

Better forecasts of range dynamics using genetic data

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The spatiotemporal response of species to past global change must be understood for adaptive management and to make useful predictions. Characteristics of past population dynamics are imprinted in genes, yet these molecular ‘log books’ are just beginning to be used to improve forecasts of biotic responses to climate change. This is despite there now being robust quantitative frameworks to incorporate such information. A tighter integration of genetic data into models of species range dynamics should lead to more robust and validated predictions of the response of demographic and evolutionary processes to large-scale environmental change. The use of these multidisciplinary methods will help conservation scientists to better connect theory to the on-ground design and implementation of effective measures to protect biodiversity.

Context: using molecular ‘log books’ in climate change research

Historical context is crucial for understanding patterns and processes of biodiversity. Disregarding or misinterpreting biotic responses to past environmental changes could impede our understanding of future ecological dynamics under global change and make accurate predictions and effective solutions difficult to formulate [1]. In many cases, the population history of species past responses to environmental changes are imprinted in their genes [2], but these data have not been exploited effectively to improve forecasts of species responses to climate change. Here we argue for the better use of ancient, historical, and contemporary genetic clues when constructing and validating models used to forecast climate change impacts on biodiversity. We also advocate for research that moves beyond using ecological niche models to improve inference from phylogeography. We show that the methods and data required for this new synthesis – weighted towards integrating ancient and historical genetic data into models of species range dynamics – are now within reach of most researchers.

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Increased access to palaeoclimatic and palaeoecological data and user-friendly ecological niche modelling software has meant that it is now common practice to use geographical information on past species distributions to interpret the spatial and temporal dimensions of genetic variation [3]. Some of the potential advantages of this approach for inferring species responses to climate change have already

Glossary

Ancient DNA (aDNA): preserved genetic records recovered from ancient materials including human and animal bones and teeth, plant remains, and sediments.

Coalescence modelling: a retrospective approach to modelling DNA variation in a population, whereby alleles of a gene shared by all members of a population are traced back to a common ancestry in the context of population demography.

Ecological niche model (ENM): use of statistical approaches to characterise the set of environmental conditions that are habitable for a species and to make inferences on range limits; also referred to ‘species distribution models’ or ‘bioclimatic envelope models’.

Effective population size (N_e): number of individuals in an idealised random mating population that has a value of a population genetic quantity equal to that of the actual population of interest. Typically substantially smaller than census population size.

Evolutionary potential: ability of a population to evolve to cope with environmental changes.

Fundamental niche: set of required environmental conditions to permit a species to exist.

Genetic stochasticity: random genetic consequences of small populations, including inbreeding, loss of genetic diversity, and mutational accumulation that may cause extinction.

Inbreeding depression: mean reduction in a life history or other fitness trait (often survival or reproduction) attributable to inbreeding.

Metapopulation: a group of spatially separated populations of the same species, which interact at some level through individuals moving between populations.

Multitemporal calibration: uses dated fossil material, matched to palaeoclimatic simulations, to more fully model, using ENMs, the breadth of climatic conditions in which a species can persist.

Niche population model (NPM): a method that dynamically couples stochastic demographic models (in some cases also capturing biophysiological processes) with ENMs to simulate spatial patterns of abundance and provide direct estimates of extinction risk.

Phylogeography: the examination of the geographic distributions and diversity of evolutionary lineages to understand evolutionary history of a taxon.

Process-based models: methods that incorporate the mechanistic links between the functional traits of species and their environments explicitly in predictions (of occurrence or abundance); also called mechanistic species distribution models.

Quaternary: a geological time period from ~2.59 million years to the recent, characterised by multiple glacial–interglacial events.

Realised niche: the set of environmental states in which a species is found at a moment in time.

Sediment (ancient) DNA (sedaDNA): ancient plant and animal DNA extracted directly from sediments.

been canvassed [4–6]. However, the methods needed to use genetic inferences to improve modelling of range dynamics have been slow to develop [7], with most attention given to conceptual frameworks [8]. The paucity of tools for such quantitative integration has meant that the new spatial modelling methods developed over the past few years [9,10] have not exploited the potential of using genetic inferences of historical demography to improve the tools for predicting climate-driven impacts on species ranges and abundances. The few models that have attempted to bridge this gap imposed simplifying assumptions about population structure and environmental and demographic heterogeneity [11,12].

