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Predicting population responses to environmental change from individual-level mechanisms: towards a standardized mechanistic approach

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1 **Predicting population responses to environmental change from individual-level**
2 **mechanisms: towards a standardised mechanistic approach**

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14

15 **Running title: Animal responses to environmental change**

16

17 **Abstract**

18 Animal populations will mediate the response of global biodiversity to environmental
19 changes. Population models are thus important tools for both understanding and predicting
20 animal responses to uncertain future conditions. Most approaches, however, are correlative
21 and ignore the individual-level mechanisms that give rise to population dynamics. Here, we
22 assess several existing population modelling approaches, and find limitations to both
23 'correlative' and 'mechanistic' models. We advocate the need for a standardised mechanistic
24 approach for linking individual mechanisms (physiology, behaviour and evolution) to
25 population dynamics in spatially explicit landscapes. Such an approach is potentially more
26 flexible and informative than current population models. Key to realising this goal, however,
27 is overcoming current data limitations, the development and testing of eco-evolutionary
28 theory to represent interactions between individual mechanisms, and standardised

29 multidimensional environmental change scenarios which incorporate multiple stressors.
30 Such progress is essential in supporting environmental decisions in uncertain future
31 conditions.

32

33 **Keywords:** individuals, population models, physiology, behaviour, evolution, environmental
34 change.

35

36 **1. Introduction**

37 Animal responses to environmental change have wide-ranging consequences for global
38 biodiversity and ecosystem functioning, through altered species interactions, richness,
39 community composition and the transfer of energy and nutrients (1). Yet, much remains
40 unknown about the selective nature of environmental changes and the interactive effects of
41 multiple stressors (2). An urgent challenge is thus to better understand the mechanisms
42 underpinning animal population responses to environmental change, in order to better
43 anticipate the effects of novel future conditions (3).

44

45 Disentangling the mechanisms that give rise to population responses is a multifaceted
46 challenge. The urgency of understanding this complexity is likely responsible for the many
47 correlative approaches to ecological forecasting (4). Yet, such approaches cannot reliably
48 extrapolate outside of the observed environmental range (5,6) and fail to represent key
49 biological and ecological mechanisms that mediate species responses in heterogeneous
50 landscapes (7). Population dynamics, however, are primarily determined by interactions
51 between individuals with each other and their environment (8). Accounting for these
52 individual-level mechanisms therefore has the potential to better describe divergent shifts in
53 species abundances and distributions in response to environmental changes.

54

55 Multiple stressors often interact with individual-level mechanisms to cause non-linear
56 population responses and may have additive, exacerbating or alleviating effects (9). For

57 instance, many species experience phenological and geographical range shifts consistent
58 with climate changes over time (10), while rapid and widespread declines of other species
59 are being driven by habitat loss and fragmentation, overexploitation, invasive species and
60 pollution (11). Honey bee colony collapses across the northern hemisphere, for example,
61 have been attributed to the combined spread of invasive parasitic mites, exposure to harmful
62 pesticides (12), climatic changes and habitat fragmentation (13). Population responses to
63 environmental changes are thus dependent on individual exposure to multiple stressors in
64 spatially explicit landscapes. Although correlative models often account for heterogeneous
65 environments, they cannot fully represent the interactive effects of multiple stressors at the
66 individual level.

67

68 Mechanistic models which incorporate individual-level mechanisms are ideal for generating
69 more informed predictions of population responses to novel environmental changes.

70 However, little progress has been made in developing an approach that is both mechanistic
71 (captures the mechanisms driving population dynamics in spatially explicit landscapes) and
72 general (can be applied to various species and environmental scenarios). Here, we first
73 discuss the importance of individual mechanisms (physiology, behaviour and evolution) in
74 driving population dynamics and then evaluate the ability of several existing population
75 modelling approaches to predict population responses to novel environmental change. We
76 suggest the need to work towards a standardised mechanistic approach so that individual
77 mechanisms inform predictions at the population-level. We then review the availability of
78 quantitative methods for the representation of these individual mechanisms in population
79 models. Finally, we discuss current limitations to developing such an approach and how
80 these could be addressed.

