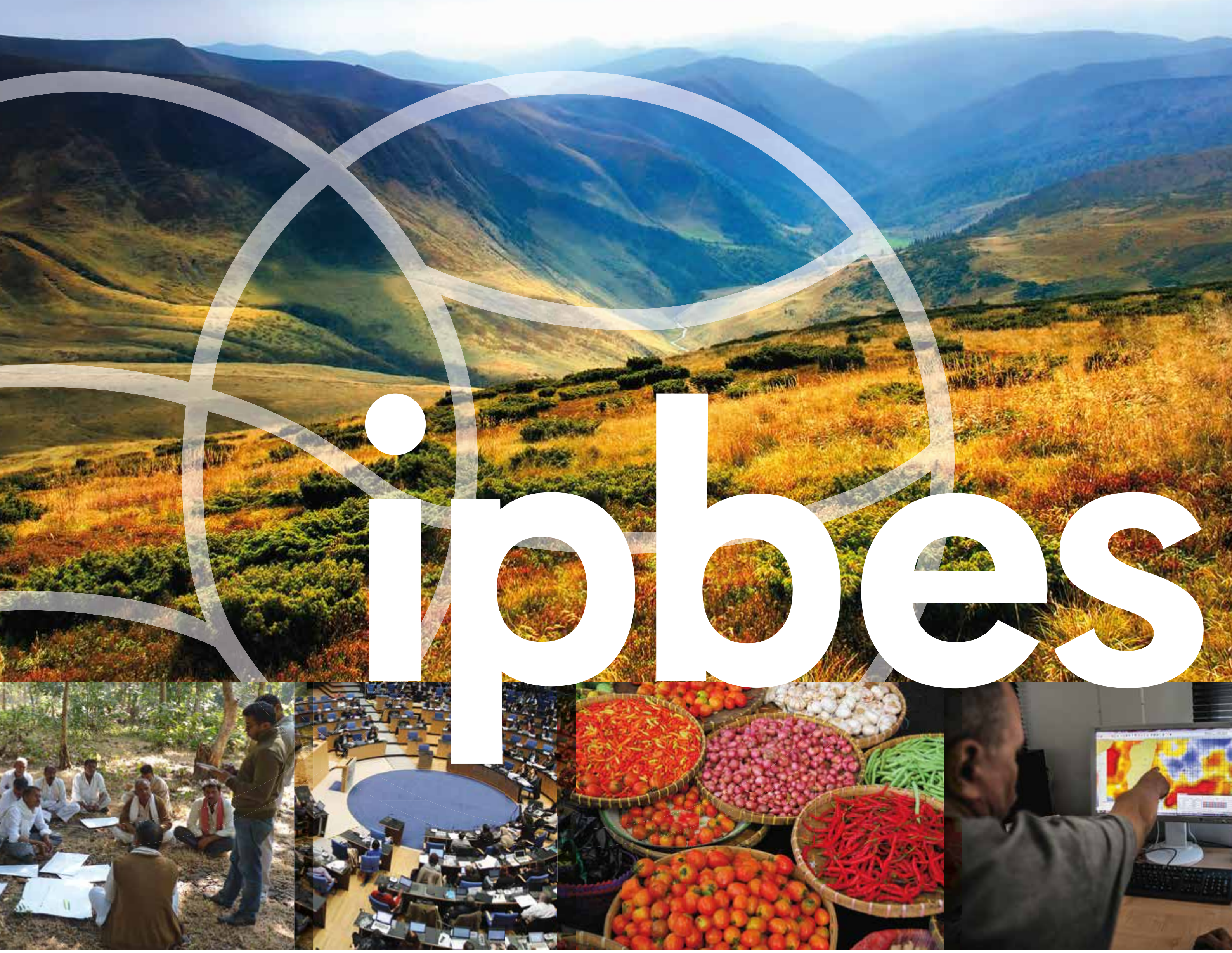

The methodological assessment report on

SCENARIOS AND MODELS OF BIODIVERSITY AND ECOSYSTEM SERVICES

CHAPTER 4

MODELLING IMPACTS OF DRIVERS ON BIODIVERSITY AND ECOSYSTEMS

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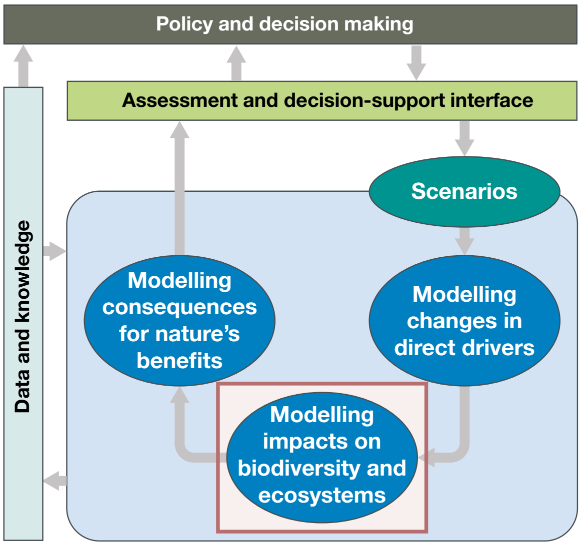
CHAPTER 4

MODELLING IMPACTS OF DRIVERS ON BIODIVERSITY AND ECOSYSTEMS

Purpose of this chapter: Explores key issues in modelling impacts of changes in direct drivers (from Chapter 3) on biodiversity and ecosystems; and critically reviews major types of models for generating outputs that are either directly relevant to assessment and decision-support activities, or are required as inputs to subsequent modelling of nature's benefits to people (covered in Chapter 5).

Target audience: Aimed mostly at a more technical audience, such as scientists and practitioners wanting to identify appropriate biodiversity and ecosystem modelling approaches for particular applications.

Scope of this chapter



KEY FINDINGS

Models of biodiversity and ecosystem function are critical to our capability to predict and understand responses to environmental change (Section 4.2). Modelling is one way of helping policymakers assess the impacts of different drivers on biodiversity and ecosystems, as well as the feedbacks on drivers generated by those impacts (from Chapter 3). Modelling provides tools that can help project future dynamics based on scenarios of direct and indirect drivers. However, the capacity of biodiversity modelling to meet policymaking needs is still affected by a lack of data and knowledge, and by model complexity and uncertainties.

There is a need to match biodiversity and ecosystem function model development to stakeholder and policy needs (Section 4.3.2.1). Biodiversity and ecosystem models rely heavily on assumptions about key processes and input data. There is a need to involve both stakeholders and modellers in representing these processes and assumptions and in identifying critical drivers (i.e. outputs from scenarios, Chapter 3) and the biodiversity/ecosystem response variables that need to be addressed. It is also important that the underlying context, uncertainties, validity, specificity, and outputs of the models are clearly and transparently interpreted and explored jointly by the modellers and stakeholders.

Biodiversity and ecosystem modelling depends heavily on our understanding of ecosystem structure, function and process and on their adequate representation in models (Section 4.2.1). Both understanding and adequate representation depend on data availability, so there is a need to generate and compile representative data for different biodiversity variables in different ecosystems at multiple locations and different scales. Observation networks, as well as long-term monitoring programmes, are therefore critical to assess the response of ecosystems to drivers of change such as climate change, land-use change, exploitation and pollution, and to inform model development.

Uncertainty in ecosystem dynamics is inherent in ecosystem modelling (Section 4.6). Uncertainty, which is inherently associated with model processes, data limitations and environmental stochasticity, can be accounted for by using multi-model ensembles, quality assurance and quality control, and by generating data from long-term observations. Different models may provide results that should be interpreted within the context of the model assumptions and input data. The biodiversity and ecosystem functioning models currently available provide a range of options to assist policymakers in understanding relationships between drivers and impacts, and in designing efficient policies.

The scientific community has recognised the importance of developing strategies to address the limitations of current models and of suitably treating the different sources of uncertainty involved. Well-established guidelines are relevant because an assessment of available approaches to modelling biodiversity and ecosystem responses to environmental changes clearly concludes that there is no single modelling approach (or model category) that can serve all assessment needs and decision-making requirements.

KEY RECOMMENDATIONS

Efforts should be made to ensure that experts involved in Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) deliverables are aware of the important role that models of biodiversity and ecosystem functioning play in formalising the complexity of living systems (Section 4.2). In particular, it is important that experts in IPBES task forces and assessments recognise the complexities linking drivers of environmental change to ecosystem dynamics. It is also important that they acknowledge the value of modelling as a method to formally represent – and therefore simplify – such complexity, and as a scientific tool to support decision making. This can be facilitated by the selection of experts for IPBES deliverables who are familiar with the limitations and use of models of biodiversity and ecosystem functioning. In addition, follow-up activities in Deliverable 3c can provide additional guidance to experts in IPBES deliverables – especially the thematic, regional and global assessments – to assist in the interpretation and correct use of biodiversity models.

Encouraging stakeholder participation in scenario and model use as early as possible in assessments would provide substantial benefits for IPBES (Section 4.7). This would maximise the correspondence between the objectives of the assessments and the outputs and limitations of the ecosystem modelling approach to be developed or interpreted. It is important that modellers and stakeholders interact in the different stages of modelling exercises concerning the selection of key questions, the context, assumptions, scale, time frame, and so on. Mechanisms for facilitating this dialogue are not yet explicitly laid out in the IPBES Work Programme.

Experts involved in IPBES assessments should critically evaluate the quality of the information used in modelling exercises. The task force on Knowledge, Information and Data could encourage long-term observations that would improve our understanding of biodiversity and ecological patterns (Section 4.3.2). This will enable models and outputs to be improved and to better fit IPBES objectives. IPBES needs to ensure that a quality chain between data type, model output and suitability for end-use exists in all assessments. Linkage of these components cannot be adequately implemented if data are scarce or of a low quality, thus leading to constraints in how model outputs feed into a given decision context (Chapter 8).

The development of consistent protocols is important for IPBES to ensure the quality of the use of models and their outputs in assessments (Section 4.3.2.2). Model intercomparison programmes would encourage increased collaboration among the modelling groups and with field ecologists to develop suitable protocols for modelling drivers impacting on biodiversity and ecosystem functions. An example could be to engage the scientific community to form model intercomparison groups similar to those developed in the context of the Intergovernmental Panel on Climate Change (IPCC) assessments, involving a large number of modelling groups working on biodiversity and ecosystem modelling.

The explicit characterisation of uncertainty should be a priority in the presentation and use of biodiversity and ecosystem model outputs within IPBES (Section 4.6). Communication of outputs needs to adequately identify the uncertainties associated with scenario development (Chapters 2 and 3), as well as clearly describe and communicate issues directly related to the choice of biodiversity and ecosystem models. To enable robust decision making and to account for uncertainty in the outcomes of biodiversity models, the integration of multi-model techniques and ensembles of multiple models and scenarios that provide a range of projections could be promoted in assessments. These practices should be encouraged, including by engaging with the scientific community through the task force on Knowledge, Information and Data and through the follow-up activities of Deliverable 3c.

The development of guidelines for integrated ecosystem modelling would be highly beneficial for IPBES assessments. There is a need to develop integrated models that can be applied in marine, terrestrial and freshwater ecosystems to assess the impact of drivers and their feedbacks on biodiversity and ecosystems. These integrated models should consider both biophysical and socio-economic drivers and their feedbacks at scales relevant to ecological processes underlying biodiversity changes and to decision-making processes.

4.1 INTRODUCTION AND CONCEPTUAL FRAMEWORK

Biodiversity and ecosystem dynamics are inherently complex, and so is their response to environmental drivers – including both natural and anthropogenic drivers. Models are powerful tools for addressing complex systems as they can be used to assess and predict the impacts of drivers on biodiversity and ecosystems, and hence the impacts on ecosystem services and human well-being. This chapter focuses on the approaches and methods currently available to explicitly link environmental changes with biodiversity and ecosystem responses, from changes in population size, to community composition and structure, to biogeochemistry fluxes. The aim is to identify the range of tools available for unravelling patterns and mechanisms of biodiversity and ecosystem change, and to incorporate this knowledge in models, allowing the projection of the future state of biodiversity and ecosystems in particular decision-making and management contexts (see Chapter 2).

The chapter first provides an introduction to the context in which biodiversity and ecosystem models are to be developed, including the relevant aspects of biodiversity response to drivers and a typology of the main modelling approaches (Section 4.2). Next, an overview of available modelling approaches relevant to IPBES – at different levels of biological organisation – is provided (Section 4.3). This comprises an explanation of model structure, scope of application and illustrating examples. To further guide the use of the most appropriate models, this section includes a critical analysis of the different modelling tools available, of model limitations, and of existing information and capacity-building needs.

Sections 4.4 to 4.6 cover the main issues in biodiversity modelling, which are modelling biodiversity feedbacks into environmental drivers, balancing model complexity and applicability, and addressing uncertainty. The issues associated with sources of uncertainty in model projections are of the utmost importance in the context of biodiversity projections for IPBES, and we describe this topic in depth in the context of biodiversity and ecosystem modelling. Finally, we identify the major challenges to biodiversity projections in the context of the IPBES programme, and highlight the main pathways available to policymakers at a range of administrative scales.

This chapter is directly linked to Chapter 3 (scenarios and models of indirect and direct drivers) and to Chapter 5 (modelling nature's benefits to people). The models discussed in this chapter provide a means of translating scenarios of drivers, as described in Chapter 3, into expected impacts on biodiversity and ecosystems. In turn, outputs (i.e. projections) from the models described in this chapter can serve as inputs to modelling changes in nature's benefits to people (including ecosystem services), as discussed in Chapter 5. Moreover, because the engagement of stakeholders in biodiversity modelling exercises and the effective communication of results to policymakers are fundamental to the successful use of models, there is a two-way link between the present chapter and Chapter 2.

The main external input when modelling biodiversity response to environmental change or pressures is the change in the state of drivers directly affecting biodiversity and ecosystems. In this chapter, we consider modelling approaches that assess the impacts of direct drivers of environmental change as identified by the Millennium Ecosystem Assessment (MA, 2005a): habitat change, climate change, overexploitation, pollution and invasive species. Scenario development and modelling methods for projecting future changes in direct drivers, to be used as inputs in biodiversity and ecosystems models, are described in detail in Chapter 3.

