

Improving assessment and modelling of climate change impacts on global terrestrial biodiversity

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Understanding how species and ecosystems respond to climate change has become a major focus of ecology and conservation biology. Modelling approaches provide important tools for making future projections, but current models of the climate-biosphere interface remain overly simplistic, undermining the credibility of projections. We identify five ways in which substantial advances could be made in the next few years: (i) improving the accessibility and efficiency of biodiversity monitoring data, (ii) quantifying the main determinants of the sensitivity of species to climate change, (iii) incorporating community dynamics into projections of biodiversity responses, (iv) accounting for the influence of evolutionary processes on the response of species to climate change, and (v) improving the biophysical rule sets that define functional groupings of species in global models.

The 'need to know' basis of climate change and biodiversity

Biodiversity, or the presence, abundance and genetic variation of organisms in an ecosystem, underpins the provision of ecological, environmental, social and economic goods and services, and is substantially responsible for the resilience of these services under climate change and other environmental stresses [1,2]. The conservation of genetic, species and ecosystem biodiversity in the face of global climate change and increasing human pressure on the land is mandated by the International Convention on Biological Diversity (<http://www.cbd.int/>). There is a large

Glossary

Adaptive capacity: the ability of a system to change in response to environmental forcing. This could include measures of genetic variation or phenotypic plasticity in a population or biodiversity in a community.

Allee effect: describes how small populations can show decreased growth rate with lower population density, potentially accelerating local extirpation. Causes can range from inbreeding depression, reduced interactions between reproductive individuals, and lower population resilience to disturbance because of reduced genetic variation.

Biome shifts: changes in the distribution of climatically-determined major vegetation types in response to a change in environmental conditions. Examples include the change from tundra to boreal forest because of increasing temperatures in high latitudes and elevations or the change from forest to savannah because of decreased precipitation or changes in disturbance regimes.

CEM: climate envelope models (also referred to as 'habitat' or 'niche' models) predict current and future species ranges based on correlations between observed species occurrences and climate variables.

DGVM: dynamic global vegetation models simulate the distribution of major vegetation types and terrestrial carbon cycling as a function of climatically-determined physiological limits on the growth of component plant functional types (PFTs) and competition between these PFTs. DGVMs can be used with some confidence to predict changes in the broad-scale behaviour of terrestrial vegetation in response to observed climate changes in the recent past, and are increasingly being used to explore the consequences of future climate scenarios.

DNA barcoding: the use of easily identified genetic markers to identify species from any material containing genetic material. This can greatly improve the efficiency in identifying species in the field.

Earth system models: numerical models that simulate the interactions between global biogeochemical cycles, climate and the biosphere.

Keystone species: a species that is thought to be essential to the functioning of a community or ecosystem.

NPP: net primary productivity refers to the change in organic mass (i.e. carbon) in an organism, community or system over time because of the absorption of carbon dioxide. NPP refers to the difference between photosynthesis (gross primary productivity) and respiration.

Palaeoecology: the field in ecology that uses data (palaeo-observations) documenting changes in past physical and biological systems to understand the response of ecosystems to changes in climate and other environmental

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factors. For example, pollen and plant macrofossils recovered from lake sediments can be used to reconstruct changes in vegetation assemblages through time. These data form a record of past ecological states.

PFT: a plant functional type is a group of species that display similar adaptations to environmental factors or perform similar functions within an ecosystem. Plant functional types are generally defined using plant functional traits related to, for example, life form, leaf form, phenology and bioclimatic limits.

Plant functional traits: are measurable characteristics of plants that are believed to be diagnostic of physiological adaptations to environmental stressors, and are thus used to identify groups of species (or plant functional types) that have specific advantages in given environments. Examples include leaf mass per area (or specific leaf area), wood density and seed mass.

and fast-growing body of evidence that anthropogenic climate change is affecting phenology and species distribution, most prominently in the northern extratropics where the registration of climate change is most marked [3,4]. Significant biome shifts (both gains and losses) have been projected as a result of anticipated 21st century climate changes [5]. However, in common with other areas of global change science, the credibility of these predictions is limited by incomplete theoretical understanding, predictive tools that are acknowledged to be imperfect, and insufficient data to test, develop and improve model projections.

IPCC Working Group 2 [4] identified some of the critical challenges to predicting climate change effects on biodiversity. These included: (i) inadequate understanding of the multiplicity of interacting drivers on changes in ecosystems, especially interactions involving land management; (ii) inadequate representation of the coupling between ecosystems and climate in models; (iii) failure of both climate-envelope models and dynamic global vegetation models (DGVMs) (see [Glossary](#)) to incorporate the range of processes known to influence species distributions; and (iv) neglect of changing disturbance regimes as a response to, and an influence on, climate-driven ecosystem changes. The Working Group went on to make specific recommendations for research priorities to reduce these uncertainties. Research in the four years since the publication of the Working Group report has begun to address some of these issues [6,7]. Nevertheless, much

still remains to be done to enhance predictive capacity. Here, we adopt the pragmatic approach of identifying gaps in relevant biological knowledge that could be filled relatively quickly because the basic tools required already exist or are being actively developed, and the obstacles to be overcome are therefore the barriers to coordination and collaboration rather than fundamental methodological issues. Although many potential gaps could be identified that would address climate impacts on particular species or biomes, we highlight generic opportunities that apply to the determination of climate-related risks to global biodiversity, and which are achievable in the medium term. These opportunities relate to: (i) improving the efficiency and accessibility of biodiversity monitoring data sets; (ii) developing tools that quantify the relative importance of climatic and non-climatic factors in governing the distribution of individual species or functional groups and account for them in making projections; (iii) incorporating community dynamics into models that project the responses of species and biodiversity; (iv) considering the influence of genetic variability, adaptive processes and phenotypic plasticity on the responses to climate change; and (v) representing functional diversity in DGVM and Earth System models. We examine each of these areas in turn and indicate ways to capitalize on recent progress, by integrating theoretical insights from diverse fields to improve our modelling capacity and using modern and palaeo-observations to test these models ([Figure 1](#)). We conclude by suggesting ten practical measures to improve predictive capacity.

