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Accepted Version

Johnston, A. S.A., Boyd, R. J., Watson, J. W., Paul, A., Evans, L. C. ORCID: https://orcid.org/0000-0001-8649-0589, Gardner, E. and Boult, V. ORCID: https://orcid.org/0000-0001-7572-5469 (2019) Predicting population responses to environmental change from individual-level mechanisms: towards a standardized mechanistic approach. Proceedings of the Royal Society B: Biological Sciences, 286. 20191916. ISSN 1471-2954 doi: https://doi.org/10.1098/rspb.2019.1916 Available at https://centaur.reading.ac.uk/86654/

To link to this article DOI: http://dx.doi.org/10.1098/rspb.2019.1916

Publisher: The Royal Society

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

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

## Abstract

Animal populations will mediate the response of global biodiversity to environmental changes. Population models are thus important tools for both understanding and predicting animal responses to uncertain future conditions. Most approaches, however, are correlative and ignore the individual-level mechanisms that give rise to population dynamics. Here, we assess several existing population modelling approaches, and find limitations to both ‘correlative’ and ‘mechanistic’ models. We advocate the need for a standardised mechanistic approach for linking individual mechanisms (physiology, behaviour and evolution) to population dynamics in spatially explicit landscapes. Such an approach is potentially more flexible and informative than current population models. Key to realising this goal, however, is overcoming current data limitations, the development and testing of eco-evolutionary theory to represent interactions between individual mechanisms, and standardised multidimensional environmental change scenarios which incorporate multiple stressors. Such progress is essential in supporting environmental decisions in uncertain future conditions.

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

## 1. Introduction

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

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

Multiple stressors often interact with individual-level mechanisms to cause non-linear population responses and may have additive, exacerbating or alleviating effects (9). For instance, many species experience phenological and geographical range shifts consistent with climate changes over time (10), while rapid and widespread declines of other species are being driven by habitat loss and fragmentation, overexploitation, invasive species and pollution (11). Honey bee colony collapses across the northern hemisphere, for example, have been attributed to the combined spread of invasive parasitic mites, exposure to harmful pesticides (12), climatic changes and habitat fragmentation (13). Population responses to environmental changes are thus dependent on individual exposure to multiple stressors in spatially explicit landscapes. Although correlative models often account for heterogeneous environments, they cannot fully represent the interactive effects of multiple stressors at the individual level.

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

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

Ecology typically describes individual variation according to species' physiological and behavioural traits (14–16). Physiology explains phenotypic plasticity of life history traits in response to environmental variables. For instance, trade-offs between individual traits (e.g. growth and reproduction) occur in response to changing food availability, quality and temperature by altering energy acquisition and expenditure (17). Behaviour then relates individuals of varying physiology to their position in the landscape and interactions with other individuals. Movement is key, as how individuals move across landscapes to fulfil their needs dictate their exposure to adverse conditions (e.g. predation, pollution, drought) (11). The physiological state of individuals also plays a central role in behavioural mechanisms, for instance by trading-off high quality resources for other factors such as finding a mate, or avoiding predation.

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

Under future environmental changes, physiology describes the sensitivity of species to stressors, behaviour describes species' exposures to those stressors, and evolution describes the potential variation of individual responses. Interactions between individual mechanisms within the landscape then describe how collective populations either acclimatise to small shifts in environmental conditions, shift their distributions or decline in response to larger changes. Population ecology has classically understood these individual-level mechanisms using a top-down approach, whereby demographic rates are related to environmental (e.g. temperature) or population-level (e.g. density) variables. More recently, however, the development of mechanistic population models use these individual-level mechanisms to predict population-level effects in a bottom-up approach.

## 3. Existing population modelling approaches

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

### *Demographic models*

Demographic population models, such as Matrix Population Models (MPMs), have played a key role in the development of ecological and evolutionary theory since their conception (25). By linking individual variation in species to changes in survival and reproduction rates, MPMs provided a basis for understanding how population dynamics shifted with demographic traits (e.g. birth and death rates, intrinsic growth rate) (26) and population density (27). Over the last few decades, MPMs have become increasingly powerful with advances in computational and statistical approaches in ecology (28). Integral projection models (IProjMs), for instance, include both continuous (e.g. mass) and discreet state variables (e.g. life stage) to more accurately represent population structure (29), whereas Integrated Population Models (IPopMs) can combine individual- and population-level data to better estimate the influence of individual variation on demographic rates (30). Classical demographic models are nevertheless based on statistical relationships between demographic rates and environmental conditions, making them more suited to understanding species dynamics under current environmental conditions than predicting population responses to novel environments in the future (5). That is, because representation of demography in response to environmental variables are constrained by the input data, they cannot reliably extrapolate outside of the environmental and/or stressor scenario in which the data was collected. It is also often necessary to parameterise MPMs for different population (e.g. pre- and post-breeding), environmental or management scenarios, because the fundamental relationships between environmental fluctuations, demographic rates and populations are not integrated (31). Inclusion of the mechanisms that underpin demographic rates thus allows for the representation of both a greater range of environmental conditions and species traits in MPMs.