A more systematic integration of genetic data into simulations of species past and future range dynamics (Figure 1) is now possible. We propose five primary applications of genetics for improving forecast responses to climate change and for gaining insight into drivers of past range dynamics: (i) calibrating ecological niche models using genetic estimates of past occurrence and abundance (effective population size), matched to palaeoclimate simulations, and then forecasting future responses; (ii) integrating genetic estimates of movement and connectivity into niche models; (iii) using molecular information to give

more robust estimates of demographic rates (inbreeding depression, dispersal capacity, etc.) and metapopulation structure (source–sink dynamics) in spatially explicit demographic models; (iv) using genetic studies to infer evolutionary and adaptive capacity (e.g., evolutionary changes in traits, rates of introgression, etc.) that can be simulated explicitly in individual-based and metapopulation models; and (v) linking genetic data with climate simulations to address whether data-intensive mechanistic models provide notably better forecasts of extinction risk than simple correlative models. The latter application could also give insight on whether the contrast between forecast high rates of extinction under anthropogenic-driven climate change [13] and apparently low extinction rates observed in the fossil record during the glacial–interglacial cycles of the Late Pleistocene [14] (with the exception of the megafauna) is the result of correlative models overpredicting biodiversity loss under climate change [15].

Forecasting range and extinction dynamics: current limitations and recent advances

Changes in species distributions and abundances are principally assessed using ecological niche models (ENMs), process-based models, or niche population models (NPMs) – see [Glossary](#) for definitions. Each approach has different advantages and limitations [16]. Being simpler and less data demanding, ENMs are easier to implement than mechanistic approaches (which typically require detailed demographic or physiological data), but have been criticised for oversimplifying assumptions and being based on largely phenomenological relationships. Process-based models that link species physiological traits with environmental conditions are more functionally realistic; however, similar to ENMs, they rarely account for important ecological processes – such as source–sink and density feedback dynamics – nor evolutionary processes (but see [17]), and are limited to inferring future extinction risk based on overlap between range areas over time, as well as crude metrics of total habitat suitability [9]. By contrast, NPMs account explicitly for metapopulation dynamics and key biotic processes, including species interactions [18], but have rarely been adapted to include evolutionary processes or loss of genetic variation. These different limitations may each cause biases or poor representation of uncertainties in their predictions of species range and abundance [19].

Despite these constraints, recent conceptual and technical advances have increased our ability to couple species spatial and genetic histories and, potentially, their future [20]. For example, (i) improvements to the spatial and temporal resolution of some general circulation models has meant that downscaled palaeoclimate data (reaching back to the Last Glacial Maximum 21 000 years ago) and future projections are available at decadal to monthly time scales [21,22]. Although there remains considerable differences across general circulation models [21], continuing refinement of these should improve predictions of species range movement and persistence through time. (ii) To address potential bias in ENM forecasts caused by occurrence records failing to capture a species fundamental ecological niche or adaptive capacity, multitemporal calibration can be used to configure ENMs [23,24]. In these

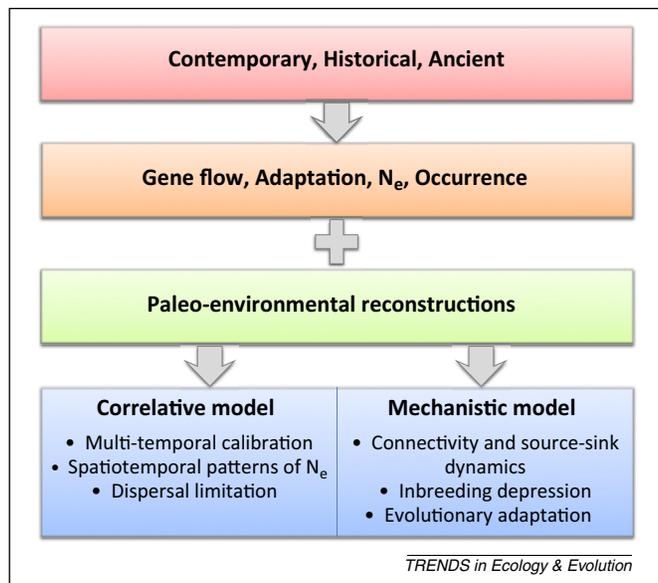


Figure 1. Integrating genetic information into correlative and mechanistic models. Three categories of genetic material (contemporary, historical, and ancient) can be used to generate alternative information on processes and patterns that can be merged with range dynamics models for climate change forecasts. Contemporary and historical genetic material is commonly used to infer dispersal rates, connectivity, source–sink dynamics, and amounts of inbreeding, using measures of gene flow and variation. Genetic information on movement can be used in correlative models to determine the biologically feasible study area and whether species can track climate pathways. Genetic information on connectivity can be used to inform the source–sink dynamics of demographic-based mechanistic models (i.e., niche population models), whereas information on genetic variation can be used to model inbreeding when subpopulations are small and habitat is fragmented. Historical DNA and ancient DNA (aDNA) can be used to infer genetically effective population sizes (N_e) along temporal and past spatial gradients using palaeoclimate data, whereas sedimentary ancient DNA (sedaDNA) can be used to identify occurrences along these gradients. Future technical [65] and analytical [61] developments could enable historical DNA and aDNA to provide information on genes under evolutionary adaptation. If alleles that strongly determine important phenotypic variation can be identified with confidence [55], this information could be incorporated into demographic-based mechanistic models that include individual heterogeneity.

