

145 time. Long-term vegetation plots can provide detailed demographic information for plants.
146 Citizen scientists can collect data over large regions on traits like flowering time or breeding
147 date, but concerns about data quality likely limit its usefulness for less easily measured traits like
148 genetic variation.

149 Certain demographic parameters are especially important. For example, adult survival
150 often affects population growth rate more than fecundity in long-lived species (37). Density-
151 dependence and generation length also strongly affect extinction risk from climate change (27).
152 Additional uncertainty stems from local adaptation, responses to novel environments,
153 mismatched phenology, community shifts, and interactions with non-climate stressors (21, 38,
154 39).

155
156 ***Evolutionary potential and local adaptation*** – Assaying genetic variation is crucial for
157 predicting future responses (32, 40) because it could allow populations to adapt to climate
158 change in situ. Unfortunately, scientists seldom know if, or how fast, populations can evolve
159 climate-sensitive traits (38). Moreover, species usually comprise many locally adapted
160 populations that each respond differently to climate change (4). Species might not shift their
161 ranges with climate change if locally adapted populations become isolated and cannot colonize
162 new habitats (4). Alternatively, individuals dispersing from locally adapted populations might
163 track optimal climates across landscapes, and thus not need to adapt locally (Fig. 2) (17).

164 The breeder's and Price equations can be used to predict responses to natural selection
165 based on selection strength and genetic (co)variances (41). Genetic (co)variances are commonly
166 measured through controlled breeding experiments or pedigrees. However, these estimates can
167 become unreliable over long timescales or in novel environments if selection regimes or adaptive

168 potential change (42). Also, genetic (co)variances often vary among populations and
169 environments, thus requiring broad sampling and careful sensitivity analyses. Other approaches
170 involve tracking evolution using long-term observations, reconstructing evolution from layered
171 propagule banks, or applying experimental evolution (43, 44). For instance, comparing *Brassica*
172 *rapa* plants grown from seeds collected before and after a drought revealed rapid evolution of
173 flowering timing (44). Past local adaptations to spatial climatic gradients are easier to assess.
174 However, these patterns suggest past adaptive potential, not future evolutionary rates (38). By
175 scanning entire genomes, next-generation sequencing offers a promising tool to uncover fine-
176 scale evolutionary diversification (45), and declining genomic costs could rapidly expand our
177 limited knowledge of adaptive potential. Other frequently applied approaches include common
178 garden experiments, natural transplants, and observations of phenotypic variation (Table 1).

179 Adaptive potential and population differentiation represent high-priority parameters
180 because ignoring them contributes high levels of uncertainty (18, 32, 38, 44). For example, the
181 Quino checkerspot butterfly was expected to become extinct from climate change, but it persists
182 after adapting to live on a new host plant (46). Given limited genetic and evolutionary
183 information, we often will need to generalize adaptive rates across species based on
184 characteristics such as generation time, genetic isolation, phenotypic variation, and phylogenetic
185 position. Fortunately, even coarse estimates of maximum adaptive rate compared to climate
186 change suggest tipping points, where minor changes in climate initiate major biological
187 disruptions and thus represent targets for facilitating adaptation in threatened populations (47).

188
189 ***Species interactions*** – Species interactions often underlie unexpected responses to climate
190 change (16, 21), and most extinctions attributed to climate change to date have involved altered

191 species interactions (48). Surprises occur when specialist interactions like mutualism constrain
192 species' responses (49), phenological mismatches alter species interactions (39), or top
193 consumers propagate climate change effects throughout food webs (14). For instance, high
194 temperatures along the Pacific Coast exacerbated predation by sea stars on mussels, which
195 caused local extirpations (50). Yet, few models account for species interactions explicitly,
196 instead assuming that each species responds independently to climate change (12, 21) (Fig. 1).

197 High-quality information on species interactions requires well-resolved information
198 across interacting species, interaction types and strengths, spatiotemporal variation, and
199 phenology. Unfortunately, such detailed information is usually missing. One approach to
200 overcome this deficit is to analyze important subsets of strongly interacting species (21). Less
201 robust alternatives include estimating trophic position using isotopes, understanding competition
202 via diet breadth or species co-occurrence patterns, extrapolating from correlations between body
203 size and trophic level, or discerning species co-occurrence patterns from meta-genomics. High-
204 priority parameters include those characterizing specialist interactions, top-down food web
205 interactions, and timing mismatches among interacting species. High uncertainty arises from
206 changes in species interactions themselves (e.g., shifts from competition to facilitation) and
207 complex indirect effects that propagate through food webs (15). Additional uncertainties arise
208 from species' differential abilities to track climate change in space, creating previously unseen
209 communities as coevolved interactions disappear and novel interactions form (16).

210

211 ***Dispersal, colonization, and range dynamics*** – To persist, species often must track suitable
212 climates into new regions through dispersal, colonization, and subsequent range shifts (51, 52).
213 Most models unrealistically assume that all organisms disperse comparably and across any

214 landscape (Fig. 1) (31). In reality, dispersal depends on the interplay between individual
215 behavior, fitness, habitat quality, and landscape configuration. Range shifts are particularly
216 sensitive to dynamics at range boundaries where low abundances challenge accurate estimation
217 (53).

218 Global positioning system units can record fine-scaled individual movement, but are
219 costly and unsuitable for many small organisms. Passive integrated transponders, acoustic tags,
220 and telemetry devices track smaller individuals at lower cost, but require strategically placed
221 recorders. Neutral genetic variation across landscapes can indicate movement patterns, but
222 demographic history can confound these estimates. Citizen science sometimes enables cost-
223 effective, coordinated, and large-scale data collection, assuming adequate quality control.
224 Dispersal distances also can be inferred from proxies (e.g., body-size-dispersal relationships in
225 animals (51) and growth form, seed mass, and vegetation type in plants (54)) until better
226 estimates become available. Long-distance dispersal and fitness at range edges are high priority
227 parameters because they introduce high uncertainty in model outcomes (31), yet are difficult to
228 measure.