Gap 1: improvement of comprehensive global biodiversity monitoring

Biodiversity monitoring is carried out for two distinct but related goals. The first is to document natural levels of global biodiversity, establishing a baseline catalogue of taxa against which to measure changes in biodiversity and determine whether targets for biodiversity conservation are being met. The second goal is to estimate rates of

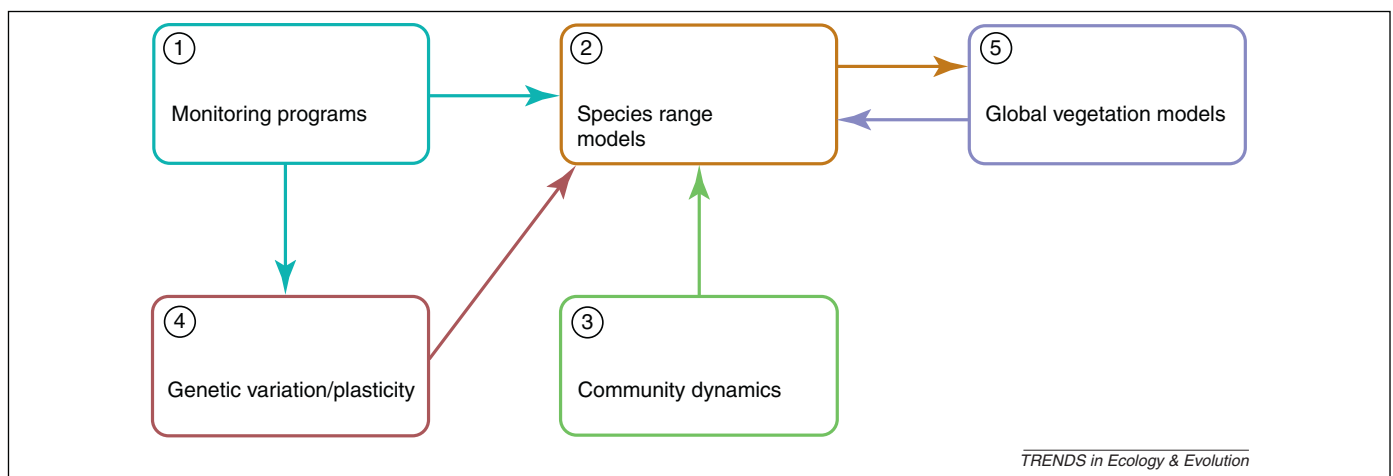


Figure 1. A diagram showing the links between the five areas identified here as ‘gaps’ in our current ability to predict the consequence of climate change for biodiversity. The arrows represent the flow of information. This information can be derived from observations or large-scale models of species viability and ecosystem change. Population monitoring (Gap 1) and genetic information (Gap 4) are the basis for descriptions of the abundance, spatial distribution and genetic variability of species. This information can inform models about community dynamics (Gap 3) and species ranges (Gap 2). We have argued for the development and use of process models to capture the mechanisms by which populations change in response to climate and other factors. These process models can, in turn, provide information about the behaviour of species with similar functional traits, information that is needed to improve the inference of large-scale (continental and global) terrestrial vegetation in response to climate change.

change in biodiversity and determine the mechanisms responsible for those changes, therefore creating quantitative links to multiple stressors involved, potentially offering an 'early warning' of the impacts of climate change on the biosphere [4]. Although monitoring is improving through the use of new technologies, such as DNA barcoding [8], camera traps (<http://www.teamnetwork.org/>), and standardized sampling protocols, many local monitoring programmes do not have a clearly articulated purpose or an approach that allows for the quantification of errors and uncertainties [9]. Furthermore, there are major gaps in the geographic coverage of monitoring sites in some high-diversity biomes, including the wet tropics and much of the Southern Hemisphere. There are also crucial gaps in terms of monitoring key taxonomic and functional groups; for example, there is almost no monitoring of soil microbial communities despite evidence that these play an important role in determining the successful establishment of vegetation [10]. Furthermore, there is little consideration of the processes that influence the response of vegetation to climate change (processes which could in turn be influenced by climate, such as fire) in the choice of monitoring sites.

New monitoring initiatives in Europe and North America (e.g. the National Ecological Observatory Network: NEON [11], <http://www.neoninc.org/>; GEO BON [12,13]) will help determine mechanisms that might put certain taxonomic or functional groups at risk. As important as these are, they do not address monitoring needs in biodiversity-rich regions of the world [14]. Global programs offer a way forward. The Smithsonian Institution Global Earth Observatory (SIGEO), which consists of 41 forest plots around the world (<http://www.sigeo.si.edu/>), has numerous sites in biodiversity-rich regions to monitor tree biodiversity. These efforts successfully catalogue an immense amount of plot-specific baseline data on tree biodiversity, but census results also highlight global monitoring challenges, especially for the second goal, understanding mechanisms that change biodiversity. For example, the 1173 identified tree species (of 356 000 total trees) in the 52 ha SIGEO plot in Lambir, Malaysia [15] offers an impressive beginning baseline data set (goal 1), but demonstrates the level of data collection necessary to infer regional species rareness, range, ecological determinants of range, and other variables important to biodiversity change (goal 2). The Forest Inventory and Analysis program (<http://fia.fs.fed.us/>) in the United States consists of over 140 000 small plots, effectively covering species presence and abundance across the entire country, but the total number of tree species in North America is less than the SIGEO site in Lambir.