Box 1. Using ancient genetics to forecast future population trends across space

The fossil record, ancient DNA (aDNA), coalescence approaches, and palaeoclimatic simulations all provide sources of evidence that, in principle, can now be effectively integrated to both calibrate ecological niche models based on past population dynamics under climate change and to forecast effective population sizes (N_e) across space under future climate change scenarios (see Figure 2 in main text). Past population trends can be estimated by extracting aDNA from dated fossil remains sampled across large regions and from different time periods, amplifying and sequencing it, and applying coalescence approaches. Various computational techniques such as Bayesian skyline or serial coalescent simulations followed by approximate Bayesian computation can trace back past population trends of genetic diversity and N_e [28], and their likely abiotic and biotic (e.g., human hunting) drivers [32]. Although previous studies focusing on aDNA have used mitochondrial DNA, recent advances allow the use of nuclear aDNA via single nucleotide polymorphisms (SNPs). Access to thousands of nuclear SNPs improves the ability to detect subtle bottlenecks and fast recoveries of populations [67]. Likewise, there is no longer a need to assume panmixia in coalescence approaches [68], allowing separate estimates of N_e for different populations. However, caution is needed when interpreting

these results because spatial heterogeneity can influence genetic diversity and population differentiation [35]. Where there is evidence that climate is likely to be the primary driver of past change in N_e (i.e., using approximate Bayesian computation methods), the geographical distribution of those population trends can be matched to high temporal resolution palaeoclimatic simulations (in millennial or centennial time bins), and the statistical relationship between N_e and climate can be modelled using a multitemporal calibration framework. Instead of using presence–absence as the response variable, we can use the value of effective population size, with climatic parameters and other environmental layers being the independent predictors. The statistical model describing the relationship between N_e and climatic condition can then be used to project future scenarios. By modelling N_e rather than presence–absence as the response variable, the influence of climate change on population dynamics and extinction vulnerability is captured more directly in future projections. By modelling N_e across a long temporal framework, uncertainty in predictions derived from (i) extrapolating to non-analogue climates and (ii) overlooking non-climate factors in model calibration will be reduced by better representing a broader range of climatic conditions within the model.

models, palaeoclimate simulations are matched to dated fossil occurrence data to broaden the breadth of climatic conditions that define a species potential niche, enhancing predictions for non-analogue climates [25]. (iii) To avoid biases in using range area type measures to draw broad inferences about the population dynamics and ultimate extinction risk of species [26], stochastic demographic models are being coupled with ENMs to estimate extinction risk directly [9].

A fourth advance has been to integrate phylogeographical analyses with complementary information from range dynamics models, to enhance evolutionary and ecological insights. This should allow conservation priorities to be set that not only conserve focal species but also historical evolutionary processes to support biodiversity over the long term [2]. A compelling and recently applied method is to use ENM projections of habitat suitability across space and time to inform spatially explicit demographic models whose parameters are then used to generate coalescent simulations [11,12]. This approach allows simulated genetic data for different habitat/demographic scenarios to be compared to observed genetic variation, providing a direct quantitative (rather than qualitative) method of validation. At the same time, new analytical tools are allowing for direct inference of historical range dynamics from modern genomic data [27].

Ancient and historical DNA: modelling effective population size and occurrence

Improvements in the bias reduction and precision of geochronological dating of fossil material and the recovery of ancient DNA (aDNA), matched with corresponding advances in the spatiotemporal resolution of palaeoclimate data (see above), are strengthening our understanding of how species and populations responded to palaeoclimate change [28,29]. On more recent time scales, analyses of DNA extracted from natural history collections can reveal climate-induced range shifts over the past few hundred years [30]. Both ancient and historical DNA can be used to infer effective population size (N_e) along temporal and past

spatial gradients, opening a direct window into prehistoric population responses to climate change. Because N_e is positively related to population size in many species [31], we could gain a deeper understanding of the implications of past climate change on species population dynamics by using estimates of N_e more directly in ENM development (rather than simply using spatiotemporal occurrence). This could be done by using DNA to elucidate species niche requirements (Box 1 and Figure 2), via the matching of information on past N_e with palaeoclimate simulations, in an analogous way to how radiometrically dated fossil material is being integrated into occurrence-based palaeodistribution models [24]. As a precautionary step, approximate Bayesian computation should be used first when possible to confirm that climate was probably the main driver of N_e dynamics rather than biotic processes such as overexploitation [32].

