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MIYADI AWARD

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Unravelling the dynamics of organisms in a changing world using ecological modelling

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Abstract Understanding and predicting the dynamics of organisms is a central objective in ecology and conservation biology, and modelling provides a solution to tackling this problem. However, the complex nature of ecological systems means that for a thorough understanding of ecological dynamics at hierarchical scales, a set of modeling approaches need to be adopted. This review illustrates how modelling approaches can be used to understand the dynamics of organisms in applied ecological problems, focussing on mechanistic models at a local scale and statistical models at a broad scale. Mechanistic models incorporate ecological processes explicitly and thus are likely to be robust under novel conditions. Models based on behavioural decisions by individuals represent a typical example of the successful application of mechanistic models to applied problems. Considering the data-hungry nature of such mechanistic models, model complexity and parameterisation need to be explored further for a quick and widespread implementation of this model type. For broad-scale phenomena, statistical models play an important role in dealing with problems that are often inherent in data. Examples include models for quantifying population trends from long-term, large-scale data and those for comparative methods of extinction risk. Novel statistical approaches also allow mechanistic models to be parameterised using readily obtained data at a macro scale. In conclusion, the complementary use and improvement of multiple model types, the increased use of novel model parameterisation, the examination of model transferability and the achievement of wider biodiversity information availability are key challenges for the effective use of modelling in applied ecological problems.

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Introduction

As ecologists, we aim to understand the dynamics of organisms and their relationships with their surroundings. We also bear a crucial responsibility to understand human impacts on, and predict future trajectories of, global biodiversity. In particular, given that the loss of biodiversity and ecosystem services is an ongoing crisis throughout the planet, the efficiency of the approaches we take matters; we need to understand what is going on with global biodiversity and take appropriate measures as soon as possible. Thus, the problem is how we can promote our understanding of ecological systems and project the future of biodiversity in an efficient, yet effective way (Starfield 1997; Evans 2012).

Modelling should be able to provide a solution to tackling this problem (Evans et al. 2012). Modelling has now become an important tool in the study of ecological systems for developing hypotheses, explaining existing data, conducting experiments, formulating predictions and consequently guiding research (Levin et al. 1997; Starfield 1997; Green et al. 2005). Typical examples include species distribution models, which aim to describe the dynamics of species spatial distribution, and population dynamics models, which are targeted to the temporal dynamics of population sizes. The critical importance of ecological modelling is well illustrated in, for example, studies on ecological phenomena at a large spatial and temporal scale. Widespread concerns about the impact of global environmental changes, including climate change, on biodiversity and ecosystem services have led to an urgent need to predict the future state of biodiversity at a global spatial scale and a temporal scale of decades to centuries for establishing effective policies (Green et al. 2005; Kerr et al. 2007). Large-scale ecological studies, however, are logistically more difficult to conduct than are small-scale studies (Root and Schneider 1995). Consequently, at a large scale, available information is usually spatially and temporally heterogeneous, often containing unknown levels of bias and large errors (Graham et al. 2004; Guisan et al. 2006). Modelling currently provides the most comprehensive and flexible approach to understanding and projecting the dynamics of organisms at a broad spatial scale while dealing with such problems that are inherent in large-scale ecological studies (Guisan and Thuiller 2005; McMahon et al. 2011).

Ecological systems, however, comprise complex networks of individuals interacting with each other and with their environment at multiple scales and, thus, can hardly be explained accurately in every aspect of time and space from a single, albeit complex, model (Guisan and Zimmermann 2000; Porté and Bartelink 2002). For example, the dynamics of organisms are affected by a wide range of environmental factors at hierarchical scales (Wiens 1989; Levin 1992), such as patch composition and configuration at a landscape scale (Dunning et al. 1992; Wiens et al. 1993) and climate and topography at a macro scale (Hawkins et al. 2003; Davies et al. 2007; Yamaura et al. 2011). The relative importance of different processes in governing ecological dynamics also differs among scales (Root and Schneider 1995; Vellend 2010). For instance, at small spatial and temporal scales, the spatial distribution of animals is driven by patch use and within-patch movements of individuals (Bernstein et al. 1988; Mueller and Fagan 2008). At a landscape scale, resource utilisation, dispersal, colonisation and population extinction compose spatial population dynamics (Turner 1989; Dunning et al. 1992; Hanski 1999) while niche shifts and conservatism, speciation and species extinction are important processes that govern species dynamics at broad spatial and temporal scales (Willig et al. 2003; Wiens and Donoghue 2004). Our survey approaches, and consequently available data, are also restricted by the scale of focal processes. Detailed information on organisms' dynamics, such as individuals' behaviour or life-history events, can usually be obtained at small spatial and temporal scales through direct observation or experiments (Sutherland et al. 2004). On the other hand, in macroecological studies, which are usually conducted at large spatial and temporal scales, available information is limited to readily measurable variables, for example, body size, abundance or geographic range for well-studied groups of organisms, such as terrestrial birds, mammals and plants (Brown 1999).

This scale-dependent nature of ecological systems and survey approaches means that it is crucial to adopt a set of modelling approaches suited to ecological processes at hierarchical spatial and temporal scales. The importance of integrative approaches in ecological studies is not a novel idea but has been argued repeatedly by earlier studies (Lawton 1999; Simberloff 2004), including those focussing on ecological models (Levins 1966; Guisan and Zimmermann 2000). However, few reviews to date have focussed on integrative approaches to modelling ecological dynamics in the field of applied ecology. Given the urgent necessity to promote the understanding of biodiversity status and human impacts on it at the global, regional and national level (Balmford et al. 2005), such integrative approaches would achieve the maximum effect in tackling applied ecological problems. Although Evans (2012) is a rare exception in that it reviews existing approaches to ecological modelling for understanding the ecological impact of environmental change, the review does not explicitly focus on the difference in dynamics, processes and available information among scales, and the consequent advantages and disadvantages of different modelling approaches.

Thus, this review focusses on how modelling approaches can be used to understand the dynamics of organisms for the purpose of tackling applied ecological problems. The aim of this review is not to cover a whole range of ecological models but to introduce applications at opposite ends of the spectrum: mechanistic models targeted to local-scale dynamics of organisms, and statistical models for macro-scale dynamics. Reviewing the pros and cons of these two extremes would highlight the necessity of integrative modelling approaches to tackling ecological processes at hierarchical spatial and temporal scales.