81

82 **2. Importance of individual-level mechanisms in driving population dynamics**

83 Ecology typically describes individual variation according to species' physiological and
84 behavioural traits (14–16). Physiology explains phenotypic plasticity of life history traits in

85 response to environmental variables. For instance, trade-offs between individual traits (e.g.
86 growth and reproduction) occur in response to changing food availability, quality and
87 temperature by altering energy acquisition and expenditure (17). Behaviour then relates
88 individuals of varying physiology to their position in the landscape and interactions with other
89 individuals. Movement is key, as how individuals move across landscapes to fulfil their
90 needs dictate their exposure to adverse conditions (e.g. predation, pollution, drought) (11).
91 The physiological state of individuals also plays a central role in behavioural mechanisms,
92 for instance by trading-off high quality resources for other factors such as finding a mate, or
93 avoiding predation.

94

95 Plastic effects through altered physiology and behaviour have been widely attributed to
96 population responses under environmental change (18), but genetic effects play an
97 important role for many species (19). That is, genetic interactions between fitness-related
98 traits and the direction of selection across multiple traits constrain an individual's potential for
99 evolutionary adaptation (20). Rapid evolutionary change has been shown for a number of
100 taxa exposed to novel environmental conditions (21), short-lived species experiencing rapid
101 changes (22), species unable to disperse to favourable habitats (23) and at landscape
102 scales (24). Physiology, behaviour and evolution thus need to be understood together to
103 build a comprehensive understanding of how individuals respond to their environment, and
104 how individual responses translate into population-level effects.

105

106 Under future environmental changes, physiology describes the sensitivity of species to
107 stressors, behaviour describes species' exposures to those stressors, and evolution
108 describes the potential variation of individual responses. Interactions between individual
109 mechanisms within the landscape then describe how collective populations either
110 acclimatise to small shifts in environmental conditions, shift their distributions or decline in
111 response to larger changes. Population ecology has classically understood these individual-
112 level mechanisms using a top-down approach, whereby demographic rates are related to

113 environmental (e.g. temperature) or population-level (e.g. density) variables. More recently,
114 however, the development of mechanistic population models use these individual-level
115 mechanisms to predict population-level effects in a bottom-up approach.

116

117 **3. Existing population modelling approaches**

118 Population modelling approaches are often reviewed in isolation because they integrate
119 different levels of biological organisation and ecological scales, but progress in population
120 modelling will rely on a combination of features from different approaches. In this section we
121 review several modelling approaches commonly used to predict population responses to
122 environmental changes. Most modelling approaches have been developed to answer
123 different ecological or evolutionary questions, and so each method reviewed here is suited to
124 its overarching purpose. Our focus, however, is on their ability to integrate individual-level
125 mechanisms and extrapolate across taxa and environmental scenarios in spatially explicit
126 landscapes, to provide informed predictions under environmental change.

127

128 *Demographic models*

129 Demographic population models, such as Matrix Population Models (MPMs), have played a
130 key role in the development of ecological and evolutionary theory since their conception (25).
131 By linking individual variation in species to changes in survival and reproduction rates,
132 MPMs provided a basis for understanding how population dynamics shifted with
133 demographic traits (e.g. birth and death rates, intrinsic growth rate) (26) and population
134 density (27). Over the last few decades, MPMs have become increasingly powerful with
135 advances in computational and statistical approaches in ecology (28). Integral projection
136 models (IProjMs), for instance, include both continuous (e.g. mass) and discrete state
137 variables (e.g. life stage) to more accurately represent population structure (29), whereas
138 Integrated Population Models (IPopMs) can combine individual- and population-level data to
139 better estimate the influence of individual variation on demographic rates (30). Classical
140 demographic models are nevertheless based on statistical relationships between