Clearly, there exists a need to establish new monitoring sites and monitoring programs, balancing coverage and sampling intensity, building off of core research, but here emphasis would be best placed on locating the sites with respect to key geographical and ecological gaps identified by current programs and research, and developing process understanding with those data. It is also crucial that monitoring sites sample data relevant to climate change threats (e.g. local climate and edaphic data). There are protocols for monitoring biodiversity [16]: a priority is to

standardize these protocols to ensure that data collected at one site are comparable to those collected elsewhere. Establishing these protocols, and providing the training that is required to implement them, will be an important community- and capacity-building effort.

Gap 2: quantifying the main determinants of the sensitivity of species to climate change

Climate can have strong and direct influence on species distributions. Limitations or shifts in the distribution of species can therefore offer a clear indicator of climate induced changes in biodiversity [3]. Most models used to predict changes in species distributions rely on climatic envelope models (CEMs; see e.g. [17–19]; also referred to as 'niche-based' or 'habitat' models) that describe statistical relations between environmental variables and observed distributions. CEMs assume that macro-climate acts as the primary determinant of the distributions of species, and offer a simple, relatively easy approach to determining basic climatic determinants of a species range and shifts in that range because of changes in the input climate variables. This most basic approach to the interface between climate and biodiversity does not attempt to establish the underlying mechanisms that determine ranges, such as functional traits, demographic vital rates, or competition. Further, CEMs treat species-climate relations as constant and species as non-interacting entities [20] (see Gap 3) and typically disregard potentially important influences of fine-scale habitat variability, temporal climate variability, and CO₂ fertilization [21]. Because of their correlative nature, CEMs can do a reasonable job linking climate to observed patterns, but future predictions derived from these models have no basis for assessment. Keenan *et al.* [22] used nine different CEM-type models to analyze distribution data on three Mediterranean tree species and found that most models serviceably predicted current distributions given observed variables (including climate and geographical data), but varied widely in how they predicted future habitat suitability (e.g. *Quercus ilex* was predicted to lose anywhere between 5.65 and 88.42 percent of its current suitable habitat by the period 2050–2080 depending on which of the nine CEM models was used).

Can more detailed models do better? Process-based models [23,24] represent a step away from the correlative foundation of CEMs by incorporating physiological or demographic mechanisms to build predictions of future changes in species distributions [25]. The trade-off is that these models require information about the physiology of species and local competitive interactions that is not always available [26]. Comparison of CEMs and process-based models suggests substantial advances can be made by directly modelling processes [27]. In the same article mentioned above, Keenan *et al.* [22] tested a model that incorporated NPP growth because of increasing CO₂ levels and found a significant influence of this mechanism on predictions of future suitable habitat.

Both correlative and mechanistic models of species distributions typically ignore biotic and abiotic influences on geographical distributions that are not related to climate [28]. Competition [26] and dispersal limitation [29] can

also play a role in defining species ranges (but see [30]). The relative importance of climatic and non-climatic factors in influencing distribution varies among species and across ranges, with some evidence that arctic/boreal species are more strongly climate limited than temperate/tropical species [31]. Furthermore, the distribution of some species shows no apparent association with climate [31,32].

Understanding what determines the sensitivity of individual species to climate is of fundamental interest [24,27], but pragmatically needs to be quantified across a wider range of functional groups. Recent statistical approaches have focused on quantifying the degree to which species distributions are in equilibrium with climate [33] or the relative contribution of climatic and non-climatic factors using appropriate null models to formulate testable hypotheses [31,32]. New applications of spatially-explicit hierarchical models offer an alternative modelling method that allows direct estimation of the relative importance of biotic and abiotic processes in shaping species distributions. Although some work is required to determine which of these statistical tools are most suitable for specific analyses, and to standardize the methods, the key task is to apply them to continental-scale datasets and identify which species are highly sensitive to climate and which are comparatively insensitive. This approach might also determine species resilience to climate change across taxonomic and functional groups, facilitating improved treatment of resilience within global-scale models.

Gap 3: community dynamics and projections of biodiversity responses

As has happened in the recent geological past (Box 1), future climate change will probably generate novel assemblages of species, as existing communities gain and lose species, and these different assemblages could affect large-scale patterns and processes such as biome boundary shifts and ecosystem function [34]. Community dynamics, the

interactions between species in an assemblage, can change radically with the loss of certain species, affecting the persistence of communities and their consequent contribution to biomes and the biosphere (Figure 1). Species are linked through interactions such as competition, predation and mutualism. Depending on the strength and structure of these links, the loss of a species because of climate change or other human interventions can radically affect the behaviour of the entire system [35]. The collapse of a community can exceptionally occur with the loss of a single 'keystone' species [36], but functional redundancy and generalist interactions, both allowing extirpated species roles in the community to be filled by other species, can buffer communities against multiple extinctions. The outcome of interactions between species, although crucial to inference about large-scale patterns, is difficult to predict and requires extensive information about population and species networks (Figure 1). Better predictions about community dynamics begins with sound ecological knowledge about which species interact and with what effect. With an increase of data from monitoring programs (Gap 1), a concerted effort should be put into systematizing this knowledge as it relates to community dynamics for predictive purposes at large scales.