Mechanistic models for local-scale dynamics

Mechanistic models explicitly capture hypothetical ecological processes (Guisan and Zimmermann 2000) and, thus, are likely to be robust under new environmental combinations in new locations, but are usually limited by the availability of data for model parameterisation (Porté and Bartelink 2002; Jongejans et al. 2008; Kearney and Porter 2009). Ecological studies at a local scale have a long history (Wiens 1989; Wu and Loucks 1995) and consequently, a wide variety of survey techniques have been established for obtaining detailed information on ecological processes at a local scale. Therefore, mechanistic models provide a powerful approach to tackling ecological dynamics at a local scale. Examples of mechanistic models in the field of applied ecology include matrix population models (Akçakaya et al. 1999), metapopulation models (Hanski 1999) and individual-based models (Grimm and Railsback 2005). The following section introduces actual applications of such mechanistic models, focusing on models based on behavioural decisions by individuals.

Behaviour-based models as an example of mechanistic models

Ecological dynamics at a local spatial scale are usually governed by processes that occur at a short temporal scale, and for animals, behavioural decisions by individuals play a fundamental role in shaping spatial population dynamics at a relatively small spatial scale (Dunning et al. 1995; Sutherland 1996). One advantage of understanding the behavioural decisions made by individuals is that it is possible to predict their behaviour and consequent spatial population dynamics in novel environments such as those resulting from environmental change (Sutherland 1998). There are also unexpected but critical findings of management consequences that cannot be derived without considering detailed behavioural processes in individuals (e.g., Goss-Custard et al. 2004). Thus, models based on behavioural decisions are a particularly powerful approach for a wide variety of applied problems in ecology (e.g., projecting spatial distribution: Railsback and Harvey 2002; Bar-David et al. 2005, assessing extinction risks: Schiegg et al. 2005; Rossmanith et al. 2006; Revilla and Wiegand 2008, measuring landscape connectivity: Kramer-Schadt et al. 2004; Revilla et al. 2004, predicting home ranges: Mitchell and Powell 2004, 2007, predicting the impact of deforestation: Satake and Rudel 2007).

Although models based on behavioural decisions by individuals have been adopted for a wide range of taxa and purposes, an outstandingly successful example of such models is the application to understanding anthropogenic impacts on the populations of bird species, particularly in coastal and farmland habitats (Stephens et al. 2003; Stillman and Goss-Custard 2010). These models are often spatially explicit individual-based models that project changes in the spatial distribution of target species and population consequences (Fig. 1). Although bahavioural processes can be incorporated in individual-based models either as empirically derived decision rules or as optimality rules (Feró et al. 2008), models of the latter category, where behaviour is predicted on the basis of short-term proxies for fitness or long-term fitness considerations, have usually been adopted by studies of birds in coastal and farmland habitats (hereafter, behaviour-based models, Goss-Custard and Sutherland 1997; Sutherland 2006). Model structures and parameters are based on knowledge acquired from intensive studies about the behavioural ecology of the target species, such as the functional response showing the relationship between food density and intake rate (Goss-Custard et al. 2006b; Stillman and Simmons 2006; Smart et al. 2008), diet and patch selection (Vickery et al. 1995; Gill 1996; Nolet et al. 2002; Amano et al. 2006a), resource dynamics (Nolet et al. 2001), interference competition (Caldow et al. 1999; Triplet et al. 1999), exploitative competition (Rowcliffe et al. 2001; Nolet et al. 2006b), behavioural responses to human disturbance (Gill et al. 2001; Stillman and Goss-Custard 2002; Amano et al. 2004), migratory behaviour (Bauer et al. 2006, 2008; Moriguchi et al. 2010) and theoretical frameworks that integrate the revealed processes (Sutherland and Anderson 1993; Sutherland and Dolman 1994). The developed models have been applied for making a wide range of predictions such as regarding carrying capacities (Sutherland and Allport 1994; Stillman et al. 2000; Nolet et al. 2006a), and the impact of habitat loss (Pettifor et al. 2000; Goss-Custard et al. 2006a), agricultural practices (Johst et al. 2001; Amano et al. 2007; Butler et al. 2010; Catry et al. 2012), human disturbance (West et al. 2002; Klaassen et al. 2006), fisheries (Stillman et al. 2001) and climate change (Durell et al. 2006; Bauer et al. 2008).

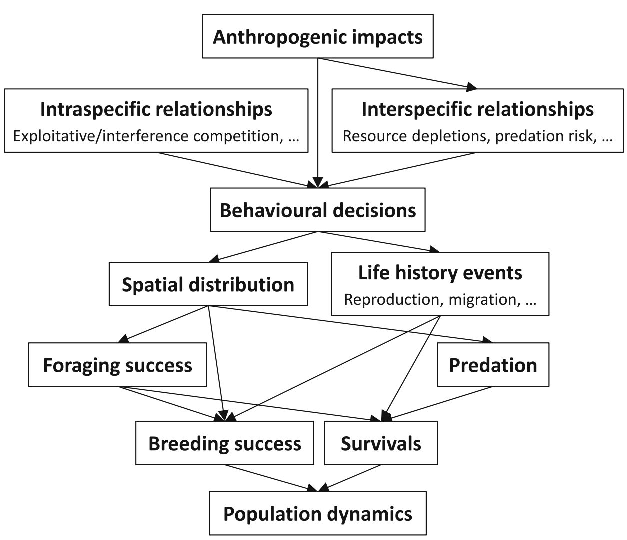

Fig. 1 Simplified sketch of processes, factors and their interrelationships included in typical behaviour-based models. Note that this schematic diagram does not necessarily represent all potential factors and processes

Limitations of and challenges for mechanistic models

Despite the success in the examples above, the relatively limited variety of species to which behaviour-based models have been applied to date clearly points to a drawback of mechanistic models. Typical behavioural-based models require detailed information on interactions both between individuals and between an individual and its environment, as well as the dynamics of prey populations, which may limit quick and widespread implementation (Bradbury et al. 2001; Feró et al. 2008). Therefore, in order to make the best use of mechanistic models like behaviour-based models, two issues—model complexity and parameterisation—need to be explored further in future studies, as highlighted by Bradbury et al. (2001).