As for connections and potential overlap with Chapter 5, it is important to note the multiple roles of biodiversity and ecosystems in the conceptual chain linking direct drivers to nature's benefits to people. Specifically, biodiversity may either regulate the ecosystem processes that generate final ecosystem services, or itself constitute a final ecosystem service, or even provide a good that is directly enjoyed by people (Mace *et al.*, 2012; Oliver *et al.*, 2015). In the first case, biodiversity attributes affect the development and maintenance of ecosystem processes (Cardinale *et al.*, 2012), such as nutrient cycling (Handa *et al.*, 2014), primary productivity (Cardinale *et al.*, 2007) or water infiltration (Eldridge and Freudenberger, 2005), which in turn give rise to final ecosystem services. In the second case, biodiversity elements are themselves material outputs with direct use value, such as medicinal plants or fish, but require human capital inputs (e.g. labour, transport) before being enjoyed by society. Finally, biodiversity elements may themselves be viewed as a good if directly enjoyed by people without any additional input, which is the case with the aesthetic enjoyment of nature, ecotourism, and so on. Therefore, outputs from biodiversity models (including future projections) can be used as inputs to ecosystem services models, or provide direct information on ecosystem services and goods, such as data on the distribution and abundance of charismatic species. It is worth noting that, often, ecosystem services models implicitly (e.g. by simplifying biodiversity components and ecosystem functions using surrogate information on land cover or use) or explicitly include biodiversity or ecosystem function sub-modules. A compilation of relevant cases is treated in further detail in Chapter 5. Moreover, although biotic and abiotic ecosystem components interact and are both essential to ecosystem functioning and therefore to modelling ecosystem services

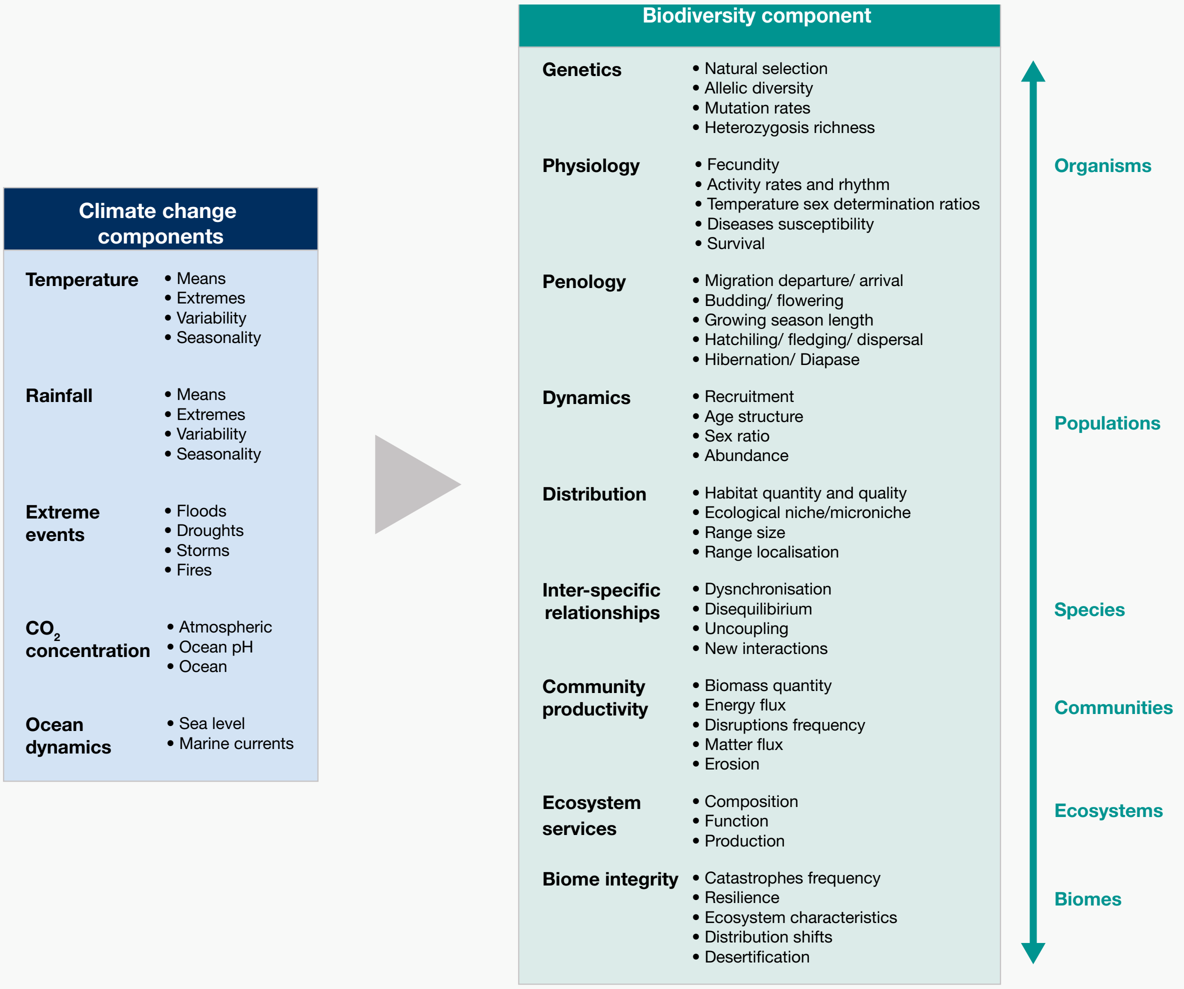
– in particular regulating services – the focus of this chapter will be on the biotic components, represented by 'nature' in the IPBES Conceptual Framework (see **Figure 1.2** in Chapter 1).

In accordance with the overall aim of Deliverable 3c to inform and guide other IPBES deliverables in the use of scenarios and models for biodiversity and ecosystem services, this chapter provides relevant information on:

- Modelling methodologies available for the IPBES Catalogue of Policy Support Tools for assessing the response of biodiversity and ecosystems to direct drivers (Deliverable 4c);
- Available modelling methodologies to evaluate scenarios of sustainable use of biodiversity and to assess responses to drivers of land degradation and to invasive species (Deliverable 3b);
- Caveats and good practices for assessments regarding the use of available data in modelling approaches and the use of modelling outputs in literature reviews and meta-analyses (Deliverables 2b, 2c, 3b);
- Capacity-building needs regarding the use of modelling approaches in decision-making processes and the engagement of stakeholders in modelling processes (Deliverables 1a, 2b);
- Current knowledge gaps, data needs and future research recommendations to improve the predictability and scope of application of models (Deliverable 1d);
- Involving indigenous and local knowledge in model development, testing and application (Deliverable 1c).

FIGURE **4.1**

Summary of biodiversity state variables and processes affected at different organisational levels by different components of climate change (Modified from Bellard *et al.*, 2012. *Impacts of climate change on the future of biodiversity.* Copyright © 2012 by John Wiley Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc).



Climate change components	
Temperature	• Means • Extremes • Variability • Seasonality
Rainfall	• Means • Extremes • Variability • Seasonality
Extreme events	• Floods • Droughts • Storms • Fires
CO_2 concentration	• Atmospheric • Ocean pH • Ocean
Ocean dynamics	• Sea level • Marine currents

Biodiversity component	
Genetics	• Natural selection • Allelic diversity • Mutation rates • Heterozygosis richness
Physiology	• Fecundity • Activity rates and rhythm • Temperature sex determination ratios • Diseases susceptibility • Survival
Penology	• Migration departure/ arrival • Budding/ flowering • Growing season length • Hatchiling/ fledging/ dispersal • Hibernation/ Diapase
Dynamics	• Recruitment • Age structure • Sex ratio • Abundance
Distribution	• Habitat quantity and quality • Ecological niche/microniche • Range size • Range localisation
Inter-specific relationships	• Dysnchronisation • Disequilibrium • Uncoupling • New interactions
Community productivity	• Biomass quantity • Energy flux • Disruptions frequency • Matter flux • Erosion
Ecosystem services	• Composition • Function • Production
Biome integrity	• Catastrophes frequency • Resilience • Ecosystem characteristics • Distribution shifts • Desertification

4.2 STRUCTURE AND COMPONENTS OF BIODIVERSITY AND ECOSYSTEM MODELS

Scientists and stakeholders supporting decision-making processes are always faced with the challenge of selecting the key processes and drivers leading to relevant impacts on their study object (Guisan *et al.*, 2013), and this is the topic of this section. Decisions on how and what to include explicitly in the modelling process, and what can be simplified or ignored, are crucial as they will impact model outcomes. The role of biodiversity as a regulator of ecosystem processes or as a material output (either a final service or good) defines the variables of interest when assessing and projecting the impacts of direct drivers. For instance, community data such as functional or species diversity (Cardinale *et al.*, 2007; Mace *et al.*, 2012) or habitat structure (Eldridge and Freudenberger, 2005) may be particularly important in assessing the impact of drivers when biodiversity has a regulatory role, while population data such as species distribution (Gaikwad *et al.*, 2011) or population structure (Berkeley *et al.*, 2004) would be more appropriate when biodiversity elements have a direct use value. It is also worth noting that, overall, a positive relationship exists between biodiversity attributes and ecosystem services (Harrison *et al.*, 2014).

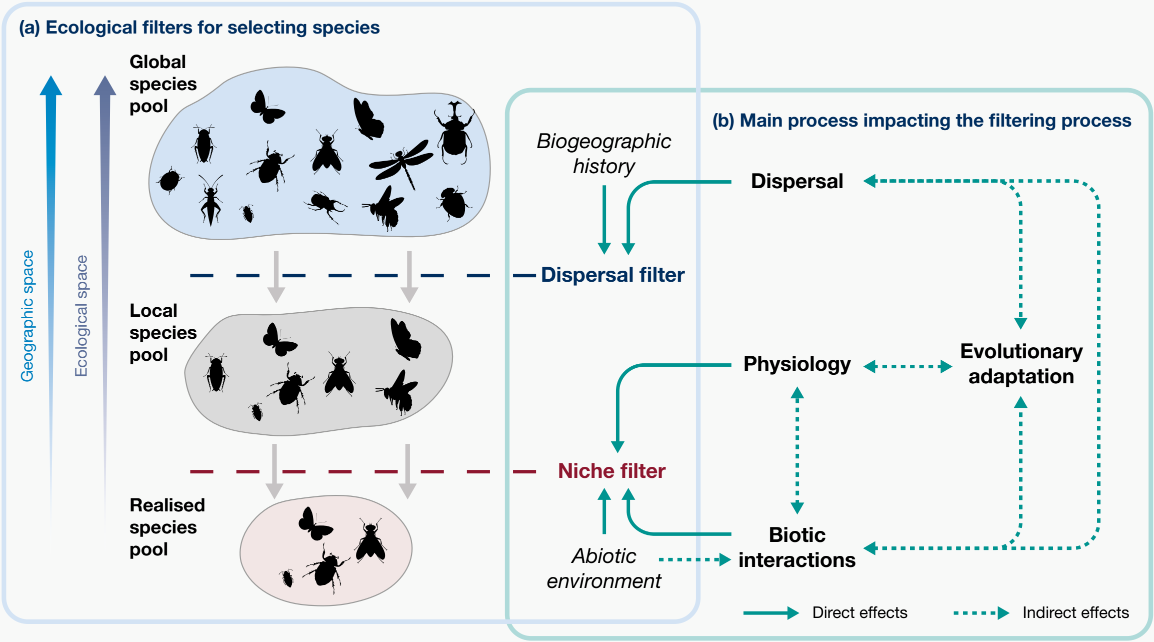
This recognition of the different roles of biodiversity follows an anthropocentric perspective that focuses on ecosystem services – the material and non-material benefits generated by nature. Like utilitarian values, biodiversity has its own intrinsic value that is independent of human demand or appreciation and that is difficult, or even impossible, to quantify through modelling, although its existence or evolutionary value may serve to maintain life.

Biodiversity models, like other mathematical models in the environmental sciences, consist of a set of components, namely state variables, external variables, mathematical equations and parameters (Jørgensen and Bendoricchio, 2001; Smith and Smith, 2007). Predictions of ecological responses to environmental changes should start with the specification of the major conceptual components of the model and the critical relationships between them. In the description of any model of this type, the following components should be identified:

1. **Elements describing the ecosystem characteristics.** These are the target state variables used to describe the biophysical components of interest, such as biomass, species richness, functional diversity or habitat structure (see **Figure 4.1**). State variables should be included based on their ability to serve as indicators of system state, their sensitivity to pressures, and the stability of their response pattern, although the consideration of available versus ideal data

FIGURE **4.2**

(a) Conceptual diagram of how dispersal and niche 'filters' select species from pools at different geographical and ecological scales. (b) Main processes that directly or indirectly impact the filtering process (Modified from Thuiller *et al.*, 2013. A road map for integrating eco-evolutionary processes into biodiversity models. Copyright © 2013 by John Wiley Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc).



often calls for a pragmatic approach given the costs and feasibility of data collection.

2. **Environmental and biotic drivers.** The spatial or temporal dynamics of these model components have a direct or indirect effect on the state variables. In the context of environmental change, changes in the value of environmental (e.g. climate change) and biotic drivers will affect the value of the state variables (e.g. species distributions).

3. **Ecosystem/ecological processes.** These model components allow the description of the changes in the stock and/or flow of materials or in the interactions between organisms and with their abiotic environment (Mace *et al.*, 2012). Processes are relevant in determining changes in the biological component (e.g. changes in species distribution after colonisation and extinction dynamics).

The impact of drivers on biological processes is key in determining the nature of the model and the inclusion of multidisciplinary expertise in the model-building process (Guisan *et al.*, 2013). In the context of environmental change, the effect of environmental pressures on state variables can be direct (e.g. loss of tree cover after deforestation, changes in climate conditions) or mediated by biophysical processes (e.g. ocean acidification and warming affecting coral recruitment and growth, and hence coral abundance and reef structure). In addition, processes also mediate interactions among state variables (e.g. biotic interactions, trophic cascades).

Using community structure as an example, the processes and scales that are important for modelling are illustrated in **Figure 4.2**, which shows how 'filters' select species from a global pool to obtain realised local communities (Thuiller *et al.*, 2013). In other words, and in the context of biodiversity response to change, drivers (input data) create or change geographic or niche filters, thus leading to changes in community composition (output data). The filters (ecological processes involved) include biogeographic and environmental aspects of the real world, and are represented as components in biodiversity models. Species response to direct drivers (box a) is mediated by dispersal and niche filters through a series of processes (box b), which may or may not be explicitly considered in biodiversity models.

4.2.1 Describing ecosystems in models: biological levels for modelling

Biodiversity and ecosystem responses to environmental change can assume many forms as a consequence of the inherent complexity; one way of addressing this diversity is to reduce it to a few meaningful dimensions. Biodiversity and ecosystem variables can be arranged along dimensions representing key aspects of biodiversity complexity: biological organisation levels (species, populations, ecosystems, etc.) and biodiversity attributes (composition, structure and function). These two dimensions define a conceptual space that can be useful for identifying relevant response variables **(see Table 4.1)**. More specifically, composition and structural elements such as species richness or biomass correspond to state variables, and functional elements such as primary productivity, herbivory or competition correspond to processes. Composition and structure emerge from processes, but also affect them (Dale and Beyeler, 2001).

From an ecological perspective, composition and structure variables describe the structural elements of ecosystems, while processes describe the fluxes of energy and matter and the interactions within and between organisation levels.

Ecosystems are open systems. They harness solar energy and transfer it through their various structural elements and organisation levels, via different biological and ecological processes. At the biosphere level, water and nutrients (e.g. carbon, nitrogen and phosphorus) are key structural elements of all living components, and key abiotic components of ecosystems. Their flux across the Earth system is described by the biogeochemical cycles. This flux of energy permits life on Earth and fuels the ecological functions that are useful for societies (i.e. ecosystem services). To model the dynamics of biodiversity, it is important that the major ecological processes involved in the transfer of energy through ecosystems are taken into account (Mokany *et al.*, 2015). These include production, consumption, respiration and recycling. Other processes such as regulation and evolution are critical to the maintenance of biodiversity and the resilience of ecosystems over time.

