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Spatially explicit models for decision-making in animal conservation and restoration

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Models are useful tools for understanding and predicting ecological patterns and processes. Under ongoing climate and biodiversity change, they can greatly facilitate decision-making in conservation and restoration and help designing adequate management strategies for an uncertain future. Here, we review the use of spatially explicit models for decision support and to identify key gaps in current modelling in conservation and restoration. Of 650 reviewed publications, 217 publications had a clear management application and were included in our quantitative analyses. Overall, modelling studies were biased towards static models (79%), towards the species and population level (80%) and towards conservation (rather than restoration) applications (71%). Correlative niche models were the most widely used model type. Dynamic models as well as the gene-to-individual level and the community-to-ecosystem level were underrepresented, and explicit cost optimisation approaches were only used in 10% of the studies. We present a new model typology for selecting models for animal conservation and restoration, characterising model types according to organisational levels, biological processes of interest and desired management applications. This typology will help to more closely link models to management goals. Additionally, future efforts need to overcome important challenges related to data integration, model integration and decision-making. We conclude with five key recommendations, suggesting that wider usage of spatially explicit models for decision support can be achieved by 1) developing a toolbox with multiple, easier-to-use methods, 2) improving calibration and validation of dynamic modelling approaches and 3) developing best-practise guidelines for applying these models. Further, more robust decision-making can be achieved by 4) combining multiple modelling approaches to assess uncertainty, and 5) placing models at the core of adaptive management. These efforts must be accompanied by long-term funding for modelling and monitoring, and improved communication between research and practise to ensure optimal conservation and restoration outcomes.

Keywords: adaptive management, biodiversity conservation, cost optimisation, ecosystem restoration, global change, predictive models

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Introduction

Biodiversity is continuing to decline worldwide (Pimm et al. 2014, Davis et al. 2018) despite repeated policy commitments to reduce the rate of loss (Mace et al. 2018). As awareness about the risks that the climate and biodiversity crises pose to societal well-being is increasing (IPBES 2019), the United Nations (UN) has called out the UN Decade on Ecosystem Restoration 2021–2030 to protect and revive ecosystems all around the world and to ensure integrity and resilience of our biosphere. Conservation and restoration actions are costly while time and financial resources for them are scarce (McCarthy et al. 2012). We should thus use our best available science to guide global actions.

A structured decision-making process can help to allocate limited resources efficiently (Fischer et al. 2009, Wintle et al. 2011, Guisan et al. 2013). Necessary steps involve identifying the problem and formulating objectives, defining possible actions and assessing their associated costs, evaluating the effectiveness of alternative actions with respect to the objective, and taking decisions based on cost–benefit trade-offs. This can be done in a purely heuristic manner or by means of quantitative modelling. Models are cost-effective and useful tools to summarise our current understanding of biological phenomena and complex ecosystem processes, to explore management options, to assess feasibility and potential success of restoration and conservation measures, and to predict the effect of multiple global change drivers on biodiversity and ecosystem functioning (IPBES 2016). Essentially, they allow us to answer 'what if' questions and to explore the potential effectiveness of different actions prior to implementation. Thus, models can help to move away from a reactive mode of decision-making to a proactive mode that aims to anticipate potential effects of global change and alternative management scenarios (Wintle et al. 2011, IPBES 2016).

In both conservation and restoration, it is crucial to identify suitable sites for action and the target biodiversity and ecosystem components and processes that should be conserved or restored. Under ongoing global change, management decisions should also consider the role of transient dynamics. First, species and ecosystems may not be at equilibrium with their environment but could exhibit legacy effects. In systems with a time-delayed response, for example, extinction debts due to past habitat loss (Semper-Pascual et al. 2021), even immediate conservation actions may not be able to halt biodiversity loss in its entirety. Second, biodiversity and ecosystems respond dynamically to global change, and conservation actions need to anticipate these dynamics (Araújo et al. 2011, Oliver et al. 2016). For example, for range shifting species, static protected areas may not be sufficient for preserving metapopulation viability into the future, but climate change-induced range shifts may need to be facilitated by adequate stepping stones and dynamic approaches to conservation (Wiens et al. 2011, Alagador et al. 2014, Synes et al. 2020). Last, restoration typically requires the identification of a reference state for species and ecosystem recovery. Yet, the historic equilibrium state of an ecosystem, for example the Pleistocene reference, might be unknown or impossible to restore due to extinctions of keystone species or might be inappropriate as a reference in the face of rapid climate change (Harris et al. 2006, Higgs et al. 2014). Effective conservation and restoration planning thus needs to incorporate considerations about transient dynamics and future climate change and needs to balance between conserving current or restoring past ecosystems in planning for resilient systems for the future.

Here, we ask how models can support conservation and restoration planning in a changing world. More specifically, we conduct a quantitative review to assess the current state of spatially explicit models for decision-support in animal conservation and ecosystem restoration. We add to recent reviews of the biodiversity modelling literature (Urban et al. 2016, Zurell 2017, Briscoe et al. 2019) by explicitly asking how different model types have been used to guide pro-active decision-making in conservation and restoration. The literature review is limited to animals to keep the breadth of available model types focussed. Models cover static to dynamic approaches on various organisational levels, from genes to ecosystems (Box 1). We consider a broad range of management applications in conservation and restoration, ranging from population reinforcement and connectivity to disease control and rewilding (Box 2). Finally, we analyse the identified case studies according to different modelling and management characteristics. More specifically, we ask whether specific model types are associated with specific management applications, what kind of prioritisation methods are typically used to inform management, and whether any biases persist in terms of considered ecological processes, ecosystems, regions, taxonomic group and threats. This will help elucidate critical gaps and biases in model-based decision support and identify future opportunities and challenges for more widespread usage.

Model-based decision support for conservation and restoration

Ecological models are often classified into correlative and process-based approaches (Dormann et al. 2012, Briscoe et al. 2019). Correlative or phenomenological models rely on statistical approaches to relate a specific biodiversity facet, for example species occurrence, to environmental predictors. Most prominent examples of correlative approaches in biodiversity and wildlife research are correlative ecological niche models (Zurell et al. 2020). In contrast, process-based or mechanistic approaches aim to establish causal links between ecological and environmental variables and explicitly describe the processes that underpin certain ecological or evolutionary phenomena. Important processes include physiology, demography, dispersal, species interactions and evolution (Urban et al. 2016, Cabral et al. 2017). Although the distinction of correlative versus process-based representations is important, models can also be classified into static models that predict equilibrium states and dynamic

Box 1: Spatially explicit model types in conservation and restoration

Static models typically assume equilibrium and predict stationary states. The modelled relationships have no independent time variable, but time can be incorporated implicitly through variation of the considered predictor variables.

- **Ecological niche models (ENM)** aim to quantify and map the determinants of the species ecological niche. We broadly summarise correlative and mechanistic niche models under this category. **Correlative species-environment relationships** relate the observed biodiversity facet (e.g. occurrences or abundances) at each site with a set of abiotic and/or biotic environmental variables (e.g. correlative species distribution model, resource selection function, static occupancy model) (Zurell et al. 2020). **Mechanistic niche models** establish causal links between species fitness and environmental, mostly (micro-) climatic, variables based on biophysical principles (Kearney and Porter 2009). As output, they predict vital rates such as survival or reproductive output.
- **Static connectivity models (Con)** assess how well habitat patches in a fragmented landscape (i.e. habitat/matrix configuration) are connected by the movement of a target species. This assessment can be based solely on Euclidian distance but often considers the site-specific resistance to dispersal, for example, modelled as a function of environmental variables (e.g. circuit theory, least-cost path analysis or graph theory measures) (McRae et al. 2008).
- **Static macroecological model (MEM)** are correlative models that relate macroecological or macroevolutionary properties (e.g. species richness, trait patterns) with spatial characteristics (e.g. species richness regression models) (D'Amen et al. 2017).

Dynamic models explicitly model processes and changes in time. The models include an independent time axis along which the modelled state evolves, such as species abundance or genetic diversity. Therefore, transient dynamics can be represented.

- **Individual-based models (IBM)** simulate the status of each single individual or agent through time and therefore model higher-level patterns (e.g. population abundance or relative proportion of genotypes) as emergent from individual behaviour (Grimm and Railsback 2005). Depending on the time scale, IBMs can consider several processes, for example annual cycles of survival, reproduction and dispersal or daily cycles of foraging and movement. They can also include genetic dynamics (Bocedi et al. 2021).
- **Patch occupancy models (POM)** describe spatial distribution of populations as the result of two underlying processes, colonisation and extinction. The colonisation and extinction probabilities are often modelled as a function of environmental variables and sometimes as a function of the patches pairwise distance (Hanski and Thomas 1994, MacKenzie et al. 2003).
- **Population-based models (PBM)** explicitly model the growth and dispersal of populations in a landscape. Each cell or patch contains a local population with site-specific reproduction and survival, and different local populations are connected by dispersal (Akçakaya 2000).
- **Integrated assessment models (IAM)** integrate models over several disciplines and aim to describe the complex relationships between environmental, social and economic drivers of biodiversity dynamics (IPBES 2016). At the moment, they are rarely used for predicting biodiversity, and in the few existing examples, biodiversity change is not always modelled as a dynamic system property (Kapitza et al. 2021).
- **General ecosystem models (GEM)** simulate ecosystem dynamics based on mechanistic relationships between environmental variables and different trophic levels within an ecosystem, from primary production to higher trophic levels. These relationships can be modelled, for example, in the form of explicit energy flow and/or nutrient cycling (Harfoot et al. 2014) or in the form of **interaction networks** (Baker et al. 2016).

models that simulate time-dependent changes in the state of a system. Both categories can include phenomenological and mechanistic aspects (Box 1). For example, niche-based models (ENM) can include not only correlative ENM, such as resource selection functions and static occupancy models, but also mechanistic ENM (Kearney and Porter 2009). We regard this distinction of static versus dynamic models as more useful in the context of conservation and restoration under global change as it emphasises the ability of the different models to take into account transitional stages, and we will thus distinguish between these two broad model categories throughout this review.