141 demographic rates and environmental conditions, making them more suited to
142 understanding species dynamics under current environmental conditions than predicting
143 population responses to novel environments in the future (5). That is, because
144 representation of demography in response to environmental variables are constrained by the
145 input data, they cannot reliably extrapolate outside of the environmental and/or stressor
146 scenario in which the data was collected. It is also often necessary to parameterise MPMs
147 for different population (e.g. pre- and post-breeding), environmental or management
148 scenarios, because the fundamental relationships between environmental fluctuations,
149 demographic rates and populations are not integrated (31). Inclusion of the mechanisms that
150 underpin demographic rates thus allows for the representation of both a greater range of
151 environmental conditions and species traits in MPMs.

152

153 Demographic models show improved predictions when incorporating physiological and
154 evolutionary processes (32). Mechanistic IProjMs, for instance, increasingly combine energy
155 budget models to describe individual life histories (33,34). Because IProjMs can also
156 account for multiple continuous state variables, trait distributions at the population-level can
157 change, either plastically or evolutionarily, according to shifts in individual life cycles and
158 inheritance functions (18). IProjMs have more recently been combined with IPopMs to
159 provide better estimates of individual-level traits and population-level density dependence
160 from multiple data sources (35). Still, model predictions are informed by the population data,
161 limiting predictions of population responses to novel environmental conditions in the future
162 for which data does not yet exist. Demographic models are also limited to representing
163 immigration and emigration rates in homogeneous environments, and so cannot incorporate
164 individual-level behavioural decisions in spatially explicit landscapes (Table 1).

165

166 *Species Distribution Models*

167 Classical Species Distribution Models (SDMs, also known as niche models, climate
168 envelope models and habitat models) were developed to better understand the relationships

169 between species distributions and environmental variables in spatially explicit landscapes
170 (36). Classical SDMs typically infer species' ecological niches, using statistical relationships,
171 from their distributions across reference landscapes for which abiotic conditions (e.g.
172 temperature, precipitation, soil type) are known. Models are then coupled with environmental
173 change forecasts to project future species distributions (37). The relative ease of building
174 SDMs make them popular tools in predicting the distributions of species under climate
175 changes (38, 39), conservation planning (40) and invasive species risk assessments (41) at
176 landscape scales. However, the relationships between species abundances and
177 distributions, on which classical SDMs are built, will likely vary outside of the spatial and/or
178 temporal extents of the data to which they were fitted. Projecting population dynamics into
179 the future with classical SDMs is therefore problematic due to the potential for environmental
180 variables and species distributions to co-vary in novel ways (37). Future species distributions
181 will also be strongly influenced by species behaviour and landscape factors which limit
182 dispersal of metapopulation dynamics (e.g. habitat fragmentation) (42). As such, classical
183 SDM predictions in novel environmental conditions are associated with high uncertainty (43).
184 These limitations of classical SDMs, alongside other caveats, have been reviewed
185 previously (44,45) and has led to the development of process-based SDMs.

186

187 Process-based SDMs aim to address the shortcomings of classical SDMs by incorporating
188 additional processes such as demographic rates, physiological and behavioural constraints
189 to movement, connectivity between suitable patches and population dynamics (46–48). For
190 a number of species both correlative and mechanistic SDMs have been developed, and
191 often give comparable predictions of future distributions under climate change (47,49). Other
192 mechanistic SDMs, however, have identified important processes for accurately predicting
193 species abundances and distributions. A mechanistic SDM developed to predict historical
194 changes in the distribution of the mosquito *Aedes aegypti* across Australia, for instance,
195 found that the incorporation of evolution in egg desiccation resistance was key to predicting
196 species distribution shifts under climate change (50). Similarly, the range dynamics of the

197 widespread North American lizard, *Sceloporus undulates*, were better predicted when
198 individual bioenergetics were incorporated in a process-based SDM (51). Most process-
199 based SDMs, however, focus on processes linked to species demographic rates rather than
200 behaviour.