First, the level of model complexity should be explored carefully. The strength of inferences from mechanistic models depends on the identification of key limiting processes (Elith et al. 2010; Kearney et al. 2010); incorporating unnecessarily detailed processes would make it difficult to parameterise models and interpret outputs (Van Nes and Scheffer 2005). Comparing the performance of models with different degrees of complexity, as has been done in some studies (Stephens et al. 2002;

Goss-Custard et al. 2003), should be encouraged further (Orzack 2012). For example, Amano et al. (2006b) developed four different behaviour-based models for white-fronted geese *Anser albifrons* with and without the assumptions of (1) individuals' complete knowledge of foraging patch quality, and (2) benefits of group foraging, and tested the ability of these models to reproduce the observed patterns in spatial distribution and fat deposition parameters, concluding that both the assumptions are necessary to predict the spatial and temporal dynamics of foraging goose populations accurately. For applied problems, the choice of the most appropriate model also depends on the management objectives (Jongejans et al. 2008). For instance, to investigate the effect of the type of agricultural land-use on the breeding success of lesser kestrels *Falco naumanni*, Rodríguez et al. (2006) used individual-based models that assume that individuals exploit only one patch type. Catry et al. (2012) expanded this model to include the dynamics of multiple land-use types and optimality-based patch selection by individuals, successfully evaluating the impact of spatial and temporal changes in agricultural practices in Portugal. Model complexity translates to cost in terms of computing resources and increased error propagation and, thus, the construction of unnecessarily complex models should be avoided (Clark and Gelfand 2006; McMahon et al. 2011).

Second, a novel approach to model parameterisation has recently opened the door to a quick and widespread implementation of mechanistic models. Although traditional mechanistic models have used parameters that are estimated statistically from different studies or sources (Fig. 2a), the novel approach integrates the traditionally disparate treatment of 'mechanistic understanding' and 'statistical parameter estimation' into a single process, making it possible to account for uncertainties in models and parameters (Fig. 2b, Clark 2005; Clark and Gelfand 2006). Typically, Bayesian methods and maximum likelihood methods (Patterson et al. 2008; Schick et al. 2008), but also other methods such as artificial neural networks (Dalziel et al. 2008) and signal processing (Boettiger et al. 2011), have been applied to parameterise mechanistic models incorporating various behavioural parameters from readily obtained distributional and trajectory data without direct behavioural observations (Table 1). Although many of these statistical approaches are based on the direct calculation of likelihoods, our ability to work out the likelihood functions is sometimes severely constrained by mathematical difficulties, particularly in models of complex stochastic systems, such as individual-based models with many hidden states (Beaumont 2010; Hartig et al. 2011). In such a case, a technique using 'Stochastic Simulation Models' is a powerful alternative approach to parameterising mechanistic models from data (see Fig. 2 in Hartig et al. 2011). Instead of calculating likelihoods directly, Stochastic Simulation Models usually take the following three steps: (1) calculate summary statistics of observed and simulated data, (2) approximate the likelihood of

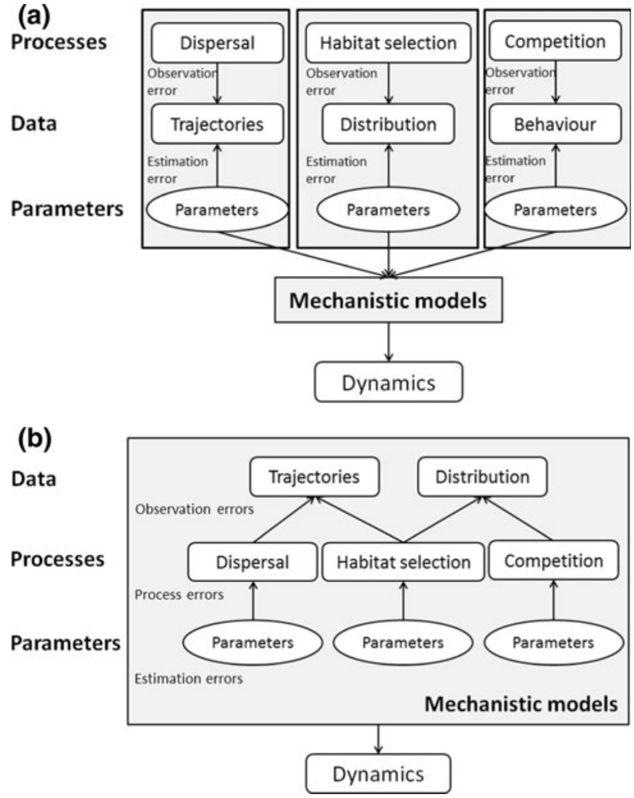

Fig. 2 **a** The approach in traditional mechanistic modelling, where parameters are estimated statistically from different studies or sources (*shaded boxes*) and then used in mechanistic models as inputs. **b** The novel approach with mechanistic models, which integrates the traditionally disparate treatment of 'mechanistic understanding' and 'parameter estimation' into a single process, making it possible to account for uncertainties in models and parameters simultaneously. Models are usually parameterised based on either the likelihood (maximum likelihood/Bayesian methods) or approximated likelihood (Stochastic Simulation Models: see main text)

obtaining the observed data from the model with parameters based on the calculated summary statistics, and (3) estimate the shape of the approximate likelihood as a function of the model parameters using computationally intensive techniques, such as Approximate Bayesian Computing (Beaumont 2010; Csilléry et al. 2010) or Bayesian calibration (van Oijen et al. 2005). Pattern-Oriented Modelling (Wiegand et al. 2003; Grimm et al. 2005) does not explicitly approximate likelihoods but also applies the same concept. For example, Martínez et al. (2011) developed an individual-based model that considers basic demographic processes and interactions such as competition and facilitation in alpine tree-line ecotones, and successfully parameterised the model using the Stochastic Simulation Model approach based on Bayesian methods. Although uncertainties in model parameters, error propagation and ad hoc methods of model selection have been the major points of criticism against complex mechanistic models like individual-based models (Wiegand et al. 2003; Grimm and Railsback 2005; Grimm et al. 2005),