Models have been frequently used in the context of conservation and risk assessments. Araújo et al. (2019) found that among the ca 6000 publications that have been published on correlative ENM between 1995 and 2015, over half of the studies had a clear focus on future scenarios, conservation or restoration. Yet, Cayuela et al. (2009) and Guisan et al. (2013) highlighted that only 1–5% of correlative ENM studies published since 1995 produced clear management decisions. Recently, Hunter-Ayad et al. (2020) reviewed static and dynamic models for informing species reintroductions and provided a modelling guide from individual to community level. However, a quantitative review on the current

Box 2: Type of management applications in conservation and restoration

- **Species conservation:** Practise of preservation and protection of wildlife and their habitats. A species conservation approach can be focused on individual species or groups of species with common needs or common ecological characteristics, thus ranging from conservation of specific populations to the protection of umbrella species or keystone species that are important for the entire ecosystem.
- **Habitat conservation:** Management practise that seeks to conserve, protect or restore landscapes and ultimately prevent ecosystem degradation. Conservation of habitat involves improving the conservation status of the habitat structure and components, as well as the interactions among these components and with the environment.
- **Spatial prioritisation:** The process of identifying priority areas where best to allocate conservation or restoration efforts as the best trade-off between available resources and conservation or restoration gain. **Reserve selection** is an application of spatial prioritisation to plan and design protected areas that contribute to species and habitat conservation.
- **Harvest management:** Conservation activity which includes protection, maintenance and sustainable utilisation of species populations through hunting and fishing. For example, reducing density and abundance of a population to keep its impact on the ecosystem at an acceptable level.
- **Connectivity:** Restoration and conservation applications that are dedicated towards managing space such that viable populations of species can survive, evolve, move and interconnect within and between suitable areas. Connectivity combines a description of the physical landscape structure with an organism's response to that structure.
- **Reintroduction/translocation:** Restoration activity that involves the intentional relocation of living organisms from one area to another (IUCN 2013). There exists a broad range of terms that highlight different purposes and circumstances of this activity, for example differentiating whether the reintroduction does or does not occur in the historical distribution range of the species (reintroduction versus assisted colonisation and ecological replacement) or whether conspecifics are present in the region or not (reinforcement versus reintroduction) (Seddon et al. 2014).
- **Ecosystem restoration:** Interventions to assist the recovery of ecosystems that have been degraded, damaged or destroyed, as well as conserving the ecosystems that are still intact (IPBES 2018). **Rewilding** is a form of ecosystem restoration that involves the reestablishment of self-regulating ecosystems by reorganising and regenerating ecosystem functionality while reducing human intervention (du Toit and Pettorelli 2019, Perino et al. 2019, Svenning 2020).
- **Disease/invasive control:** Activity of regulation or management of an organism or pathogen that impacts adversely on ecosystems. Activities include exclusion, repulsion, physical treatment or removal (e.g. management techniques to control invasive alien species).

usage of static and dynamic models in decision-making for various conservation and restoration applications, and from the gene to ecosystem level, is still missing.

We assessed the state-of-the-art of model-based decision support for conservation and restoration using a quantitative literature review. To this end, we conducted a Web of Science search on 9 February 2021, searching for studies employing different model types (Box 1) for specific management applications (Box 2) in the period 1900–2021 (for a complete list of keywords cf. Supporting information). We initially identified 5179 papers, which we further refined to papers that fell under the Web of Science category 'biodiversity conservation', yielding a list of 650 papers. We screened these and only kept papers that had a clear management application (Box 2) and that provided some form of spatial planning and decision support. The latter requirement was met when at least a map of the status quo was derived from the model and presented. Papers that had potential implications for conservation but did not provide a basis for spatial planning and management decisions were excluded. The final list contained 217 research articles that met our inclusion criteria.

For each selected research article, we recorded different information about the models and case studies. First, we recorded model type (static versus dynamic; represented as 0/1), the ecological level being modelled (genes – individual – population – community – ecosystem; represented as an ordinal variable), the processes considered (sensu Urban et al. 2016: environmental response, physiology, demography, dispersal, interspecific interactions and evolution; each represented as 1 if the process was considered and 0 otherwise), the number of species covered and the spatial resolution and spatial extent (all three variables were represented as ordinal variables). Based on these 11 variables, we ran a non-metric multidimensional scaling (NMDS) analysis to identify gradients of the highest variation between typical model types, processes, and scales (Supporting information). From the 217 reviewed articles, 155 studies contained information for all relevant variables and were included in the NMDS. Second, we recorded additional information for each paper related to the type of management application (Box 2), prioritisation method (mapping, gap analysis, global change scenario, management scenario, cost optimisation), threats (land/sea use change, overexploitation, pollution, invasive species and disease, climate change), essential biodiversity variable (genetic composition, species populations, species traits, community composition, ecosystem function, ecosystem structure), ecosystem type, geographic region, taxonomic group, and temporal dimension. To identify spatial and thematic gaps and biases in the concurrent literature, we analysed the relative proportion of papers falling into these categories (using all identified papers n = 217) and how these categories correlated with the NMDS axes (n = 155). A full list of information recorded in the review is provided in Supporting information. The final list of papers including their classifications is available from Dryad (Data availability statement).

Overall, we found substantial variation in the relative frequency of model types, management applications, ecosystem types, taxonomic groups, relevant threats, and the focal level of ecological organisation. The ordination converged with a stress value of 0.172, indicating a fair but not excellent representation of pairwise dissimilarities in two-dimensional Euclidean space (Clarke 1993, Dexter et al. 2018). The first NMDS axis mainly represented the gradient from static to dynamic and the processes dispersal and demography, while the second axis mainly represented spatial resolution and extent and the inclusion of environmental responses (Fig. 1a). Static models were used more often than dynamic models (79% vs 21%), with a particularly