Careful interpretation of past population trends using DNA-based coalescence simulations [33,34] is needed when using information on N_e in ENMs, because genetic diversity can change as a result of admixture or spatial restructuring, independent of any variation in demography [35]. Furthermore, the relationship between N_e and true population size can vary temporally; however, fossil abundance can be used to validate [36] or calibrate this relationship. Palynological time series abundance data are widely accessible for hundreds of plant taxa [37], but animal fossils are far rarer and scattered. In the absence of independent estimates of abundance from the fossil record, N_e should be interpreted carefully or restricted to multitemporal calibration of species occurrence–climate relationships.

Uncertainty in estimates of N_e must also be factored into N_e –ENM projections. This could be done by calibrating ENMs separately with the upper and lower confidence limits for N_e , providing a projection range to span the likely relationship between N_e and climate. Because trends in N_e are calculated as the mean of thousands of independent sampled estimates, consensus methods can also be used to avoid underestimating uncertainty in the relationship

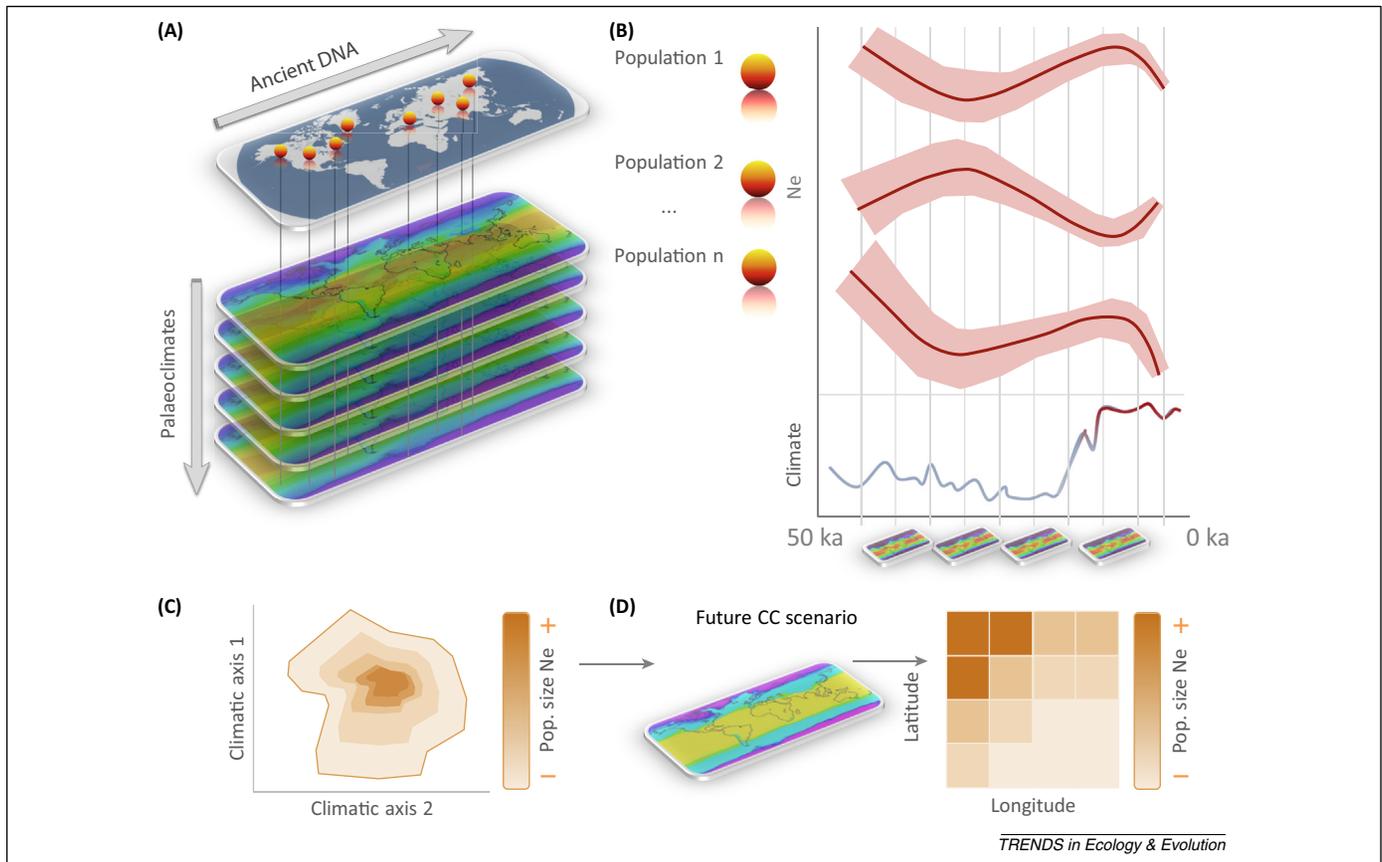


Figure 2. Illustration of the integration of ancient DNA (aDNA), palaeoclimatic simulations, and estimated genetically effective population sizes (N_e) through time in an environmental niche model framework, which can be used to forecast population responses to future climate change. **(A)** Localities with aDNA data (red spheres) and palaeoclimatic simulations from general circulation models can be organised in an explicitly spatial framework using a geographical information system. **(B)** aDNA can be used to infer N_e through time, matched to palaeoclimatic conditions for multiple populations. **(C)** By pooling climatic conditions and N_e across time and space, a climatic niche based on the variation of N_e across spatiotemporal climatic gradients can be inferred. This climatic niche can be statistically quantified using several mathematical algorithms (e.g., regression-based functions). Orange colours show different N_e values across climatic space. **(D)** Finally, the model-based characterisation of the environmental climatic niche can be transferred back into a geographical space for future climate change scenarios. Orange colours show the variability of projected abundances across geographical space.

between climate and N_e [28]. Both approaches are analogous to how uncertainty in climate futures is being integrated into adaptation assessments [38].

In the absence of fossil material, sedimentary ancient DNA (sedaDNA) can be used to identify species presence, mainly in regions with soil permafrost conditions [39]. Although sedaDNA may be of limited use in reconstructing past population dynamics, it can provide important temporal markers of species occurrence–climate relationships that are not well captured by the fossil record for a wide variety of taxa that existed in suitable regions [39]. These data can be used to map the past distribution of species, and when implemented in a multitemporal calibration framework, sedaDNA could provide an effective way to improve model performance and generality.