A number of new methods estimate how changes in the physical environment can affect species interactions. Stochastic demographic models combine information about life-history change over time under different environmental conditions and can be built in such a way (e.g. using hierarchical Bayesian methods) that they offer extrapolation of output over space and into the future [37,38]. As the taxonomic and geographical scope of local and regional models of communities increases, output from these models should provide insight into common behaviours of communities that can be applied broadly. Thébaud and Fontaine [39] demonstrated that mutualistic networks of plants and pollinators and trophic networks of herbivores

Box 1. Palaeoecological evidence

There has been wide recognition that palaeoecological studies have an important role to play in conservation strategies: providing baseline information about natural ecosystems, documenting the range of responses to natural variability, and identifying situations in which critical changes in ecosystem functioning occur [74]. The past does not provide direct analogues for the future, but past climate changes have been as large and as fast as those projected in the future [75]. During the Last Glacial, for example, temperature shifts of up to 10–16 °C occurred in Greenland and the northern extratropics, sometimes within a few decades [76]. The response of terrestrial ecosystems to past climate changes is documented by pollen, plant macrofossils and organic biomarkers in, and the carbon isotopic composition of, dated sedimentary deposits [77]. Changes in disturbance through fire are documented by recalcitrant charcoal in sedimentary deposits [78]. These records show that both vegetation and disturbance adjusted to rapid climate changes during the Last Glacial within 50–200 years of the initial disturbance ([79–81]; Figure 1). The rapid vegetation response implies either rapid long-distance migration or rapid expansion of small *in situ* refugial populations in local microhabitats; both have been documented in the fossil record and the latter mechanism is supported by both fossil evidence (see e.g. [82]) and genetic studies of modern populations (see e.g. [83,84]). Rapid climate changes have occurred in past warm (interglacial) periods [85] and have also given rise to rapid changes in

ecosystems and disturbance (e.g. [86]). Detailed studies of the response of terrestrial vegetation to climate changes since the Last Glacial Maximum (ca 21 000 years ago) show that species respond in an individualistic way to climate changes, giving rise to assemblages that do not occur today [87]. At certain times in the past, vegetation types that are today confined to small areas expanded to occupy very large areas of the northern continents [88]. Palaeodata provide an observational basis for understanding the multi-faceted responses to diverse, large and sometimes very rapid climate changes, far beyond the limited palette represented by the instrumental record [18]. Although there have been examples where palaeoecological information has been used to guide conservation or restoration activities (e.g. [89]), only limited use has been made of palaeoecological evidence to date in the context of biodiversity studies [90]. This is partly because palaeoecology has, until recently, largely been site focused and descriptive. With the advent of global data sets documenting key aspects of the terrestrial biosphere (e.g. vegetation distribution; fire: [78,80]), and statistical tools to analyze such data sets, palaeoecological data can now be used to quantify the relations between climate change and ecosystem responses. Furthermore, the large-scale synthesis facilitated by these data sets provides concrete tests of the ability of DGVMs to simulate processes, such as migration, which operate at timescales precluding the use of historic records.