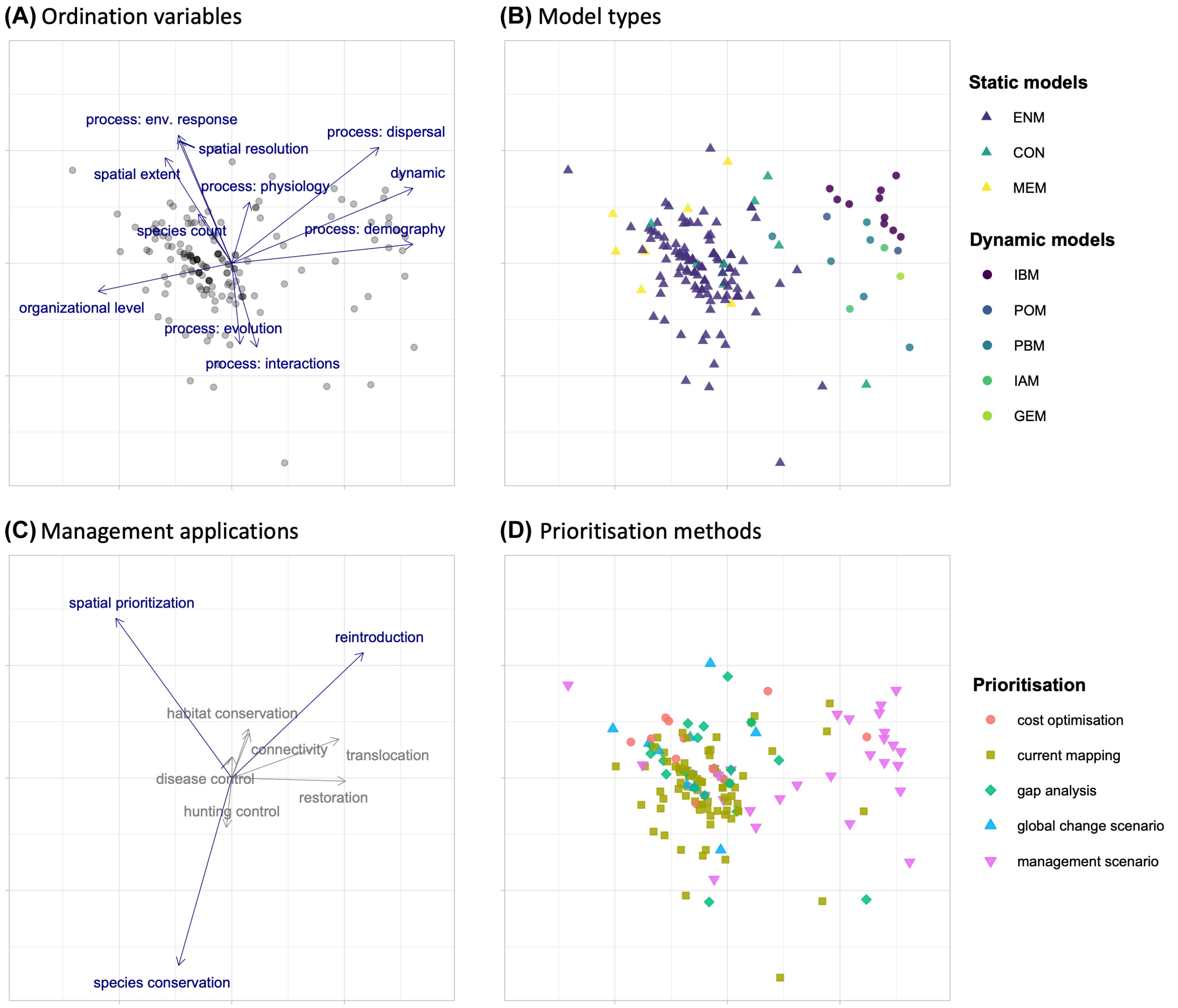

Figure 1. Ordination results. (A) Biplot showing the ordinated studies (points) and considered variables projected into ordination space (arrows). (B)–(D) Distribution of model types (B), management applications (C) and prioritisation method (D) across ordination space. Arrow lengths in plots (A) and (C) are proportional to the correlation of the respective variables with the ordination configuration but adjusted to fit the size of the plot. Thus, arrow lengths are not comparable among plots. Instead, significant variables are highlighted in blue. We only included those studies in the ordination (non-metric multidimensional scaling, NMDS) that contained information for all relevant ordination variables (n = 155). (ENM: ecological niche model; CON: connectivity model; MEM: macroecological model; IBM: individual-based model; POM: patch-occupancy model; PBM: population-based model; IAM: integrated assessment model; GEM: general ecosystem model).

strong representation of niche-based models (65%; Fig. 1b). In line with Urban et al. (2016), we found that the environmental response of the focal ecological unit was most frequently modelled (93% of studies). Among the other processes, dispersal (19%) and demography (20%) were considered regularly, while interspecific interactions (7%), as well as physiology and evolution, were rarely considered (both <1%). Only 29% of studies modelled multiple processes simultaneously.

Most studies focussed on conservation rather than restoration, with species and habitat conservation being the most frequent applications (44% and 31%, respectively), while applications related to ecosystem restoration made up less than 5% of the studies, reintroduction 3%, and translocation less than 1%. There was a tendency that restoration applications such as reintroductions were rather addressed with more complex dynamic models while species conservation applications mostly relied on static models (Fig. 1c). Recommendations and decision-making were typically informed by current mapping (46%) or exploration of different management scenarios (26%), whereby management scenarios were primarily explored in dynamic models (Fig. 1d). Explicit cost–benefit optimisation was only used in 10% of the studies, a gap analysis was carried out in 12%, and global change scenarios were addressed in 5% of the studies.

Commonly cited (non-mutually exclusive) threats were land/sea use change (56%) and overexploitation (27%), while climate change (11%), pollution (5%), and invasive species and disease (7%) were mentioned less frequently as study motivation (Fig. 2a). In 16% of the studies, the threats could not be assigned to one of the major five threat categories (marked as 'other' in Fig. 2a). Studies covered all continents whereby half of them were carried out in Europe and North America (Fig. 2b). Also, there was a bias towards (semi-) natural terrestrial ecosystems, in particular towards forests (47%) and grasslands (41%). The spatial resolution was ≤ 10 km for 90% of the studies. Most studies focus on the population level and, thus, from the six classes of essential biodiversity variables (EBVs) (Pereira et al. 2013), the EBV class 'species populations' was overrepresented (72%; Fig. 2c). Taxonomically, the majority of studies focussed on a single taxonomic group (82%), and most studies included mammals (62%) and birds (30%), followed by reptiles (11%), amphibians (9%), invertebrates (9%), fishes (4%), and microbes (< 1%). Half of all studies focused on single species (Supporting information). We could not find any temporal trends in the relative use of static versus dynamic models or for attempting predictions into the future (Supporting information).

A model typology for animal conservation and restoration

Increasing awareness of the importance of predicting conservation and restoration outcomes, together with the increasing availability of spatial data, has led to the development and application of a broad range of spatially explicit models to inform conservation and restoration actions (Box 1). Our quantitative review highlighted important gaps and biases in the current use of these models with a strong bias towards static models, towards the species and population level, and towards conservation (rather than restoration planning). Some advantages and disadvantages of different model types have been discussed in a few recent reviews (Cabral et al. 2017, Zurell 2017), and some authors also provide initial guidance for selecting appropriate models for specific applications and goals (Briscoe et al. 2019, Hunter-Ayad et al. 2020). Yet, we are still missing a model typology that captures the entire breadth of spatially explicit models and matches these with ecological levels and relevant processes and, in particular, with specific management applications in animal conservation and restoration. Such a model typology could pave the road for more cost-effective and targeted use of modelling in systematic conservation and restoration planning in order to safeguard animal species and communities as well as entire ecosystems against ongoing global change.

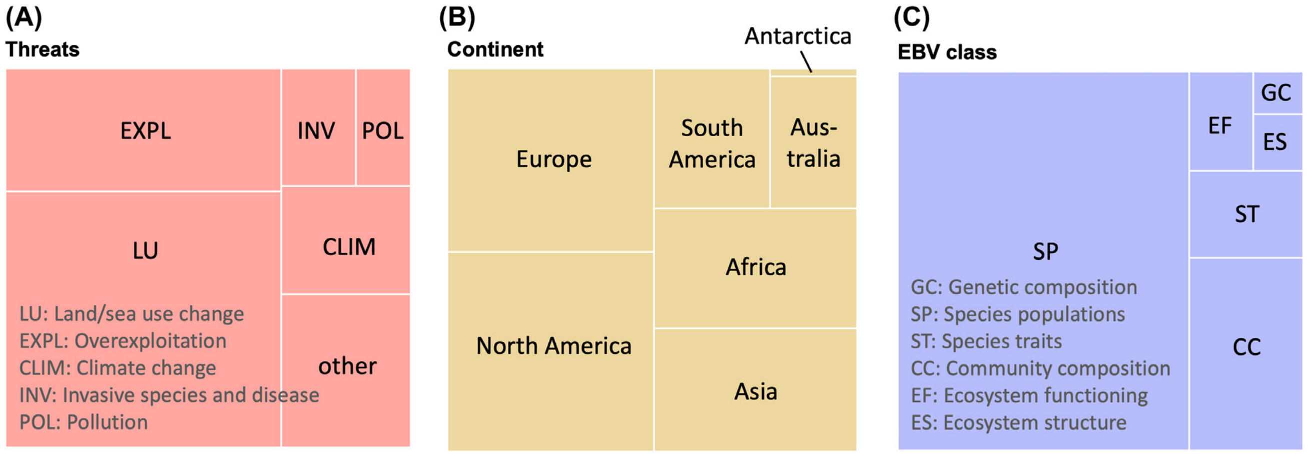

Figure 2. Relative proportions of studies addressing different (A) focal threats, (B) continents and (C) essential biodiversity variables (EBVs). Focal threats (A) were non-mutually exclusive across the considered studies (n = 217).