Contemporary DNA: gene flow and genetic variation Improving the representativeness and realism of ENMs using gene flow

Genetic tools are commonly used to quantify dispersal rates and distances based on gene flow [40]. These estimates of past dispersal success could be used to determine the potential for a species to track future climate pathways, providing

more realistic estimates of range shifts and identification of refugia. Species-specific dispersal constraints (i.e., fixed dispersal distance and least cost pathways) are now commonly integrated into projections of ENMs under environmental change and/or landscape fragmentation scenarios, reducing uncertainty in projections of species distributions [41]. However, acquiring field-based species-level long-distance dispersal information (e.g., via tagging, radio-tracking, or seed traps) is difficult and expensive. Therefore phylogenetic relatedness or morphology similarity to species with direct dispersal estimates is often used to extrapolate dispersal information across species [42]. Estimates of movement using gene flow data provide an underutilised alternative for incorporating dispersal information, at the level of the metapopulation, into ENMs. Furthermore, estimates of movement and connectivity, based on gene flow, could also be used to delimit biologically feasible study areas for calibrating presence-only ENMs, thereby ensuring that the background (or pseudo-absence) localities for model parameterisation is constrained to the conditions likely to have been experienced by the species, but not necessarily occupied [43]. Because the spatial extent from which pseudo-absence data are drawn can influence the accuracy of

ENM predictions [44], using genetically inferred dispersal rates to inform the selection of pseudo-absence localities would constrain an important source of bias in ENM forecasts. The range of uncertainty in dispersal estimates could be used to bracket the likely spatial extent from which pseudo-absence data are taken, thereby avoiding the use of arbitrary threshold rules when determining model sensitivity to pseudo-absence data [44].

Simulating source–sink dynamics and inbreeding depression in mechanistic models

Metapopulation theory asserts that emigration will be higher for source populations and lower for sink populations, largely reflecting differences in intrinsic population growth rates and local density. Sink populations persist because of immigration, having in some cases a detrimental and others a stabilising effect on metapopulation persistence [45]. Genetic data have been used to identify source and sink populations by estimating migration rates using coalescent approaches or assignment tests [46]. Coupling gene flow estimates with direct measures of movement provides multiple lines of evidence on the complex role of dispersal in natural populations [47]. However, the idea of using genetic estimates of connectivity to provide independent validation or calibration (by modifying immigration and emigration rates) of source–sink dynamics in climate–demographic modelling approaches remains largely unexplored. This is despite accommodating frameworks having been developed [48] and climate change forecasts of extinction risk and range movement being sensitive to inherent uncertainties in estimates of source–sink dynamics [26,49].