Primary production and respiration are major ecological processes, occurring at the organism level but affecting population dynamics and community structure. Organic matter from primary production forms the basis of all life on Earth. Numerous factors such as light, the availability of inorganic nutrients, water and temperature influence primary production. Respiration, which encompasses all the living processes using oxygen, is at the core of metabolism. While occurring at the organism level, both processes can be considered at every level of organisation. Primary productivity, for instance, is often used as an indicator of ecosystem functioning and modelled at the level of communities or ecosystems to assess the impacts of land-use change, climate change and management practices on vegetation. Regarding respiration, at the organism level respiration processes are influenced by many factors, including the species considered (body-size scaling rules imply that many metabolic processes vary with the maximum size that a species can reach (Kearney *et al.*, 2010), the size of individuals, their condition, the availability of food, oxygen levels and temperature. At the population level, respiration integrates the metabolism of all individuals. It is therefore highly dependent on the size and state structure of the population. At the community level, respiration integrates the metabolism of all populations and is therefore controlled by their relative abundance and the structure of the community. Consumption and recycling are the main processes associated with trophic interactions, and are therefore modelled at the community and ecosystem levels (Sarmiento and Gruber, 2006). Consumption constitutes a major process of ecosystem dynamics that transfers solar energy along food chains, from primary producers up to top predators. Trophic interactions are influenced by various factors, including the spatial-temporal co-occurrence of grazers/predators and their food/prey, which is often constrained by environmental features.

In addition to the metabolic processes described above, processes related to biodiversity responses to environmental changes can be broadly divided into population and community responses (Lavergne *et al.*, 2010). The first of these are mechanisms related to the ecology of the species populations, including dispersal, plasticity and population dynamics. These processes are primarily determined by biological traits expressing the capability of the target species to deal with environmental variability in space and time (e.g. Thuiller *et al.*, 2013; Hanski *et al.*, 2013). Secondly, species interactions can restrict or expand the set of places that the species is able to inhabit (Davis *et al.*, 1998). Competition, facilitation or trophic relationships are site- and species-specific and account for a great deal of variability in the capability of a species to survive in a given environment.

4.2.2 Introducing drivers of environmental change

The world has experienced global environmental change due to human activities, and this has encouraged research on scenarios and models to study the new challenges that biodiversity is exposed to (Pereira *et al.*, 2010). Assessments of links between these drivers and biodiversity responses are central to IPBES. Change in biodiversity is determined both by changes in the environment and by the ecological and physiological processes contributing to the dynamics of these ecological systems (Lavergne *et al.*, 2010). Thus, biodiversity change may be either related to changes in the environment itself, to the biological processes acting within ecosystems or, more frequently, to a combination of both (Leung *et al.*, 2012). It is therefore important to distinguish between changes caused by anthropogenic drivers and changes emerging from the natural dynamics of ecological systems. This is particularly important because, although biodiversity and ecosystem services experience change due to natural causes, anthropogenic drivers increasingly dominate current environmental changes.

Following the IPBES Conceptual Framework, natural and anthropogenic drivers directly affect biodiversity. Both natural and anthropogenic direct drivers of impacts on ecosystem processes explicitly cause measurable changes in ecosystem properties.

Natural direct drivers emerge from natural biophysical and geophysical processes, while anthropogenic drivers result from the trajectory and interactions of socio-economic drivers (indirect drivers).

Biodiversity models use variables describing properties of direct drivers as inputs to predict their impact on biodiversity variables. Historically, the largest impacts on biodiversity have been through land-use change in terrestrial ecosystems (Pereira *et al.*, 2012) and through resource exploitation in marine ecosystems (MA, 2005b). Freshwater ecosystems have been strongly impacted by a range of factors including, most notably, habitat modification, invasive species and pollution. Climate and land-use changes have probably now reached a similar level of pressure on ecosystems, but during the last three centuries land-use change has exposed 1.5 times as many landscapes to significant modifications as climate change (Ostberg *et al.*, 2015).

TABLE **4.1**
Examples of biological levels for modelling (compositional, structural and functional biodiversity variables, from (Noss, 1990; Dale and Beyeler, 2001), selected to represent levels of biodiversity that warrant attention in environmental monitoring and assessment programmes.

Level	Composition	Structure	Function
Individuals	Genes	Genetic structure	Genetic processes, metabolism
Populations	Presence, abundance, cover, biomass, density	Population structure, range, morphological variability	Demography, dispersion, phenology
Communities	Species richness, evenness and diversity, similarity	Canopy structure, habitat structure	Species interactions (herbivory, predation, competition, parasitism), decomposition
Ecosystems	Habitat richness	Spatial heterogeneity, fragmentation, connectivity	Ecosystem processes (hydrologic processes, geomorphic processes), disturbances

Human impacts on the global environment are operating at a range of rates and spatial scales. Scaling issues are particularly important when assessing impacts on biodiversity and ecosystem services because drivers have different impacts at different scales. For example, while climate change is a driver that acts at the global scale, habitat modification has an impact on biodiversity and ecosystem services at regional and local scales. The consequences of habitat modification have been significant for many aspects of local, regional and global environments, including the climate, atmospheric composition, species composition and interactions, soil condition, and water and sediment flows. However, global-scale assessments typically mask critical sub-global variations, thus underestimating the effects of drivers acting at local scales. Local and regional case studies can provide the spatial and temporal resolution required to identify and account for major environmental sources of variation in cause-to-cover relationships and the consequence for biodiversity. Single-factor explanations, at the macro or the micro scale, have not proven adequate (Bellard *et al.*, 2015). Many models assessing the impact of environmental drivers on terrestrial ecosystems and biodiversity elements, including those dealing with climate and trace-gas dynamics, require projections of land-cover change as inputs. In this context, Loreau *et al.* (2003) highlighted that knowledge of spatial processes across ecosystems at the local scale is critical to predict the effects of landscape changes on both biodiversity and ecosystem functioning and services.

4.2.3 Dealing with processes: the model continuum from correlative to process-based approaches

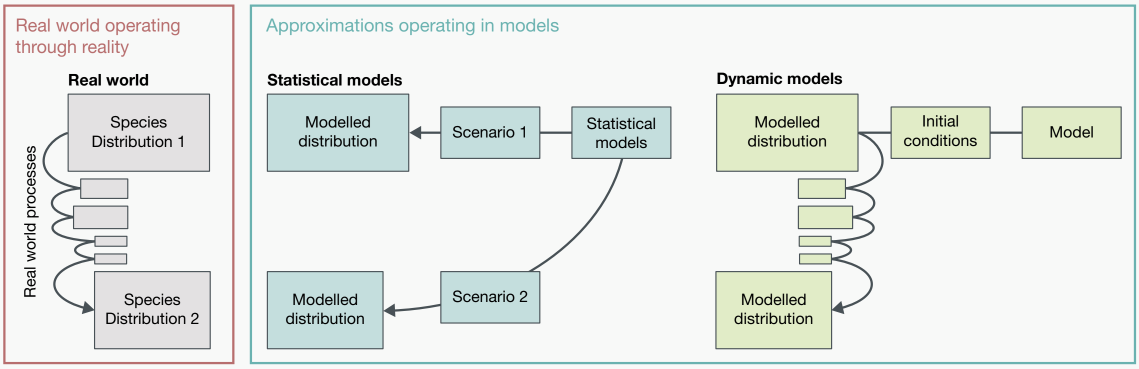
There are a wide variety of ecological models available for assessing impacts of direct drivers on biodiversity and ecosystem functioning. These can be categorised based on their complexity and degree of formalisation, from expert-based systems that rely on experience (including in the form of local knowledge), to complex integrated ecosystem models.

Quantitative models are generally classified in two broad categories: correlative and process-based models (e.g. Pereira *et al.*, 2010; Dormann *et al.*, 2012). To distinguish between these model types, we follow the model definitions of Dormann *et al.* (2012). These state that correlative models are characterised by having parameters with no predefined ecological meaning, and for which processes are implicit, whereas process-based models use explicitly-stated mechanisms, and their parameters have a clear, predefined ecological interpretation.

In the literature, the terms process-based model and mechanistic model are often used as synonyms. Here, we use the term process-based for any model type with explicit implementation of ecological processes in the model (i.e. encompassing both process-based and purely mechanistic models), and we reserve the mechanistic category for the subset of models that are developed based on ecological theory only and that do not use correlative approaches at all for parameterisation. The primary difference along this modelling axis is the inductive versus deductive approach to processing information. The main advantage of correlative models, also termed phenomenological or statistical models, is that there is no need for a fundamental understanding of the ecosystem and relationships between system elements, as these are derived inductively from empirical observations. With process-based models, there is a deductive process involved in which the process is determined and the relationship derived, quantified and explicitly modelled (Jørgensen and Bendoricchio, 2001). At the other end of the formalisation gradient, pure mechanistic models – also called theoretical models – are axiomatic constructions (Gallien *et al.*, 2010). As in theoretical physics,

FIGURE **4.3**

Schematic representation of the relationship between two observations of a species distribution in the ‘real world’, ‘correlative (statistical) models’ and ‘dynamic, process-based models’ (Modified from McInerny and Etienne, 2012. *Ditch the niche – is the niche a useful concept in ecology or species distribution modelling?* Copyright © 2012 by John Wiley Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc).



they apply the hypothetico-deductive scientific method, starting from a hypothesis (the axiom) to deduce predictions that can be tested empirically, either to falsify or conversely to corroborate the hypothesis made (but never to prove or 'validate' it).

To illustrate how models are both abstractions and representations of reality, **Figure 4.3** shows how real-world processes change an entity (here a distribution) from one state to another. In a correlative model, the two distribution states are modelled with two alternative scenarios (e.g. before and after a forest fire). In the process-based dynamic model, the model builds on a set of initial conditions to derive a modelled distribution, which then is altered through specified processes that aim to replicate the real-world phenomena in order to predict the second modelled distribution. It must be noted that the real-world processes are often unknown and indeed never can be fully known or emulated. Process-based modelling therefore cannot be expected to fully replicate the real-world situation, but it may provide a useful approximation (McInerny and Etienne, 2012).

In practice, the categorisation of ecological models is rarely as clear-cut as depicted in **Figure 4.3**, but rather tends to fall along a continuum from correlative to process-based, depending on available data and parameters, purpose and model philosophy. This model continuum, however, forms the basis for the presentation here, which also describes a spectrum of how the broad model types rely on empirical data versus ecological knowledge.

Whether modelling is based on correlative or process-based approaches (or any intermediate type), there are a number of issues that should be considered as part of the model building process **(Table 4.2)**. For instance, statistical assumptions about error structure and unbiased sampling apply to both broad types of modelling approaches. The same is not true regarding the assumption that species are in equilibrium with their environment, which applies only to correlative models, at the risk of losing predictive ability.

4.2.3.1 Expert-based systems

The most common approach for evaluating impacts of alternative management procedures related to predictions and decision support is often based on information provided by experts (Cuddington *et al.*, 2013). An expert is defined here as someone who has achieved a high level of knowledge on a subject through his or her life experience (Kuhnert *et al.*, 2010), and may be a person with local knowledge or a scientist. It is assumed that the expert is a reliable source of information in a specific domain, though it appears that experts tend to be far more confident in their opinions than is warranted (Burgman, 2005).

Eliciting expert information usually involves dealing with multiple expert judgements, with different sources of bias and uncertainty around expert estimates (Martin *et al.*, 2012). For instance, expertise may vary geographically, with relevant information restricted to the region of interest of the experts (Murray *et al.*, 2009). Structuring how multiple expert opinions are used, for example through a Delphi approach (MacMillan and Marshall, 2006), can make the modelling much more rigorous and less likely to result in arbitrary predictions (Sutherland, 2006).

The expert-based approach typically includes five steps: considering how the information will be used; deciding what to elicit; designing the process for the elicitation; the

TABLE **4.2**
Summary of aspects to be considered during the model building process (Modified from Dormann *et al.* (2012) *Correlation and process in species distribution models: bridging a dichotomy.* Copyright © 2012 by John Wiley Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc).

Topic	Relevant issues
Assumptions	Error structure, structure of functional relationships, relevant processes/predictors, equilibrium with environment
Information required	Data on distribution, populations, environments, environmental data, ecological and biological knowledge
Determination of model structure	Variable selection, alternative functional relationships, submodels
Verification	Technical correctness, model diagnostics
Validation	Cross-validation, external validation, parameter validation, sensitivity, specificity
Sources of uncertainty in model predictions	Input data, model misspecification, regression dilution, stochasticity
Equifinality	Over-parameterization, collinearity, non-identifiability
Extrapolation	Model domain, (micro-)evolution, stationarity of limiting factors and interactions, phenotypic plasticity
When to stop: accuracy versus complexity	Deployment time, re-parameterization, sensitivity analysis
Communicability and model transparency	Documentation, open source code/software
Knowledge potentially gleaned from the model	Surprise, emergence
Common errors and misuses	Lack of uncertainty analysis, use beyond purpose, overconfidence in communication

actual undertaking of the elicitation; and finally translating the elicited information into quantitative statements that can either be used directly or in an integrative or participatory modelling approach (Martin *et al.*, 2012).

Expert knowledge-based species-habitat relationships are used extensively to guide conservation planning, particularly when data are scarce (Iglecia *et al.*, 2012). Expert knowledge is quite commonly utilised in conservation science (Janssen *et al.*, 2010; Aizpurua *et al.*, 2015), and has frequently been incorporated in aquatic habitat suitability modelling to link environmental conditions to the quantitative habitat suitability of aquatic species (Mouton *et al.*, 2009).

Indigenous and local knowledge (ILK)

Indigenous people, with collective knowledge of the land, sky and sea, are excellent observers and interpreters of changes in the environment. Their knowledge may offer valuable insights, complementing scientific data with chronological and landscape-specific precision and detail that is critical for verifying models and evaluating scenarios developed by scientists at much broader spatial and temporal scale.

Moreover, ILK provides a crucial foundation for community-based actions that sustain the resilience of social-ecological systems at the interconnected local, regional and global scales (Raygorodetsky, 2011). Indigenous and local observations and interpretations of ecological phenomena at a much finer scale have considerable temporal depth and highlight elements that may be marginal or even new to scientists.

ILK can potentially supplement other scientific data in modelling, as input to the model but also in the interpretation and understanding of the outputs of model runs. Traditional or indigenous knowledge is a result of a long series of observations transmitted from generation to generation (Berkes *et al.*, 1995). Such ‘diachronic’ observations (i.e. observations over time) can be of great value and complement the ‘synchronic’ observations (i.e. observations made at the same time, but at different locations) that are often used for model construction and testing (Gadgil *et al.*, 1993). Knowledge holders have not only developed a stake in conserving biodiversity, but also in understanding the complexities and interrelations among the varied entities that an ecosystem encompasses (Slobodkin, 1961). Modelling for biodiversity conservation and ecosystem services can therefore benefit significantly from the application of ILK, which may fill gaps in biodiversity modelling (Thaman *et al.*, 2013; WWF, 2013).

ILK thus has the potential to contribute to global environmental assessments, posing the challenge of how to integrate different scales and how to connect different knowledge systems to complement each other. One of the approaches of IPBES, the ‘Multiple Evidence Base approach’ was developed at the Stockholm Resilience Centre as a conceptual framework for connecting diverse knowledge systems (Tengö *et al.*, 2013).

Integration of ILK in research techniques such as modelling and remote sensing can provide a robust contribution to informed decision making. An example is animal herd management in the Arctic, where remote satellite sensing, meteorology and modelling are complemented with the indigenous knowledge of Sami and Nenets reindeer herders to co-produce datasets. The indigenous observers are able to make sense of complex changes in the environment through the qualitative assessment of many factors, complementing the quantitative assessment of variables made by scientists (Magga *et al.*, 2011). Case studies from Canada and New Zealand also provide evidence that a combination of traditional ecological knowledge and science to understand and predict population responses can greatly assist co-management for sustainable customary wildlife harvests by indigenous peoples (Moller *et al.*, 2004).