201

202 Dynamic range models (DRMs) have recently been introduced to address the lack of
203 behaviour in SDMs, by incorporating the effects of dispersal on species abundance and
204 distribution alongside population demography (52). That is, species abundance and
205 distribution data are used to estimate statistical relationships between environmental
206 variables and demographic rates, density dependence and dispersal rates in a statistical
207 model (52). There are relatively few examples of operational DRMs, but a recent evaluation
208 of several approaches found DRMs, compared to classical and process-based SDMs, to
209 improve predictions under current climate conditions (53). However, model results were
210 evaluated using simulated rather than real data, while predictions under climate change
211 scenarios were comparable across models (53). Pagel & Schurr (52) suggested that the use
212 of mechanistic submodels, for both niche and population dynamics, would increase the
213 predictive power of DRMs under environmental change.

214

215 *Individual Based Models*

216 Individual-based models (IBMs; also known as agent-based models, ABMs) consider
217 individuals and their variation as the fundamental building blocks of ecological systems,
218 while landscapes are often dynamic and characterised by environmental drivers [54]. During
219 model simulations, individuals interact with one another and their environment and make
220 decisions about how to maximise their fitness in a given environment, resulting in emergent
221 predictions at the population level. IBMs can thus describe the bottom-up mechanisms that
222 give rise to population dynamics in novel environmental and management scenarios (8).
223 Accounting for individual variation explicitly further allows for predictions of population
224 distributions according to individual characteristics across heterogeneous environments.

225 IBMs have thus proven to be particularly useful in addressing land management and
226 conservation scenarios, where the consequences of individual exposures to multiple
227 stressors on species populations can be predicted (3,55). Despite their many advantages,
228 however, IBMs are far less commonly used for predicting environmental change effects on
229 species abundances and distributions than MPMs and SDMs (3).

230

231 A key limitation of IBMs is the need for sufficient, and precise, individual-level data to
232 parameterise species life cycles and behaviours under various environmental scenarios
233 (56). Data availability at the individual- and population-level is often limited for different
234 species, and so most IBMs are developed ad-hoc with the models purpose (i.e. species,
235 environmental and management scenarios) and data availability in mind (57). IBMs are thus
236 less standardised than demographic models or SDMs, and can be time-intensive to develop.
237 IBMs are also not necessarily mechanistic, and demographic rates are widely used to
238 parameterise IBMs. However, demographic models are being increasingly replaced by
239 physiological and behavioural mechanisms which better describe fundamental relationships
240 across species and environmental variables (58–60). These ‘mechanistic’ IBMs are better
241 able to make predictions outside of the range of environmental conditions for which they
242 were parameterised because the individual-level mechanisms remain unchanged across
243 scenarios.

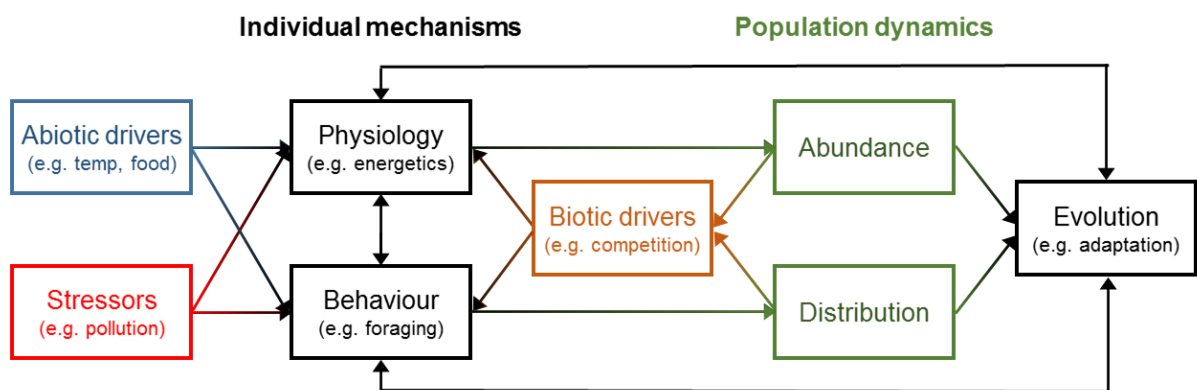
Table 1. Summary of modelling approaches typically used in predicting animal population responses to environmental change. Different approaches are categorised according to their ability to describe the individual-level mechanisms (physiology, behaviour and evolution) that drive population responses to environmental changes in spatially explicit landscapes.