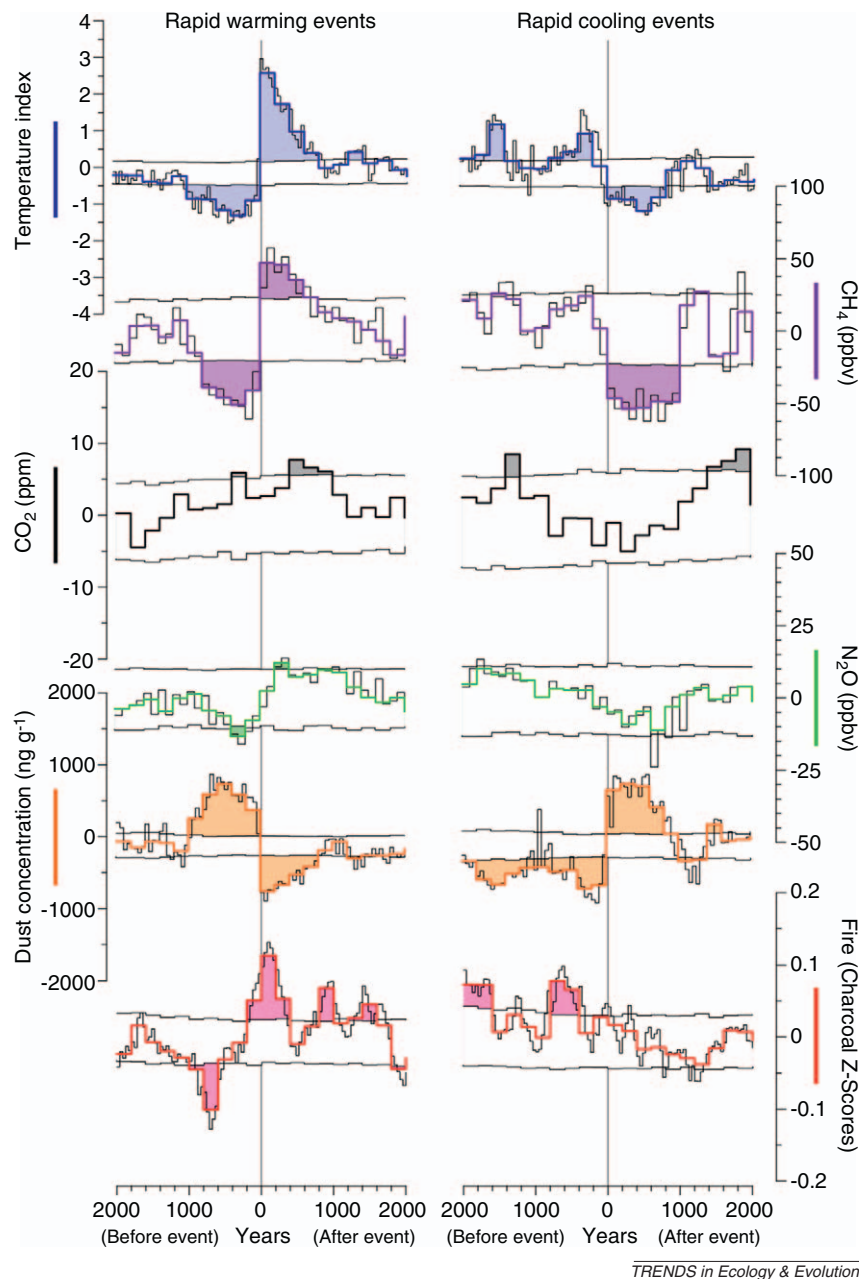


Figure 1. Superposed epoch analysis of ice-core and biomass-burning records over the interval 80 ka to 10 ka. This analysis shows the consistent response of a time series to the repeated occurrence of the abrupt warming and cooling events that define the Dansgaard-Oeschger (D-O) cycles during the Last Glacial period. The Greenland oxygen-isotope record (a), an index of regional temperature, shows the characteristic saw-tooth pattern of an individual D-O cycle, is compared to ice-core records of (b) CH_4 , (c) CO_2 , (d) N_2O , and (e) dust concentration (an index of vegetation cover, with more vegetation meaning less dust erosion and transport), and (f) a composite curve of transformed and standardized charcoal concentrations (an index of biomass burning) from a global network of terrestrial and marine cores. All of these records show distinctive responses associated with the occurrence of abrupt warming or cooling in Greenland [79].

and plants are stable over time with very different interaction architectures. Mutualist networks show greater stability with highly connected and nested network architecture, whereas trophic networks show greater stability when highly modular and loosely connected. Combining quantified expectations of interaction outcomes using new modelling approaches with theoretical expectations of community stability and resilience based on interaction architecture offers a promising way to build predictions about ecosystem changes. These quantified links can then inform large-scale simulations that cannot explicitly model the complexity of fine-scale community dynamics.

Gap 4: accounting for the influence of genetic variability and adaptive processes on species responses to climate change

Populations of nearly all species of sexually reproducing organisms exhibit considerable genetic variation. Estimates of genetic variation, based on selection studies [40], quantitative genetic studies [41], and studies of neutral markers and quantitative trait loci [42], suggest that most populations of most species have significant potential to respond evolutionarily to changing climate, given enough time and selective pressure [43]. For a given level of genetic variation, a functionally significant evolutionary

response to climate change is inversely proportional to generation time and positively correlated with the magnitude of environmental change, contingent upon demographic contributions to fitness [44]. The most probable candidates for evolutionary response to rapid climate change will therefore be short-lived species, such as bacteria, arthropods and annual plants, and species experiencing the largest shifts in climate or disturbance regime. Plasticity, the development of a range of phenotypes from one genotype [41], is an alternative response to climate change. Plasticity can be non-adaptive (e.g. reduced reproductive output in stunted organisms) or adaptive (e.g. smaller leaves increasing survival in heat- or drought-stressed plants). Selection for greater plasticity has been demonstrated for breeding dates of passerine birds in response to climate change [45].

The process of change in range can itself lead to evolution, particularly at the leading and trailing edges of the species range [46], albeit with a cost in effective population size and genetic variation. Selection pressures at leading and trailing edges are different because the environments are different: at the leading edge, the species is migrating into an already established community, whereas at the trailing edge it is suffering demographic decline and potential Allee effects. Evolutionary potential at the leading edge can be enhanced or impeded by gene flow from the main range of the species, but at the trailing edge evolution will depend on existing genetic variation and can be affected by isolation of populations.

Genetic variation and micro-evolutionary capacity are rarely taken into account in predictions of species or ecosystem responses to climate change, partly because of a lack of systematized information. The role of genetic diversity and phenotypic plasticity in buffering communities against the effects of changing climate could be assessed by combining experimentally derived data and knowledge of spatial processes in ecosystem and vegetation models. Taxonomic patterns of plasticity and adaptive capacity can be identified by meta-analysis of existing population-genetic data, with broad representation across clades, supplemented by laboratory tests of species responses to specific climate stresses. A particularly promising advancement in this type of analysis involves the mathematical integration of population-genetic and phylogenetic-comparative methods for assessing both short-term and long-term evolutionary response of populations and species to changing climate [47].