229

230 ***Environmental responses*** – Responses to climate change depend on species-specific sensitivities
231 and exposures to climate and habitat variation at relevant spatiotemporal scales. For instance,
232 butterflies and moths responded idiosyncratically to different climate variables, which accurately
233 predicted their observed responses to climate change (55). Researchers must carefully identify
234 which specific climate components actually affect species. Many organisms respond not to
235 average annual temperature or precipitation, but rather to temperature thresholds, season length,
236 humidity, potential evapotranspiration, or extreme events like droughts. Species also differ in the

237 relevant spatiotemporal scales of environmental variation. Researchers should evaluate the
238 environment through the eyes of the organism. The scales relevant to focal organisms often are
239 meters and minutes rather than the measurements in kilometers and months typically available.
240 Despite the increasing availability of fine-scaled information, most predictions are still made at
241 coarse scales, which can substantially reduce predictive accuracy (56). Hierarchical sampling can
242 maximize information content by combining large-scale sampling with targeted fine-scale
243 measurements that capture relevant gradients. Species characteristics like body size or generation
244 length also can provide proxies for missing data on species' environmental responses.

245 In addition, we need to integrate predictions of climate change with other human
246 disturbances, including land use, pollution, invasive species, and harvesting, to gauge the full
247 extent of future environmental change. Improving predictions of these disturbances and
248 downscaling data to relevant ecological resolutions is critical for reducing future uncertainty.

249

250 ***Interacting mechanisms*** – Each mechanism potentially interacts with many others. Specifically,
251 climate responses depend proximately on dispersal and demography; demography in turn
252 depends on physiology, species interactions, and environments; and each trait can evolve. For
253 example, great tit birds in the Netherlands do not lay eggs earlier in warmer springs (involving
254 demography, phenology, and environmental responses), while their caterpillar prey (species
255 interaction) emerge earlier. This phenological mismatch between birds and their prey decreases
256 nestling fitness (demography) (39). Yet, great tits from the United Kingdom do breed earlier in
257 warmer springs, suggesting population genetic differentiation (57). A challenge is to integrate
258 multiple interacting mechanisms without unnecessarily increasing model complexity (Fig. 2).

259

260 **A practical way forward**

261 We recognize that the complexity of natural systems will add uncertainty even to the best-
262 parameterized and most realistic models (58). Collecting the relevant information and developing
263 realistic biological models will require substantial investment in time and resources. Despite
264 these challenges, we believe that collecting mechanistic data will jointly enhance our
265 fundamental understanding of the biological processes that underlie climate responses and
266 contribute to more accurate, longer-term projections that facilitate more effective conservation.
267 Mechanistic models might not make accurate predictions initially, but learning from those
268 failures provides the insights that ultimately improve projections. Predictive science advances
269 most quickly via iterative prediction-failure-improvement cycles, and mechanistically grounded
270 models often quicken the pace of these advances (8, 9, 24). Even small gains in understanding
271 can improve future models by indicating critical missing information, highlighting key
272 uncertainties, suggesting general trait-based predictions for non-modeled organisms, and
273 delimiting the best options for retaining biodiversity under a range of future policy scenarios.

274 Given limited time and resources, however, we need to develop strategies that leverage
275 existing data and target essential information. Toward this end, we advocate for an adaptive
276 modeling scheme that facilitates cost-effective model development and data collection (Fig. 4).
277 The process of model testing and revision – steps rarely taken today, but facilitated by a more
278 systematic approach – can reveal data of particular importance for improving predictions.
279 Researchers first parameterize models with available data. In Table 1, we demonstrate how to
280 tailor data collection efforts to system-specific constraints by listing ideal methods along with
281 more easily collected proxies. Researchers then use independently collected variables from
282 monitoring efforts to test outcomes and fit uncertain relationships. Sensitivity analyses identify

283 the most important parameters to collect, ensuring that resources go toward producing the
284 greatest gains in accuracy. Based on these analyses, researchers can collect improved or new
285 parameter estimates and revise the model through successive iterations of the approach.
286 Crucially, results from multiple independent models should be combined because ensemble
287 forecasts often prove more accurate (9, 59). Researchers also need to articulate clearly how
288 uncertainty in parameter estimates and model choice propagates at each modelling step. We
289 recommend adopting the IPCC's standards for classifying model confidence and probabilistic
290 uncertainty.

291 Several approaches are available to extend projections from a few carefully studied
292 species to many unstudied ones. We often possess extensive information spread across many
293 species, but which is incomplete for any particular species. Emerging phylogenetic and trait-
294 based approaches could fill these data gaps. Trait-based approaches use trait correlations (e.g.,
295 between adult survival and fecundity) to predict missing parameters for species (51). Researchers
296 also can simulate the climate responses of virtual species with realistic combinations of traits.
297 For example, this virtual approach predicted that 30% of terrestrial mammals might not keep
298 pace with climate change (60). Minimally, these efforts provide qualitative insights about which
299 types of species are most vulnerable to climate change and therefore should be targeted for
300 future, in-depth study (27). Another cost-effective strategy is to prioritize research on species
301 with both high climate sensitivity and disproportionately large impacts on ecosystems. These so-
302 called biotic multipliers, often top predators and other keystone species, amplify small changes
303 in climate to produce large ecological effects (14) such that their future dynamics drive overall
304 ecosystem changes (15).

305 Conservation sometimes focuses on overall biodiversity rather than focal species.
306 Estimates from subsets of species might be extrapolated cautiously to overall biodiversity,
307 assuming suitable representation across taxonomic and phylogenetic diversity. However, trait-
308 based approaches might more efficiently suggest species with vulnerable trait combinations or
309 that amplify community-wide impacts of climate change. For example, focusing on top
310 consumers and other keystone species can indicate how their responses reverberate through
311 entire food webs (14), thus further extending the value of single-species forecasts.

312 Lastly, hybrid correlative-mechanistic approaches offer a pragmatic, initial approach to
313 improving predictions by adding key mechanisms to simple models. For example, adjusting
314 predicted ranges from correlative models with species-specific dispersal abilities (61) or
315 interacting species' ranges (49) can add realism and improve predictions. Given the simplicity of
316 most current approaches (Fig. 1), even minimally more realistic models might improve
317 projections until more complicated models can be developed (19, 24).