Modelling approach	Spatially explicit	Vital rates	Individual variation	Physiology	Behaviour	Evolution	Examples
<i>Demographic Models</i>							
Matrix Population Models (MPMs)	N	Y	N	N	N	N	Crouse et al. (61)
Mechanistic MPMs	N	Y	N	N	N	Y	De Vries & Caswell (62)
Integrated Population Models (IPopMs)	N	Y	N	Y	N	Y	Schaub et al. (63)
Mechanistic IPopMs	N	Y	Y	Y	N	Y	Plard et al. (35)
Integral Projection Models (IProjMs)	N	Y	Y	Y	N	Y	Smallegange et al. (33) (34) Ozgul et al. (18) Coulson et al. (64)
<i>Species Distribution Models (SDMs)</i>							
Classical SDMs	Y	N	N	N	N	N	Elith & Leathwick (36)
Process-based SDMs	Y	Y	Y	Y	N	Y	Buckley (51) Kearney et al. (50) Fordham et al. (65)
Dynamic range models	Y	Y	N	N	Y	N	Zurell et al. (53)
<i>Individual Based Models (IBMs)</i>							
Classical IBMs	Y	Y	Y	N	Y	N	Liu et al. (66) Becher et al. (67)
Mechanistic IBMs	Y	Y	Y	Y	Y	Y	Bocedi et al. (68) Galic et al. (58) Johnston et al. (59) Boyd et al. (60)

246 **4. Towards a standardised mechanistic approach in population modelling**

247 Progress in mechanistic population modelling has been made by integrating individual-level
248 mechanisms in historically correlative or demographic approaches (Table 1). Indeed, a
249 common feature of the population modelling approaches reviewed in the previous section is
250 the recent integration of mechanisms to provide better predictive power. However, there is
251 little consensus on how to integrate the full range of mechanisms within population models.
252 There is thus an overarching need to work towards a standardised mechanistic approach
253 across existing population models. Such an approach would consider different individual-
254 level mechanisms (physiology, behaviour and evolution), and the interactions between them
255 (Figure 1). A key benefit to a standardised approach is that current ad-hoc development of
256 mechanistic approaches is time-consuming. Also, because population models are typically
257 developed to answer specific questions they are often species- and site-specific. By
258 integrating fundamental and general eco-evolutionary rules (e.g. thermodynamics and
259 energy conservation, stoichiometry, natural selection), a standardised mechanistic approach
260 would be applicable across taxa and environmental scenarios, and have better predictive
261 power under environmental change.

262



263

264 **Figure 1.** Conceptual standardised mechanistic approach for predicting animal population dynamics in
265 response to spatially explicit abiotic drivers (blue) and multiple stressors (red). Individual mechanisms
266 (black) interact to drive shifts in population abundance and distribution (green), and biotic drivers
267 (orange) cause feedbacks between population dynamics and individual mechanisms.

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5. Mechanistic submodels for representing individual-level mechanisms within population models

Individual mechanisms need to be represented using quantitative submodels in mechanistic population models. Ideally, a toolkit of standardised mechanistic submodels would be available for modellers to integrate in population models and test for different species and scenarios. A synthesis of existing submodels, however, is needed to better understand how these could be linked in a standardised mechanistic population model (Figure 1). Here, we review approaches currently used to describe physiological, behavioural and evolutionary mechanisms at the individual-level. While these individual mechanisms interact with one another, the methods to model each often come from disparate fields and so are considered separately in the following section.