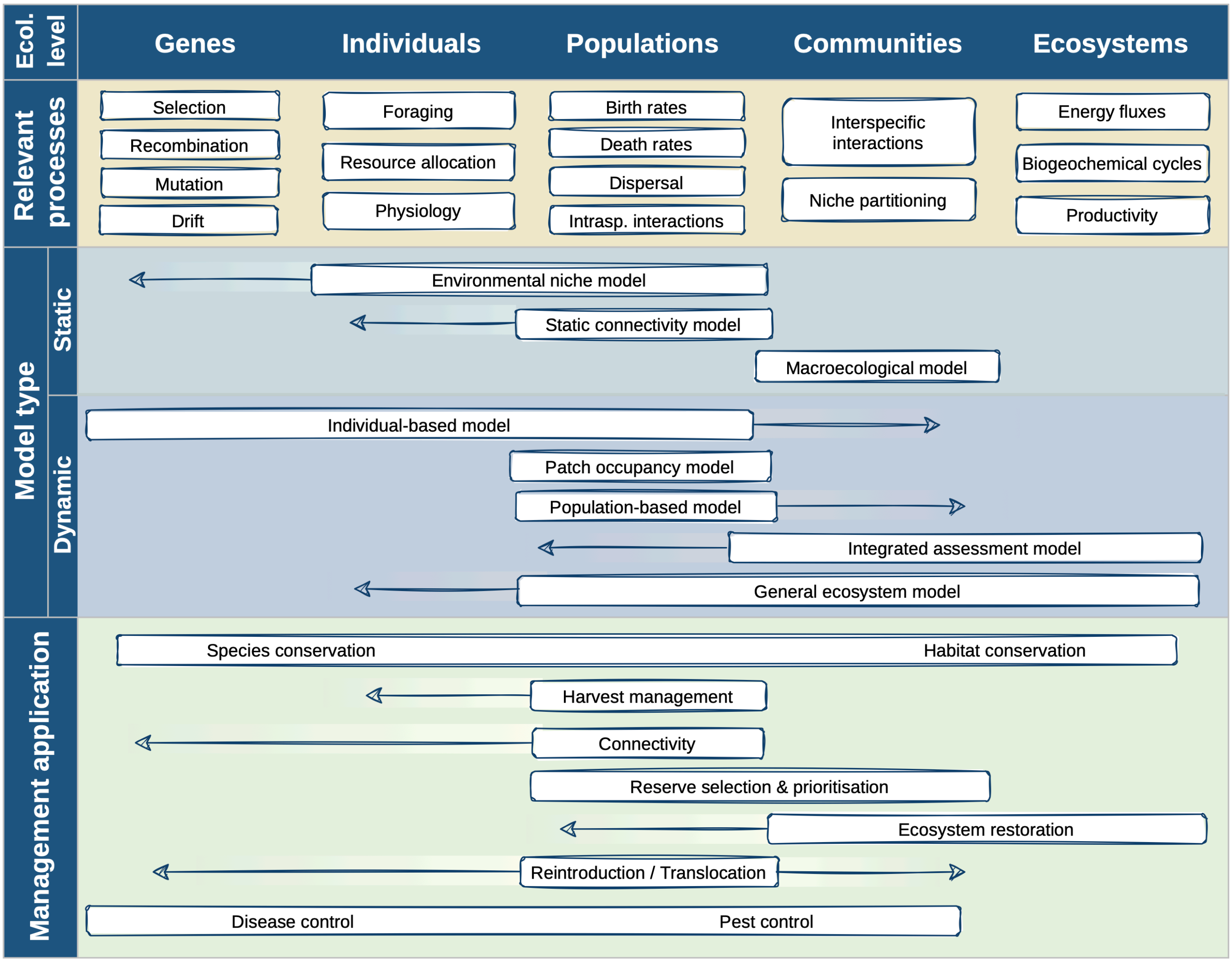

Figure 3. Typology of spatially explicit models for conservation and restoration, typical management applications and relevant ecological processes at different ecological levels. We list the relevant ecological processes at those ecological levels where they would most naturally be modelled. Boxes for model types and management applications indicate the ecological levels at which these models and applications are typically used or the ecological processes that are typically considered when making model-based decisions, while the arrows indicate the potential to consider other ecological levels and processes.

Here, we aim to fill this gap and provide a new model typology matching available spatially explicit model types with animal conservation and restoration goals (Fig. 3). This model typology recognises the different ecological levels from genes to ecosystems and the relevant ecological and evolutionary processes that are relevant at these organisational levels. It allows matching conservation and restoration goals with different static and dynamic model types. We deliberately kept the model typology rather general, indicating useful model types but without identifying specific model implementations, although a non-exhaustive list of current implementations is provided in the Supporting information. In the model typology, we indicate which spatially explicit model types could be extended to lower or higher ecological levels than is currently done (Fig. 3). Most of the conservation and restoration applications have been approached at the population level, using static models. However, dynamic models are generally better suited to capture patterns or processes at the far end of the ecological spectrum (genes, and ecosystems; Fig. 3). The outstanding questions are thus why dynamic models are not more routinely used in animal conservation and restoration and likewise why the gene-to-individual and the community-to-ecosystem level are underrepresented in the literature although the modelling frameworks are principally available. In the following, we briefly discuss the potential advantages of dynamic models as well as recent advances in modelling frameworks across ecological levels, while we reflect on further challenges and opportunities in the next section.

From static to dynamic models

It is important to acknowledge that choosing between a static or dynamic modelling approach will determine the kind of

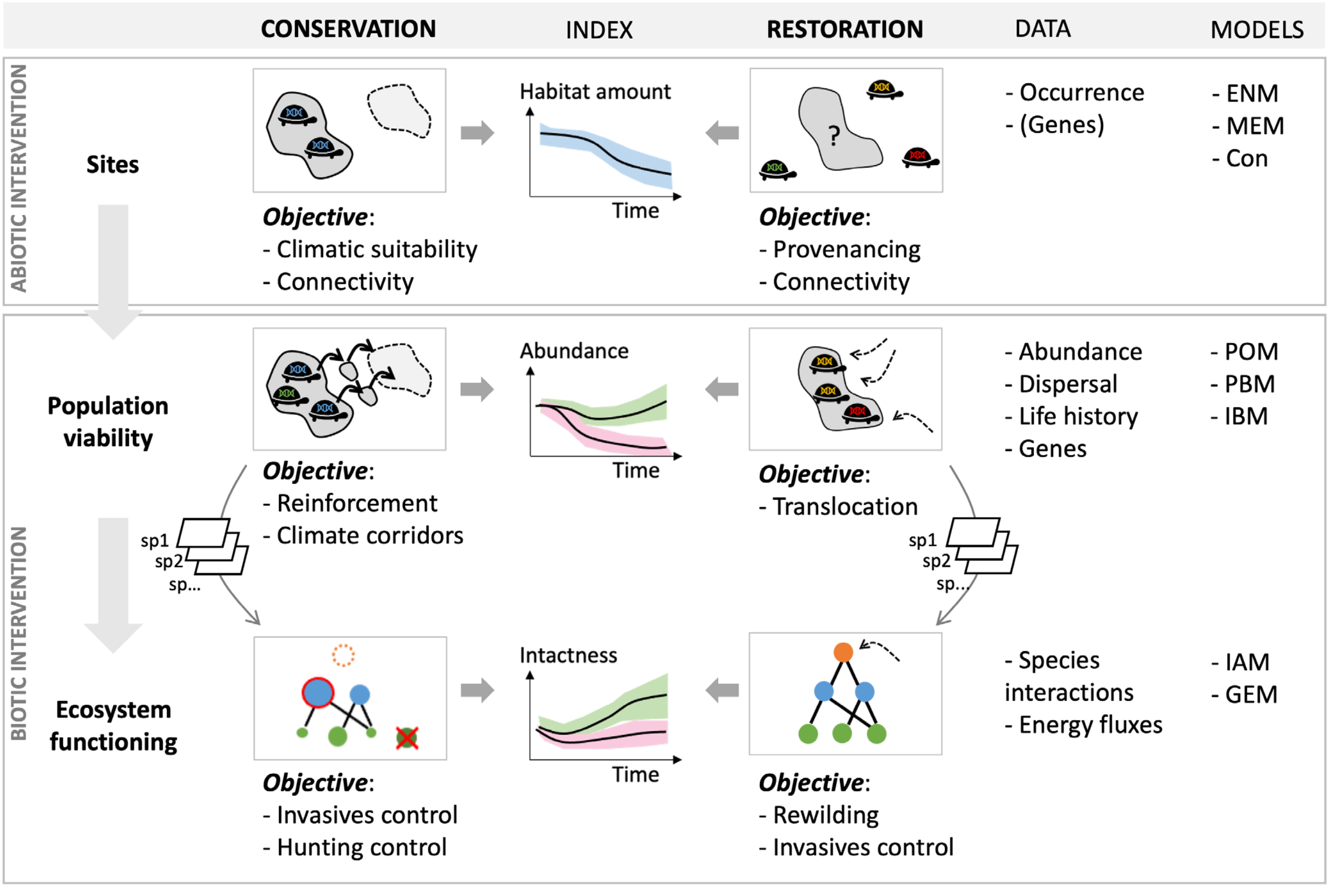

Figure 4. The use of spatially explicit models to inform different conservation and restoration objectives. Static models (ENM: ecological niche model; MEM: macroecological model; Con: connectivity model) are most useful at selecting sites and planning abiotic interventions. These models require comparably simple information for model calibration. Dynamic approaches (POM: patch-occupancy model; PBM: population-based model; IBM: individual-based model; IAM: integrated assessment model; GEM: general ecosystem model) can help planning biotic interventions, for example, designing conservation and restoration measures to ensure or increase population viability or ecosystem functioning over time. These dynamic modelling approaches require increasingly complex data for calibration. The listed objectives are not exhaustive. All management objectives can be optimised by comparing model outputs against desired targets, for example specific targets for habitat amount, population abundance or ecosystem intactness.

management goals that can be informed by models (Fig. 4). Static models will be most useful to inform site selection in the widest sense (e.g. habitat or climate suitability, corridors) and plan abiotic interventions (e.g. building habitat, remediating physical conditions). By contrast, dynamic models can inform biotic interventions that are necessary to conserve or restore population viability and ecosystem functioning, for example quantifying the required number, timing, and locations of reintroductions to ensure viable populations (Ovenden et al. 2019) or ecosystem recovery. The strong bias towards static models in the reviewed literature indicates that currently model-based decision support in animal conservation and restoration is focusing on selecting sites and site management, while modelling population viability and ecosystem functioning in a spatially explicit way is less often done. This means that management decisions are mostly based on predicted habitat extent or quality and less so on predicted temporal population dynamics or community stability and ecosystem intactness (Fig. 4).

Generally, dynamic models for decision support would be preferable over static models in cases where the timing of a certain management action is of importance (e.g. in sequential recovery) or when the success and time horizon of a certain management action for population viability or ecosystem functioning should be assessed a priori (e.g. in reintroduction planning). Also, under scenarios of global change, dynamic models have been shown to outperform the predictive performance of static models (Zurell et al. 2016, Fordham et al. 2018). By explicitly accounting for transient dynamics of biological processes such as dispersal, demography and evolution, among others, dynamic models are better able to predict the response of different ecological levels to management actions or external threats and to predict potential time lags (Briscoe et al. 2019). Yet, dynamic modelling approaches typically need more data to inform the different biological processes being modelled (Fig. 4) (Urban et al. 2016, Briscoe et al. 2021) and also a solid a priori understanding of the system or extensive model testing to adequately capture the structural uncertainty, meaning defining the adequate model complexity (Zurell et al. 2016). Thus, data availability and accessibility of methods remain key barriers that prevent more widespread use of dynamic modelling approaches (Briscoe et al. 2019).