318

319 **Global coordination**

320 Global coordination will be critical at all stages, including defining projection goals, developing
321 better models, collating and incorporating existing data, determining which additional data might
322 improve forecasts, collecting new data, monitoring biodiversity changes, and organizing and
323 maintaining data. Researchers and policymakers first must agree on the nature of the projection
324 itself, including the accuracy, coverage, and time horizon of forecasts. A global clearinghouse
325 would be useful to organize trait data, standardize terminology (e.g., dispersal vs. migration), and
326 monitor climate responses.

327 It would also be useful to form regional working groups with local experts. Regional
328 working groups would define representative ecosystems and climatic and environmental
329 gradients in their region, while taking advantage of existing data and long-term monitoring sites.
330 Groups would select species representing a broad range of regional trait diversity and build
331 initial models with available data to estimate parameter sensitivity. To address immediate
332 extinction threats, regional working groups might also characterize the climate change risk for
333 threatened species on The International Union for Conservation of Nature Red List. Groups
334 should then develop plans to refine sensitive parameters through targeted funding opportunities
335 and citizen science. Collected biological information must be accessible, quality-checked,
336 standardized, and maintained in databases such as Encyclopedia of Life's TraitBank (traits) and
337 Global Biodiversity Information Facility (species' occurrences).

338 The IPCC's development of climate change predictions provides a template for how to
339 achieve comparable progress in biodiversity projections. The IPCC's biodiversity analogue, the
340 Intergovernmental Platform on Biodiversity and Ecosystem Services, can also help coordinate
341 this effort. Already the Group on Earth Observations – Biodiversity Observation Network is
342 developing a list of Essential Biodiversity Variables (EBVs) for monitoring global biodiversity
343 (30), and are working to address monitoring gaps (24). Despite some overlap between the
344 modeling parameters outlined here and EBVs, the two collection schemes differ given divergent
345 objectives. The EBVs monitor changes in biodiversity and provide variables for initializing and
346 testing mechanistic predictions. Mechanistic models, however, also require parameters governing
347 key processes, which often mandate more detailed observations or experiments than monitoring
348 programs currently entail.

349

350 **Combining predictive modeling with robust scenario analysis**

351 Collecting the data necessary to inform mechanistic biological models presents an enormous
352 challenge given the vast diversity of life, its complexity, and our inadequate knowledge about it.
353 This inherent complexity and stochasticity limits the accuracy of biological predictions for policy
354 and management (58, 62), especially over long forecast horizons (9). We must accept that even
355 the best-informed predictions could fail for a variety of unanticipated reasons.

356 An alternative approach to planning for climate change develops conservation strategies
357 robust to a broad range of future scenarios (63), thus insuring against inevitable surprises. For
358 example, applying this ‘robust scenario’ approach might include maintaining dispersal corridors,
359 preserving existing natural habitat and genetic diversity, and facilitating monitoring and flexible,
360 adaptive management (58, 64). This strategy broadly protects biodiversity and depends less on
361 accurate predictions. However, practical considerations will often limit which options are
362 feasible, especially when management options for one species trade off against another.

363 The two approaches are not mutually exclusive, and we believe that they work best in
364 tandem. Mechanistic approaches likely will improve predictions at intermediate time horizons,
365 e.g., 25-50 years, when current environmental correlations break down, and correlative
366 approaches become less accurate (9). Beyond this timeframe, even the best mechanistic models
367 become uncertain as key parameters can shift and uncertainty propagates. Yet, predictive models
368 are still needed to delimit plausible expectations, place bounds on uncertainty, and direct limited
369 resources toward strategies that target the most threatened regions and species (28, 58). Hence, a
370 tandem approach builds general insights from key, representative species while preserving
371 flexible options that work when models fail.

372

373 **Conclusions**

374 Analogously, climate scientists in 1975 acknowledged their inability to predict climate
375 accurately and highlighted the many challenges to reaching this objective (65). Despite these
376 challenges, they outlined an ambitious long-term research program aimed at understanding key
377 mechanisms governing climate change and collecting key pieces of missing information. This
378 program ultimately produced the improvements in forecasting weather and climate change that
379 society benefits from today. We believe that biology can and must do the same.

380 Here, we advocate for a renewed global focus on targeting the natural history information
381 needed to predict the future of biodiversity. Such efforts would more than compensate for their
382 cost by improving our ability to understand, anticipate, and thereby prevent biodiversity loss and
383 damage to ecosystems from climate change as well as other disturbances. Ultimately,
384 understanding how nature works will provide innumerable benefits for long-term sustainability
385 and human wellbeing.

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389 **References and Notes:**

390

- 391 1. M. Kearney, W. P. Porter, C. Williams, S. Ritchie, A. A. Hoffmann, Integrating
392 biophysical models and evolutionary theory to predict climatic impacts on species'
393 ranges: the dengue mosquito *Aedes aegypti* in Australia. *Funct. Ecol.* **23**, 528 (2009).
- 394 2. D. Murray-Rust *et al.*, Combining agent functional types, capitals and services to model
395 land use dynamics. *Environmental Modelling & Software* **59**, 187 (2014).
- 396 3. M. Kearney *et al.*, Modelling species distributions without using species distributions: the
397 cane toad in Australia under current and future climates. *Ecography* **31**, 423 (2008).
- 398 4. S. L. Pelini, J. A. Keppel, A. E. Kelley, J. J. Hellmann, Adaptation to host plants may
399 prevent rapid insect responses to climate change. *Glob Change Biol* **16**, 2923 (2010).
- 400 5. S. Jenouvrier *et al.*, Demographic models and IPCC climate projections predict the
401 decline of an emperor penguin population. *Proc. Natl. Acad. Sci. USA* **106**, 1844 (2009).
- 402 6. G. Bocedi *et al.*, RangeShifter: a platform for modelling spatial eco-evolutionary
403 dynamics and species' responses to environmental changes. *Method Ecol Evol* **5**, 388
404 (2014).
- 405 7. J. Settele *et al.*, in *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Fifth*
406 *Assessment Report of the Intergovernmental Panel of Climate Change*, C. B. Field *et al.*,
407 Eds. (Cambridge University Press, New York, 2014), pp. 1-153.
- 408 8. N. Mouquet *et al.*, Predictive ecology in a changing world. *J. Appl. Ecol.* **52**, 1293
409 (2015).