Physiology

Phenotypic plasticity is often described using energy budget models (also known as energy allocation, bioenergetics or biophysical models), which integrate fundamental principles of physiological ecology. Energy budget models represent how individual animals acquire energy from food resources and expend assimilated energy on different life cycle processes in order to maximise Darwinian fitness (69,70). For instance, when food is limited r-selected species often allocate energy to reproduction before growth. Because physiological and biochemical properties are widely shared across taxa and/or species, energy budgets also provide a general framework for representing individual life cycles (71). When coupled with heterogeneous landscapes, energy budgets integrated in population models are useful for predicting population responses to changing resource distributions and temperature regimes (58,59). However, current energy budget approaches are limited to describing life cycles in response to a small number of abiotic drivers (temperature, resource amount and energy contents).

296 Nutrition, together with energy, plays a central role in physiology through the need to
297 maintain nutrient homeostasis (72). Ecological Stoichiometry (ES) is used to investigate
298 environmental effects on the nutrient (carbon, nitrogen, phosphorous) stoichiometry of
299 organisms, and how nutrients flow through individuals and populations (73). Combinations of
300 energy budget and ES concepts in a unified framework have been suggested to predict the
301 influence of nutrition on animal populations, but have not yet been applied within a
302 population model (74). Similar approaches have been suggested to combine the metabolic
303 theory of ecology (MTE) and ES (75). Still, metabolic submodels do not currently integrate
304 mechanisms of acclimatisation, adaptation or genetic plasticity, whereby the expression of
305 physiological traits vary with environmental stress.

306

307 *Behaviour*

308 Behavioural plasticity plays a central role in the ability of animals to cope with environmental
309 changes (11). Classical behavioural ecology theories such as optimal foraging, ideal free
310 distribution (IDF) and kin selection provide testable submodels for describing animal
311 behaviour in population models. Yet, most assume that animals will always move in order to
312 optimise their fitness and that they have perfect knowledge of the profitability of their
313 environment (76). IDF, for example, assumes equilibrium distribution of organisms among
314 patchy resources or habitats (77). Many animals, however, have shown maladaptive
315 behavioural responses to environmental changes (78), suggesting the need to understand
316 animal behaviour according to trade-offs between an individual's fitness and their position in
317 a rapidly changing environment.

318

319 State-space models (SSMs) of animal movement integrate unobserved interactions between
320 individual fitness and environmental variables to better understand movement patterns (79).
321 Coupling SSMs with robust individual physiology and evolution submodels could thus
322 improve the mechanistic basis for understanding animal abundances and distributions in
323 future conditions. On the other hand, energy budget models coupled with spatially explicit

324 IBMs can be used to understand how animals forage to maximise their fitness in
325 heterogeneous environments (70). However, the profitability of landscape patches, and
326 trade-offs between different environmental variables, need to be described (55). Patch
327 profitability then needs to be linked to the probability of moving, together with movement
328 metrics such as speed, direction and turning angles (80). Nutritional ecology has addressed
329 some of these questions through the Geometric Framework, which was developed to
330 understand how individual behaviour (e.g. foraging) responded to changes in the nutritional
331 value (energetic macronutrients, micronutrients and non-nutritional components) of available
332 food resources (81).

333

334 Animal groups are influenced by additional behaviours such as collective decisions and
335 sociality. Many studies have stressed the importance of quorum responses as a key feature
336 of collective decisions at the group-level, which are modelled as non-linear probabilities of an
337 individual choosing a particular action according to the number of individuals already
338 committed to the same decision (82), although this is just one means by which collective
339 decisions are made. In other groups, the age-structure of populations can be critical in group
340 responses to environmental changes, particularly in long-lived species where changes in
341 behaviour can occur faster than evolution (83). In such cases, the loss of leaders can lead to
342 an overall loss of information from the group (84). Although animal sociality is an important
343 mechanism driving population responses to environmental change (85), there are
344 currently very few approaches for linking animal culture to behavioural decisions.