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

*Species Distribution Models*

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

Process-based SDMs aim to address the shortcomings of classical SDMs by incorporating additional processes such as demographic rates, physiological and behavioural constraints to movement, connectivity between suitable patches and population dynamics (46–48). For a number of species both correlative and mechanistic SDMs have been developed, and often give comparable predictions of future distributions under climate change (47,49). Other mechanistic SDMs, however, have identified important processes for accurately predicting species abundances and distributions. A mechanistic SDM developed to predict historical changes in the distribution of the mosquito *Aedes aegypti* across Australia, for instance, found that the incorporation of evolution in egg desiccation resistance was key to predicting species distribution shifts under climate change (50). Similarly, the range dynamics of the widespread North American lizard, *Sceloporus undulates*, were better predicted when individual bioenergetics were incorporated in a process-based SDM (51). Most process-based SDMs, however, focus on processes linked to species demographic rates rather than behaviour.

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

### *Individual Based Models*

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

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

A key limitation of IBMs is the need for sufficient, and precise, individual-level data to parameterise species life cycles and behaviours under various environmental scenarios (56). Data availability at the individual- and population-level is often limited for different species, and so most IBMs are developed ad-hoc with the models purpose (i.e. species, environmental and management scenarios) and data availability in mind (57). IBMs are thus less standardised than demographic models or SDMs, and can be time-intensive to develop. IBMs are also not necessarily mechanistic, and demographic rates are widely used to parameterise IBMs. However, demographic models are being increasingly replaced by physiological and behavioural mechanisms which better describe fundamental relationships across species and environmental variables (58–60). These ‘mechanistic’ IBMs are better able to make predictions outside of the range of environmental conditions for which they were parameterised because the individual-level mechanisms remain unchanged across 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)<br>Ozgul et al. (18)<br>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)<br>Kearney et al. (50)<br>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)<br>Becher et al. (67) |
| Mechanistic IBMs | Y | Y | Y | Y | Y | Y | Bocedi et al. (68)<br>Galic et al. (58)<br>Johnston et al. (59)<br>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.

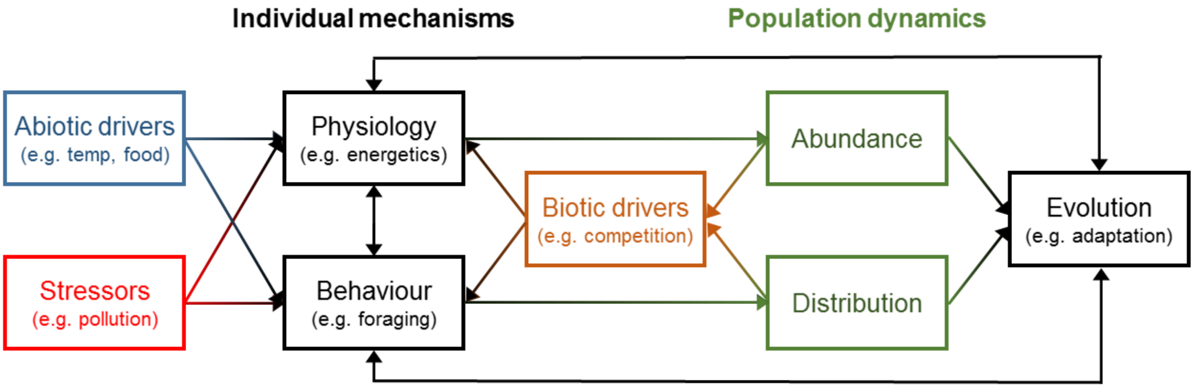

**Figure 1.** Conceptual standardised mechanistic approach for predicting animal population dynamics in response to spatially explicit abiotic drivers (blue) and multiple stressors (red). Individual mechanisms (black) interact to drive shifts in population abundance and distribution (green), and biotic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

## 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).

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

### *Behaviour*

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

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

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

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

### *Evolution*

Evolutionary processes moderate species responses to environmental change via complex eco-evolutionary dynamics (86). Genetic variation and heritability are often studied at the population-level (20), and observations can be used to predict the selection response of a population given single or multiple trait heritability and a specified selection pressure (87). Approaches such as the breeders equation have enabled identification of the genetic and non-genetic components of phenotypic changes in response to novel environments. Demographic processes within populations, however, play a key role in evolutionary change. The mechanistic MPM of de Vries & Caswell (62) addresses this issue by integrating a demographic genetic model which accounts for genotype-stage dynamics and allows for the maintenance of a genetic polymorphism. Adaptive population responses to environmental change, however, rely on interactions between different levels of biological organisation in the same way as nonadaptive population responses (88). That is, evolutionary change at the population level will feedback to a number of mechanisms operating at the individual level (89, Figure 1).