4.2.3.2 Correlative models

Correlative models are generally easy to apply and do not require extensive knowledge of underlying processes, but instead use statistical methods to establish direct relationships between environmental variables and biodiversity data such as species richness, abundance or distribution (Morin and Lechowicz, 2008). These models produce information on biodiversity patterns and responses to drivers based on empirical observations, and do not attempt to explain the mechanisms underlying those patterns and responses (Rahbek *et al.*, 2007). When using the correlative modelling approach, it is recognised that there are clear limitations to ecological knowledge for model development, and often the focus is on ensuring a pragmatic model implementation that will capture current existing ecological patterns, which often provides good – if narrow – projections (Araújo and Pearson, 2005; Elith and Leathwick, 2009).

Correlative models are frequently used to assess the impacts of human activities on biodiversity, forecast future impacts of environmental changes, support human productive activities (e.g. enhance agricultural production) and conservation actions (e.g. identify sites for translocations and reintroductions, or predict the location of rare and endangered species), and understand species’ ecological requirements, among other uses (Peterson, 2006; de Souza Muñoz *et al.*, 2011). Correlative models have the advantage of being tractable and easy to interpret, and permit the predictability of phenomena that depend on differences between components – for example the invasive potential of a species depends on the difference between potential and actual distributional areas (Peterson, 2006).

Correlative models can be applied at all spatial scales after careful assessment of relevant environmental predictors and response variables relevant to the question addressed (Elith and Leathwick, 2009; Guillera Arroita *et al.*, 2015). For instance, the effect of climate variables is better assessed at large spatial extents, such as regions, and coarse resolution data may be acceptable, whereas the effect of land use or soil nutrients requires fine resolution data to cover fine-scale variations, and is usually modelled at smaller extents such as landscapes. When the selected environmental predictors act at different scales, hierarchical models with nested sub-models can be used (Elith and Leathwick, 2009). Regarding temporal scales, correlative models are often static (i.e. assume that the species-environment relationships do not change over time), and therefore often fail to capture species or community dynamics such as species dispersal. Nevertheless, temporal predictors – such as variability of food resources – may be added to models to capture variation in the state of biodiversity variables.

Correlative models should be used carefully when extrapolating biological descriptors to new spatial areas and time frames (i.e. hindcasting and forecasting applications). This is due to the possibility that conditions (e.g. climatic conditions) associated with the training data (i.e. the data used to fit the model) may not remain constant over time (Elith and Leathwick, 2009; Araújo and Peterson, 2012), or may be inadequate to represent the conditions found outside their area of distribution. Moreover, correlative models are data demanding, requiring robust datasets. However, because the data required by correlative models are often available across a range of scales, and because the models can implicitly capture many complex ecological responses, Elith *et al.* (2010) anticipate the continued use of correlative models for biodiversity projections.

4.2.3.3 Process-based models

Process-based models are generally more complex to develop than correlative models as they require more knowledge of the processes that shape biodiversity patterns, including an explicit consideration of selecting which processes to include. These models nevertheless allow a more explicit representation than correlative approaches of ecological processes mediating biodiversity and ecosystem responses to environmental drivers. As they tend to build on a formal framework with varying levels of theoretical underpinning, they are also more capable of explaining why biodiversity patterns occur, rather than simply demonstrating that they do. The golden standard for modelling, however, frequently includes the degree to which models can be used for predictive purposes, and while this is an area in which process-based models may have an advantage over correlative models, it should also be acknowledged that the capabilities of process-based models with regard to predicting the consequences of anthropogenic impacts for biodiversity and ecosystems are uncertain and under continuous development. In response to climate change, species may change their climatic niches along three non-exclusive axes: time (e.g. phenology), space (e.g. range) and self (e.g. physiology), as described by Bellard *et al.* (2012). Of these, the physiological axis in particular calls for the capacity to handle evolutionary adaptations (see for more detail Section 4.3.1.1). It should also be noted that data availability generally places limits on how reliably models can be parameterized.

One example of an approach used to overcome the limitations of correlative methods is the dynamic energy budget theory (e.g. Kooijman, 2009). This is a good example of mechanistic theory that aims to capture the quantitative aspects of metabolism at the organism level from a small set of key assumptions (Sousa *et al.*, 2008). The dynamic energy budget theory makes it possible to account for the effects of environmental variability on organisms through food and temperature changes and captures the diversity of all possible living forms on Earth in a single mechanistic framework. This allows the representation of the energetics and major life history traits of all possible species in a community with the same set of unspecific taxa-dependent dynamic energy budget parameters.

Overall, process-based models are limited by the number of processes that are explicitly included, the sensitivity of the system dynamics to the mathematical form used to represent the process, the sensitivity to the data used to estimate the parameters, and the limited capacity to predict beyond the range of observed conditions. Despite the wide use of process-based ecosystem models in biology and ecology they, as do all other model developments, suffer from fundamental and practical limitations.

Various strategies and approaches for process formalisation can be distinguished among the available process-based models:

Box models. This is the simplest and most developed category. It describes ecosystem dynamics using a set of state variables (e.g. fish biomass) that are connected together by fluxes (e.g. consumption or predation) based on given functional responses that are either predefined (Holling, 1959) or emergent properties (Ahrens *et al.*, 2012). The most common use of this type of model is to simulate mass balances and energy fluxes at the scale of the system represented, and this is one of its main advantages.

On the other hand, they tend to use highly aggregated representations of state variables (e.g. lumping all fish species at a trophic level together) and therefore neglect phenomena such as the importance of size in controlling metabolism, predator-prey interactions and life history omnivory (i.e. dietary changes as organisms grow).

Age/stage/size-structured models. These models are box models that are structured along a dimension that is assumed to be functionally important. They explicitly account for some processes of metabolism such as growth, reproduction and the age-dependence of respiration. Age/stage-structured models are widely used for fisheries management (see Hilborn and Walters, 1992), as well as for food web models (e.g. Walters *et al.*, 2010). Size-structured models emphasise the impact of size as a structuring element in ecosystems. In marine and freshwater ecosystems, size is usually a good predictor of trophic level at the community level (Jennings *et al.*, 2001) because many predators are size-selective, leading to this biological trait to exert a strong influence on predation and metabolism. Size-based models are easier to parameterise than functional group or age/stage-structured food-web models, though in particular applications there may be more interest for species than for size per se. Size-structured models can, however, be constructed with explicit species considerations to make them more suitable for addressing questions of direct relevance to biodiversity research (Shin and Cury, 2001; Blanchard *et al.*, 2014).

4.2.3.4 Hybrid models: combining correlative and process-based modelling

Hybrid models combine correlative and process-based modelling approaches (Schurr *et al.*, 2012) in order to represent complex, integrated systems with a focus on biophysical as well as human components (Parrott, 2011). Such models tend to be highly data-driven and help build on our understanding of important factors and synthesise knowledge, as well as providing a structural link between data sources and decision-support systems. Hybrid model development takes a pathway in which some of the ecological processes defining the ecological system under study (e.g. the realised niche) are modelled explicitly (i.e. process-based), while others are based on correlative niche modelling (Thuiller *et al.*, 2013). Hybrid approaches derive from the interest to balance realism and flexibility in model building with limited knowledge, but this approach also comes with important challenges.

How different models are integrated into hybrid approaches is often a difficult issue. Gallien *et al.* (2010) indicate that one of the current limitations of the hybrid approach is the form and strength of the relationship between habitat suitability and demographic parameters. Changes in habitat suitability are normally integrated with population processes by limiting carrying capacity. Furthermore, the response of ecological processes (e.g. growth, dispersal and thermal tolerance) to environmental changes is unclear, and is often assumed to be unimodal or linear. Non-linear functional response could make the model more complex.

Broadly speaking, mechanisms determining ecosystem dynamics can be related to the ecology of species, species interactions and evolutionary processes (Lavergne *et al.*, 2010). Any biological process of interest should have an explicit link with the components formulated in the model. However, this link does not need to be one-on-one (Lurgi *et al.*, 2015). The implementation of these processes in the model may be carried out in a wide variety of ways spanning a broad range of complexities, from cellular automata (Iverson and Prasad, 2001), meta-population models (e.g. Wilson *et al.*, 2009) and structured meta-population models (Akçakaya *et al.*, 2004), to spatially-explicit population models (e.g. Cabral and Schurr, 2010), individual-based models (e.g. Grimm *et al.*, 2005), trophic models (e.g. Albouy *et al.*, 2014) and reaction-diffusion models (e.g. Wikle, 2003; Hui *et al.*, 2010). For example, the recently introduced ‘dynamic range modelling’ framework (Pagel and Schurr, 2012), based on a Bayesian approach, overcomes several of these limitations as it uses species distribution data and time series of species abundance to statistically estimate both distribution dynamics and the underlying response of demographic rates to the environment. This approach is particularly relevant when dispersal limitation or source-sink dynamics cause disequilibrium between species distributions and environmental conditions (Pulliam, 2000).

The dynamic bioclimate envelope model developed by Cheung *et al.* (2008b) simulates changes in the relative abundance of marine species through changes in population growth, mortality, larval dispersal and adult movement following the shifting of the bioclimate envelopes induced by changes in climatic variables. The model does not account for species interactions and potential food web changes, which are however considered in a combined food web and habitat capacity model (Christensen *et al.*, 2014). Dynamic bioclimatic envelope models are also being developed to account for effects of ocean biogeochemistry, such as oxygen level and pH, on the eco-physiology and distribution of marine fish (Stock *et al.*, 2011). Models with emergent dynamics may also include species interactions (e.g.Albert *et al.*, 2008) or abiotic processes included via feedbacks (e.g. wildfires versuss vegetation growth; Grigulis *et al.*, 2005).

4.3 AVAILABLE APPROACHES TO MODELLING THE IMPACT OF DRIVERS ON BIODIVERSITY AND ECOSYSTEM FUNCTIONING

4.3.1 Modelling approaches addressing biological levels of particular relevance to IPBES

4.3.1.1 Individual-level models and evolutionary adaptation

Populations are not static, but evolve. As a consequence, species may be able to adapt to conditions different from those previously experienced (Hoffmann and Sgrò, 2011). As introduced in **Figure 4.2**, evolution can alter dispersal patterns, physiology and biotic interactions (Thuiller *et al.*, 2013), and this poses a clear problem for predictive modelling at all levels, from genes to ecosystems: how to make predictions that go beyond current conditions?

There has been considerable research aimed at addressing this question, notably theoretical models that explicitly account for biological processes such as mutation, dispersal and interactions within and between species (e.g. mating and competition) (Bürger, 2000). Such models can account for environmental change and allow projections about future scenarios, beyond the range of what is currently observed. They also provide a means of assessing the robustness of predictions across uncertain parameters and processes.

Short-term evolutionary projections focus on the response to selection within a population based on the initial ('standing') genetic variance, and can account for selection acting on multiple traits (Lande and Arnold, 1983). Assuming that several genes underlie these traits, quantitative genetic models can accurately predict short-term evolutionary responses to a changing environment, given information about the genetic variance for each trait, the covariance among traits, and the strength of selection induced on each trait (see, for example, Shaw and Etterson, 2012). In practice, this information is unavailable for most species and over large spatial extents. Thus, ranges of plausible values must be inferred – with uncertainty – based on data from other species.

Longer-term projections are made difficult by the need to account for the dynamics of genetic variation. Processes such as mutation and migration that build genetic variance must be modelled (Barton and Turelli, 1989). Selection itself causes allele frequency changes that can increase or decrease genetic variance (de Vladar and Barton, 2014).

While many of these models assume a stable population size, more relevant to our understanding of biodiversity change are models that explicitly account for the feedback between population dynamics and evolutionary change. One theoretical approach focuses on key ecological traits (e.g. resource acquisition traits) that impact population dynamics and whose optimum values shift in a changing environment (Pease *et al.*, 2008; Duputié *et al.*, 2012). Such models that account for population dynamics are essential for addressing the extinction risk faced by a population. How far and how fast can a population be pushed by environmental change before it collapses (Bürger and Lynch, 1995; Lande and Shannon, 1996; Gomulkiewicz and Houle, 2009)? These models identify the critical speed of environmental change above which evolutionary lags grow over time until populations can no longer persist.

While the above models focus on standing genetic variance, some environmental changes require novel genetic solutions. Recent models have asked when new mutations can 'rescue' a population before it goes extinct following an environmental perturbation (e.g. Bell and Collins, 2008; Bell, 2013). These models provide key insights into the factors that promote evolutionary rescue, including the population size, the severity of environmental degradation, and the array of possible rescue mutations (Carlson *et al.*, 2014). Results from these combined evolutionary and population dynamic models can be counterintuitive. For example, while evolutionary adaptation generally works best when the environment changes slowly, evolutionary rescue can be more likely when an environmental shift occurs rapidly, because the release from density-dependent competition helps establish rescue mutations (Uecker *et al.*, 2014).

While the simplest evolutionary models are not spatially explicit, models are increasingly examining how the arrangement of populations and migration rates among them influence evolutionary processes in the face of a changing environment. For example, models have explored the process of evolution to a new or altered environment in the face of migration from the rest of the species range (Gomulkiewicz *et al.*, 1999). Such models can inform policy decisions about the maintenance of gene flow and the importance of migration corridors. Other models explore how the geographical range of a species evolves over time in the face of environmental change. Interestingly, these models are highly sensitive to assumptions made about the dynamics of genetic variance and whether it is held fixed, allowed to evolve deterministically, or subjected to random genetic drift (Polechová *et al.*, 2009, Polechová and Barton, 2015). The latter paper clarifies how demographic and evolutionary processes combine to predict whether a species will persist or undergo range contraction when the environment varies over space.

Many evolutionary models focus on genetic changes within a single species. Clearly, it is useful to clarify what might happen in simplified scenarios before adding the complexity of species interactions. To fully account for evolution in climate change models, however, we need to account for interactions among species co-occurring within a community. Those models that have considered species interactions suggest that evolutionary responses to environmental change can be fundamentally altered. For example, interspecific competition can hinder evolutionary adaptation and drive extinct a species that would be able to persist if it were on its own (Johansson, 2008). Other models demonstrate that accurate predictions require an understanding of how selection is shaped by both species interactions and environmental change (Osmond and de Mazancourt, 2013; Mellard *et al.*, 2015).

The results of any model, particularly evolutionary models, are sensitive to the details assumed. What are the selection processes and life strategies? How far do individuals migrate? How patchy is the environment? Which mutations are neutral or functional? These details matter when predicting whether a species will persist or become extinct.

Evolutionary processes thus raise a great deal of uncertainty in our projections of future biodiversity change in the face of major environmental drivers. Models such as those described above allow us to explore the range of possibilities. Not accounting for evolutionary change is, in most cases, the most conservative assumption for the maintenance of biodiversity (Shaw and Etterson, 2012). On the other hand, allowing evolutionary change under generous assumptions about current and future levels of genetic variance allows us to delimit the most optimistic scenarios for biodiversity in the face of human-caused environmental change.

4.3.1.2 Species- or population-level models

Populations are groups of organisms, all of the same species, that live in a given area and interact. Biodiversity change at the species or population level is often measured using data on population demography and species distribution (i.e. the distribution of populations within a species). Populations change in size and distribution due to the interaction between internal (e.g. growth rate, reproduction) and external (e.g. resources, predation, diseases) factors. Models building from the simple exponential function, including the logistic population model, life table matrix modelling, the Lotka-Volterra models of community ecology, meta-population theory, and the equilibrium model of island biogeography and many variations thereof, are the basis for ecological population modelling to predict changes over time (Gotelli, 2008).