Table 1 Examples of studies where behavioural processes were estimated by directly fitting mechanistic models to data

Behavioural processes incorporated	Data type	Methods for parameterisation	References (target species)
Movement modes	Trajectories	Bayesian method	Morales et al. 2004; Fryxell et al. 2008 (elk)
	Trajectories	Bayesian method	Jonsen et al. 2005 (hooded seal), 2007 (leatherback turtle)
	Trajectories	Bayesian method	Eckert et al. 2008 (loggerhead turtle)
	Trajectories	Bayesian method	Block et al. 2011 (tuna, shark, sea turtle, seal and whale)
Habitat specific mortality and survival rates	Mark-recapture	Bayesian method	Ovaskainen et al. 2008 (Glanville fritillary butterfly)
	Distribution	Bayesian method	Kuroe et al. 2011 (harvest mouse)
Responses to resource distribution, disturbances and predators	Trajectories	Maximum likelihood method	Forester et al. 2007 (elk)
	Trajectories	Artificial neural networks	Dalziel et al. 2008 (elk)
	Trajectories	Signal processing	Boettiger et al. 2011 (African elephant)
Responses to edges/barriers	Mark-recapture	Bayesian method	Ovaskainen et al. 2008 (Glanville fritillary butterfly)
	Trajectories	Bayesian method	Pedersen et al. 2011 (Bluefin tuna)
Spatial memory	Trajectories	Artificial neural networks	Dalziel et al. 2008 (elk)
Conspecific interaction	Trajectories	Maximum likelihood method	Moorcroft et al. 2006 (coyote)
Density-dependent colonisation	Distribution	Bayesian method	Bled et al. 2011 (Eurasian collared-dove)

the implementation of Stochastic Simulation Models provides a robust framework that allows such statistical inference even for complex mechanistic models (Hartig et al. 2011; Martínez et al. 2011).

Statistical models for macro-scale dynamics

Widespread concerns over the possible impacts of global environmental changes on biodiversity have led to the increasing importance of understanding spatial and temporal dynamics of organisms at broad (typically from country to global) scales (Kerr et al. 2007; Kühn et al. 2008). This is also well reflected in recent global efforts to assess the status of global biodiversity and ecosystem services, such as the Convention on Biological Diversity's 2010 target (UNEP 2002) and the Millennium Ecosystem Assessment (2005). Macroecology, which searches for ecological patterns in the spatial and temporal dynamics of organisms at broad spatial scales and develops theoretical explanations for these patterns, is a powerful approach to tackling applied problems at a broad spatial scale (Brown and Maurer 1989; Lawton 1999). Macroecological studies often rely on readily obtainable data, such as abundance, distribution or phenology of common species (Graham et al. 2004; Dickinson et al. 2010). Data-hungry mechanistic models are not necessarily easy to develop with such data (Urban 2005; Wiens et al. 2009). More importantly, such data are usually based on citizen science or natural history collections and suffer from sampling bias and errors (Dickinson et al. 2010; Snäll et al. 2011), which should be addressed to identify ecological patterns accurately. Statistical models thus play an important role in dealing with problems that are often inherent in macroecological data.

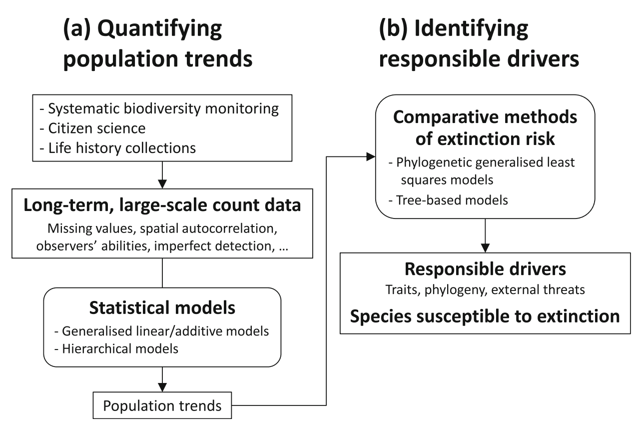

Fig. 3 A statistical approach to assessing the status of populations and species at a macro scale, which typically comprises two steps: **a** quantifying population trends, and **b** identifying the drivers responsible for the revealed trends

Statistical approaches to assessing the status of populations and species

For example, assessing the status of populations and species at a macro scale typically comprises two steps: quantifying population trends (changes in population sizes), and identifying drivers that are responsible for the revealed trends (Fig. 3). Population trends of species at a broad spatial scale are quantified using long-term, large-scale count data, which usually include several problems that have recently been recognised increasingly, such as spatial autocorrelation (Kissling and Carl 2008), incomplete samples (ter Braak et al. 1994), differences in observers' abilities (Sauer et al. 1994) and imperfect detection of species (Royle et al. 2005). Consequently, a wide range of statistical models have been applied to quantifying population trends while dealing with those

Table 2 Problems that need to be dealt with when quantifying population trends using macro-scale data, and example studies that have tackled each challenge

Problem	Example studies
Spatial autocorrelation	Thogmartin et al. (2004)
Differences in population trends among sites	Link and Sauer (2002); Amano et al. (2012)
Differences in observers' abilities	Link and Sauer (2002)
Imperfect detection of species	Kéry et al. (2009)
Spatial variation in survey efforts	Link et al. (2006)
Temporal variation in survey efforts	Kéry et al. (2010)
Changes in data collection procedure	Brun et al. (2011)

problems. Conventional approaches have used either generalised linear models or generalised additive models to estimate population trends from data with missing values (ter Braak et al. 1994; Fewster et al. 2000). More recently, hierarchical models have had a wide application for overcoming a number of problems that had not been addressed in the conventional approaches when estimating population trends (Table 2). These statistical models have contributed successfully to assessing the status of populations and species at national (Conrad et al. 2004; Battersby and Partnership 2005; Van Dyck et al. 2009; Amano et al. 2010; Baillie et al. 2010; Kasahara and Koyama 2010; Sauer and Link 2011), regional (Van Strien et al. 2001; Gregory et al. 2005) and global scales (Collen et al. 2009; Butchart et al. 2010).