345

346 *Evolution*

347 Evolutionary processes moderate species responses to environmental change via complex
348 eco-evolutionary dynamics (86). Genetic variation and heritability are often studied at the
349 population-level (20), and observations can be used to predict the selection response of a
350 population given single or multiple trait heritability and a specified selection pressure (87).
351 Approaches such as the breeders equation have enabled identification of the genetic and

352 non-genetic components of phenotypic changes in response to novel environments.
353 Demographic processes within populations, however, play a key role in evolutionary change.
354 The mechanistic MPM of de Vries & Caswell (62) addresses this issue by integrating a
355 demographic genetic model which accounts for genotype-stage dynamics and allows for the
356 maintenance of a genetic polymorphism. Adaptive population responses to environmental
357 change, however, rely on interactions between different levels of biological organisation in
358 the same way as nonadaptive population responses (88). That is, evolutionary change at the
359 population level will feedback to a number of mechanisms operating at the individual level
360 (89, Figure 1).

361

362 The influence of trait variation on demographic rates and their heritability are increasingly
363 accounted for in population models which integrate evolutionary processes. IProjMs which
364 link demography to trait variation, for instance, can incorporate eco-evolutionary dynamics
365 using statistical relationships between vital rates and environmental variables and estimates
366 of heritability (90). Likewise, the Reaction Norm (RN) concept for quantifying genotype-
367 phenotype relationships are typically expressed as simple linear regressions between trait
368 value in the average environment and the change in phenotype across an environmental
369 gradient (91). While statistical relationships between demographic rates and evolutionary
370 change allows for models to account for the influence of population dynamics on adaptive
371 responses, they cannot describe the fundamental relationships influencing genetic structure
372 (92). An alternative approach, typically applied to macroevolutionary processes, is the direct
373 representation of alleles coding for a phenotypic trait of individuals that are then inherited by
374 their offspring (68,93). Although applications of such models have so far been largely
375 theoretical, Coulson et al. (64) recently set out a framework for incorporating developmental
376 and inheritance rules for both genetic and environmental components of a phenotype in
377 IProjMs. Such an approach can predict both plastic and adaptive population responses to
378 environmental change.

379

380 **6. Current limitations and future directions**

381 Representing how animal population dynamics emerge from interactions between individual
382 mechanisms in spatially explicit landscapes will improve the predictive power of population
383 models. Such mechanistic approaches are potentially more flexible and informative than
384 existing population modelling approaches which rely on correlative relationships and/or ad-
385 hoc model development. A number of current limitations, however, need to be overcome
386 before progress in the development of a standardised mechanistic approach in population
387 modelling can be made.

388

389 *Data availability*

390 A key limitation in population modelling is the availability of data to parameterise, calibrate
391 and validate models. Historically, SDMs have relied only on presence-absence data,
392 demographic models were built with snapshots of abundance over time, and IBMs have
393 focused on a single well-studied system to fulfil high data needs. A standardised mechanistic
394 approach, however, necessitates data at the individual-level for parameterisation and the
395 population-level for validation. For most species, data is often limiting at one level. For
396 instance, short-lived species are often well-studied at the individual-level in laboratory
397 conditions and less so at the population and field-level (e.g. invertebrates and fish), whereas
398 population data may be available for wild animals but individual-level data is scant (e.g. large
399 mammals). Another limitation is that most empirical studies are conducted over short
400 timescales, while the processes influencing population responses to environmental changes
401 operate over longer time-scales.

402

403 Individual-based and long-term field studies represent an important resource for the
404 development and evaluation of a standardised mechanistic approach in population modelling
405 (94). In particular, datasets for diverse species and scenarios will be crucial in testing
406 whether such an approach can identify how different mechanisms influence a population's
407 response to different environmental changes. Individual-based studies, for instance, have

408 played a key role in identifying the role of individual variation, age-related fitness and social
409 structures on population dynamics (95–99). Still, mechanistic submodels often require more
410 detailed information at the individual level than is recorded in the field. Energy budget
411 models, for example, often require prior knowledge about ingestion, assimilation, growth and
412 reproduction rates in optimal environmental conditions. An advantage of developing a
413 standardised mechanistic approach in population modelling, however, is in providing a
414 consensus on how to address data gaps using robust statistical techniques and calibration
415 tools (e.g. 55).