Without the influence of external factors (thus in a density-independent situation), population growth can be modelled as exponential (Vandermeer and Goldberg, 2004). However, as the population size increases, density-dependence factors – such as resource limitation, competition or disease – frequently impact population growth because births and deaths are dependent on population size. Under density-dependence, growth rates slow down and reach a maximum, depicting a sigmoid curve of population size against time, in other words logistic growth. In the logistic model, the maximum number of individuals in the population is based on the carrying capacity of the system.

The logistic model is frequently used to study the impact of harvesting a population by removing individuals from it (Giordano *et al.*, 2003). Important modifications to the original model include the introduction of critical threshold densities, fluctuations in the carrying capacity and discrete population growth. A popular, but also much debated, example of the logistic growth model is the application to managing fisheries by finding the optimal strategy that maximises the population growth rate and the long-term yields achieving the maximum sustained yield (Gotelli, 2008). Discussions around this concept are large and include the importance of including species interactions to calculate this reference point in the context of fisheries management (Walters *et al.*, 2005).

Because species do not occur in isolation, the dynamics of any one species affects the dynamics of other sympatric species. In these cases, the logistic equation can be modified to consider the interaction of a population with interspecific competitors, with predators and with prey (Otto and Day, 2007). Lotka and Volterra models for interspecific competition and prey-predator interactions are the classical initial frameworks for competition and predation studies in ecology. These models build from the logistic equations and incorporate the interactions with other populations of competitors, predators and prey, modifying population growth rates. A classic example of the predator-prey interactions Lotka-Volterra model is the prediction of the regular cycling of the population size of Canada lynx (Lynx canadensis) and the snowshoe hare *(Lepus americanus)* (Sinclair and Gosline, 1997). An important concept in predator-prey interactions is the functional response of the predator as a function of the prey abundance. This response can be represented as a linear function of prey abundance (called the Type I response). More realistic assumptions incorporate handling time, under which the response of the predator increases to a maximum prey consumption rate (Type II response). A variation of the latter incorporates switching with an acceleration of the feeding rate at intermediate prey density and a decrease at high prey density as an asymptote is reached (Type III; Holling, 1959). These responses are key elements when modelling the ability of predator species to control prey populations (Gotelli, 2008).

Additionally, populations are often not closed, so that individuals tend to move between populations, influencing their persistence and survival. Different ways to model sets of populations (or meta-populations) exist. This approach is applied to study linkages of populations at the landscape scale, both in terrestrial and aquatic systems. Methodologies quantify the fraction of all population sites that are occupied, and have been notably applied to study the impacts of protected areas to inform biodiversity conservation (Royle and Dorazio, 2008; Kritzer and Sale, 2010). In addition, the number of species interacting in a specific place depends on the area available for those species to survive and the relationship between species and area holds in most assemblages of organisms worldwide.

This is at the origin of island biogeography that states that the larger an island, the more species it will hold, and the more potential interactions there will be. The original explanation for this pattern was related to habitat types, considering that larger islands include a higher diversity of habitats, and thus species restricted to those habitat types will only occur on larger islands (Gotelli, 2008). However, an alternative hypothesis developed with the equilibrium model of island biogeography includes the immigration of new species and the extinction of resident species as the main force behind the relationship between area, habitat heterogeneity and the number of species in a community (Simberloff, 1976; Allouche *et al.*, 2012).

When survival and fecundity rates depend on the age of individuals affecting population growth, age-structured models using the analysis of life table matrices are applied (Otto and Day, 2007; Gotelli, 2008). However, many other parameters can affect vital rates and their variability in space and time, which is at the core of estimating the risk of extinction or decline of a population.

Population viability analysis, a form of risk assessment analysis, estimates these risks by identifying major threats faced by a population and by evaluating the likelihood of future population persistence (Beissinger and McCullough, 2002; Morris and Doak, 2002).

Population viability analyses are often applied to the conservation and management of threatened or rare species (Akçakaya *et al.*, 2004), with the aim to evaluate options for how to improve the chance of survival of populations or species at risk (Akçakaya and Sjögren-Gulve, 2000; Drechsler and Burgman, 2004).

Species occurrence and abundance are often modelled using correlative methods generally described as species distribution models. Species distribution models are mainly used to evaluate 1) overall species distributions; 2) historic, present and future probability of occurrence; and 3) to gain an understanding of ecological niche limits, which is why this approach is also called ecological niche modelling (Aguirre-Gutiérrez *et al.*, 2013).

Species distribution models are widely used to model the effects of environmental changes on species distribution across all realms (Pearson and Dawson, 2003; Brotons, 2014). The multiple applications of species distribution models are reflected in the diversity of designations used to refer to this type of modelling approach, including ecological niche models, bioclimatic envelope models, and habitat (suitability) models (Elith and Leathwick, 2009). Modelling approaches that incorporate species abundance data along with species distribution data, for a joint prediction of the effects of environmental drivers on population demography and consequently on the overall species distribution, are also being pursued (Ehrlén and Morris, 2015).

Research that incorporates expert knowledge into species distribution models is relatively limited. However, in a study on species distribution modelling, Niamir *et al.* (2011) incorporated existing knowledge into a Bayesian expert system to estimate the probability of a bird species being recorded at a finer resolution than the original atlas data. They noted that knowledge-based species distribution maps produced at a finer scale using a hybrid model/expert system had a higher discriminative capacity than conventional approaches, even though such an approach might be limited to well-known species. Furthermore, in a study to evaluate trade-offs for using species occurrence data in conservation planning, Rondinini *et al.* (2006) noted that the geographic range data of species generated by expert knowledge had the advantage of avoiding the potential propagation of errors through data processing steps.

4.3.1.3 Community-level models

Community-level modelling offers an opportunity to move beyond species-level predictions and to predict broader impacts of environmental changes (e.g. Hilbert and Ostendorf, 2001; Peppler-Lisbach and Schröder, 2004; D'Amen *et al.*, 2015), which may be relevant in certain decision-making contexts.

For example, it can be used to predict the impact of losing a top predator in the structure of a trophic network or the impacts of land-use change in native communities. Community-level approaches are also recommended when time and financial resources are limited, when existing data are spatially sparse or when the knowledge on individual species distribution is limited (Ferrier *et al.*, 2002a) or even absent, as in the case of non-described species in highly diverse environments, and when species diversity is beyond what can feasibly be modelled at the individual species level. Overall, assessing changes in community composition, including both species presence and abundance, and how those changes affect ecosystem processes, provides a more detailed understanding of the impacts of drivers (Newbold *et al.*, 2015). Moreover, species richness – a community-level metric – is a commonly used biodiversity indicator (Mace *et al.*, 2012).

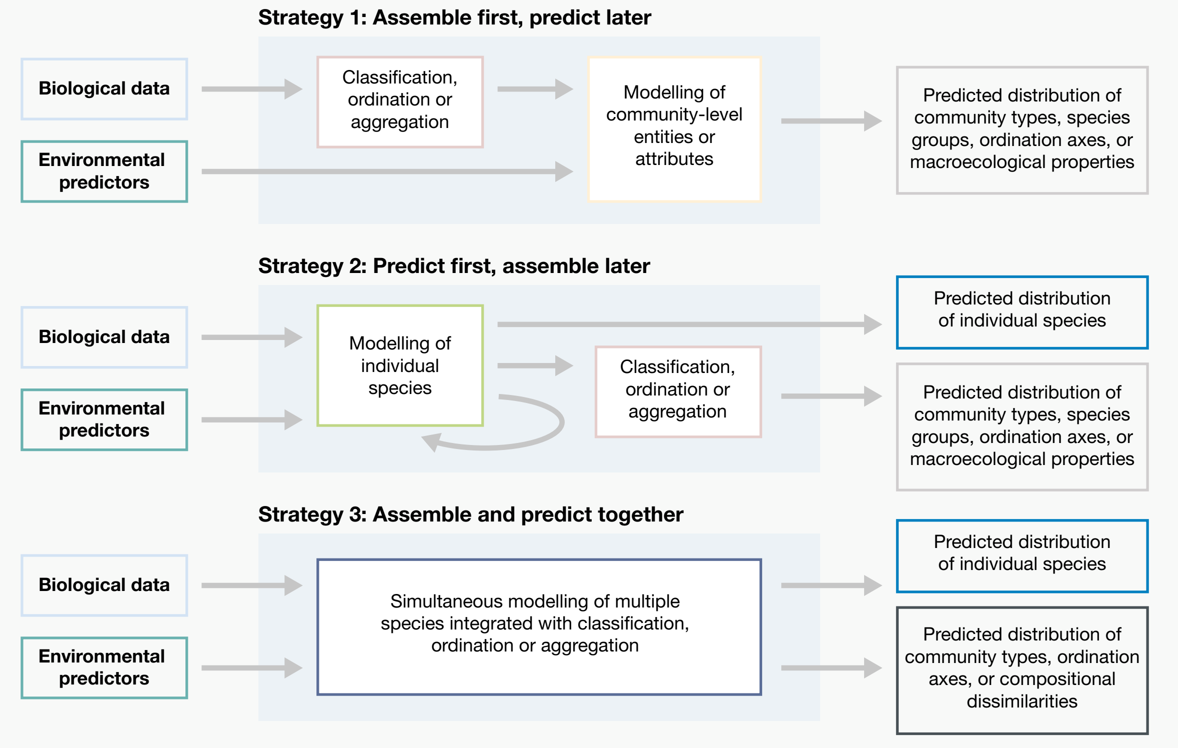
Community-level distribution models, as for species distribution models, use environmental data to predict the distribution of species assemblages or communities. Data input needs are similar to species distribution model inputs but model outputs are more diverse and can be classified into five main types (Ferrier and Guisan, 2006): community types (groups of locations with similar species composition), species groups (groups of species with similar distributions), axes or gradients of compositional variation (reduced space dimensions of compositional patterns), levels of compositional dissimilarity between pairs of locations, and various macro-ecological properties (e.g. species richness) and even phylogenetic diversity.

Ferrier and Guisan (2006) and D'Amen *et al.* (2015) identify three approaches to community-level modelling **(Figure 4.4)**: 1) 'assemble first, predict later', whereby species data are first combined with classification or ordination methods and the resulting assemblages are then modelled using machine learning or regression-based approaches, 2) 'predict first, assemble later', whereby individual species distributions are modelled first and the resulting potential species distributions are then combined (i.e. the result is in fact the summation of individualistic models), and 3) 'assemble and predict together', whereby distributions of multiple species are modelled simultaneously using both environmental predictors and information on species co-occurrence patterns.

These approaches have different strengths (D'Amen *et al.*, 2015). The first and third approach are more able to capture overall patterns of response and are better options if rare species, for which distribution data may be scarce, represent a significant fraction of the species assemblage.

FIGURE **4.4**

Main approaches to community-level distribution models (Modified from Ferrier and Guisan, 2006. *Spatial modelling of biodiversity at the community level.* Copyright © 2006 by John Wiley Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc).



However, the second approach allows more flexibility in how different species respond to different environmental factors, though it may fail to produce reliable projections of rare species distributions (Ferrier and Guisan, 2006). Similar reasoning can be used when deciding whether to use species distribution models or community-level models to assess community responses. Species distribution models can provide more reliable predictions of well-sampled species, but may fail with rare species and are resource-demanding when applied at the community level.

The strengths and weaknesses of community-level modelling approaches and the applicability of community models are discussed by Ferrier *et al.* (2002b) and by Ferrier and Guisan (2006). More recently, D'Amen *et al.* (2015) have highlighted potential research avenues and proposed novel integrative frameworks to encourage the state-of-the-art in spatial predictions at the community level. As in species distribution models, correlative community-level distribution models can also integrate ecological processes such as meta-community dynamics and species interactions (Mokany and Ferrier, 2011) to enhance their predictive ability (D'Amen *et al.*, 2015).

4.3.1.4 Ecological interaction networks

Ecological interaction networks include, among other examples, trophic webs and plant-pollinator webs (Ings *et al.*, 2009). Species interactions within communities can be explicitly modelled using process-based approaches that describe the links between species and the dynamics that determine species coexistence in the network, such as predator-prey oscillations (Verhoef and Olff, 2010).

Network topology is also an important consideration when building interaction models, since the links between elements may follow a non-random pattern. In food webs, interactions patterns are shaped by body size, which justifies the use of size-structured models (Woodward *et al.*, 2005; Loreau, 2010).

Correlative approaches are also frequent in studies of interaction networks, due to their lower information requirements, but Ings *et al.* (2009) advocate against the use of inferential approaches and recommend pursuing more mechanistic approaches that build on first principles and ecological theory. Similarly, applications in modelling marine ecosystems will require the coupling of different trophic levels that may have different characterisations. One way to represent biodiversity in complex marine systems would be to concentrate the detail of representation at the target species level and their main interactions at the community level (FAO, 2008). Community interaction network approaches have been used to assess the impacts of, for example, invasive species (Woodward and Hildrew, 2001), the overfishing of top predators (e.g. Bascompte *et al.*, 2005), biodiversity and ecosystem function relationships (Fung *et al.*, 2015), freshwater pollution (e.g. Scheffer *et al.*, 1993) and global warming (Petchey *et al.*, 1999).

Outputs from community-level distribution models can be used to inform species traits approaches, assessing the composition of impacted communities. Species traits approaches can also be linked to interaction network models to predict how changes in community traits will affect ecosystem functioning (Harfoot *et al.*, 2014b). Species traits approaches move the focus from species composition in a community to the distribution of traits or average trait values in the community. Species traits underlie species responses to drivers, that is, their ability to cope with environmental change, but also their role in environmental processes. Therefore, the distribution of trait values in a community (e.g. root depth, body size or forage range) may not only inform on the vulnerability of the community to changes in drivers, but also on the effects of community compositional change to ecosystem functioning, and consequently to ecosystem services (Lavorel and Garnier, 2002; Suding *et al.*, 2008; Oliver *et al.*, 2015). Trait-based ecological risk assessment is an example of a trait-based approach to assess ecological responses to natural and anthropogenic stressors based on species characteristics related to their functional roles in ecosystems (Baird *et al.*, 2008).

Another approach commonly used to assess community change over time is through species-area relationship models. These are used to predict species richness as a function of habitat area. Species-area relationship models have been tested and applied to a wide range of taxa and across all scales, from local to global (e.g. Brooks *et al.*, 2002; Brooks *et al.*, 1997). Species-area relationship models are often used to predict the impacts of changes in habitat availability, driven by land-use change (e.g. van Vuuren *et al.*, 2006; Desrochers and Kerr, 2011) or climate change (e.g. Malcolm *et al.*, 2006; van Vuuren *et al.*, 2006), on community richness, but also to assess the impacts of direct exploitation on community parameters such as species turnover rates (e.g. Tittensor *et al.*, 2007). Reviews on the use of species-area relationships can be found in Rosenzweig (2010), Drakare *et al.* (2006) and Triantis *et al.* (2012).

The most common species-area relationship model is the power function (Arrhenius, 1921), $S=cA^z$, where S is species richness, A is habitat area, and c and z are model parameters (Rosenzweig, 2010). Notwithstanding the general use of the power function, species-area relationship models may be best described by other functions or by averaging the predictions of alternative models (i.e. multi-model species-area relationship approaches) when there is no single best model (Guilhaumon *et al.*, 2008). Another important caveat relates to the risk that species-area relationship models may overestimate predicted species loss due to habitat loss (Pereira and Daily, 2006). This limitation can be addressed through the use of modified species-area relationship approaches that better represent community dynamics, such as the species-fragmented area relationship (Hanski *et al.*, 2013) – which considers the effects of habitat fragmentation on species diversity patterns – and the countryside species-area relationship (Proença and Pereira, 2013) – which accounts for the differential use of habitats in a landscape by different species groups.