- 410 9. O. L. Petchey *et al.*, The ecological forecast horizon, and examples of its uses and
411 determinants. *Ecol. Lett.* **18**, 597 (2015).
- 412 10. M. C. Urban, Accelerating extinction risk from climate change. *Science* **348**, 571 (2015).
- 413 11. A. L. Angert *et al.*, Do species' traits predict recent shifts at expanding range edges? *Ecol.*
414 *Lett.* **14**, 677 (2011).
- 415 12. A. J. Davis, L. S. Jenkinson, J. H. Lawton, B. Shorrocks, S. Wood, Making mistakes
416 when predicting shifts in species range in response to global warming. *Nature* **391**, 783
417 (1998).
- 418 13. S. D. Veloz *et al.*, No-analog climates and shifting realized niches during the late
419 quaternary. *Glob Change Biol* **18**, 1698 (2012).
- 420 14. P. L. Zarnetske, D. K. Skelly, M. C. Urban, Biotic multipliers of climate change. *Science*
421 **336**, 1516 (2012).
- 422 15. E. Post, *Ecology of climate change: the importance of biotic interactions*. (Princeton UP,
423 Princeton, 2013).
- 424 16. M. C. Urban, J. J. Tewksbury, K. S. Sheldon, On a collision course: competition and
425 dispersal differences create no-analogue communities and cause extinctions during
426 climate change. *Proc. R. Soc. Lond. B.* **279**, 2072 (2012).
- 427 17. J. Norberg, M. C. Urban, M. Vellend, C. A. Klausmeier, N. Loeuille, Eco-evolutionary
428 responses of biodiversity to climate change. *Nat Clim Change* **2**, 747 (2012).
- 429 18. G. Bocedi *et al.*, Effects of local adaptation and interspecific competition on species'
430 responses to climate change. *Ann N Y Acad Sci* **1297**, 83 (2013).

- 431 19. D. Zurell *et al.*, Benchmarking novel approaches for modelling species range dynamics.
432 *Glob Change Biol*, doi: 10.1111/gcb.13251 (2016).
- 433 20. J. W. Williams, S. T. Jackson, J. E. Kutzbach, Projected distributions of novel and
434 disappearing climates by 2100 AD. *Proc. Natl. Acad. Sci. USA* **104**, 5738 (2007).
- 435 21. S. E. Gilman, M. C. Urban, J. Tewksbury, G. W. Gilchrist, R. D. Holt, A framework for
436 community interactions under climate change. *Trends Ecol. Evol.* **25**, 325 (2010).
- 437 22. D. Purves *et al.*, Ecosystems: time to model all life on earth. *Nature* **493**, 295 (2013).
- 438 23. M. Kearney, W. Porter, Mechanistic niche modelling: combining physiological and
439 spatial data to predict species' ranges. *Ecol. Lett.* **12**, 334 (2009).
- 440 24. S. M. McMahon *et al.*, Improving assessment and modelling of climate change impacts
441 on global terrestrial biodiversity. *Trends Ecol. Evol.* **26**, 249 (2011).
- 442 25. J. Pagel, F. M. Schurr, Forecasting species ranges by statistical estimation of ecological
443 niches and spatial population dynamics. *Global Ecol. Biogeography* **21**, 293 (2012).
- 444 26. H. R. Pulliam, On the relationship between niche and distribution. *Ecol. Lett.* **3**, 349
445 (2000).
- 446 27. R. G. Pearson *et al.*, Life history and spatial traits predict extinction risk due to climate
447 change. *Nat Clim Change* **4**, 217 (2014).
- 448 28. A. Singer *et al.*, Community dynamics under environmental change: How can next
449 generation mechanistic models improve projections of species distributions? *Ecol Model*,
450 (2015).

- 451 29. L. B. Buckley *et al.*, Contrasting correlative and mechanistic models of species ranges:
452 putting concepts into practice. *Ecol. Lett.* **13**, 1041 (2010).
- 453 30. H. M. Pereira *et al.*, Essential biodiversity variables. *Science* **339**, 277 (2013).
- 454 31. M. C. Urban, P. L. Zarnetske, D. K. Skelly, Moving forward: Dispersal and species
455 interactions determine biotic responses to climate change. *Ann N Y Acad Sci* **1297**, 44
456 (2013).
- 457 32. A. A. Hoffmann, C. M. Sgro, Climate change and evolutionary adaptation. *Nature* **470**,
458 479 (2011).
- 459 33. M. J. Angilletta, *Thermal adaptation: a theoretical and empirical synthesis*. (Oxford UP,
460 Oxford, 2009).
- 461 34. L. Crozier, G. Dwyer, Combining population-dynamic and ecophysiological models to
462 predict climate-induced insect range shifts. *Am. Nat.* **167**, 853 (2006).
- 463 35. B. Sinervo *et al.*, Erosion of lizard diversity by climate change and altered thermal
464 niches. *Science* **328**, 894 (May 14, 2010, 2010).
- 465 36. D. A. Keith *et al.*, Predicting extinction risks under climate change: coupling stochastic
466 population models with dynamic bioclimatic habitat models. *Biology Letters* **4**, 560
467 (2008).
- 468 37. B.-E. Sæther, Ø. Bakke, Avian life history variation and contribution of demographic
469 traits to the population growth rate. *Ecology* **81**, 642 (2000).
- 470 38. J. Merilä, A. P. Hendry, Climate change, adaptation, and phenotypic plasticity: the
471 problem and the evidence. *Evol Appl*, (2014).