Gap 5: improving the biophysical rule sets that define functional groupings of plant species in global models DGVMs (e.g. [48]) simulate changes in vegetation distribution, allowing for competition between different plant functional types (PFTs) rather than species (Box 2). The current generation of DGVMs employs a limited set of PFTs (< 15 PFTs, Table S1), as do land-surface schemes in climate models (see e.g. [49]) (Table S1). This simplification of biodiversity is an elegant solution that provides credible simulations of biogeochemical processes and ecosystem structure, but constrains their usefulness for predicting how future climate changes might affect vegetation distribution and biodiversity. One way to improve the biological realism of DGVMs is to increase the number

Box 2. Plant functional types and global modelling

Functional classification of plant species has been seen as a necessary tool for monitoring the effects of environmental change and ecosystem management (e.g. [91]), for mapping vegetation patterns (e.g. [88]), and most particularly, for the construction of global vegetation models (e.g. [55]). It is now widely recognized that there are two broad, non-congruent, categories of functional types: functional effect types and functional response types [54]. Functional effect types group together species that have a common impact on one or more aspects of ecosystem functioning, such as productivity, decomposition or nutrient availability (see e.g. [92]). Functional response types group together species that have a common response to one or more environmental factors, such as climate stressors, resource availability or disturbance (see e.g. [53]). Plant functional types can be classified *a priori* based on assumptions about functionality or based on correlations between morphological, physiological, biogeochemical, reproductive or demographic characteristics or traits. Several functional classification schemes have been proposed (see e.g. [50,93]), adapted for specific purposes. Global models, whether these are stand-alone equilibrium or dynamic vegetation models (DGVMs) or representations of vegetation dynamics within the land-surface schemes of earth system models, use a scheme related to the functional response to climate and assuming *a priori* that life form (e.g. tree, shrub, herb), leaf type (e.g. broadleaf, needleleaf, scaleleaf) and phenology (e.g. deciduous, evergreen) are key traits with climatic significance (see [50]). These schemes could additionally recognize categories related to bioclimatic thresholds, for example tolerance with respect to extreme low or high temperatures (e.g. cold hardiness, heat stress mortality). In general, through computational limitations and lack of empirical data, the number of plant functional types used in global models (see Table S1) is considerably smaller in number than the number of such types used for vegetation mapping or monitoring purposes. This opens up the possibility of using existing empirical research on plant response types with respect to, for example, disturbance through grazing or fire, nutrient status, and atmospheric CO₂ concentration (e.g. [53]), to expand these classifications. The recognition that both functionality and response are expressed through readily observable traits [54] means that the ever-growing datasets on trait distribution could also be exploited to refine functional classification schemes.

of PFTs by representing more types that are important for a specific ecological function and/or are responsive to particular aspects of climate or disturbance. PFT definition in a modelling context has emphasised 'top-down' classifications based on traits such as life form, leaf form and phenology, with some attempt to incorporate bioclimatic limits based on current spatial distribution patterns or on limited physiological data [50]. Statistical studies of trait abundance with respect to climate (Figure 2; [51]), nutrient [52] or disturbance gradients [53,54] demonstrate that it is possible to derive empirical PFT classifications. However, additional work will be required to establish robust relations between traits measured in the field and physiological quantities represented in the models. Once robust relations have been established it will still be necessary to provide quantitative values for a number of other parameters relating to phenology, allocation strategy and response to disturbance [55]. Data availability has been a key limitation on the number of PFTs included in DGVMs, but the development of global trait databases (e.g. GLOPNET [52]; TRY [http://www.try-db.org/]) can now redress this situation. Quantitative trait data have already been used to improve the representation of photosynthetic capacity and nitrogen use efficiency in the vegetation module of the ECHAM climate model [56]. DGVMs are