4.3.1.5 Ecosystem-level models and integrated models

Ecosystem-level models may focus on the biophysical dimension of ecosystems (e.g. dynamic global vegetation models), or they can be developed to also include economic and social aspects (e.g. EwE models, see Chapter 5).

> Dynamic Global Vegetation Models (DGVMs) are process-based models that simulate various biogeochemical, biogeophysical and hydrological processes such as photosynthesis, heterotrophic respiration, autotrophic respiration, evaporation, transpiration and decomposition.

DGVMs are the most advanced tool for estimating the impact of climate change on vegetation dynamics at the global scale (Smith *et al.*, 2001). They simulate shifts in potential vegetation and the associated biogeochemical and hydrological cycles as a response to shifts in climate. DGVMs use time series of climate data and, given the constraints of latitude, topography and soil characteristics, simulate monthly or daily dynamics of ecosystem processes. DGVMs are most often used to simulate the effects of future climate change on natural vegetation and carbon and water cycles, and are increasingly being coupled with atmosphere-ocean general circulation models to form Earth system models.

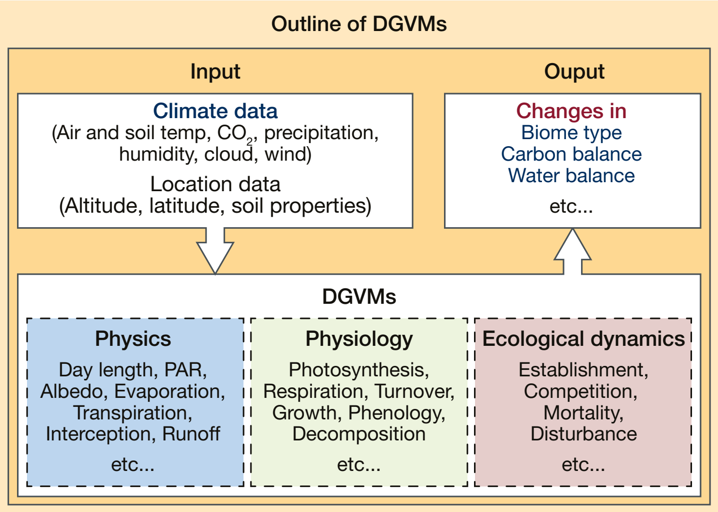
The basic structure of a DGVM is shown in **Figure 4.5**.

DGVMs capture the transient response of vegetation to a changing environment using an explicit representation of key ecological processes such as establishment, tree growth, competition, death and nutrient cycling (Shugart, 1984; Botkin, 1993). Plant functional types are central to DGVMs as, on the one hand, they are assigned different parameterisations with respect to ecosystem processes (e.g. phenology, leaf thickness, minimum stomatal conductance, photosynthetic pathway, allocation and rooting depth) while, on the other hand, the proportion of different plant functional types at any point in time and space defines the structural characteristics of the vegetation (Woodward and Cramer, 1996).

The key advantages of using DGVMs include the capacity to simultaneously model the transient responses related to dynamics of plant growth, competition and, in a few cases, migration. As such, this allows the identification of future trends in ecosystem functioning and structure and these models can be used to explore feedbacks between biosphere and atmospheric processes (Bellard *et al.*, 2012). DGVMs are, however, focused on a limited number of plant functional types, which induces a high level of abstractedness (Thuiller *et al.*, 2013).

FIGURE **4.5**

Structure of Dynamic Global Vegetation Models (Modified from: http://seib-dgvm.com/oview.html).



Adding a further level of complexity beyond ecosystem modelling is achieved through integrated assessment models (IAMs, see **Figure 4.6**), which were defined in the IPCC Third Assessment Report (IPCC, 2001) as 'an interdisciplinary process that combines, interprets, and communicates knowledge from diverse scientific disciplines from the natural and social sciences to investigate and understand causal relationships within and between complicated systems'.

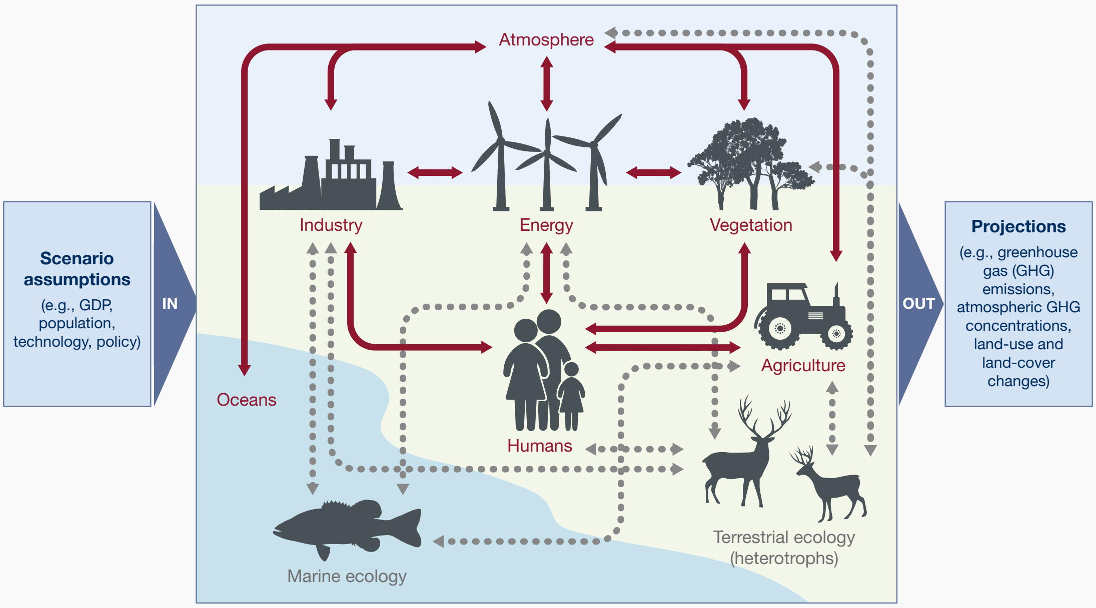
It is generally agreed that there are two main principles to integrated assessment: integration over a range of relevant disciplines, and the provision of information suitable for decision making (Harremoes and Turner, 2001). IAMs therefore aim to describe the complex relationships between environmental, social and economic drivers that determine current and future states of the system and the effects of climate change, in order to derive policy-relevant insights (van Vuuren *et al.*, 2009). One of the essential characteristics of integrated assessment is the simultaneous consideration of the multiple dimensions of environmental problems. At the global level, IAMs could potentially be a valuable tool for modelling biodiversity dynamics under different drivers; however, current IAMs are not developed for this application (Harfoot *et al.*, 2014a). Existing IAMs are largely used for modelling climate change and investigating options for climate mitigation. Key outputs from IAMs include anthropogenic greenhouse gas emissions. However, these also provide projections for other variables, such as land cover and land use (including deforestation rates).

One of the most noticeable limitations of IAMs is that they focus largely on terrestrial systems, not marine or freshwater aquatic ecosystems (as shown in **Figure 4.6**, which provides a schematic representation of a typical IAM). Another notable limitation is the lack of feedback from changes in biodiversity, ecosystem functions and terrestrial ecology on other drivers such as climate change and land-use change. For example, actions that reduce the number or composition of species in natural systems may compromise ecosystem functioning, as the ability of ecosystems to provide services may depend on both these aspects (Tilman *et al.*, 2001; Loreau *et al.*, 2001; Hooper *et al.*, 2005; Isbell *et al.*, 2011). At the European level, CLIMSAVE not only integrates sectoral models, but also has feedbacks and can be used to explore the impacts of selected adaptation options (Harrison *et al.*, 2015).

IAMs typically describe the cause-effect chain from economic activities and emissions to changes in climate and related impacts on, for example, ecosystems, human health and agriculture, including some of the feedbacks between these elements. To make their construction and use tractable, many IAMs use relatively simple equations to capture relevant phenomena, for example for the climate system and carbon cycle (Goodess *et al.*, 2003). However, the behaviour of these components can have a

FIGURE **4.6**

Schematic representation of a typical full-scale integrated assessment model. Red labels and arrows represent existing model components and interactions, while grey labels and greydashed arrows indicate important components and interactions not currently included (Modified from Harfoot *et al.*, 2014a. *Integrated assessment models for ecologists: the present and the future.* Copyright © 2014 by John Wiley Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc).



significant impact on IAM results and the quality of policy advice, with the possibility of simplifications in the Earth system projections leading to imprecision (or even error) in projecting impacts and costs of mitigation.

Over the last decade, IAMs have expanded their coverage in terms of land use and terrestrial carbon cycle representation, non-CO_2 gases and air pollutants, and by considering specific impacts of climate change. Some IAMs have a stronger focus on economics, such as multi-sectoral computable general equilibrium models that are combined with climate modules and models focused on cost-benefit analysis; others focus on physical processes in both the natural system and the economy (integrated structural models/biophysical impact models). Examples of IAMs are IMAGE (Integrated Model to Assess the Global Environment), DICE (Dynamic Integrated model of Climate and the Economy), FUND (Climate Framework for Uncertainty, Negotiation and Distribution) and MERGE. All of these models include key drivers of change such as population and macro-economy that can be derived from various external and internal sources.

However, as IAMs aim to integrate different aspects of the environment, they run the risk of becoming extremely complex. The developers of such models therefore have to make decisions about the focus of their study and how to express the impacts they estimate, whether it is through the reporting of physical changes in emissions, shifts in land-use activity or mortality rates, or through cost-benefit analyses of damages resulting from climate change (Goodess *et al.*, 2003). The data requirements for these IAMs are also large and not always feasible.

4.3.2 Modelling options, strengths and limitations

4.3.2.1 Meeting policy information needs

Models allowing the assessment of impacts of changes in drivers on biodiversity or ecosystem processes are important tools to support decision making **(Table 4.3)**. To be effective, models should be able to address the policy or decision-making needs that motivate their use. A formal and accurate definition of the decision-making context is therefore essential in this process (Guisan *et al.*, 2013). A precise definition of the policy or decision context should inform the selection of modelling framework, including model complexity, spatial and temporal scales or response variables and data requirements (Chapter 2). State variables should be sensitive to the pressures underlying alternative management scenarios or addressed by policies and, if possible, be responsive at temporal and spatial scales that are relevant for policy strategies. For example, small farmland birds are responsive to agro-environmental schemes implemented at the field scale, while large farmland birds are more affected by activities over larger spatial scales (Concepción and Díaz, 2011). Moreover, state variables should also be representative of the biodiversity attributes underpinning the benefits of nature that are valued in a given decision-making context.

Regarding model scope, models should be adjusted to the specific requirements of the decision-making context. Models could rely on observed data to describe the relationship between pressures and response variables, explicitly describe the processes linking those variables, or follow an intermediate approach. The explicit inclusion of mechanisms in modelling approaches will be relevant whenever the understanding of the underlying dynamics is necessary to guide management and where changing environmental conditions call for a mechanistic approach (Gustafson, 2013; Collie *et al.*, 2014). The use of correlative approaches, on the other hand, is suitable where there is limited knowledge about the underlying mechanisms or when model outputs are able to capture the dominant response patterns that are needed to inform policy, such as the evaluation of large-scale conservation initiatives (Araújo *et al.*, 2011; Dormann *et al.*, 2012).

As for model complexity, input data requirements should be balanced against data availability and quality – namely the spatial and temporal resolution of available data – as a lack of adequate input data may compromise model feasibility and the quality of results (Collie *et al.*, 2014). The ongoing development of new technologies and remote sensing to monitor species and ecosystems, as well as platforms for data sharing, is encouraging as it is resulting in increased data availability and accessibility (Pimm *et al.*, 2014). The integration of local observations and remote sensing products can provide a more complete view of the responses of biodiversity to environmental change and can improve the modelling of ecosystem processes across scales (Pereira *et al.*, 2013; Pimm *et al.*, 2014).

4.3.2.2 Predictability

No model can capture the full complexity of ecosystems and perfectly predict biodiversity patterns and ecosystem function as impacted by a suite of drivers, such as through climate change or habitat modification (Bellard *et al.*, 2015). However, models are useful to synthesise data, evaluate alternative hypotheses, and provide projections about potential future states.

This is illustrated by the study of Bellard *et al.* (2012), who reviewed the approaches most commonly used for estimating future biodiversity at global and regional scales. They found that projections from the different approaches vary considerably, depending on method, taxonomic group, biodiversity loss metrics, spatial scales and time periods. Nevertheless, the overall projections from the majority of the models indicated that future trends for biodiversity were alarming. This reiterates a general finding from the IPCC, which is that projections from individual models should not be taken at face value. Instead, an ensemble approach accommodating uncertainty in multi-model prediction is required for interpreting trends and for comparisons between models. Comparisons that involve applying numerous models to evaluate a given policy question (e.g. related to the efficiency of alternative measures for minimising the impact of climate change) provide a means not just for evaluating uncertainty, but just as importantly for studying why the models produce different answers. This may indeed lead to feedback that impacts not just the individual models, but also the underlying theory that is used to develop the models (see **Figure 4.7**).

It is becoming standard practice in many research fields for model fitting and statistical procedures to test model predictions on a known, typically simulated, data set in order to assess model behaviour and characteristics (e.g. in fisheries assessment, Hilborn and Walters, 1992). For models of complex natural systems, it is often not possible to test model predictions against simulated data, but a minimum requirement is that the models are 'validated' by a demonstration of each model's capability to at least exhibit the same behaviour as that which has been observed historically (Rykiel, 1996). Validation here means consistency with observation (for instance as tested through time series fitting with formal information criteria evaluation).

TABLE **4.3**
Summary of major biodiversity models and modelling approaches.