Once population trends are quantified, the underlying drivers can be explored effectively by comparative methods of assessing extinction risk, which aim to identify factors associated with species showing serious population declines (Fisher and Owens 2004). Factors related to the risk of decline and extinction include species life-history and ecological traits, such as body mass or geographical range (Bennett and Owens 1997; Reynolds 2003), evolutionary history (Purvis et al. 2000; Purvis 2008), external anthropogenic threats (Cardillo et al. 2004, 2005) and large-scale climate variability (Brander 2007; Waite et al. 2007). Statistical models again play an important role in untangling the effects of these multiple drivers of population decline. For example, since related species cannot be assumed to be independent data points, phylogenetic generalised least-squares models (Grafen 1989; Martins and Hansen 1997) have been adopted in comparative methods to identify correlates of population decline while dealing with phylogenetic non-independence among species (Shultz et al. 2005; Amano and Yamaura 2007; Purvis 2008).

Recently, comparative methods of extinction risk have shown further development in two aspects. First, an increasing number of studies has found that there are non-linear effects of species characteristics (Cardillo et al. 2005) and interaction effects of intrinsic and external factors (Murray et al. 2010) on species extinction risk. Such non-linearities and interactions of potential drivers can be explored effectively by machine learning methods (Olden et al. 2008). Tree-based models such as Decision Trees (De'ath and Fabricius 2000) and Random Forests (Liaw and Wiener 2002) have been applied in particular to a wide range of ecological topics (Olden et al. 2008). In fact, recent studies have applied tree-based approaches successfully to model population declines (e.g. Jones et al. 2006b; Sullivan et al. 2006; Davidson et al. 2009; Murray et al. 2010). However, although for practical purposes it is an advantage that tree-based models do not require phylogenetic information, which is often difficult to obtain (Davidson et al. 2009), the inability to account for phylogenetic non-independence also means that tree-based models cannot reduce the influence of clade-specific relationships in data (Bielby et al. 2010). Thus, tree-based models may be used effectively as a first step in identifying non-linearities and interaction terms of drivers for inclusion in phylogenetic generalised least-squares models in future efforts to assess species susceptibility to extinction (Bielby et al. 2010).

Second, disentangling the effects of species traits, phylogeny and spatial context on population decline and species extinction would be a challenge to be addressed in comparative methods (Purvis 2008). Species traits, phylogeny and space are related closely to each other through phylogenetic trait conservatism (Freckleton et al. 2002; Maherali and Klironomos 2007) and phylogenetic niche conservatism (Peterson et al. 1999; Wiens 2004), making it difficult to evaluate the independent effect of each factor. Recent advances in statistical models for quantifying the relative effect of traits and phylogeny (Desdevises et al. 2003; Diniz-Filho and Bini 2008) and space and phylogeny (Freckleton and Jetz 2009) could be a breakthrough to solve the problem, although only a few studies to date have adopted these modelling techniques to quantify the relative contribution of these factors to species extinction risk (e.g. Safi and Pettorelli 2010).

The examples above focus on the status of populations and species, but macroecological approaches described in this section also play an important role in assessing the loss of functional diversity (Şekercioğlu et al. 2004; Flynn et al. 2009) and consequent decline in ecosystem services (Butchart et al. 2010; Garibaldi et al. 2010; Keesing et al. 2010).

Limitations of and challenges for statistical models in macroecological studies

Obviously, one big disadvantage of correlation-based statistical models is the lack of mechanistic structures, making it difficult to extrapolate to novel conditions (Sutherland 2006). This is particularly critical in applied ecological problems, which often require predictions under novel conditions (e.g. impact of climate change: Thomas et al. 2004; spread of invasive species: Bradley et al. 2010). For instance, climate envelope models have typically been used in efforts to assess biodiversity consequences of climate change (Heikkinen et al. 2006). However, recent studies have pointed out that the reliance on such correlation-based statistical models can lead to inaccurate projections of changes in species spatial distribution (Beale et al. 2008; Duncan et al. 2009). Consequently, there is an increasing awareness that, for the accurate understanding of the impact of climate change, it is necessary to incorporate biotic interactions (Davis et al. 1998; Araújo and Luoto 2007), physiology (Kearney and Porter 2009), dispersal limitations (Svenning and Skov 2007) and plasticity and evolution of niches (Pearman et al. 2008; Wiens et al. 2010) in predictive models.

Incorporating such mechanistic structures in ecological models at a macro scale is not at all an easy task, considering the general lack of information at this spatial scale. Nevertheless, recent studies have successfully enhanced predictions about the spatial population dynamics of organisms by incorporating information derived from mechanistic models in statistical models (Amano et al. 2008; Kearney and Porter 2009; Morin and Thuiller 2009; Elith et al. 2010). The use of meta models, such as graph models, which extract key processes from but are much simpler than detailed mechanistic models, will also be a promising approach to applying a mechanistic understanding over large spatial scales (Urban 2005). Novel statistical approaches to model parameterisation, such as Bayesian methods and Stochastic Simulation Models as described earlier in this paper, also offer an alternative and promising modelling method that allows the development of mechanistic models with macroecological data (Hartig et al. 2011; McMahon et al. 2011). Bled et al. (2011) represents one excellent example of such a novel modelling approach for assessing processes underlying the spatial population dynamics of organisms at a macro scale. Their hierarchical Bayesian model explicitly incorporates the invasion process of Eurasian collared doves *Streptopelia decaocto* through the estimation of site-persistence probability, initial colonisation and recolonisation, and their relationship with local population density, while accounting for the detection probability of the species. The model was fitted, using a Bayesian method, to distribution data derived from the North American Breeding Bird Survey, and the density-dependent nature of the invasion process was successfully inferred from the estimated parameters (Bled et al. 2011). Kadoya and Washitani (2010) also adopted a Bayesian method to estimate parameters of the immigration and establishment processes of alien bumblebees *Bombus terrestris* in Japan from spatio-temporal presence/absence data.