- 472 39. M. E. Visser, A. J. van Noordwijk, J. M. Tinbergen, C. M. Lessells, Warmer springs lead
473 to mistimed reproduction in Great Tits (*Parus major*). *Proc. R. Soc. Lond. B.* **265**, 1867
474 (1998).
- 475 40. S. P. Carroll *et al.*, Applying evolutionary biology to address global challenges. *Science*,
476 (September 11, 2014, 2014).
- 477 41. M. B. Morrissey *et al.*, The prediction of adaptive evolution. *Evolution* **66**, 2399 (2012).
- 478 42. J. P. Reeve, Predicting long-term response to selection. *Genet. Res.* **75**, 83 (2000).
- 479 43. W. E. Bradshaw, C. M. Holzapfel, Evolutionary response to rapid climate change.
480 *Science* **312**, 1477 (2006).
- 481 44. S. J. Franks, S. Sim, A. E. Weis, Rapid evolution of flowering time by an annual plant in
482 response to a climate fluctuation. *Proc. Natl. Acad. Sci. USA* **104**, 1278 (2007).
- 483 45. J. Buckley, R. K. Butlin, J. R. Bridle, Evidence for evolutionary change associated with
484 the recent range expansion of the British butterfly, *Aricia agestis*, in response to climate
485 change. *Mol. Ecol.* **21**, 267 (2012).
- 486 46. C. Parmesan, in *Butterfly Conservation 7th International Symposium*. (Southampton
487 University, 2014).
- 488 47. C. A. Botero, F. J. Weissing, J. Wright, D. R. Rubenstein, Evolutionary tipping points in
489 the capacity to adapt to environmental change. *Proc. Natl. Acad. Sci. USA* **112**, 184
490 (2015).
- 491 48. A. E. Cahill *et al.*, How does climate change cause extinction? *Proc. R. Soc. Lond. B.*
492 **280**, 20121890 (2012).

- 493 49. O. Schweiger, J. Settele, O. Kudrna, S. Klotz, I. Kuhn, Climate change can cause spatial
494 mismatch of trophically interacting species. *Ecology* **89**, 3472 (2008).
- 495 50. C. D. G. Harley, Climate Change, Keystone Predation, and Biodiversity Loss. *Science*
496 **334**, 1124 (November 25, 2011, 2011).
- 497 51. C. A. Schloss, T. A. Nunez, J. J. Lawler, Dispersal will limit ability of mammals to track
498 climate change in the Western Hemisphere. *Proc. Natl. Acad. Sci. U. S. A.* **109**, 8606
499 (2012).
- 500 52. B. J. Anderson *et al.*, Dynamics of range margins for metapopulations under climate
501 change. *Proc. R. Soc. Lond. B.*, (2009).
- 502 53. J. P. Sexton, P. J. McIntyre, A. L. Angert, K. J. Rice, Evolution and ecology of species
503 range limits. *Annu. Rev. Ecol. Syst.* **40**, 415 (2009).
- 504 54. F. J. Thomson *et al.*, Chasing the unknown: predicting seed dispersal mechanisms from
505 plant traits. *J. Ecol.* **98**, 1310 (2010).
- 506 55. G. Palmer *et al.*, Individualistic sensitivities and exposure to climate change explain
507 variation in species' distribution and abundance changes. *Science Advances* **1**, (2015).
- 508 56. R. Early, D. F. Sax, Analysis of climate paths reveals potential limitations on species
509 range shifts. *Ecol. Lett.* **14**, 1125 (2011).
- 510 57. A. Charmantier *et al.*, Adaptive phenotypic plasticity in response to climate change in a
511 wild bird population. *Science* **320**, 800 (2008).
- 512 58. D. E. Schindler, R. Hilborn, Prediction, precaution, and policy under global change.
513 *Science* **347**, 953 (2015).

- 514 59. M. B. Araújo, M. New, Ensemble forecasting of species distributions. *Trends Ecol. Evol.*
515 **22**, 42 (2007).
- 516 60. L. Santini *et al.*, A trait-based approach for predicting species responses to environmental
517 change from sparse data: how well might terrestrial mammals track climate change? *Glob*
518 *Change Biol*, doi:10.1111/gcb.13271 (2016).
- 519 61. S. Dullinger *et al.*, Extinction debt of high-mountain plants under twenty-first-century
520 climate change. *Nat Clim Change* **2**, 619 (2012).
- 521 62. B. Beckage, L. J. Gross, S. Kauffman, The limits to prediction in ecological systems.
522 *Ecosphere* **2**, 1 (2011).
- 523 63. R. J. Lempert, M. E. Schlesinger, Robust strategies for abating climate change. *Climatic*
524 *Change* **45**, 387 (2000).
- 525 64. B. Rayfield, D. Pelletier, M. Dumitru, J. A. Cardille, A. Gonzalez, Multipurpose habitat
526 networks for short-range and long-range connectivity: a new method combining graph
527 and circuit connectivity. *Method Ecol Evol* **7**, 222 (2016).
- 528 65. U. S. N. A. o. Sciences, U. S. C. f. t. G. A. R. P. Panel on Climatic Variation, National
529 Research Council, Ed. (National Academy of Sciences, Washington, D.C., 1975), pp.
530 239.

531

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541

542 **Supplementary Materials:**

543 Fig. S1

544 Table S1

545 **Fig. 1: Most models of biological responses to climate change omit important biological**
546 **mechanisms.** Only 23% of reviewed studies (10) included a biological mechanism. Models that
547 included one mechanism usually incorporated others, but no model included all six mechanisms.
548 All models included environmental variation, generally via correlations, but usually did not
549 explicitly incorporate species' sensitivities to environmental variation at relevant spatiotemporal
550 scales.

551
552 **Fig. 2: A generic model integrates six biological mechanisms to predict climate change**
553 **responses.** The six mechanisms A) are matched by color to their representation in equations (B)
554 simplified from (17) (see Table S1 for symbol descriptions). Results suggest how dispersal (blue-
555 purple), adaptive evolution (yellow), and their combination (red-orange) determine the match
556 between community-wide thermal traits and changing local temperatures (C). Temperatures
557 increase before stabilizing at the white dotted line. Black indicates no trait change. In cold
558 regions, warm-adapted species disperse into newly suitable, warmer habitats. In warm regions,
559 evolution dominates because no species with higher thermal tolerances exist. D) shows
560 equilibrium abundances of five hypothetical species (each indicated by differently colored lines)
561 following climate change.