Models across ecological levels

Our quantitative literature review further indicated that the gene-to-individual level as well as the community-to-ecosystem level were particularly underrepresented (Fig. 2c). This strong bias towards populations and species allows only a limited view of biodiversity changes as set out by the EBV framework (Pereira et al. 2013). Successful conservation and restoration of ecosystems need to move beyond single species or habitat approaches, since biological impoverishment and threats act at multiple levels of organisation (Noss 1990).

To date, genetics are rarely considered in spatially explicit models, although genetic and evolutionary processes are now recognised to be key elements to consider in designing effective conservation and restoration strategies (Hoffmann and Sgrò 2011, Mijangos et al. 2014, Hoffmann et al. 2015, 2021). Conservation and restoration strategies that take into account genetics and evolution are operating across two main objectives: increasing current population fitness through genetic rescue and increasing genetic diversity to maintain adaptive potential in the face of changing environments (i.e. evolutionary rescue) (Weeks et al. 2011, Derry et al. 2019, Gaitán-Espitia and Hobday 2020). Hitherto, relevant evolutionary processes such as variation and loss of genetic diversity by genetic drift, reduction in fitness due to inbreeding depression, and adaptive evolution have mostly been considered in spatiallyimplicit simulations to perform 'genetic viability analyses' in single small and often isolated populations (Hoban et al. 2012, Grueber et al. 2018). Spatially explicit models including genetics have rarely been used (here, <1% of reviewed studies) but show large potential. For example, Mims et al. (2019) assessed how reintroduction strategies, life-history variation, and riverscape structure affect the demography and genetic diversity and structure of reintroduced bull trout populations in Washington State, USA. At a larger scale and considering adaptive genetic variation, Bush et al. (2016) projected the distribution of 17 species of Australian drosophilids with genetic variation underlying their climatic tolerances and showed that drosophilids might have the capacity to adapt under realistic scenarios of climate change. Thus, models that consider evolutionary responses to changing or new environments and in a spatially explicit way are particularly useful for studying the interaction between genetic and demographic processes and alternative management strategies (Pavlova et al. 2017, Kelly and Phillips 2019).

Genetic threats and adaptive potential are two fundamental pieces of the puzzle for managing and restoring species, communities, and ecosystems, such as guiding provenancing and identifying reinforcement needs (Fig. 4). Yet, active interventions aimed at genetic restoration in the broader sense have been rarely implemented in practise because of uncertainties related to potential negative effects such as outbreeding depression, swamping of locally adapted genotypes, and genetic homogenisation (Weeks et al. 2011, Bell et al. 2019, Hoffmann et al. 2021). Dynamic and process-based models can be a powerful tool for shedding light on the complex interactions between evolutionary and ecological processes as well as feedbacks and trade-offs (Tallmon et al. 2004, Whiteley et al. 2015, Hoffmann et al. 2021) and on the likely response of the system to specific management strategies and future global change scenarios. Additionally, using spatially explicit models can help to evaluate the potential genetic consequences of higher-level management interventions, meaning actions that are not explicitly aimed at genetic restoration but, for example, at restoring or conserving habitat or connectivity between populations. As promising new applications are emerging that integrate genetic and evolutionary processes with other relevant processes such as physiology, demography, dispersal and/or interspecific interactions in different combinations and levels of sophistication (Bush et al. 2016, Landguth et al. 2017, Okamoto and Amarasekare 2018, Haller and Messer 2019, Cotto et al. 2020, Bocedi et al. 2021, Malchow et al. 2021), modelling biodiversity from the gene to ecosystem-level becomes progressively more feasible and opens exciting new perspectives for conservation and restoration.

At the other end of organisational levels, community-level and ecosystem models were underrepresented in the reviewed applications in animal conservation and restoration. General ecosystem models (GEMs, Box 1) aim to predict the complex interactive effects of multiple species and trophic levels in the landscapes (Geary et al. 2020) and are thus particularly useful to plan and assess the potential efficiency of restoration measures for ecosystem functioning (Fig. 4). For example, Baker et al. (2016) devised an ensemble ecosystem modelling method integrating a large number (ensemble) of ambiguous species interaction networks and dynamic community simulations to explore potential effects of wolf reintroduction to Yellowstone National Park and dingo reintroduction to a national park in Australia. The simulations allowed assessing relative increases and decreases of plant species abundance, as well as of different herbivores and meso-predators abundance, and identifying species that would be important to monitor to avoid any negative effects from reintroduction. Pesendorfer et al. (2017) used a similar approach to assess how the reintroduction of seed dispersers could accelerate the recovery and expansion of natural tree communities (passive restoration) in California's Channel Islands National Park. Such ecosystem models allow ecologists to complement individual-to-population level analysis of biodiversity patterns with community and ecosystem-level modelling that builds on ecological theory. For example, in the mechanistic GEM 'Madingley', ecosystem structure and functions emerge from individual-level (or cohort-level) processes such as foraging and growth and interspecific interactions within grid cells, and dispersal between grid cells (Harfoot et al. 2014, Hoeks et al. 2021). The Madingley model is not species-specific but relies on functional groups of similar body mass and trophic level. It could thus be particularly useful in understudied regions where species data are sparse, but knowledge of ecosystem-level properties can be applied (Purves et al. 2013). Recently, a novel application of the Madingley model assessed the sustainability of bushmeat hunting across environmental gradients in Africa (Barychka et al. 2019). These examples show that ecosystem-level modelling provides the means to assess the efficiency and resilience of ecosystems and their functioning and thus has a high potential to inform ecosystem restoration efforts.

Challenges and opportunities

Despite the potential of dynamic approaches to predict population viability and ecosystem functioning and manage for transient dynamics (Fig. 4), our results indicated a strong bias towards static models. Also, most studies focus on single or few species and few taxonomic groups (Supporting information). This underlines that important data and modelling challenges remain and need to be overcome for operationalising models over multiple taxonomic and spatiotemporal scales (Urban et al. 2016, Briscoe et al. 2019). Additionally, our results indicated underuse of cost optimisation frameworks such as spatial conservation prioritisation (Ball et al. 2009). Broader exploration of modelling options paired with explicit prioritisation methods seems particularly promising as this could provide cost-effective tools to assess efficiency of different management options to achieve clear conservation and restoration objectives (Guisan et al. 2013). In the following, we discuss current challenges and opportunities for using spatially explicit models for informing animal conservation and restoration. Overall, we believe that the challenges go beyond the availability of appropriate model frameworks, data integration and optimisation methods, but we need more knowledge transfer between modellers and practitioners as well as applied scientists to make existing and newly emerging modelling frameworks more accessible and easier to use and to provide (best-practise) guidelines for their usage.

Data challenges

Previous reviews proposed that the lack of data is hampering more widespread use of dynamic models in global change research (Urban et al. 2016, Briscoe et al. 2019). It is undisputed that dynamic and mechanistic models require more complex data than simple correlative models (Dormann et al. 2012). For example, while correlative species distribution models require only simple snapshot occurrence data, patch-occupancy models need time-series data of occurrence and population-based models need demographic information and/or time series of abundance for calibration (Box 1, Fig. 4). Further, model evaluations on simulated data as well as on empirical data have shown that predictive accuracy of dynamic models increases when fitted to longer time series, with more information content on transient dynamics (Pagel and Schurr 2012, Briscoe et al. 2021). Such time series data are only available for limited taxonomic groups and regions. Typically, spatiotemporal data are particularly scarce for rare species that often are of high conservation concern. Recent studies show promise for using habitat and demographic proxies in such cases (Bleyhl et al. 2021). Additionally, we see great potential for extending available time-series data through emerging new sensor and genetic techniques and approaches that will improve our ability to document biodiversity dynamics and patterns but will also provide a more complete, holistic picture of ecosystem restoration (Pimm et al. 2015). Emerging techniques include citizen science, efficient automated and semi-automated bioacoustics and camera-trap devices, remote sensing techniques (e.g. spaceborne, airborne, radar, lidar), genomics (population genomics, meta-omics and genome editing) (Breed et al. 2019), and the accessibility of retrieving DNA from environmental samples (environmental DNA – eDNA) (Bush et al. 2017, Kissling et al. 2018a, b). These methods allow sampling and biomonitoring of ecosystems at high resolution and in real-time, filling data gaps between fine-scale and ecosystem-scale observations and detecting systematic changes in ecosystems. An outstanding challenge is to improve the integration of these data types in monitoring and modelling. Here, a promising and still underexploited avenue is provided by more flexible computational methods such as Approximate Bayesian Computation and pattern-oriented modelling that can help integrating heterogeneous data sources into simulation models (Hartig et al. 2011, Grimm and Railsback 2012, Gallagher et al. 2021).