Future challenge for applied ecological modelling

This review has briefly introduced the application of two types of ecological models to applied problems. As indicated above, no single type of model is sufficient to understand and predict ecological dynamics at hierarchical scales, given the difference in processes operating and information available among scales. Thus, the complementary use of mechanistic models and statistical models according to the scale, available information and skills would be an effective approach to tackling the dynamics of organisms in a changing world (Bradbury et al. 2001; McMahon et al. 2011, Fig. 4). Considering that all models, including the mechanistic and statistical models introduced here, inevitably contain a black box, which hides the underlying details, no type of model should be dismissed automatically as inferior just because it does not include all of the mechanistic details (Orzack 2012). What truly matters is where to use such black boxes in model structures, and the consequent predictive performance of the models (Orzack 2012), both of which should be taken into account more explicitly in future modelling studies. At the same time, efforts to overcome the drawbacks of each type of model represent a major challenge for the next decade. Novel approaches to model parameterisation, such as Bayesian methods and Stochastic Simulation Models, improve the chances of a quick and widespread implementation of mechanistic models even for ecological dynamics at large spatial and temporal scales. In fact, these approaches break down the boundaries between statistical models and traditional mechanistic models, providing a comprehensive framework for the field of ecological modelling (Fig. 4).

One of the largest challenges faced by ecological modelling and, more broadly, conservation science, are

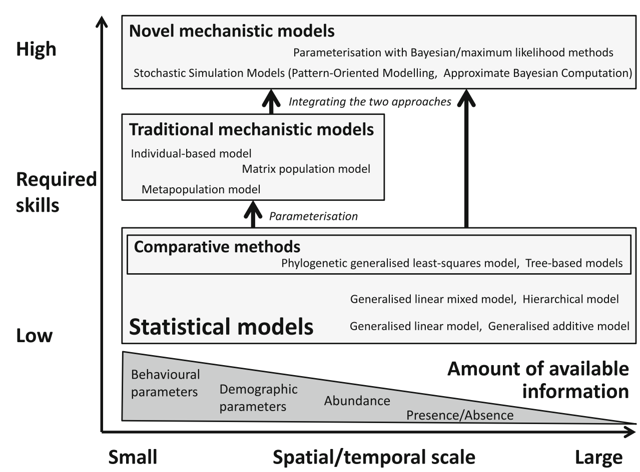

Fig. 4 A diagram of the amount of available information, statistical models, traditional mechanistic models and novel mechanistic models along the gradient of temporal/spatial scales and skills required for modelling. The amount of available information is generally large at small spatial and temporal scales. Statistical models, including the comparative methods, can be applied to a wide range of scales but are particularly important for ecological dynamics at large spatial and temporal scales, where it is usually difficult to implement traditional mechanistic models due to the lack of necessary information. Novel statistical approaches to model parameterisation allow a quick implementation of mechanistic models even with information available at large spatial and temporal scales, consequently providing a comprehensive framework for the field of ecological modelling

the reported gaps and heterogeneity in the geographical and taxonomical coverage of existing information (Collen et al. 2009; Pennisi 2010). For example, 18% (7,976/45,301 species) of animal species that have been evaluated to date by the IUCN have so little information available for assessing population status that they can be judged only as Data Deficient (IUCN 2011). Thus, the challenge is how to effectively understand and predict the dynamics of organisms with ecological modelling under such uncertain and temporally and financially constrained conditions. Although many studies (e.g. Ludwig 1999; Brook et al. 2000; Coulson et al. 2001) have explored the validity of ecological models for predicting future status of organisms, surprisingly few studies to date have tested if ecological models that have been developed for a particular species in a particular region can be used to effectively predict the dynamics of other species or in other regions (Amano et al. 2011). In this regard, efforts to test the predictability of species' extinction risk using trait-based comparative methods (e.g. Cardillo et al. 2008; Pocock 2011) and the spatial transferability of predictive models (Broennimann et al. 2007; Whittingham et al. 2007), though still rare, should be encouraged further.

Finally, special emphasis should be placed on the importance of improving biodiversity information across the globe. As discussed above, the possibilities and applicabilities of ecological modelling are restricted largely by the amount of information available for a target system. Systematic biodiversity monitoring (Pereira and Cooper 2006; Lindenmayer and Likens 2009), citizen science (Dickinson et al. 2010) and natural history collections (Graham et al. 2004) all have the potential to provide invaluable information for developing effective ecological models. Improving the accessibility of existing but isolated empirical data by overcoming technological and cultural challenges (Jones et al. 2006a; Reichman et al. 2011) is also an effective strategy.

In conclusion, the complementary use and improvement of multiple model types, increased use of novel model parameterisation, examination of the applicability of models to species and regions with little information, and the achievement of wider biodiversity information availability are important challenges for the effective use of modelling in applied ecological problems. Enhancing collaborative partnerships among empirical ecologists, theoretical ecologists and ecological modellers would promote the exchange of information and ideas for these purposes (Green et al. 2005; Lindenmayer and Likens 2011). However, considering recent declines in fundamental fields such as taxonomy and natural history (Noss 1996; Hopkins and Freckleton 2002; Uniyal 2011), encouraging inter-field collaborations may not be enough. To borrow Weiner (1995)'s phrase, individual ecologists should aim to be both modellers and empiricists. Modellers should learn as much as possible about the natural history of the systems they are trying to model, and empiricists should learn as much as possible about models that may be relevant to their research (Weiner 1995). Such pluralism, not only within ecological modelling but across the field of ecology, might be the best strategy for unraveling the dynamics of organisms in a rapidly changing world.

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References

Akçakaya HR, Burgman MA, Ginzburg LR (1999) Applied population ecology: principles and computer exercises using RAMAS EcoLab 2.0, 2nd edn. Sinauer, Sunderland

Amano T, Yamaura Y (2007) Ecological and life-history traits related to range contractions among breeding birds in Japan. Biol Conserv 137:271–282

Amano T, Ushiyama K, Fujita G, Higuchi H (2004) Factors affecting rice grain density unconsumed by white-fronted geese in relation to wheat damage. Agric Ecosyst Environ 102:403–407

Amano T, Ushiyama K, Fujita G, Higuchi H (2006a) Foraging patch selection and departure by non-omniscient foragers: a field example in white-fronted geese. Ethology 112:544–553

Amano T, Ushiyama K, Moriguchi S, Fujita G, Higuchi H (2006b) Decision-making in group foragers with incomplete information: test of individual-based model in Geese. Ecol Monogr 76:601–616