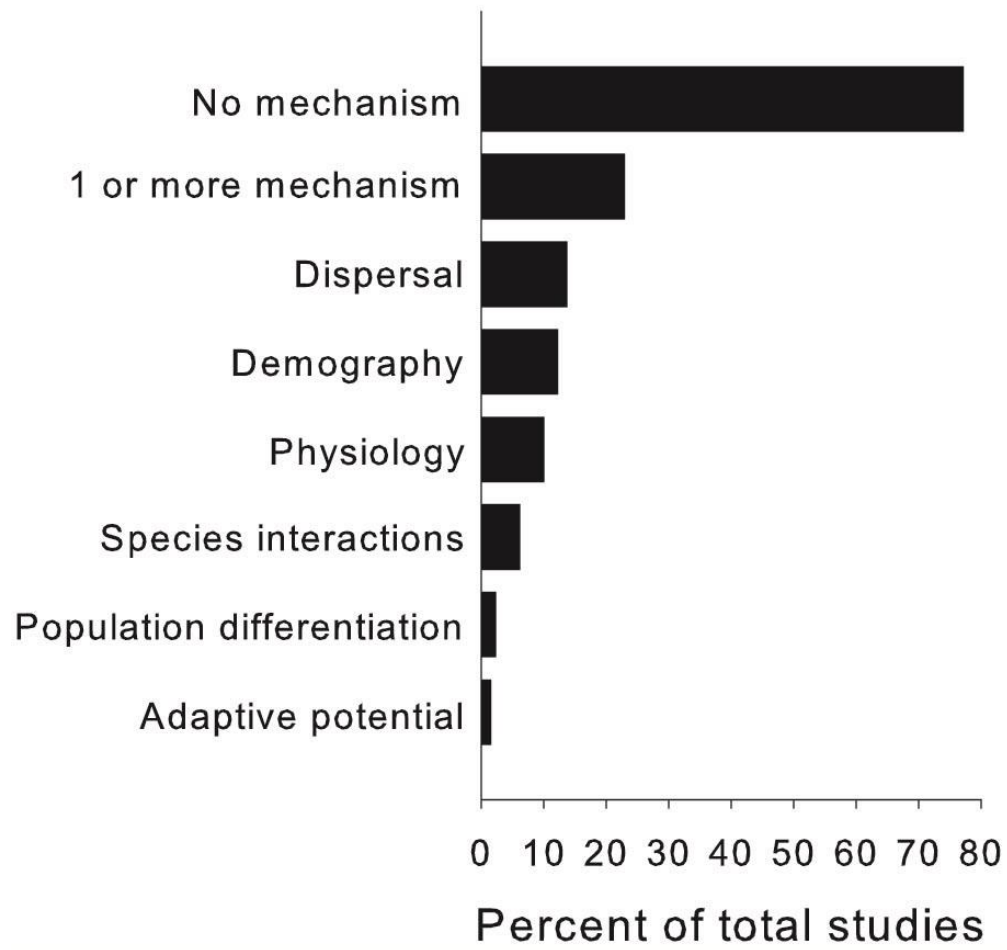
562
563 **Fig. 3: Data gaps exist even for well-studied species.** We rated data quality for some of the
564 best-studied species in climate change research: a) fence lizard, b) sockeye salmon, c) speckled
565 wood butterfly, and d) European beech. Data quality: high = near-complete information, medium
566 = information available but missing critical components, low = information mostly absent. We

567 evaluated data availability by examining models of climate responses, reviewing species-specific
568 literature, and contacting experts.

569

570 **Fig. 4: Biological models improve iteratively through time by applying an adaptive**
571 **modeling scheme.** Steps include parameterizing models using available data, estimating
572 parameter sensitivities, targeting better measurements for sensitive parameters, validating
573 projections with observations, and iteratively refining and updating the model to improve
574 predictive accuracy and precision through time.

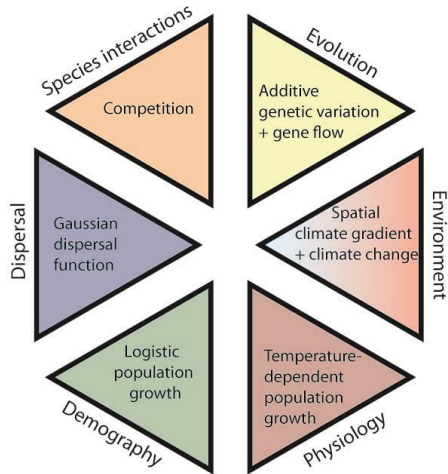
575 Figure 1



576

A synthetic model of climate change responses

A) Model components



B) Model equations

$$\frac{\partial N_i}{\partial t} = g_i N_i + D_i \frac{\partial^2 N_i}{\partial x^2}$$

Change in population (N)
population dynamics
dispersal

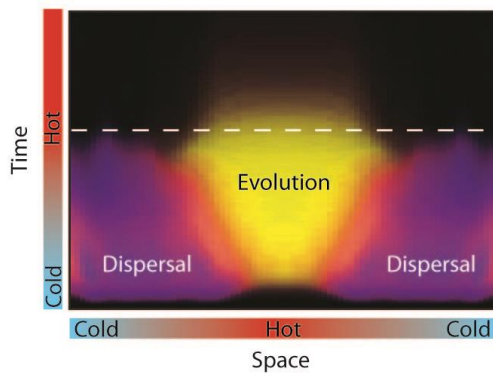
$$g_i(x, t) = r_{max} N_i \exp\left(\frac{-(TC(x, t) - z_i(x, t))^2}{\omega^2}\right) \left(1 - \sum_j \alpha_{ij} N_j(x, t)\right)$$

Fitness
temperature-dependent growth
competition

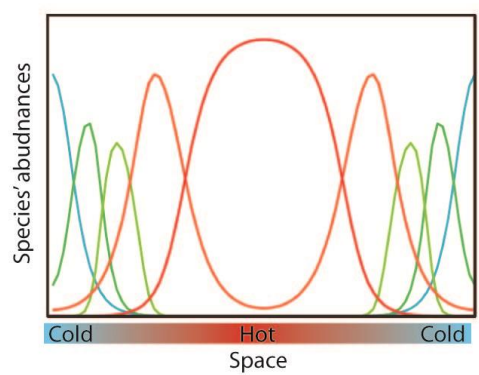
$$\frac{\partial z_i}{\partial t} = q_i V_i \frac{\partial^2 g_i}{\partial z} \Big|_{z=z_i} + D_i \left(\frac{\partial^2 z_i}{\partial x^2} + 2 \frac{\partial \log N_i}{\partial x} \frac{\partial z_i}{\partial x} \right)$$