Model	Level of organiza-tion	Model type	Level of integration	Required level of expertise	Examples	References
Evolutionary models	Organisms	Mixed (hybrid)	Integrated models	High	How demographic and evolutionary processes combine to predict whether a species will persist or not	Polechová and Barton, 2015; Barton, 2001
Dynamic Energy Budget models	Organisms	Mechanistic	Integrated models	High	To understand evolution of metabolic organisation	Kooijman, 2009
Aquatic habitat suitability	Community	Expert-based models	Single model	Basic	To link environmental conditions to the quantitative habitat suitability of aquatic species	Mouton et al., 2009
Species Distribution Models	Species/ Populations	Mainly correlative	Single or integrated models	Basic – Moderate	Used to model the effects of environmental change on species distribution	Pearson and Dawson, 2003; Elith and Leathwick, 2009; Stockwell and Peters, 1999; Phillips *et al.*, 2006
Dynamic bioclimate envelope model	Species/ Populations	Mixed (hybrid)	Integrated models	Moderate	Changes in the relative abundance of marine species induced by change in climatic variables	Cheung *et al.*, 2008a, 2008b, 2011; Gallego-Sala, 2010; Notaro et al., 2012; Fernandes *et al.*, 2013
Age/stage-structured models	Species/ Populations	Correlative	Single model	Basic	Widely used for fisheries management	Hilborn and Walters, 1992; Getz, 1988; Barfield *et al.*, 2011
Food web models	Ecosystems	Process-based	Integrated models	Moderate	Widely used for ecosystem-based management	Christensen and Walters, 2011
Size-based models	Community	Correlative	Single model	Basic	Impact of size in marine and freshwater ecosystems management	Duplisea *et al.*, 2002; Rochet *et al.*, 2011
Species-Area Relationship models	Community	Correlative	Single model	Moderate	Used to predict the impacts of changes in habitat availability, driven by land use change or climate change	van Vuuren *et al.*, 2006; Desrochers and Kerr, 2011; Pereira *et al.*, 2013; Huth and Possingham, 2011
Biodiversity metric models	Community	Correlative	Integrated models	Moderate	A quantitative and integrated approach to assess the biodiversity with multiple indicators	Janse et al., 2015
Lotka-Volterra	Community	Process-based	Integrated models	High	For interspecific competition and prey-predator interactions	Sinclair and Gosline, 1997
Dynamic Global Vegetation Models	Ecosystem	Process-based	Integrated models	High	To estimate the impact of climate change on vegetation dynamics at global scale and its carbon and water cycles	Botkin, 1993; Bellard *et al.*, 2012; Cramer *et al.*, 2001
General ecosystem model	Global	Process-based	Integrated models	High	Uses a unified set of fundamental ecological concepts and processes for any ecosystem to which it is applied, either terrestrial or marine, at any spatial resolution	Harfoot *et al.*, 2014a
Integrated Assessment Models	Global and regional	Integrated	Multiple models	High	Interdisciplinary assessment	Harremoos and Turner, 2001; Tilman *et al.*, 2001

As an example of a comprehensive model validation exercise, Elith and Graham (2009) constructed the distribution of an artificial plant species based on its affinity along three axes, related to preference for moisture, aspect ('southness') and geology, to obtain a 'true' spatial distribution for the plant. They constructed a spatial subsample of parameters (along the three axes), and used this to parameterize five different, commonly applied Species Distribution Models. By next predicting the full distribution for each method, they were able to validate model performance using true-false positive and negative patterns as well as the evaluation of predictions versus true values. This study, in addition to the direct evaluation of model performance, also demonstrated that model comparisons can be used to evaluate why different models give different predictions – which can be used for the further development of models as well as the refinement of ecological theory (see **Figure 4.7**).

While model comparisons are both needed and feasible, as demonstrated by the study of Elith and Graham (2009), they are difficult to conduct by any one research group as soon as the models involved are complex and in practice require both specific capacity and experience to be run optimally. For this reason, it is extremely important to build capabilities for inter-model comparisons, following in the footsteps of the Coupled Model Intercomparison Projects (CMIP) of the IPCC. Similar activities are now underway for biodiversity research as part of the Inter-Sectoral Impact Model Intercomparison Project (ISI-MIP), which is a community-driven modelling effort that brings together impact models across sectors and scales to create consistent and comprehensive projections of climate change impacts.

4.4 MODELLING FEEDBACKS AND INTERACTIONS

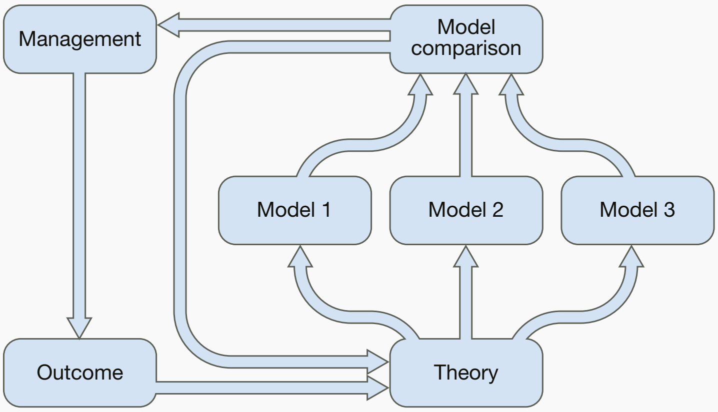
Both human and non-living environmental drivers influence biodiversity and ecosystem functions through a number of processes. In turn, biodiversity exerts feedbacks on both systems **(Figure 4.8)**. Consideration of the feedbacks is important as they may cause non-linearity in interaction dynamics, which can potentially move a system beyond thresholds and tipping points (e.g. regime shift: Lenton, 2011).

Changes in biodiversity interact with different drivers of biodiversity change (e.g. climate change, disturbance regimes such as forest fires, invasive species and pests, and ecosystem processes) over different temporal and spatial scales. Changes in biodiversity and shifts in the distribution of plant traits can influence the climate at global and regional scales. For instance, General Circulation Models based on simulations indicate that the widespread replacement of deep-rooted tropical trees by shallow-rooted pasture grasses would reduce evapotranspiration and lead to a warmer, drier climate (Shukla *et al.*, 1990). Similarly, the replacement of snow-covered tundra by a dark conifer canopy at high latitudes may increase energy absorption sufficiently to act as a powerful positive feedback to regional warming (Foley *et al.*, 2000).

Feedbacks between drivers and biodiversity or ecosystem levels usually involve a high level of complexity in the models because changes in state variables at different levels (either

FIGURE **4.7**

An overview of relationships between ecological theory, models, comparison and management. There may be numerous models to represent a given theory, and both the model comparisons and the management outcome may provide feedback to theory (Modified from Cuddington *et al.*, 2013. *Process-based models are required to manage ecological systems in a changing world.* Copyright © 2013 by John Wiley Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc).



biological or others) should be able to interact and cause emergent dynamics. Changes in biodiversity, for instance, can impact disturbance regimes such as fire, which in turn are strongly determined by climate (Pausas and Keeley, 2009) and fire-suppression efforts (Brotons *et al.*, 2013).

Biodiversity and ecosystem models as discussed in Section 4.3 describe the impact of abiotic drivers such as climate, nutrient cycling, atmospheric concentration of greenhouse gases including CO_2, water resources, fire, and land use on the biotic systems, including their biodiversity and ecosystem services. Many of the modelling approaches are capable of simulating the feedback of the biotic system on abiotic and human drivers as well. For example, many of the process-based models simulate carbon sequestration in vegetation and soils, and thus the impact on atmospheric greenhouse gas concentrations. Process-based models can also simulate feedbacks, from vegetation change to forest fires (LANDIS). Furthermore, many of the Dynamic Global Vegetation Models (ex-IBIS Foley *et al.*, 1996; Kucharik *et al.*, 2000; Sitch *et al.*, 2003) are able to simulate feedback between the biotic system and water resources. However, only a few Dynamic Global Vegetation Models include detailed feedback to nutrient cycling. Dynamic Global Vegetation Models have been also used to study feedback between vegetation and past climate. General Circulation Models/ Atmosphere-Ocean General Circulation Models too include vegetation feedbacks to climate. Neither the process-based models (including Dynamic Global Vegetation Models) nor the General Circulation Models/ Atmosphere-Ocean General Circulation Models include the feedback of biodiversity and ecosystems to human societies. However, IAMs are capable of simulating impacts of changes in biodiversity and ecosystems on human systems, including economic activities.

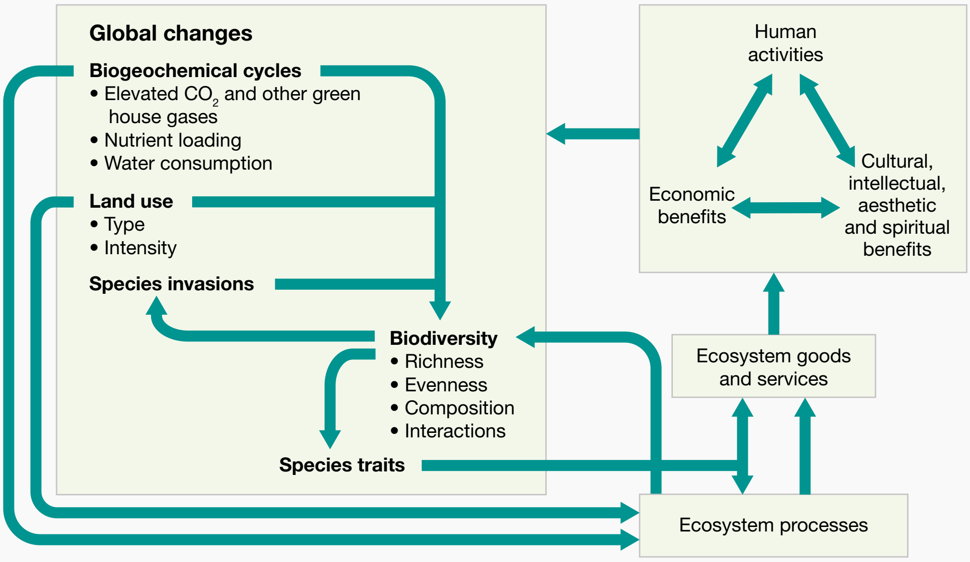
4.5 MODEL COMPLEXITY

Matching model complexity to policy and decision-making needs while keeping the model as simple as possible is a major challenge in the future development of biodiversity and ecosystem models (Merow *et al.*, 2014). We here describe three general strategies that should help limit model complexity: model what matters, adopt hierarchical modular modelling approaches, and standardise protocols for model communication.

The first general strategy is the formulation of critical biological processes directly relevant to the question addressed or the problem to be dealt with. Avoiding unnecessary increases in model complexity requires a careful assessment of the biological processes that most directly affect species distributions at the spatial and temporal scales of interest for each particular study (Guisan and Thuiller, 2005). Although there is no general recipe

FIGURE **4.8**

Schematic diagram of interactions between biodiversity, the human system and the non-living environment used for evaluating feedbacks related to species invasions. The figure represents feedbacks between biodiversity, drivers of biodiversity change and the interactions between these drivers (Modified by permission from Macmillan Publishers Ltd: [Nature] Chapin *et al.*, 2000, 405, 234-242, copyright 2000).



to select the relevant biological processes, those related to species auto-ecology will always have a central role. Habitat selection and population dynamics in species-level models may be formulated with more or less detail, but are fundamentally important to predict species distribution dynamics (Willis *et al.*, 2009; Kunstler *et al.*, 2011).

Biological processes should only be modelled explicitly and internally (i.e. using process-based models) if they are critical for the question at hand. The remaining processes can be modelled externally and formulated into the model by means of input spatial layers or parameters modified by additional modelling frameworks (Smith *et al.*, 2001). Such an approach may facilitate the flexible structuring of models by allowing sub-models to be plugged into one another (e.g. McRae *et al.*, 2008). In this modular structure, the upper levels provide external contextual information (and hence external dynamics) to the lower ones. Hierarchical modular structures have the advantage of 1) being easier to integrate across different spatial and temporal scales (e.g. to downscale the results of processes formulated at higher levels (del Barrio *et al.*, 2006)), and 2) being able to assess the levels of uncertainty added at each stage (Larson *et al.*, 2004; Chisholm and Wintle, 2007). However, modularity may be limited for those target species that modify their environment or interact with other biotic entities (Midgley *et al.*, 2010). Research is needed to compare the outputs of models with different degrees of complexity in the light of validation data appropriate to the process or driver under study (Roura Pascual *et al.*, 2010). Only in this case will it be possible to build a body of reference regarding the minimum acceptable levels of complexity to analyse a given problem.

4.6 ACCOUNTING FOR UNCERTAINTY

Policymaking related to biodiversity and ecosystem functioning must take place based on the currently available knowledge. It must also be done recognising that uncertainty is associated with all science, including modelling, due to data limitations, the representation of processes, and the resolution of the ecosystem scale. Environmental complexity is an emergent property of the environment – it is not just that our models have limitations.

The fact remains that the environment is incredibly complex and interconnected. However, policymakers have to make decisions even in the face of uncertainty, to act on drivers in order to conserve ecosystems and biodiversity. To support decision making, models aim to synthesise this complexity into a reasonable number of dimensions.

In biodiversity and ecosystem modelling, the uncertainty arises from two primary sources: model uncertainty and uncertainty in the input parameters (or scenario uncertainty). Different models represent different physical processes differently, and to varying extents and levels of detail. This leads to model uncertainty. Input parameters, for example climate projections, add to the modelling uncertainty. An example of model uncertainty is that models generally do not take into account tipping points and non-linearity (Whiteman *et al.*, 2013). Additionally, many models generally leave out the natural processes and feedbacks that are difficult to model given the current state of knowledge, even though these processes may cause large impacts. An example of uncertainty arising from input parameters is the uncertainty inherent in climate or land-use change projections. In addition, existing impact assessment studies – including the biophysical and integrated assessment models (IAM) – generally tend to work with the mean of the probability distribution of projected impacts, neglecting the low-probability, high-impact tails of the distribution (Weitzman, 2009; Ackerman *et al.*, 2010; Marten *et al.*, 2012). Impact studies generally focus on single-sector or single region-based assessments. The potential interactions among sectors and regions, which can adversely impact biodiversity and ecosystems, are therefore not adequately included in the quantitative estimates (Warren, 2011).

Similarly, the ambient policy and management practices and socio-economic stresses leading to the degradation of natural resources are also not included in most sectoral impact assessment models. Also, although key human-related issues such as armed conflict, migration and loss of cultural heritage have a lot of potential to impact natural ecosystems, impact assessment models do not include these human system-related stresses (Hope, 2013). IAM-based economic analyses of impacts are generally conservative, as these studies make optimistic assumptions about the scale and effectiveness of adaptation (Marten *et al.*, 2012; Hope, 2013). In this section, we present the sources of uncertainty in models of biodiversity and ecosystems, some options to address uncertainty, and approaches to communicating uncertainty.

4.6.1 Sources of uncertainty

Link *et al.* (2012) and Leung *et al.* (2012) highlighted six major sources of uncertainty confronting ecosystem modellers **(Figure 4.9)**.

4.6.1.1 Natural variability

Natural variability or stochasticity includes biological differences among individuals, either within the same environment (genetic differences) or between environments (plasticity), differences among populations within a community, changes in spatial distributions with time, density-dependent or independent variation in a vital rate, seasonal or inter-annual variability in realised environmental conditions, or shifts in productivity regimes. Natural variability increases ecosystem model uncertainty by reducing the precision of parameter estimates.

4.6.1.2 Observation error

Observation error is inevitable when studying organisms in either a single species or an ecosystem context (e.g. Morris and Doak, 2002; Ives *et al.*, 2003, as cited in: Link *et al.* (2012)). The environmental characteristics of a particular area (even those that we can measure fairly accurately) are difficult to relate directly to the full experience of mobile organisms that move into and out of that area. Thus, natural variability can actually exacerbate observation error. Observation error adds uncertainty to ecosystem models through reduced precision, misspecified parameter distributions, and biased parameter estimates.

4.6.1.3 Structural complexity

The structural complexity of a model arises from many factors, such as the number of parameters it includes; the number of ecosystem components and processes it simulates; the temporal scale; the nonlinearities, log effects, thresholds and cumulative effects incorporated in those processes; and whether or not it includes features such as spatial dynamics or stochasticity (Fulton *et al.*, 2003). Structurally complex ecosystem models are gaining in use, in part due to improved computing capabilities and also due to the intricate, multi-sector, cross-disciplinary questions commonly being addressed in ecosystem-based management.

