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

Article

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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

3

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 discreet 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
Demographic Models							
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)
Species Distribution Models (SDMs)							
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)
Individual Based Models (IBMs)							
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)

4. Towards a standardised mechanistic approach in population modelling

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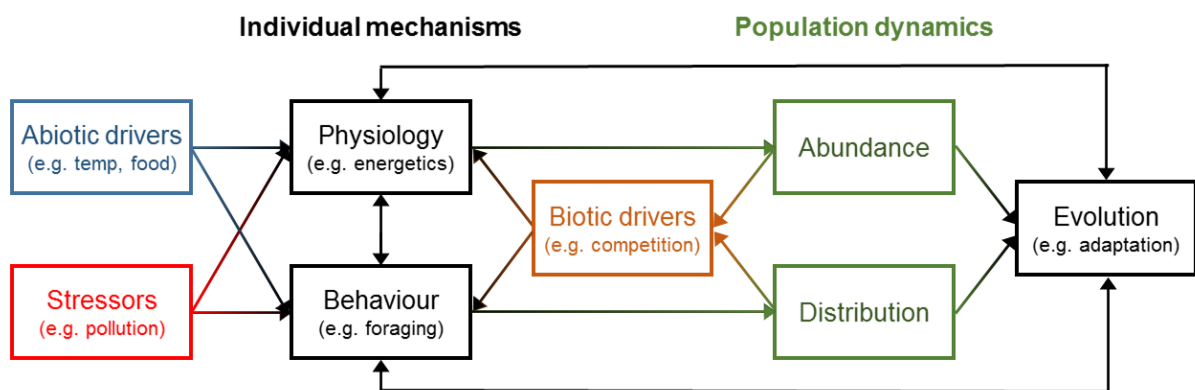

Figure 1. Conceptual standardised mechanistic approach for predicting animal population dynamics in response to spatially explicit abiotic drivers (blue) and multiple stressors (red). Individual mechanisms (black) interact to drive shifts in population abundance and distribution (green), and biotic drivers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

11

268

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.

280

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).

295

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

13

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

6. Current limitations and future directions

380

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 populations

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 CO_2 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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