Change in trait (z)
directional selection
gene flow

C) Model spatiotemporal dynamics



D) Model results



578

579

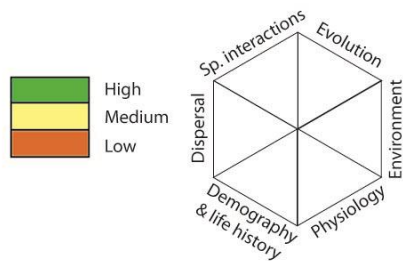
580

581 Figure 3

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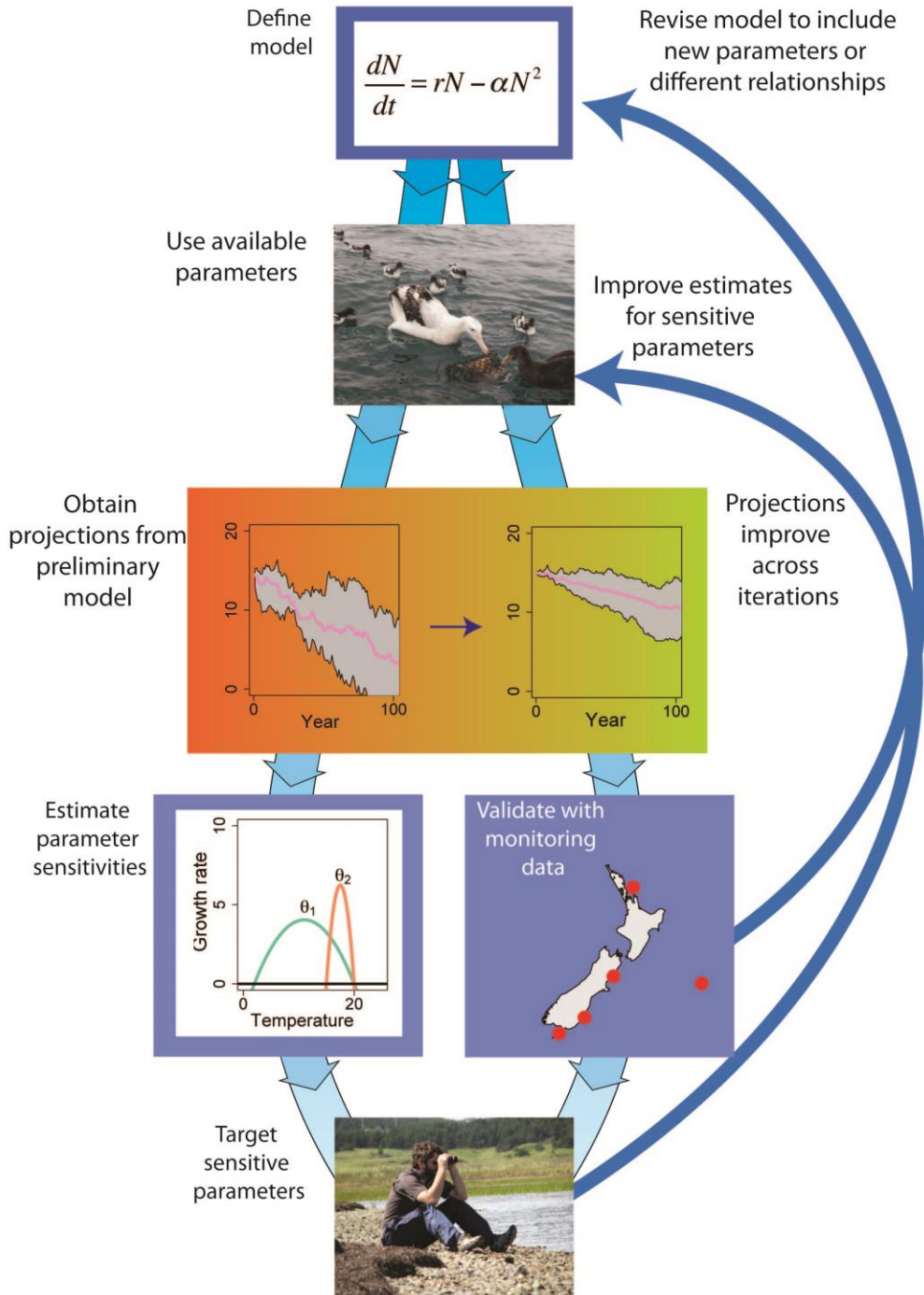
Quality of information



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Adaptive parameterization of biotic models



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Table 1. Biological Parameters, Collection Methods, Proxies, Priorities, and Key Uncertainties

We list six classes of biological modeling parameters, example parameters, methods to collect them, possible proxy relationships that could fill in gaps for poorly studied taxa, priority parameters, and key remaining uncertainties.