Data challenges also remain for improving data availability of relevant environmental drivers, in past, present, and future (Urban et al. 2016). While most studies in our review mentioned direct effects of human activities (e.g. land-use change, overexploitation) as the dominant threat in the studied system, the impact of indirect anthropogenic effects such as climate change and ocean acidification is becoming increasingly relevant (Uthicke et al. 2013, Urban 2015). Designing effective conservation measures under these dynamic and non-local threats requires a detailed understanding of their individual and joint effects (Oliver and Morecroft 2014). For example, habitat loss and fragmentation not only lead to local extinctions and reduced gene flow among populations but also limit the ability of species to track their environmental niche under climate change (Warren et al. 2001). Similarly, habitat degradation and climate change may put the native fauna at a competitive disadvantage against potential and already-established invasive species (Foley 2005, Bellard et al. 2013). Likewise, rewilding apex predators may be unsuccessful in a policy context that does not regulate poaching (Bleyhl et al. 2021), and riparian habitat restoration may be inefficient when pollution sources are not eliminated first. Quantifying whether stressors affect biodiversity additively or synergistically requires improved environmental data, including past time series when studying legacy effects (Semper-Pascual et al. 2021) and future scenarios to inform decision-making. A key challenge is thus to provide integrated scenarios of climate, land use, and other anthropogenic pressures at finer spatial resolution in order to inform regional conservation and restoration efforts.

Modelling challenges

The comparably simple data requirements of static models, in particular correlative ENMs, are an important but likely not the only reason for their popularity compared to dynamic modelling approaches. Another major difference is the accessibility of easy-to-use software implementations and extensive guidance to use ENMs (Zurell et al. 2020). By contrast, many open-source and cross-platform implementations of dynamic modelling approaches have only been released comparably recently, and less guidance is currently available for applying them in practise (Supporting information). This means that it will take time for less experienced modellers and practitioners to accustom with these approaches. Knowledge transfer could be improved by providing more dedicated modelling support in form of extended tutorials and textbooks (as has happened for correlative ENMs) or in form of support teams. For example, the Climate Change Specialist Group (CCSG) of the International Union for Conservation of Nature (IUCN) has established a modelling support activity providing useful resources and advice to modelling carried out by the IUCN specialist groups (<http://ccsg-iucn.com/themes/modelling-support/>). Development of best-practise guidelines (Araújo et al. 2019) and standard protocols (Grimm et al. 2010, 2014, Zurell et al. 2020) can further facilitate planning, implementation, documentation, and communication of models and thus improve confidence in their adequacy for decision-making.

Additionally, several items are still missing from the toolbox of spatially explicit, dynamic modelling approaches, including easy-to-use routines for model calibration and model selection (Hartig et al. 2011, 2012) as well as for model validation. While model selection, model averaging and ensemble modelling, and validation of predictive performance are common practise for correlative ENMs (Roberts et al. 2017, Dormann et al. 2018), fitting complex simulation models to data and assessing their predictive performance is still regarded as cutting-edge and rarely done. Yet, these topics should receive much more attention in dynamic modelling approaches. The more complex the models, the more complex are decisions regarding the necessary process detail in the models (Zurell et al. 2016). This structural uncertainty could be dealt with by designing adequate model selection strategies for simulation models, or it could be accounted for by ensemble approaches. Validating predictive performance is particularly important for assessing uncertainty, when transferring models to different places and times and when model predictions are used to inform conservation and restoration projects, such as species reintroductions (Yates et al. 2018). For example, measures for preventing invasions and spread of aliens can be designed based on predictions of invasibility and establishment potential (Medley 2010, Villemant et al. 2011). Also, hindcasting to past and forecasting to future climates can help to benchmark and plan trophic rewilding and to select suitable sites for species reintroduction (Jarvie and Svenning 2018). Model transferability has received much attention in static modelling (Sequeira et al. 2018), and methodological advances have been made by introducing, for example, block cross-validation that explicitly tests predictive accuracy to different places, times, or environments (Wenger and Olden 2012, Roberts et al. 2017). By contrast, transferability and predictive accuracy in dynamic modelling approaches have rarely been assessed explicitly (Trotsiuk et al. 2020), although benchmarking studies showed that model fit to calibration data is not indicative of predictive accuracy under changing environmental conditions (Zurell et al. 2016). More routinely assessing limits to transferability of both static and dynamic models in space and time in a standardised way will be crucial for defining their forecast horizon (Petchey et al. 2015) and for adequately guiding conservation and restoration efforts under global change. A major step in this direction will be implementing standard routines for model validation within dynamic modelling platforms.

Decision-making challenges

As only limited funds and resources are available to spend on conservation and restoration efforts (McCarthy et al. 2012), it is crucial to invest the available means efficiently, for example by relying on explicit prioritisation approaches. In our review, most studies provided decision support only in the form of mapping the status quo, for example by identifying hotspots and coldspots of biodiversity and threats (Romero-Muñoz et al. 2020), or in the form of a gap analysis, for example by comparing hotspots with currently implemented protected areas and management plans. Cost optimisation approaches were rarely used as a formal decision support tool (10%), although their proportional use increased compared to former evaluations (Guisan et al. 2013). Well-validated spatial models allow the exploration of alternative, predefined management options either by comparing scenarios or by adopting a cost optimisation strategy that aims to find the optimal solution between maximising conservation and restoration gains and minimising costs (e.g. financial, human and spatial resources). Cost optimisation relies on defining an appropriate conservation goal that should ideally reflect different biodiversity facets, for example taxonomic, phylogenetic, and functional diversity (Pollock et al. 2017). Yet, most studies reviewed here only considered species richness as model response or focussed on only a single species. Here, we argue that multi-faceted conservation and restoration targets should be considered more routinely in decision-making. For example, complex models that incorporate processes from gene to ecosystem level (Fig. 3) will allow cost optimisation based on multiple EBVs and can effectively trade off different biodiversity facets in conservation as well as the provision of different ecosystem functions and services in ecosystem restoration. Additionally, using dynamic models will help anticipating transient dynamics in response to global change (Fig. 4) and thus bear the potential to plan sequential restoration measures (Higgs 2016) and to more effectively guide adaptative management strategies.

A range of optimisation software is available (Ball et al. 2009, Moilanen et al. 2011) that has traditionally been applied to static biodiversity information, such as optimising the representation or number of species or sites. Alagador and Cerdeira (2020) showed how existing prioritisation software such as 'Marxan' (Ball et al. 2009) and 'Zonation' (Moilanen et al. 2011) could be reformulated to optimise persistence goals under transient climate change dynamics, yet at the expense of high computational load. New prioritisation methods are currently being developed to make use of machine learning and artificial intelligence (Chadès et al. 2017). For example, deep reinforcement learning approaches (Rolnick et al. 2019) can be applied to the complex challenges of conservation and restoration of ecological systems. Again, a key challenge will be making these methods accessible to applied modellers and practitioners in the form of easy-to-use interfaces or modelling support groups and establishing best-practise guidelines for aiding model-based decision-making.

Discussion and conclusion

As ecosystems further deteriorate and our focus shifts from conservation to restoration, we urgently need more advanced models to support planning and decision-making under transient dynamics. To meet the challenges posed by the climate and biodiversity crises and the growing human population, we need to provide effective tools for quantifying the trade-offs between economic and societal well-being, biodiversity, climate adaptation, and climate mitigation (Leclère et al. 2020, Poertner et al. 2021). Models can greatly aid this decision-making and uncertainty quantification and should be used more routinely for guiding conservation and restoration actions at the local to global level (IPBES 2016).

Our literature review highlighted advances and opportunities of available spatially explicit modelling approaches and applications in animal conservation and restoration. This resulted in a new model typology for matching models with conservation and restoration goals and for facilitating model-based decision support. Thereby, our review focussed on applications in animal conservation and restoration and thus does not cover the entire breadth of available modelling frameworks in ecology, ignoring for example the wide field of vegetation modelling (Snell et al. 2014). Also, we only considered modelling studies that had a clear management application and were spatially explicit. We took care to define a set of general taxonomic keywords that would not bias our search towards terrestrial animals but cannot exclude that the keywords related to 'space' (Supporting information) have reduced the number of freshwater and marine studies considered. Nevertheless, we are confident that the identified studies provide a representative picture of the current state of spatially explicit models in animal conservation and restoration across regions and realms.

Important gaps for modelling and forecasting biodiversity at the gene to ecosystem level could be closed by improved integration of relevant ecological and evolutionary processes at the different organisational levels (Urban et al. 2016), improved data integration, and improved integration of cost optimisation strategies that include multiple biodiversity facets and transient dynamics. We conclude with a list of explicit recommendations for improving model-based decision support in conservation and restoration.

1) *Develop a toolbox for conservation and restoration modelling:* For a widespread adoption of models to inform effective animal conservation and restoration activities, it is critical that accessibility of modelling tools is improved and their use is facilitated. This would be substantially enhanced by the provision of an integrated platform or easy-to-use toolbox that provided ready access to a suite of models from across the modelling typology. Strong documentation, examples of effective model applications, and forum pages could all be helpful for developing a supportive developer and user community.
2) *Improve calibration and validation of dynamic modelling approaches:* Operationalising dynamic models over large numbers of species and ecosystems will require efficient and automated parameterisation and model selection and will need to integrate different sets of heterogeneous data. This requires easy access and guidance on advanced calibration methods such as pattern-oriented modelling and Approximate Bayesian Computation. Additionally, more routine model validation methods for dynamic modelling approaches need to be developed to explicitly assess predictive accuracy in a standardised way and increase confidence in these models. Without this information, it is impossible to know when it is necessary to collect additional data for updating model parameterisation and consequent model-based decisions.
3) *Develop and harmonise best-practise guidelines across modelling approaches:* When using models to project the state of biodiversity and ecosystems in time and space, we need to make sure that models are aligned with the intended use and are robust. Best-practise guidelines and standard protocols for model reporting will facilitate model implementation and communication and will ensure transparency and reproducibility. Such best-practise guidelines are needed in all aspects of model-based conservation and restoration planning, including the spatially explicit ecological models as well as the decision-making approaches.
4) *Use multiple models in combination:* For most conservation and restoration projects that we can envisage, it is likely that results from more than one model type can be useful as each model approach has specific strengths and weaknesses and can inform different aspects of the project. For example, if a reintroduction is being planned, an ENM may help inform where it is best to reintroduce while an IBM including genetics may help determine how many individuals should be reintroduced and at what temporal schedule to ensure effective establishment and long-term

genetic viability. An ecosystem model may then be useful to determine the likely broader impacts of the reintroduction of a species. Further, model validation may result in varying levels of confidence for alternative model types or alternative model implementations. Similar to other disciplines, epistemic uncertainty in the models could be considered by comparing results from, or by combining, multiple model types and algorithms in ensemble approaches.