In addition to including adaptive evolutionary potential, extinction forecasts also need to properly account for inbreeding, which reduces reproductive fitness and leads to a loss of genetic diversity that reduces adaptive potential [50]. In connected populations, gene flow can offset genetic drift, maintain beneficial mutations, and mitigate inbreeding depression [50] but, at the same time, potentially obstruct local adaptation [51]. Genetic markers can be used to infer levels and impact of inbreeding by comparing fitness of individuals in matching environmental conditions [52]. Inbreeding depression has not been incorporated into any case study of demographic model forecasts of range dynamics in climate change settings to date, despite its important role in driving the extinction vortex in small or fragmented populations [53]. Thus, the survival prospects and distributions of threatened species are likely to be overestimates, especially when full life cycle impacts on reproductive fitness are properly accounted [54]. More focus is needed on routinely incorporating individual-level genetic information in metapopulation-level models of persistence and range movement, particularly for species in highly fragmented populations that are forecast to experience large shifts in climatic conditions, and when modelling populations at the contracting range boundary. Default estimates of inbreeding or rules of thumb (i.e., populations with $N_e > 100$ and > 1000 individuals will avoid inbreeding in the short and long term, respectively) [53] should be used cautiously and only in the absence of more detailed information,

because they can overstate or understate the risk of extinction depending on the level of metapopulation connectedness.

Considering adaptive evolution in models of range dynamics

Evolutionary adaptation and genetic diversity can influence range dynamics on medium- to long-term time scales, by giving species the capacity to counter stressful conditions or realise ecological opportunities [55]. There is some evidence to suggest that climate change has caused genetically based adaptive evolution in demographic traits so that species can exploit or tolerate new conditions [56]. These rare examples are important, because in the near future many species are unlikely to survive solely on phenotypic plasticity or their ability to track their preferred environment in space, attributable to the rapidity of anthropogenic climate change and the overlay of contemporary habitat fragmentation [57]. This means they must adapt evolutionarily, *in situ*, to avoid extinction. Therefore, reliable forecasts of species distributions and extinction risk will require adaptive evolution to be considered in range dynamics models [7], particularly for species with large population sizes and short generation times that are more likely to sustain the demographic cost of selection [56].

Model architectures have been developed to use information on adaptive capacity in simulations of species range dynamics. Estimates of heritable variation and selection intensity for ecologically important phenotypic traits can be calculated using quantitative genetics models [55], and this information can be used in simulation frameworks to condition vital rates (i.e., dispersal, survival, and fecundity) as they affect species distributions [17]. These models have recently been extended to include phenotypic plasticity [58] and environmental and demographic stochasticity [59]. For example, Vedder *et al.* [60] found that great tits (*Parus major*) are likely to adapt in the face of climate change through a combination of phenotypic plasticity and microevolutionary response in egg-laying date, allowing them to track changes in caterpillar densities.

Technical advances in population genomics will continue to provide increasing power to identify ‘large-effect’ alleles that underlie heritable variation within populations and divergence among them [61]. More specifically, the use of historical DNA from museum specimens and next-generation sequencing for monitoring full genomes can provide relevant insights on genes involved in adaptive responses and on the speed of those adaptations across many species [62]. However, evolution often acts via large numbers of small effect polygenes, and often epigenetic influences, potentially causing misleading interpretations of how alleles affect phenotypes and hence adaptive capacity [63]. Furthermore, disentangling the signature of local adaptation from other important but confounding genetic processes, such as founder effects (and mutation surfing), bottlenecks, and gene introgression, can be difficult [64]. As such, there is certainly a need for ongoing technical [65] and analytical [61] work in this area if range dynamics models are to routinely capture evolutionary processes. In

Box 2. Validating simple versus complex models under past climatic changes

The Quaternary (~2.59 million years ago to Recent) is the best-studied past period for biodiversity dynamics under multiple bouts of global climate change, making it an ideal natural setting for examining how model-based assumptions affect the integrated predictions of species responses to climate change. The glacial–interglacial cycles of the Quaternary were characterised by large globally averaged climatic shifts of 4–6°C [69]. The dominant response of species was idiosyncratic shifts in geographical range with concomitant shuffling of community composition [1]. There were few signals of elevated extinction rates [14], with the exception of the Late Pleistocene and megafauna and later Holocene losses, where human impacts (probably in synergy with climate change) led to a temporally staggered mass extinction of large-bodied fauna across many continents and large islands [23,28]. Anthropogenic greenhouse gas emissions are forecast to cause a further major shift in mean global temperature by 2100, this time hotter than any Quaternary epoch [70], which has the potential to cause widespread biodiversity loss [13]. Whether the contrast between high future forecast and lower observed biodiversity loss attributable to Quaternary climate change is an artefact of models bias inflating extinction risk, or reflects ongoing lags, is an important question that needs to be urgently resolved [15]. Genetic data could help resolve this issue by providing crucial independent validation data on the expansion and contraction of effective population size (N_e). Our hierarchical framework proposes using hindcasts of change in past range sizes based on models of