Biological mechanisms	Example parameters	Alternative and complementary methods*	Proxy relationships	Priority parameters	Key uncertainties
1. Physiology	Thermal, desiccation, and chemical tolerances; environment-dependent performance and metabolic rate; photosynthesis	1. Experimental understanding of physiological responses to environmental conditions in nature or laboratory 2. Observed correlations between physiological responses and environmental conditions in time or space 3. Trait-based proxies (e.g., body mass for metabolism)	1. Body mass correlates strongly with energy requirements 2. Water and light requirements in vegetation models	Physiological responses in extreme environments (e.g., performance under hot or dry conditions)	How does behavior modify physiology? To what degree do organisms evolve different physiological responses across a range? How do physiological sensitivities of different performance traits scale to whole-organism fitness?
2. Demography, life history, and phenology	Birth and death rates, including age or stage structure, age of maturity, development and growth rates, environmental dependence, timing,	1. Long-term mark recapture parentage studies or long-term demographic data from vegetation plots 2. Experimental studies of environment-dependent birth and death rates in nature (best) or in the laboratory	1. Demographic parameters correlate with life history traits (e.g., slow-fast continuum) and niche specialization	vital rates most influencing population growth rates – e.g. adult survival for long-lived organisms,	To what degree do organisms evolve different life histories across a range? Does rapid adaptation to climate change play a role?

	and individual variability	3. Population growth rates from observed abundance data		generation length, mismatches in timing of life history events	<p>When does phenology depend on climate versus non-climate triggers (e.g., day length)?</p> <p>How do other environmental changes (e.g., habitat degradation) interact with climate responses?</p>
3. Evolutionary potential and selection	Additive genetic trait (co)variance/heritability and additive genetic covariance between traits and fitness	<p>1. Quantitative genetic variation in key traits estimated from controlled breeding designs, populations with pedigrees, or from individuals raised under common conditions</p> <p>2. Experimental or correlational estimation of selection gradients</p> <p>3. Gene expression patterns for understanding functional trait variation under different environmental conditions</p> <p>4. Phenotypic variation within populations</p>	<p>1. Evolutionary rates correlate negatively with generation length</p> <p>2. Genetic variation within populations positively correlated with population size</p> <p>3. Space-for-time substitutions</p>	Adaptive potential, local adaptation of climate-sensitive parameters across species' range	<p>To what degree is trait change determined by genetics versus environment?</p> <p>How well do short-term measurements of adaptive mechanisms perform in the long run?</p> <p>How does local adaptation within a range alter species-</p>

Population differentiation	Fitness differences among populations and environments, genetic variation among populations, phenotypic variation, including plasticity, among populations	<ol style="list-style-type: none"> 1. Reciprocal transplant and common garden experiments that reveal fitness and trait differences among populations in response to relevant environmental gradients 2. Statistical search for variation in loci under selection 3. Gene expression patterns for understanding functional trait variation under different environmental conditions 4. Population genetics with neutral loci to understand population differentiation through barriers to gene flow 5. Observation of phenotypic variation within and among populations 	<ol style="list-style-type: none"> 1. Genetic variation among populations positively correlated with range size. 		level responses to climate change?
4. Species interactions	Interaction webs with spatiotemporal variation and phenology, interaction types and strengths, community module, diet or resource	<ol style="list-style-type: none"> 1. Experimental evaluation of species interaction strength and direction in nature (best) or laboratory 2. Natural history observations of interactions 	<ol style="list-style-type: none"> 1. Trophic level increases with body size 2. Similar trophic levels shared by phylogenetically similar species 	Specialist interactions, sensitivity of top consumers, phenological mismatches between	<p>What happens as coevolved interactions disappear and new species interactions form?</p> <p>How sensitive are food webs to top-</p>

	overlap, trophic position	<p>3. Isotope analysis to reveal trophic levels and food web links</p> <p>4. Statistical co-occurrence patterns (e.g., checkerboard patterns for competition)</p>		interacting species	<p>down versus bottom-up climate disturbances?</p> <p>To what degree can species adapt to novel species interactions?</p>
5. Dispersal, colonization, and range dynamics	Dispersal behaviors, movement and settlement rules, inter-individual variability, environment-, density- and condition-dependent dispersal, landscape permeability (e.g., least-cost path analysis)	<p>1. Satellite telemetry of moving organisms to reveal landscape movement tracks</p> <p>2. Mark-recapture and relocations to evaluate absolute movement</p> <p>3. Experiments (e.g., linked mesocosms) to understand movement</p> <p>4. Landscape genetics to reveal landscape connectivity among populations</p> <p>5. Historical reconstruction of movement patterns during expansion</p> <p>6. Incidence functions in metapopulations to determine population connectivity</p> <p>7. Citizen science to track organisms (e.g., tagged birds)</p>	<p>1. Larger bodied animals disperse farther</p> <p>2. Smaller seeds travel farther</p> <p>3. Animal dispersed seeds travel farther</p> <p>4. Larger winged organisms disperse farther</p> <p>5. Pelagic animals disperse farther than benthic ones</p>	Long-distance dispersal, fitness at range boundaries	<p>How important is long-range dispersal for range dynamics?</p> <p>How does fitness vary across a range?</p>

6. Responses to environmental variation	Functional relationships between traits and environments, identification and quantification of key environmental gradients across species-relevant scales of space and time	<ol style="list-style-type: none"> 1. Experimental manipulation of key environments to understand functional responses 2. Statistical analysis of environmental gradients and responses 3. Characterization of environmental gradients at biologically relevant scales <ol style="list-style-type: none"> a. Surveys of environmental parameters conducted at relevant spatial and temporal scales b. Ground-truthed maps to be used in environmental gradient analyses c. Statistical interpolation of coarse map data 	<ol style="list-style-type: none"> 1. Determining networks of co-acting environmental variables 2. Correlating easily collected GIS data to other factors such as resources 	Identifying key gradients, spatial scale-dependence of environmental responses, dynamic change in gradients	<p>Are there general ways to predict the relevant scales that species will respond to environmental variation?</p> <p>What biological parameters are linked with the environmental factors and how?</p> <p>How are important environmental gradients changing through time?</p>
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592 Note that each of these mechanisms likely interacts with other mechanisms.

593 * We list methods in an illustrative descending order of data accuracy. The ordering of collection methods are considered illustrative
594 only and will clearly change depending on the particular attributes of species and systems. The best methods however might not be
595 easily implemented for some taxa, necessitating more practical methods, followed by sensitivity analysis. They will also change
596 through time, for example, as emerging methods become less costly. In reality, the ideal approach for collecting data on a key process
597 will involve joint use of more than one method. For example, for dispersal we might currently want to collect high quality telemetry
598 data for the movement of a relatively small number of dispersers due to cost constraints while also obtaining population-level

599 estimates of dispersal through either landscape genetics or mark-release-recapture methods (or both). We encourage readers to tailor
600 costs and benefits of the alternative and complementary approaches to their own system and adjust decisions for investment of
601 resources appropriately.

602