416

417 Other promising advances being made in the collection and sharing of data include remote
418 sensing and citizen science projects (100). For example, satellite tracking technology such
419 as that used in the recently launched International Cooperation for Animal Research Using
420 Space (ICARUS) project (101), can provide valuable data for parameterising the movements
421 and dispersal ability of individuals. A growing data sharing culture and the growth of freely
422 available online databases such as Add-my-pet (102) and Movebank (103) present another
423 promising source of data for population models. A standardised mechanistic approach,
424 developed and tested for diverse species and scenarios simultaneously, would provide
425 additional consensus on data requirements and availability from diverse sources. Such an
426 approach would also identify key knowledge gaps in physiological, behavioural and
427 evolutionary ecology which could be addressed through coupled modelling-empirical studies.

428

429 *Eco-evolutionary theory*

430 Quantitative methods for representing individual mechanisms and the interactions between
431 them as in Figure 1 need to be developed and tested. A number of current approaches,
432 based on fundamental eco-evolutionary theory, have been developed to address single
433 mechanisms. A pragmatic way forward, therefore, is to establish which of these competing
434 approaches for representing physiology, behaviour and evolution can be used within a single
435 framework. Because different approaches have been designed to address different

436 questions, however, components from a variety of approaches may need to be integrated.
437 Using established and extensive datasets for different species and scenarios, as discussed
438 above, provides a way to develop a unified approach by testing their assumptions and
439 predictions. Novel eco-evolutionary theory will likely emerge from such an exercise, because
440 interactions between physiology, behaviour and evolution need to be accounted for to
441 understand diverse population responses.

442

443 *Environmental scenarios*

444 There is an overarching need for realistic and multidimensional environmental scenarios.
445 Climate forecasts, from a range of earth system models and for numerous greenhouse gas
446 emission scenarios, are well developed as inputs to population models. A general lack of
447 standardised multiple stressor scenarios, however, limit many population modelling
448 approaches to focusing on the effects of climate changes alone. Multidimensional
449 environmental change scenarios would include multiple environmental drivers and stressors,
450 and could be developed by integrating key drivers of biodiversity change (e.g. land use,
451 atmospheric CO₂ concentration, nitrogen deposition and climate) using different scenarios
452 generated by global models of climate, vegetation and land use. Such scenarios could
453 identify how global drivers interacted in the past (e.g. antagonistically or synergistically), to
454 inform more realistic environmental scenarios in the future. Hypothetical scenarios of
455 additional stressors such as habitat fragmentation, pollution and invasive species could be
456 further integrated for projection purposes. Such standardised landscape-scale environmental
457 scenarios will be key to objectively evaluating different modelling approach predictions under
458 environmental change.

459

460 **7. Concluding remarks**

461 Mechanistic population models are needed to better anticipate, and mitigate, the ecological
462 consequences of future environmental changes. Currently, population models tend to be
463 either 'correlative' or 'mechanistic'. Correlative models assess how current ecological ranges

464 of species will shift or disappear with changing climatic conditions, and provide useful
465 assessments of species' exposure to environmental changes but are limited to
466 extrapolations of historical population patterns into the future. Mechanistic models, on the
467 other hand, provide more robust predictions about a species' vulnerability to future
468 environmental changes by incorporating individual-level mechanisms, but are time- and
469 data-intensive and limited to finer ecological scales compared to correlative approaches. A
470 standardised mechanistic approach is needed for more informed predictions of animal
471 population responses to novel environmental conditions. Progress in predictive population
472 modelling should thus focus on identifying extensive datasets for different species and
473 scenarios for model development and evaluation, the conception of a unified approach for
474 integrating current eco-evolutionary theory to represent individual mechanisms and the
475 interactions between them and the construction of multidimensional environmental scenarios
476 for informing population predictions in the uncertain future.

477

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479

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