5) *Use models as a core part of adaptive management:* Effective adaptive management requires long-term projects that couple management, monitoring, and research. The proposed toolbox with improved modelling methods and best-practise guidelines will allow model-based adaptive management, which should become an integral part of conservation and restoration projects. By monitoring and validating model predictions, and updating model assumptions and decision-making in an iterative fashion, model-based adaptive management will allow to identify and react to early warning signals of a system's shift and ensure ecosystem resilience into the future. The availability of long-term funding for modelling and monitoring and improved communication between research and practise will be key for achieving desired conservation and restoration outcomes.

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References

Akçakaya, H. R. 2000. Viability analyses with habitat-based metapopulation models. – Popul. Ecol. 42: 45–53.

Alagador, D. and Cerdeira, J. O. 2020. Revisiting the minimum set cover, the maximal coverage problems and a maximum benefit area selection problem to make climate-change-concerned conservation plans effective. – Methods Ecol. Evol. 11: 1325–1337.

Alagador, D. et al. 2014. Shifting protected areas: scheduling spatial priorities under climate change. – J. Appl. Ecol. 51: 703–713.

Araújo, M. B. et al. 2011. Climate change threatens European conservation areas. – Ecol. Lett. 14: 484–492.

Araújo, M. B. et al. 2019. Standards for distribution models in biodiversity assessments. – Sci. Adv. 5: eaat4858.

Baker, C. M. et al. 2016. Ensemble ecosystem modeling for predicting ecosystem response to predator reintroduction. – Conserv. Biol. 31: 376–384.

Ball, I. R. et al. 2009. Spatial conservation prioritization: quantitative methods and computational tools. – In: Moilanen, A. et al. (eds), Oxford Univ. Press, pp. 185–195.

Barychka, T. et al. 2019. Modelling variation in bushmeat harvesting among seven African ecosystems using the Madingley model: yield, survival and ecosystem impacts. – bioRxiv 695924, <https://www.biorxiv.org/content/10.1101/695924v1>.

Bell, D. A. et al. 2019. The exciting potential and remaining uncertainties of genetic rescue. – Trends Ecol. Evol. 34: 1070–1079.

Bellard, C. et al. 2013. Will climate change promote future invasions? – Global Change Biol. 19: 3740–3748.

Bleyhl, B. et al. 2021. Reducing persecution is more effective for restoring large carnivores than restoring their prey. – Ecol. Appl. 31: e02338.

Bocedi, G. et al. 2021. RangeShifter 2.0: an extended and enhanced platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. – Ecography 44: 1453–1462.

Breed, M. F. et al. 2019. The potential of genomics for restoring ecosystems and biodiversity. – Nat. Rev. Genet. 20: 615–628.

Briscoe, N. J. et al. 2019. Forecasting species range dynamics with process-explicit models: matching methods to applications. – Ecol. Lett. 22: 1940–1956.

Briscoe, N. J. et al. 2021. Can dynamic occupancy models improve predictions of species' range dynamics? A test using Swiss birds. – Global Change Biol. 27: 4269–4282.

Bush, A. et al. 2016. Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. – Ecol. Lett. 19: 1468–1478.

Bush, A. et al. 2017. Connecting Earth observation to high-throughput biodiversity data. – Nat. Ecol. Evol. 1: 0176.

Cabral, J. S. et al. 2017. Mechanistic simulation models in macroecology and biogeography: state-of-art and prospects. – Ecography 40: 267–280.

Cayuela, L. et al. 2009. Species distribution modeling in the tropics: problems, potentialities and the role of biological data for effective species conservation. – Trop. Conserv. Sci. 2: 319–352.

Chadès, I. et al. 2017. Optimization methods to solve adaptive management problems. – Theor. Ecol. 10: 1–20.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. – Austral Ecol. 18: 117–143.

Cotto, O. et al. 2020. NEMO-AGE: spatially explicit simulations of eco-evolutionary dynamics in stage-structured populations under changing environments. – Methods Ecol. Evol. 11: 1227–1236.

D'Amen, M. et al. 2017. Spatial predictions at the community level: from current approaches to future frameworks. – Biol. Rev. 92: 169–187.

Davis, M. et al. 2018. Mammal diversity will take millions of years to recover from the current biodiversity crisis. – Proc. Natl Acad. Sci. USA 115: 11262–11267.

Derry, A. M. et al. 2019. Conservation through the lens of (mal) adaptation: concepts and meta-analysis. – Evol. Appl. 12: 1287–1304.

Dexter, E. et al. 2018. The trouble with stress: a flexible method for the evaluation of nonmetric multidimensional scaling. – Limnol. Oceanogr. Meth. 16: 434–443.

Dormann, C. F. et al. 2012. Correlation and process in species distribution models: bridging a dichotomy. – J. Biogeogr. 39: 2119–2131.

Dormann, C. F. et al. 2018. Model averaging in ecology: a review of Bayesian, information–theoretic and tactical approaches for predictive inference. – Ecol. Monogr. 88: 485–504.

du Toit, J. T. and Pettorelli, N. 2019. The differences between rewilding and restoring an ecologically degraded landscape. – J. Appl. Ecol. 56: 2467–2471.

Fischer, J. et al. 2009. Integrating resilience thinking and optimisation for conservation. – Trends Ecol. Evol. 24: 549–554.

Foley, J. A. 2005. Global consequences of land use. – Science 309: 570–574.

Fordham, D. A. et al. 2018. How complex should models be? Comparing correlative and mechanistic range dynamics models. – Global Change Biol. 24: 1357–1370.

Gaitán-Espitia, J. D. and Hobday, A. J. 2020. Evolutionary principles and genetic considerations for guiding conservation interventions under climate change. – Global Change Biol. 27: 475–488.

Gallagher, C. A. et al. 2021. From theory to practice in pattern-oriented modelling: identifying and using empirical patterns in predictive models. – Biol. Rev. 96: 1868–1888.

Geary, W. L. et al. 2020. A guide to ecosystem models and their environmental applications. – Nat. Ecol. Evol. 4: 1459–1471.

Grimm, V. and Railsback, S. F. 2005. Individual-based modeling and ecology. – Princeton Univ. Press.

Grimm, V. and Railsback, S. F. 2012. Pattern-oriented modelling: a 'multiscope' for predictive systems ecology. – Phil. Trans. R. Soc. B 367: 298–310.

Grimm, V. et al. 2010. The ODD protocol: a review and first update. – Ecol. Model. 221: 2760–2768.

Grimm, V. et al. 2014. Towards better modelling and decision support: documenting model development, testing and analysis using TRACE. – Ecol. Model. 280: 129–139.

Grueber, C. E. et al. 2018. Complex problems need detailed solutions: harnessing multiple data types to inform genetic management in the wild. – Evol. Appl. 12: 280–291.

Guisan, A. et al. 2013. Predicting species distributions for conservation decisions. – Ecol. Lett. 16: 1424–1435.

Haller, B. C. and Messer, P. W. 2019. SLiM 3: forward genetic simulations beyond the wright–fisher model. – Mol. Biol. Evol. 36: 632–637.

Hanski, I. and Thomas, C. D. 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. – Biol. Conserv. 68: 167–180.

Harfoot, M. B. J. et al. 2014. Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. – PLoS Biol. 12: e1001841.

Harris, J. A. et al. 2006. Ecological restoration and global climate change. – Restor. Ecol. 14: 170–176.

Hartig, F. et al. 2011. Statistical inference for stochastic simulation models – theory and application. – Ecol. Lett. 14: 816–827.

Hartig, F. et al. 2012. Connecting dynamic vegetation models to data – an inverse perspective. – J. Biogeogr. 39: 2240–2252.

Higgs, E. 2016. Novel and designed ecosystems. – Restor. Ecol. 25: 8–13.

Higgs, E. et al. 2014. The changing role of history in restoration ecology. – Front. Ecol. Environ. 12: 499–506.

Hoban, S. et al. 2012. Computer simulations: tools for population and evolutionary genetics. – Nat. Rev. Genet. 13: 110–122.

Hoeks, S. et al. 2021. MadingleyR: an R package for mechanistic ecosystem modelling. – Global Ecol. Biogeogr. 30: 1922–1933.

Hoffmann, A. A. and Sgrò, C. M. 2011. Climate change and evolutionary adaptation. – Nature 470: 479–485.