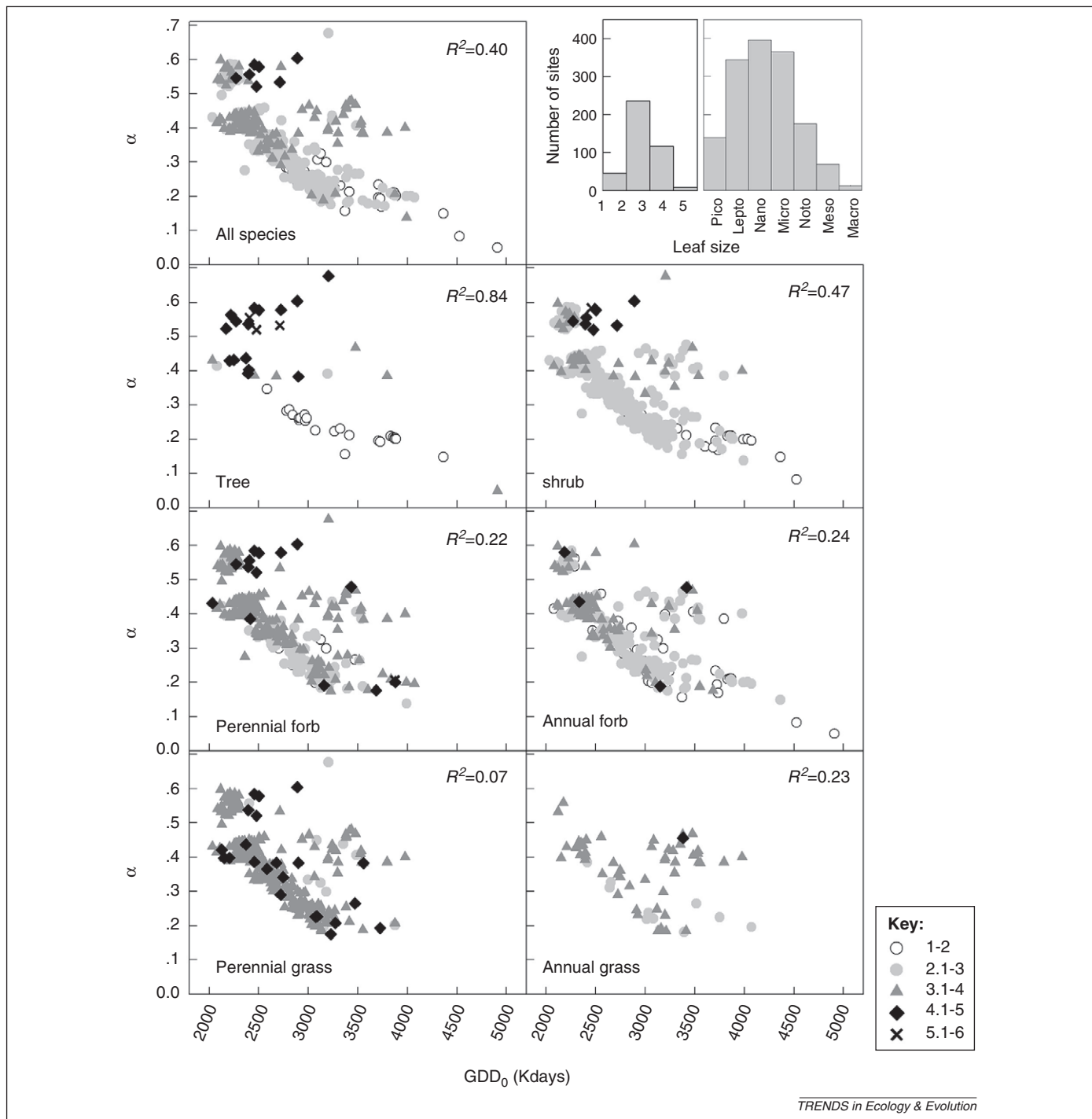


Figure 2. An example of climate-trait relations along climate gradients in China (from [51]). Expression of average leaf size as a function of aridity (as measured by the ratio of actual to potential evapotranspiration, α) and summer temperature (as measured by the accumulated temperature sum during the growing season above 0 °C, GDD₀) across all species and within different life forms. For analytical purposes, leaf size was divided into 7 categories: 1 = pico (leaf area < 5 mm²), 2 = lepto (leaf area 5–25 mm²), 3 = nano (leaf area 25–250 mm²), 4 = micro (leaf area 250–2000 mm²), 5 = noto (leaf area 2000–4500 mm²), 6 = meso (leaf area 4500–20 000 mm²), and 7 = macro (leaf area 20 000–150 000 mm²). Leaf size decreases with increasing aridity and with increasing summer temperature, overall and within most life forms. The relations are all statistically significant ($p < 0.001$).

also moving beyond ‘hard-wired’ specification of parameter values for PFTs to allow environmentally plastic traits to adapt to environmental changes [57,58], in which case quantitative trait data are equally important to test modelled trait values (Gap 4).

Improved PFT representation in DGVMs will require systematic studies of trait relations with key environmental factors, and the refinement of the rule sets that define PFTs in the current generation of DGVMs. Further devel-

opment of existing trait databases will be needed to have sufficient coverage of all pertinent traits. Table S2 lists a subset of traits we have identified as the most crucial, and the availability of measurements of these traits in the TRY database. (This is not a comprehensive list but does represent a growing consensus on the most important primary information likely to be needed, and obtainable, to represent PFTs in next-generation DGVMs. Measurements on all of these traits however are available for only about 50

species. Additional field measurements might need to be made in key ecosystems, but should be complemented by exploitation of other resources such as regional floras or herbaria [51]; this is increasingly feasible, given the rapid growth of digital resources. Until recently, trait research has focused on how the possession of particular traits, or trait combinations, affects plant performance. Additional

research is required on how traits or suites of traits possessed collectively by co-existing species influence ecosystem function. Meta-analyses will be needed to link traits, demographic characteristics and environmental factors in a phylogenetic context. There needs to be a closer integration between statistical analyses of traits and process studies relating traits explicitly to plant performance, to

Table 1. Description of existing models used to predict the distribution of populations, species or vegetation types. Each model has specific characteristics (drivers, spatial scale) and specific purposes, gaps and advantages

Type of model	Examples	Level of development	Drivers	Spatial scale	Purposes	Advantages	Gaps
Demographic models	Sortie [66] ForClim [67] ED [68]	Individual/ population	Abiotic (climate, nutrient, soil conditions, water availability, land-use) and biotic (intra- and inter-specific competition)	Landscape/ regional	Relative abundance of species in a community	Explicit representation of population dynamics and competition	Progress to be made on the effect of climate, link with species distribution [Gap 1, 3,4]
SDMs	<i>Climatic envelope habitat-based</i>	BIOCLIM [69] BIOMOD [70]	Species	Regional/ continental	Predicting the impact of climate change on species distribution	Possible to calibrate for many organisms / widely used in conservation plans	Validation problematic, progress to be made on incorporation of ecological processes and incorporation of genetic variability improvement of migration processes/ evolutionary processes [Gap 2–4]
	<i>Process-based</i>	NicheMapper [71] Phenofit [72,73]	Individual/ population/ species		Understanding current species distributions and predicting the impact of climate change on distributions	External validation is possible, identifying limiting factors and processes for observed species ranges and for predictions, can incorporate climate factors but also other factors (e.g. land-use), can take account of genetic variability across individuals/ populations	Requires ecological knowledge (which increases as spatial scale becomes finer), relevant ecological data, currently developed for only a few taxa, lack of migration processes [Gap 2–3]
DGVMs	LPJ [48]	Functional types/ biomes	Abiotic (climate, soil conditions, land-use) and biotic (only among functional types)	Continental/ global	Identifying limiting factors and processes for observed biomes/ predicting the impact of global change on biome distribution	Global picture of vegetation-disturbance regimes	Definition of functional types, only broad-scale changes [Gap 3, 5]

be able to use trait data operationally for ecosystem modelling. Ideally, a new rule set for PFT definition should account for trade-offs between investment in key traits that underpin both simulation of PFT performance under a range of climate conditions and the outcome of competitive interactions between them.