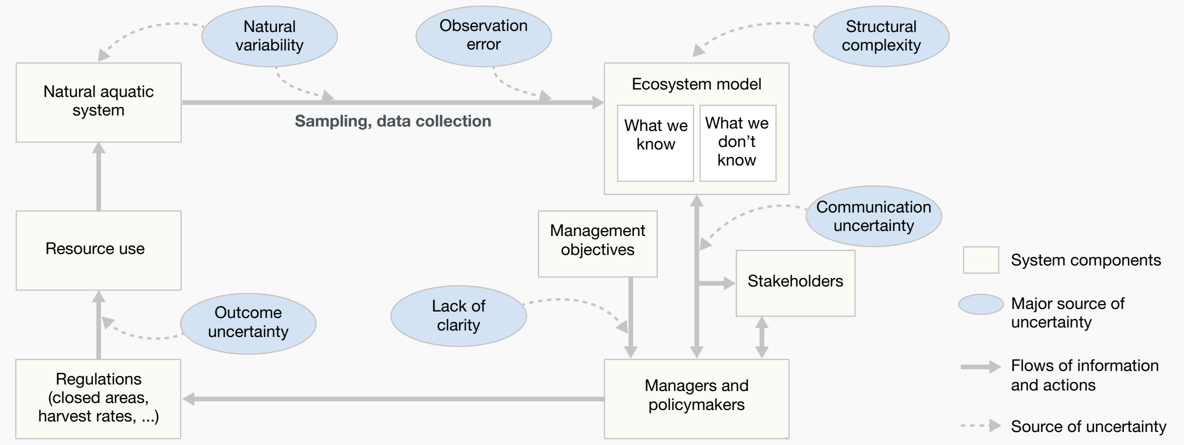
Ecosystem models are diverse in terms of scope and approach, but share the general feature of a large number of parameters with complex interactions. These models are necessarily built with imperfect information. Given these inevitable uncertainties, large and complex ecosystem models must be evaluated through sensitivity analyses with independent data before their output can be effectively applied to conservation problems (McElhany *et al.*, 2010). Uncertainty in climate change scenarios arises from different greenhouse gas emission storylines and from differences between climate models, even if driven with the same storylines (McElhany *et al.*, 2010). This can be partly addressed by using climate change scenario data from several emission storylines, but also by using results from multi-model studies (i.e. an ensemble of climate models). Process-based models are widely used to assess the impacts of climate change on forest ecosystems (McElhany *et al.*, 2010). Climate change impact studies that do not integrate parameter uncertainty may overestimate or underestimate climate change impacts on forest ecosystems.

4.6.2 Options for reducing uncertainty

All model types carry multiple uncertainties, but there are potential options for reducing uncertainty, as discussed by

FIGURE **4.9**

A conceptual diagram of the flow of information and actions in a typical Living Marine Resources management system. Rectangles represent components of the system, solid arrows indicate flows of information and actions between components, and ellipses represent major sources of uncertainty (Modified from Link *et al.*, 2012. *Dealing with uncertainty in ecosystem models: The paradox of use for living marine resource management.* Copyright © 2012 by John Wiley Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc).



Beale and Lennon (2011). It is important to establish the full range of model behaviours by carrying out a sensitivity analysis and considering different combinations of models and parameters. Sensitivity analysis is useful to determine the importance of each source of uncertainty. Apart from the sensitivity analysis of the model parameters, it is also important to consider the interaction between models and the data. Furthermore, running each model multiple times can assess the full range of model behaviour, parameter uncertainty and natural variability. One way of assessing uncertainty is to apply a mixed approach to uncertainty assessment comprising both the model and scenario uncertainty (Dunford *et al.*, 2014). In addition, bifurcation points and decision nodes in models and scenarios need to be identified, and this should be supplemented by monitoring the system as it approaches these nodes to verify system behaviour. Monitoring can reduce the model and scenario uncertainty by adjusting the model in the light of the observations through a process of 'data assimilation'.

One way of reducing uncertainty is to use multi-model ensembles (averages/weighted average), where it is suggested to avoid averaging model results unless the distribution of results suggested by all models is unimodal. Multi-model ensemble is not the only way of combining multiple model types, as different model types can also be joined statistically. For example, niche-based models and demographic- or process-based models could be integrated across spatial scales in a hierarchical framework or, more simply, Dynamic Global Vegetation Model output could feed into species distribution models to better predict the reliance of species on particular biomes.

4.6.3 Communicating uncertainty

An important consideration is the effective communication of these uncertainties when presenting assessment and modelling results. The purpose of the study strongly determines what uncertainty information is relevant and when to communicate uncertainty to policymakers and decision makers, and it is important to convey at least the robust main messages from a modelling assessment (Kloprogge *et al.*, 2007).

The main challenge in developing a generic guideline for communicating uncertainty is that each assessment or decision-support context is unique. For example, in the case of species distribution modelling, Gould *et al.* (2014) report that the spatial distribution of uncertainty is not homogeneous and can vary substantially across the predicted habitat of a species, and that this depends on how the uncertainty impacts the model specification. Furthermore, modellers often encounter situations in which a number of potential sources of uncertainties cannot be quantified. In these situations, Gould *et al.* (2014) recommend that all potential sources of uncertainty should at least be systematically reported, along with model outputs.

Communicating uncertainty not only involves reporting on the uncertain aspects of the models themselves, but also provides insight into these aspects by elaborating on questions such as: Where do the uncertainties originate? What significance or implications do they have in a given policy or decision context? How might a reduction in uncertainty affect the decisions to be made? Can uncertainty be reduced? And how is uncertainty dealt with in the assessment or decision-support activity?

Communicating uncertainty to policymakers is different from communicating with scientists as far as the content and the form of presentation is concerned. Knowing the target audience and what matters to them is therefore important. Furthermore, the policy relevance of information on specific types of uncertainty depends on the phase of the policy cycle. Early in the cycle, for example, the focus would probably be on the nature and causes of a problem, while later on the focus may shift to the effects and costs of intervention options (Kloprogge *et al.*, 2007).

It is important to adopt a systematic approach to the provision of information, for example through the 'progressive disclosure of information' (PDI; Kloprogge *et al.*, 2007). Under this approach, a report and associated publications are subdivided into several 'layers'. The 'outer' layer consists of the press releases, executive summaries, and so on. Here, it is advisable that non-technical information be presented with uncertainties integrated into the main messages and with the context emphasised. An example is the emphasis on the significance and consequences of assessment findings by the IPCC in summaries for policymakers. The 'inner' layers, comprising of appendices, background reports, and so on, can then provide detailed technical information and elaborate on the types, sources and extent of uncertainty. With regard to any of these layers, bear in mind when writing the purpose of the layer the purpose of the uncertainty communicated within it, the information needs of the target group, and the target group's expected interest in the layer. It is desirable that the target community's views are canvassed while designing the scenarios and recommendation as to what level of uncertainty is acceptable, both to the target community and scientifically.

4.7 WAYS FORWARD IN BIODIVERSITY AND ECOSYSTEM MODELLING

Modelling allows policymakers to assess the implications of scenarios of drivers and policy options for the future of biodiversity and ecosystems (Pereira *et al.*, 2010). A diverse range of modelling approaches, from local to global scales, and from individual to ecosystem levels, have been developed to assess the impacts of direct drivers on biodiversity and ecosystem functioning and to investigate the feedback effects of biodiversity on these drivers. However, important challenges still remain in the link between biodiversity modelling and policymaking due to model complexity, uncertainty, and the lack of available data and knowledge (Mouquet *et al.*, 2015).

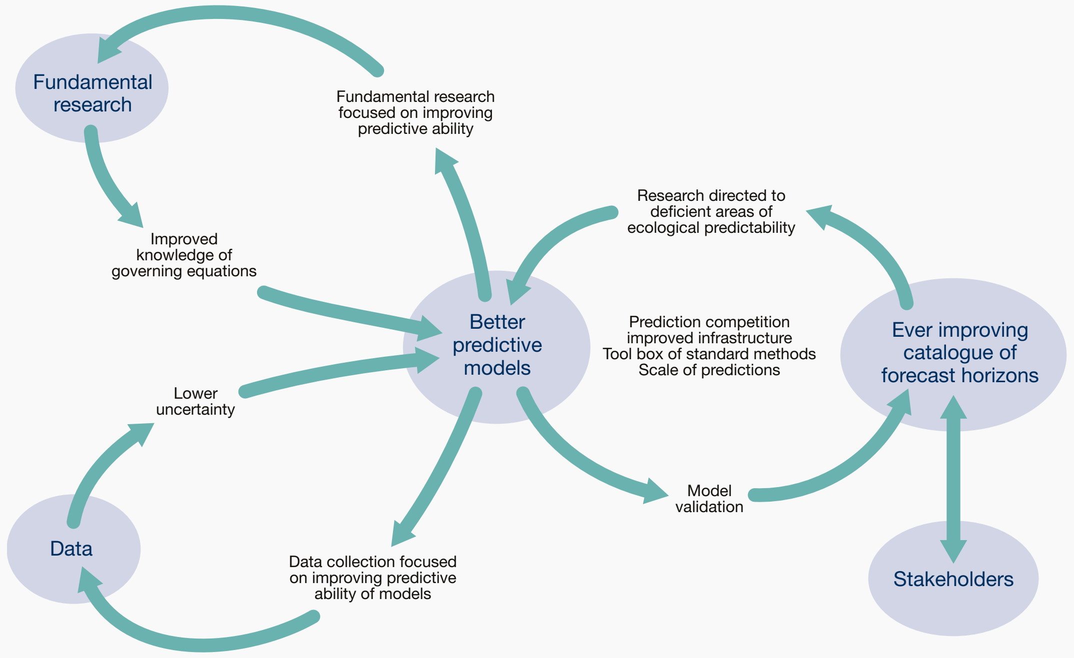
Despite the availability of modelling approaches and applications developed in recent years, the biodiversity community needs to develop a common road map to better integrate predictive modelling with the challenges and needs derived from the current biodiversity crisis. A good example is seen in climate change research, where Global Circulation Models and Earth System Models have helped significantly in advancing understanding of the role of greenhouse gas emissions in driving the future climate.

Petchey *et al.* (2015) have introduced a road map for ecological predictability research. The road map describes the feedbacks and interactions between fundamental research on which the models are based, the data feeding into such models, and using evaluation of model outputs to inform development of new models, thereby improving the accuracy and usefulness of predictions. These feedbacks and interactions point to the need for an integrated approach to making models that meet the predictive requirements of stakeholders and policy **(Figure 4.10)**.

IPBES needs to recognise the complexities linking drivers of environmental change to biodiversity and ecosystem dynamics, and acknowledge the value of modelling as a method of producing a formal abstraction of such complexity and as a scientific tool for supporting decision making. When adequately framed, modelling approaches can be used as robust policy support (Guisan *et al.*, 2013). However, IPBES also needs to keep in mind the significant capacity constraints and important gaps in the formalisation of the links between ecosystem models and policymaking. Therefore, future efforts should strongly encourage stakeholder participation as early as possible. This should be done to maximise the correspondence between the assessment objectives and the outputs and limitations of the modelling approaches (Guillera Arroita *et al.*, 2015). Furthermore, the contextual interpretation of the modelling

FIGURE **4.10**

Schematic outline for improving model predictability in ecological research. The indirect interactions and feedbacks (e.g. between fundamental research and data and predictive models) are left implicit, yet are extremely important (Modified from Petchey *et al.*, 2015. The ecological forecast horizon, and examples of its uses and determinants. Copyright © 2015 by John Wiley Sons, Inc. Reprinted by permission of John Wiley & Sons, Inc).



results and model uncertainty needs to be a joint activity of modellers and decision makers.

Finally, biodiversity and ecosystem modelling urgently requires adequate guidance regarding the typology of models used in isolation or combined in each of the assessments. Model intercomparison programmes should lead to increased collaboration among modelling groups and also with field ecologists to develop suitable protocols for modelling impacts of drivers on biodiversity and ecosystem functions, for example regarding scale, time frame, data collection and validation protocols, agreed processes, uncertainty analysis, and standardised outputs of the modelling studies. The promotion of model intercomparison groups will be vital for developing consistent protocols and standardised data, parameters and scenarios, as well as for incorporating long-term observation data and addressing and communicating uncertainty.

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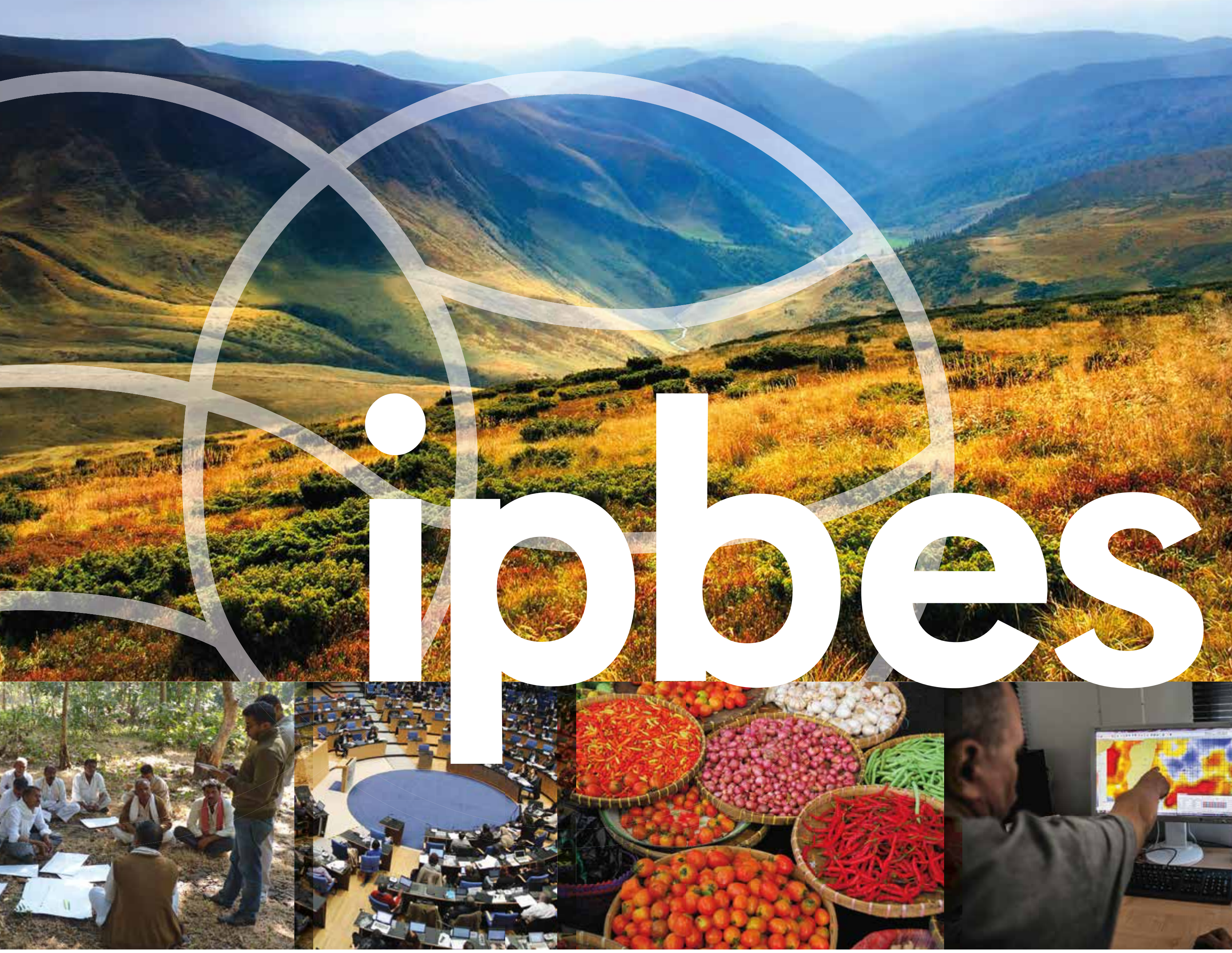

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