varying complexity, with simulated trends in N_e using genetic data (see Figure 3 in main text). The assumption is that range expansion and contraction affects N_e and these changes are reflected in the time series of genetic diversity [28]. Because the identification of temporal genetic signatures can be difficult, particularly for metapopulations with low average densities [35], this approach could initially be applied to a small number of species with good fossil abundance data that can be used to interpret [36], and potentially calibrate, the temporal relationship between N_e and total population abundance, or for species with large metapopulations. At one end of the continuum there would be environmental niche models, parameterised using occurrence data for the present day. At the other end would be mechanistic models that account for demographic and biophysical responses (and potentially evolutionary adaptation) to climate change and shifts in biotic responses, such as hunting by humans [9,10]. By applying this approach to diverse groups of species (small in number owing to data limitations, but representing a range of ecological–evolutionary milieu), our understanding of the environmental and life history conditions that determine when estimates of shifts in potential range area are likely to provide a good approximation of population expansion or contraction (and when they might be static) will be improved. Furthermore, comparing hindcast estimates of simulated population size (i.e., from niche population models) with genetic estimates of N_e should help define the circumstances when range area is a useful proxy for change in population abundance.

particular, more empirical data are urgently required to identify evolutionary potential across groups of individual species. This should be collected using a targeted approach, focused on case study species that are likely to be most sensitive to changes in thermal or hybrid conditions, thermal extremes, and whose climate preferences are forecast to change rapidly.

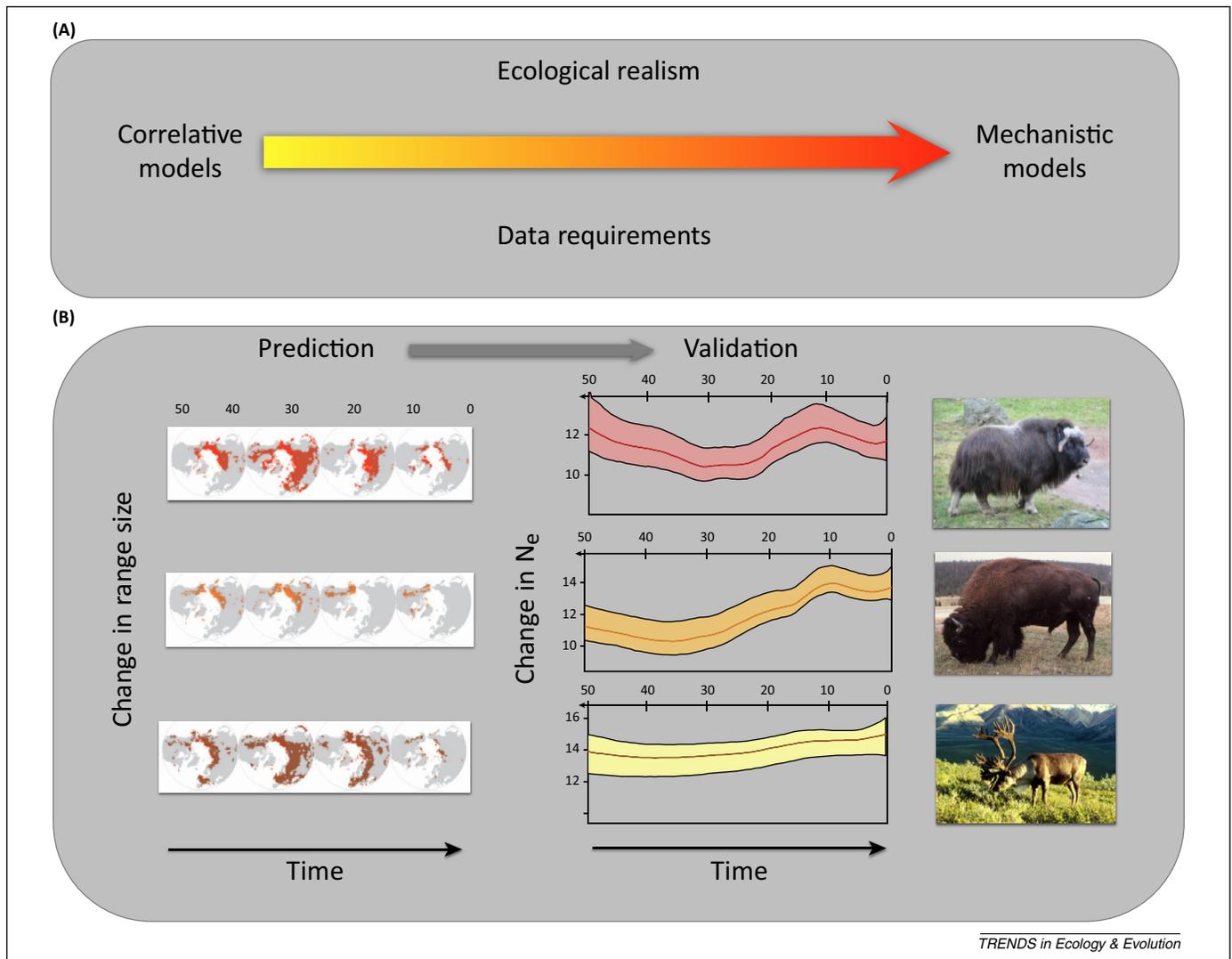
Past genetic signatures, model validation, and the dilemma of model complexity