Modelling future changes in biodiversity: considerations and caveats

Modelling currently provides the most comprehensive and flexible approach to generating probabilistic projections of changes in biodiversity under future climate scenarios. Models can use new information derived from observations or other model output to forecast dynamics in complex contexts, such as global change. To advance estimates of biodiversity loss under climate change, existing models need to take into account the importance of climatic and non-climatic factors to species ranges, the influence of disturbance on species and ecosystems, of species interactions in determining population dynamics, and the potential for species to adjust to climate changes through plastic responses, adaptive evolution and migration. However, the construction of ever more complex models incorporating all of these multifarious interactions and processes is not necessarily a good solution. Model complexity has a cost, in terms of computing resources and increased error propagation.

As in climate modelling (see e.g. [59]), it is probable that understanding the impact of climate change on biodiversity will require the application of a hierarchy of ecological models; the choice of model being dependent on the type of question being asked and the spatio-temporal scale of interest [25]. Existing models (Table 1) have been designed for various purposes and operate at different scales. Linking existing models that operate at compatible scales could provide a way forward: for instance, linking species distribution and demographic models to take biotic interactions into account [46], and linking mechanistic dispersal models with DGVMs to simulate migration processes [60]. The incorporation of dispersal processes and constraints in DGVMs has been extensively discussed [34]; the required theory development is advancing [61] and has been incorporated to some degree in landscape-scale modelling [62].

Genetic diversity and the potential effects of climate change on biodiversity as mediated through plastic or evolutionary responses are not yet considered at any level in this hierarchy of models. Advances in evolutionary ecology need to be incorporated within the modelling framework. We have argued that increasing the number of PFTs within existing DGVMs, particularly if this expansion is based on analyses of trait–climate relations, will produce a major improvement in our ability to model future changes in biodiversity. It should also be possible to incorporate genetic diversity and adaptive plasticity within PFTs through probabilistic representation of key processes. It should be possible now to incorporate dispersal and migration explicitly (perhaps probabilistically) into DGVMs as well. We suspect the main limitation to doing this has been the lack of relevant observations to test the response of ecosystems and species to rapid climate changes. However, the palaeorecord offers useful

targets [62] and a global perspective on such response is now possible thanks to the collection and compilation of palaeoecological data covering multiple episodes of rapid climate change (see Box 1).

Perhaps the opportunity for the most rapid progress through a hierarchical approach lies in applying process representations that have been developed for DGVMs to local and regional scale analyses by translating dynamically modelled ‘species envelopes’ into DGVM parameters. One variant of this approach has been successfully implemented for relatively depauperate tree floras of northern Europe [63] and proposed as feasible for the tree flora of North America [64]. In this variant, the aim is dynamic simulation using the full DGVM with species substituted for PFTs, but this would be impractical for large and diverse assemblages. An alternative approach would only predict changes in species ranges (dynamically determined [Gaps 2 and 3]) but would do so with improved predictive confidence. Further, this approach would allow inclusion of directly measured quantitative trait information (e.g. extreme cold tolerance) where available and generalization to a wider set of organisms through the substitution of climate controlled variables for different life-history characteristics [65].

Conclusions and recommendations

We have identified five research areas in which substantial progress could be made in the near future that would improve understanding of large-scale biodiversity–climate relations and advance the predictive ability of climate–biosphere models (Figure 1). Progress requires action, and we have identified ten measures (1–10 below) that need to be taken. (1) Creating on-line repositories for data from existing monitoring sites will allow real-time access to global datasets on biodiversity and also assist in ensuring data quality and facilitating synthesis. (2) The global monitoring of biodiversity will also benefit from standardizing protocols for measuring biodiversity, accompanied by provision of training in their implementation. This will also facilitate capacity building in developing regions that contain the majority of the species on earth. (3) Establishing monitoring sites that fill key geographical and ecological gaps is crucial to understanding species ranges and community dynamics. (4) The development and application of methodological and statistical toolkits that can use monitoring data will aid in the quantification of species sensitivity to climatic and non-climatic factors. The application of new statistical tools will also help (5) quantify the sensitivity of individual species to climate across taxonomic and functional groups. (6) Meta-analyses of laboratory and field observations of genetic diversity can begin to determine the relation between genetic patterns and resilience to climate change across broad geographic regions and taxonomic units. (7) Expanding trait databases by adding information from regional floras and herbaria and targeted field campaigns will (8) help derive improved parameterizations and more realistic PFT classifications in DGVMs. (9) Incorporating demographic processes, plasticity, genetic variability and dispersal within DGVMs will also aid in developing better large-scale models of vegetation change. Finally, (10) the application of hierarchical

modelling approaches using multiple sources of data, including palaeodata, to address biodiversity responses to environmental changes at different temporal and spatial scales will critically improve predictive models of biodiversity change under current and future climate scenarios.

We do not wish to suggest that these are the only measures that would improve understanding of how climate change will affect biodiversity. Rather, these actions address tractable problems that through enhanced collaborations between different scientific communities can more effectively address global changes in biodiversity. This 'big science' effort will require collaboration between ecologists, physiologists, climatologists, statisticians, computer scientists, and other disciplines. Above all, we must incorporate isolated, place-based study of communities and populations into continental and global frameworks of quantitative biodiversity modelling. Such an effort can incorporate the abundance of insights gained from ecological field studies into a quantitative framework applicable to conservation policy.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.tree.2011.02.012](https://doi.org/10.1016/j.tree.2011.02.012).

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