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

## 6. Current limitations and future directions

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

### *Data availability*

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

Individual-based and long-term field studies represent an important resource for the development and evaluation of a standardised mechanistic approach in population modelling (94). In particular, datasets for diverse species and scenarios will be crucial in testing whether such an approach can identify how different mechanisms influence a populations response to different environmental changes. Individual-based studies, for instance, have played a key role in identifying the role of individual variation, age-related fitness and social structures on population dynamics (95–99). Still, mechanistic submodels often require more detailed information at the individual level than is recorded in the field. Energy budget models, for example, often require prior knowledge about ingestion, assimilation, growth and reproduction rates in optimal environmental conditions. An advantage of developing a standardised mechanistic approach in population modelling, however, is in providing a consensus on how to address data gaps using robust statistical techniques and calibration tools (e.g. 55).

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

### *Eco-evolutionary theory*

Quantitative methods for representing individual mechanisms and the interactions between them as in Figure 1 need to be developed and tested. A number of current approaches, based on fundamental eco-evolutionary theory, have been developed to address single mechanisms. A pragmatic way forward, therefore, is to establish which of these competing approaches for representing physiology, behaviour and evolution can be used within a single framework. Because different approaches have been designed to address different questions, however, components from a variety of approaches may need to be integrated. Using established and extensive datasets for different species and scenarios, as discussed above, provides a way to develop a unified approach by testing their assumptions and predictions. Novel eco-evolutionary theory will likely emerge from such an exercise, because interactions between physiology, behaviour and evolution need to be accounted for to understand diverse population responses.

*Environmental scenarios*

There is an overarching need for realistic and multidimensional environmental scenarios. Climate forecasts, from a range of earth system models and for numerous greenhouse gas emission scenarios, are well developed as inputs to population models. A general lack of standardised multiple stressor scenarios, however, limit many population modelling approaches to focusing on the effects of climate changes alone. Multidimensional environmental change scenarios would include multiple environmental drivers and stressors, and could be developed by integrating key drivers of biodiversity change (e.g. land use, atmospheric $CO_2$ concentration, nitrogen deposition and climate) using different scenarios generated by global models of climate, vegetation and land use. Such scenarios could identify how global drivers interacted in the past (e.g. antagonistically or synergistically), to inform more realistic environmental scenarios in the future. Hypothetical scenarios of additional stressors such as habitat fragmentation, pollution and invasive species could be further integrated for projection purposes. Such standardised landscape-scale environmental scenarios will be key to objectively evaluating different modelling approach predictions under environmental change.

## 7. Concluding remarks

Mechanistic population models are needed to better anticipate, and mitigate, the ecological consequences of future environmental changes. Currently, population models tend to be either ‘correlative’ or ‘mechanistic’. Correlative models assess how current ecological ranges of species will shift or disappear with changing climatic conditions, and provide useful assessments of species' exposure to environmental changes but are limited to extrapolations of historical population patterns into the future. Mechanistic models, on the other hand, provide more robust predictions about a species' vulnerability to future environmental changes by incorporating individual-level mechanisms, but are time- and data-intensive and limited to finer ecological scales compared to correlative approaches. A standardised mechanistic approach is needed for more informed predictions of animal population responses to novel environmental conditions. Progress in predictive population modelling should thus focus on identifying extensive datasets for different species and scenarios for model development and evaluation, the conception of a unified approach for integrating current eco-evolutionary theory to represent individual mechanisms and the interactions between them and the construction of multidimensional environmental scenarios for informing population predictions in the uncertain future.

**Competing interests.** We declare no competing interests.

**Author contributions.** ASAJ conceived the review idea and led the writing of the manuscript. RJB, JWW, AP, LCE, ELG and VLB equally contributed ideas, discussions and to the writing of the manuscript.

**Acknowledgements.** The authors thank the editor and two anonymous reviewers for helpful suggestions which greatly improved the manuscript.

**Funding.** A.S.A.J. has been financially supported by an NERC fellowship (grant no. NE/N019504/1), V.L.B., R.J.B. & J.W.W. by NERC Scenario studentships (grant no. NE/L002566/1), L.C.E by a BBSRC CASE studentship (grant no. BB/N504129/1), A.P. by an NERC NPIF studentship (grant no. NE/R012229/1) and E.L.G. by a BBSRC grant (grant no. BB/R00580X/1).

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