Hoffmann, A. et al. 2015. A framework for incorporating evolutionary genomics into biodiversity conservation and management. – Clim. Change Respon. 2: 1.

Hoffmann, A. A. et al. 2021. Genetic mixing for population management: from genetic rescue to provenancing. – Evol. Appl. 14: 634–652.

Hunter-Ayad, J. et al. 2020. Reintroduction modelling: a guide to choosing and combining models for species reintroductions. – J. Appl. Ecol. 57: 1233–1243.

IPBES 2016. The methodological assessment report on scenarios and models of biodiversity and ecosystem services. – Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.

IPBES 2018. The IPBES assessment report on land degradation and restoration. – Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.

IPBES 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. – Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.

IUCN 2013. Guidelines for reintroductions and other conservation translocations. – IUCN Species Survival Commission.

Jarvie, S. and Svenning, J.-C. 2018. Using species distribution modelling to determine opportunities for trophic rewilding under future scenarios of climate change. – Phil. Trans. R. Soc. B 373: 20170446.

Kapitza, S. et al. 2021. Assessing biophysical and socio-economic impacts of climate change on regional avian biodiversity. – Sci. Rep. 11: 3304.

Kearney, M. and Porter, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. – Ecol. Lett. 12: 334–350.

Kelly, E. and Phillips, B. 2019. How many and when? Optimising targeted gene flow for a step change in the environment. – Ecol. Lett. 22: 447–457.

Kissling, W. D. et al. 2018a. Building essential biodiversity variables (EBVs) of species distribution and abundance at a global scale. – Biol. Rev. 93: 600–625.

Kissling, W. D. et al. 2018b. Towards global data products of essential biodiversity variables on species traits. – Nat. Ecol. Evol. 2: 1531–1540.

Landguth, E. L. et al. 2017. CDMetaPOP: an individual-based, eco-evolutionary model for spatially explicit simulation of landscape demogenetics. – Methods Ecol. Evol. 8: 4–11.

Leclère, D. et al. 2020. Bending the curve of terrestrial biodiversity needs an integrated strategy. – Nature 585: 551–556.

Mace, G. M. et al. 2018. Aiming higher to bend the curve of biodiversity loss. – Nat. Sustain. 1: 448–451.

MacKenzie, D. I. et al. 2003. Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. – Ecology 84: 2200–2207.

Malchow, A.-K. et al. 2021. RangeShiftR: an R package for individual-based simulation of spatial eco-evolutionary dynamics and species' responses to environmental change. – Ecography 44: 1443–1452.

McCarthy, D. P. et al. 2012. Financial costs of meeting global biodiversity conservation targets: current spending and unmet needs. – Science 338: 946–949.

McRae, B. H. et al. 2008. Using circuit theory to model connectivity in ecology, evolution and conservation. – Ecology 89: 2712–2724.

Medley, K. A. 2010. Niche shifts during the global invasion of the Asian tiger mosquito, *Aedes albopictus* Skuse (Culicidae), revealed by reciprocal distribution models. – Global Ecol. Biogeogr. 19: 122–133.

Mijangos, J. L. et al. 2014. Contribution of genetics to ecological restoration. – Mol. Ecol. 24: 22–37.

Mims, M. C. et al. 2019. Simulating demography, genetics and spatially explicit processes to inform reintroduction of a threatened char. – Ecosphere 10: e02589.

Moilanen, A. et al. 2011. Spatial prioritization of conservation management. – Conserv. Lett. 4: 383–393.

Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. – Conserv. Biol. 4: 355–364.

Okamoto, K. W. and Amarasekare, P. 2018. A framework for high-throughput eco-evolutionary simulations integrating multilocus forward-time population genetics and community ecology. – Methods Ecol. Evol. 9: 525–534.

Oliver, T. H. and Morecroft, M. D. 2014. Interactions between climate change and land use change on biodiversity: attribution problems, risks and opportunities. – WIREs Clim. Change 5: 317–335.

Oliver, T. H. et al. 2016. Are existing biodiversity conservation strategies appropriate in a changing climate? – Biol. Conserv. 193: 17–26.

Ovenden, T. S. et al. 2019. Improving reintroduction success in large carnivores through individual-based modelling: how to reintroduce Eurasian lynx *Lynx lynx* to Scotland. – Biol. Conserv. 234: 140–153.

Pagel, J. and Schurr, F. M. 2012. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. – Global Ecol. Biogeogr. 21: 293–304.

Pavlova, A. et al. 2017. Severe consequences of habitat fragmentation on genetic diversity of an endangered Australian freshwater fish: a call for assisted gene flow. – Evol. Appl. 10: 531–550.

Pereira, H. M. et al. 2013. Essential biodiversity variables. – Science 339: 277–278.

Perino, A. et al. 2019. Rewilding complex ecosystems. – Science 364: eaav5570.

Pesendorfer, M. B. et al. 2017. Oak habitat recovery on California's largest islands: scenarios for the role of corvid seed dispersal. – J. Appl. Ecol. 55: 1185–1194.

Petchey, O. L. et al. 2015. The ecological forecast horizon, and examples of its uses and determinants. – Ecol. Lett. 18: 597–611.

Pimm, S. L. et al. 2014. The biodiversity of species and their rates of extinction, distribution and protection. – Science 344: 1246752.

Pimm, S. L. et al. 2015. Emerging technologies to conserve biodiversity. – Trends Ecol. Evol. 30: 685–696.

Poertner, H. O. et al. 2021. IPBES-IPCC co-sponsored workshop report synopsis on biodiversity and climate change. – IPBES and IPCC.

Pollock, L. J. et al. 2017. Large conservation gains possible for global biodiversity facets. – Nature 546: 141–144.

Purves, D. et al. 2013. Time to model all life on Earth. – Nature 493: 295–297.

Roberts, D. R. et al. 2017. Cross-validation strategies for data with temporal, spatial, hierarchical or phylogenetic structure. – Ecography 40: 913–929.

Rolnick, D. et al. 2019. Tackling climate change with machine learning. – arXiv preprint, <https://arxiv.org/abs/1906.05433>.

Romero-Muñoz, A. et al. 2020. Increasing synergistic effects of habitat destruction and hunting on mammals over three decades in the Gran Chaco. – Ecography 43: 954–966.

Seddon, P. J. et al. 2014. Reversing defaunation: restoring species in a changing world. – Science 345: 406–412.

Semper-Pascual, A. et al. 2021. How do habitat amount and habitat fragmentation drive time-delayed responses of biodiversity to land-use change? – Proc. R. Soc. B 288: 20202466.

Sequeira, A. M. M. et al. 2018. Transferring biodiversity models for conservation: opportunities and challenges. – Methods Ecol. Evol. 9: 1250–1264.

Snell, R. S. et al. 2014. Using dynamic vegetation models to simulate plant range shifts. – Ecography 37: 1184–1197.

Svenning, J.-C. 2020. Rewilding should be central to global restoration efforts. – One Earth 3: 657–660.

Synes, N. W. et al. 2020. Prioritising conservation actions for biodiversity: lessening the impact from habitat fragmentation and climate change. – Biol. Conserv. 252: 108819.

Tallmon, D. A. et al. 2004. The alluring simplicity and complex reality of genetic rescue. – Trends Ecol. Evol. 19: 489–496.

Trotsiuk, V. et al. 2020. Assessing the response of forest productivity to climate extremes in Switzerland using model–data fusion. – Global Change Biol. 26: 2463–2476.

Urban, M. C. 2015. Accelerating extinction risk from climate change. – Science 348: 571–573.

Urban, M. C. et al. 2016. Improving the forecast for biodiversity under climate change. – Science 353: aad8466.

Uthicke, S. et al. 2013. High risk of extinction of benthic foraminifera in this century due to ocean acidification. – Sci. Rep. 3: 1769.

Villemant, C. et al. 2011. Predicting the invasion risk by the alien bee-hawking yellow-legged hornet *Vespa velutina nigrithorax* across Europe and other continents with niche models. – Biol. Conserv. 144: 2142–2150.

Warren, M. S. et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. – Nature 414: 65–69.

Weeks, A. R. et al. 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. – Evol. Appl. 4: 709–725.

Wenger, S. J. and Olden, J. D. 2012. Assessing transferability of ecological models: an underappreciated aspect of statistical validation. – Methods Ecol. Evol. 3: 260–267.

Whiteley, A. R. et al. 2015. Genetic rescue to the rescue. – Trends Ecol. Evol. 30: 42–49.

Wiens, J. A. et al. 2011. Protected areas in climate space: what will the future bring? – Biol. Conserv. 144: 2119–2125.

Wintle, B. A. et al. 2011. Ecological–economic optimization of biodiversity conservation under climate change. – Nat. Clim. Change 1: 355–359.

Yates, K. L. et al. 2018. Outstanding challenges in the transferability of ecological models. – Trends Ecol. Evol. 33: 790–802.

Zurell, D. 2017. Integrating demography, dispersal and interspecific interactions into bird distribution models. – J. Avian Biol. 48: 1505–1516.

Zurell, D. et al. 2016. Benchmarking novel approaches for modelling species range dynamics. – Global Change Biol. 22: 2651–2664.

Zurell, D. et al. 2020. A standard protocol for reporting species distribution models. – Ecography 43: 1261–1277.

Zurell, D. et al. 2021. Data from: Spatially explicit models for decision-making in animal conservation and restoration. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.crjdfn34p>.