There is strong theoretical support for using mechanistic–range dynamics models (e.g., NPMs) to explore species potential responses to climate change. Yet whether such added sophistication results in more consistently reliable forecasts of range movement and extinction risk, given inherent data and knowledge limitations, remains largely unknown [19]. Contrary to simple correlative habitat suitability models, the data needed to parameterise complex mechanistic models can be time consuming and expensive to collect, meaning that the majority of forecasts of biodiversity loss are inferred based on change in potential range size and not directly estimated from declines in population size or extinction risk. Establishing the environmental and demographic settings that determine when a more complex mechanistic model is preferable to a simple correlative association is crucial for improving forecasts of species range movement and persistence [26] and economic prioritisation. For example, recent work on commercially exploited molluscs showed that ENMs predict range and density expansion in response to global warming but the reverse when limiting biophysical and metapopulation processes are included [19]. In this example, a simple model would lead to adverse management decisions.

Genetic signatures of the timing and intensity of past population size changes, episodes of range shifts (e.g.,

expansion from, or contraction to, refugia), and admixture of previously isolated populations provide crucial independent data for validating spatiotemporal predictions. If repeated on many species, this could deliver vital insights into the balance between model complexity (i.e., niche models versus data intensive mechanistic models) and predictive skill. However, separating these effects independent of a spatial model can be difficult. Genetically derived validation data can yield superior spatial coverage and temporal resolution compared with other independent data sources (such as repeat surveys, fossil or space-for-time substitution data), by using after-the-fact sampling, which does not require intensive field work. Genetic data can also give a deep temporal perspective (in the case of aDNA) by providing estimates of local to range wide population changes during periods when the global climate was substantially different to the present [28]. Box 2 and Figure 3 show how temporal reconstructions of past genetic diversity and estimated population sizes could be used to assess the predictive ability (bias reduction and precision) of different families of models of species range dynamics.

A challenge will be developing ways to represent and interpret uncertainty in fossil dates, palaeoclimate simulations, and genetic estimates of spatiotemporal population size changes. Some of these uncertainties can be addressed directly, and their effect minimised [28], for example, by using Late Quaternary palaeoclimate simulations (with high temporal resolution) to calculate average climatic conditions over the exact range of uncertainty in fossil dates. However, for some species the uncertainty intervals in validation data and model parameters will be so wide that validating hindcasts will yield little information about the capacity of models to predict extinction probabilities [66]. Due diligence on candidate species is thus needed.



TRENDS in Ecology & Evolution

Figure 3. Schematic illustration of the integration of population genetics and geographical range models for independently validating projections of species responses to climate change. Reconstructions of change in past geographical distributions through time can be compared against effective population trends, N_e (see Box 2). Similarly, population trends estimated by methods that predict spatial patterns of abundance (e.g., niche population models) can be directly validated against genetic-based estimates of N_e . The framework allows for comparison of key assumptions of each model family and the assessment of the predictive ability (bias reduction and precision) of simple versus complex models. Based on Lorenzen *et al.* [28].

Concluding remarks

New approaches are emerging at the frontier between population genetics and ecological modelling that are useful for both uncovering the processes governing the past responses of species and populations to global environmental change, and showing the way to better integrate these disciplines for prediction. Inference of past population and range dynamics using multiscale genetic data will both strengthen ecological forecasting methods and enhance biological understanding of species demographic responses to climate change for well-studied species, and lend general insights into the expected behaviour of others. Wider application of models that incorporate evolutionary and ecological mechanisms – for cases where sufficient data exist – should allow conservation scientists to develop useful generalisations on the importance of these processes for extinction risk attributable to climate change and thus to achieve better on-ground implementation of effective measures to protect biodiversity.

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