Amano T, Ushiyama K, Fujita G, Higuchi H (2007) Predicting grazing damage by white-fronted geese under different regimes of agricultural management and the physiological consequences for the geese. J Appl Ecol 44:506–515

Amano T, Ushiyama K, Higuchi H (2008) Methods of predicting risks of wheat damage by white-fronted geese. J Wildl Manag 72:1845–1852

Amano T, Székely T, Koyama K, Amano H, Sutherland WJ (2010) A framework for monitoring the status of populations: an example from wader populations in the East Asian-Australasian flyway. Biol Conserv 143:2238–2247

Amano T, Kusumoto Y, Okamura H, Baba YG, Hamasaki K, Tanaka K, Yamamoto S (2011) A macro-scale perspective on within-farm management: how climate and topography alter the effect of farming practices. Ecol Lett 14:1263–1272

Amano T, Okamura H, Carrizo SF, Sutherland WJ (2012) Hierarchical models for smoothed population indices: the importance of considering variations in trends of count data among sites. Ecol Indic 13:243–252

Araújo MB, Luoto M (2007) The importance of biotic interactions for modelling species distributions under climate change. Glob Ecol Biogeogr 16:743–753

Baillie SR, Marchant JH, Leech DI, Renwick AR, Joys AC, Noble DG, Barimore C, Conway GJ, Downie IS, Risely K, Robinson RA (2010) Breeding birds in the wider countryside: their conservation status 2010. BTO Research Report No. 565, Thetford, UK. (http://www.bto.org/birdtrends)

Balmford A, Bennun L, ten Brink B, Cooper D, Côté I, Crane P, Dobson A, Dudley N, Dutton I, Green R, Gregory R, Harrison J, Kennedy E, Kremen C, Leader-Williams N, Lovejoy T, Mace G, May R, Mayaux P, Morling P, Phillips J, Redford K, Ricketts T, Rodriguez J, Sanjayan M, Schei P, van Jaarsveld A, Walther B (2005) The convention on biological diversity's 2010 target. Science 307:212–213

Bar-David S, Saltz D, Dayan T (2005) Predicting the spatial dynamics of a reintroduced population: the Persian fallow deer. Ecol Appl 15:1833–1846

Battersby J, Partnership TM (2005) UK mammals: species status and population trends: first report by the tracking mammals partnership. JNCC/Tracking Mammals Partnership, Peterborough, UK

Bauer S, Madsen J, Klaassen M (2006) Intake rates, stochasticity, or onset of spring—what aspects of food availability affect spring migration patterns in Pink-footed Geese *Anser brachyrhynchus*? Ardea 94:555–566

Bauer S, Van Dinther M, Hogda KA, Klaassen M, Madsen J (2008) The consequences of climate-driven stop-over sites changes on migration schedules and fitness of Arctic geese. J Anim Ecol 77:654–660

Beale CM, Lennon JJ, Gimona A (2008) Opening the climate envelope reveals no macroscale associations with climate in European birds. Proc Natl Acad Sci USA 105:14908–14912

Beaumont MA (2010) Approximate Bayesian computation in evolution and ecology. Annu Rev Ecol Evol Syst 41:379–406

Bennett PM, Owens IPF (1997) Variation in extinction risk among birds: chance or evolutionary predisposition? Proc R Soc B Biol Sci 264:401–408

Bernstein C, Kacelnik A, Krebs JR (1988) Individual decisions and the distribution of predators in a patchy environment. J Anim Ecol 57:1007–1026

Bielby J, Cardillo M, Cooper N, Purvis A (2010) Modelling extinction risk in multispecies data sets: phylogenetically independent contrasts versus decision trees. Biodivers Conserv 19:113–127

Bled F, Royle JA, Cam E (2011) Hierarchical modeling of an invasive spread: the Eurasian Collared-Dove *Streptopelia decaocto* in the United States. Ecol Appl 21:290–302

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison AL, Ganong JE, Swithenbank A, Castleton M, Dewar H, Mate BR, Shillinger GL, Schaefer KM, Benson SR, Weise MJ, Henry RW, Costa DP (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90

Boettiger AN, Wittemyer G, Starfield R, Volrath F, Douglas-Hamilton I, Getz WM (2011) Inferring ecological and behavioral drivers of African elephant movement using a linear filtering approach. Ecology 92:1648–1657

Bradbury RB, Payne RJH, Wilson JD, Krebs JR (2001) Predicting population responses to resource management. Trends Ecol Evol 16:440–445

Bradley BA, Blumenthal DM, Wilcove DS, Ziska LH (2010) Predicting plant invasions in an era of global change. Trends Ecol Evol 25:310–318

Brander KM (2007) Global fish production and climate change. Proc Natl Acad Sci USA 104:19709–19714

Broennimann O, Treier UA, Muller-Scharer H, Thuiller W, Peterson AT, Guisan A (2007) Evidence of climatic niche shift during biological invasion. Ecol Lett 10:701–709

Brook BW, O'Grady JJ, Chapman AP, Burgman MA, Akçakaya HR, Frankham R (2000) Predictive accuracy of population viability analysis in conservation biology. Nature 404:385–387

Brown JH (1999) Macroecology: progress and prospect. Oikos 87:3–14

Brown JH, Maurer BA (1989) Macroecology: the division of food and space among species on continents. Science 243:1145–1150

Brun M, Abraham C, Jarry M, Dumas J, Lange F, Prévost E (2011) Estimating an homogeneous series of a population abundance indicator despite changes in data collection procedure: a hierarchical Bayesian modelling approach. Ecol Model 222:1069–1079

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque J-F, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vie J-C, Watson R (2010) Global biodiversity: indicators of recent declines. Science 328:1164–1168

Butler SJ, Mattison EHA, Glithero NJ, Robinson LJ, Atkinson PW, Gillings S, Vickery JA, Norris K (2010) Resource availability and the persistence of seed-eating bird populations in agricultural landscapes: a mechanistic modelling approach. J Appl Ecol 47:67–75

Caldow RWG, Goss-Custard JD, Stillman RA, Durell SEALeV-dit, Swinfen R, Bregnballe T (1999) Individual variation in the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and susceptibility to interference. J Anim Ecol 68:869–878

Cardillo M, Purvis A, Sechrest W, Gittleman JL, Bielby J, Mace GM (2004) Human population density and extinction risk in the world's carnivores. PLoS Biol 2:909–914

Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis A (2005) Multiple causes of high extinction risk in large mammal species. Science 309:1239–1241

Cardillo M, Mace GM, Gittleman JL, Jones KE, Bielby J, Purvis A (2008) The predictability of extinction: biological and external correlates of decline in mammals. Proc R Soc B Biol Sci 275:1441–1448

Catry I, Amano T, Franco A, Sutherland W (2012) Influence of spatial and temporal dynamics of agricultural practices on the lesser kestrel. J Appl Ecol 49:99–108. doi:10.1111/j.1365-2664.2011.02071.x

Clark JS (2005) Why environmental scientists are becoming Bayesians. Ecol Lett 8:2–14

Clark JS, Gelfand AE (2006) A future for models and data in environmental science. Trends Ecol Evol 21:375–380

Collen B, Loh J, Whitmee S, McRae L, Amin R, Baillie JEM (2009) Monitoring change in vertebrate abundance: the Living Planet Index. Conserv Biol 23:317–327

Conrad K, Woiwod I, Parsons M, Fox R, Warren M (2004) Long-term population trends in widespread British moths. J Insect Conserv 8:119–136

Coulson T, Mace GM, Hudson E, Possingham H (2001) The use and abuse of population viability analysis. Trends Ecol Evol 16:219–221

Csilléry K, Blum MGB, Gaggiotti OE, François O (2010) Approximate Bayesian Computation (ABC) in practice. Trends Ecol Evol 25:410–418

Dalziel BD, Morales JM, Fryxell JM (2008) Fitting probability distributions to animal movement trajectories: using artificial neural networks to link distance, resources, and memory. Am Nat 172:248–258

Davidson AD, Hamilton MJ, Boyer AG, Brown JH, Ceballos G (2009) Multiple ecological pathways to extinction in mammals. Proc Natl Acad Sci USA 106:10702–10705

Davies RG, Orme CDL, Storch D, Olson VA, Thomas GH, Ross SG, Ding TS, Rasmussen PC, Bennett PM, Owens IPF, Blackburn TM, Gaston KJ (2007) Topography, energy and the global distribution of bird species richness. Proc R Soc B Biol Sci 274:1189–1197

Davis AJ, Jenkinson LS, Lawton JH, Shorrocks B, Wood S (1998) Making mistakes when predicting shifts in species range in response to global warming. Nature 391:783–786

De'ath G, Fabricius KE (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192

Desdevises Y, Legendre P, Azouzi L, Morand S (2003) Quantifying phylogenetically structured environmental variation. Evolution 57:2647–2652

Dickinson JL, Zuckerberg B, Bonter DN (2010) Citizen science as an ecological research tool: challenges and benefits. Annu Rev Ecol Evol Syst 41:149–172

Diniz-Filho JAF, Bini LM (2008) Macroecology, global change and the shadow of forgotten ancestors. Glob Ecol Biogeogr 17:11–17

Duncan RP, Cassey P, Blackburn TM (2009) Do climate envelope models transfer? A manipulative test using dung beetle introductions. Proc R Soc B Biol Sci 276:1449–1457

Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. Oikos 65:169–175

Dunning JB, Stewart DJ, Danielson BJ, Noon BR, Root TL, Lamberson RH, Stevens EE (1995) Spatially explicit population models: current forms and future uses. Ecol Appl 5:3–11

Durell SEALeVdit, Stillman RA, Caldow RWG, McGrorty S, West AD, Humphreys J (2006) Modelling the effect of environmental change on shorebirds: a case study on Poole Harbour, UK. Biol Conserv 131:459–473

Eckert SA, Moore JE, Dunn DC, van Buiten RS, Eckert KL, Halpin PN (2008) Modeling loggerhead turtle movement in the Mediterranean: importance of body size and oceanography. Ecol Appl 18:290–308

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342

Evans MR (2012) Modelling ecological systems in a changing world. Philos Trans R Soc B 367:181–190

Evans MR, Norris KJ, Benton TG (2012) Predictive ecology: systems approaches. Philos Trans R Soc B 367:163–169

Feró O, Stephens PA, Barta Z, McNamara JM, Houston AI (2008) Optimal annual routines: new tools for conservation biology? Ecol Appl 18:1563–1577

Fewster RM, Buckland ST, Siriwardena GM, Baillie SR, Wilson JD (2000) Analysis of population trends for farmland birds using generalized additive models. Ecology 81:1970–1984

Fisher DO, Owens IPF (2004) The comparative method in conservation biology. Trends Ecol Evol 19:391–398

Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N, Mayfield MM, DeClerck F (2009) Loss of functional diversity under land use intensification across multiple taxa. Ecol Lett 12:22–33

Forester JD, Ives AR, Turner MG, Anderson DP, Fortin D, Beyer HL, Smith DW, Boyce MS (2007) State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. Ecol Monogr 77:285–299

Freckleton RP, Jetz W (2009) Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. Proc R Soc B Biol Sci 276:21–30

Freckleton RP, Harvey PH, Pagel M (2002) Phylogenetic analysis and comparative data: a test and review of evidence. Am Nat 160:712–726

Fryxell JM, Hazell M, Börger L, Dalziel BD, Haydon DT, Morales JM, McIntosh T, Rosatte RC (2008) Multiple movement modes by large herbivores at multiple spatiotemporal scales. Proc Natl Acad Sci USA 105:19114–19119

Garibaldi LA, Aizen MA, Klein AM, Cunningham SA, Harder LD (2010) Global growth and stability of agricultural yield decrease with pollinator dependence. Proc Natl Acad Sci USA 108: 5909–5914

Gill JA (1996) Habitat choice in pink-footed geese: quantifying the constraints determining winter site use. J Appl Ecol 33:884–892

Gill JA, Norris K, Sutherland WJ (2001) Why behavioural responses may not reflect the population consequences of human disturbance. Biol Conserv 97:265–268

Goss-Custard JD, Sutherland WJ (1997) Individual behaviour, populations and conservation. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach. Blackwell Science, Oxford, pp 373–395

Goss-Custard JD, Stillman RA, Caldow RWG, West AD, Guillemain M (2003) Carrying capacity in overwintering birds: when are spatial models needed? J Appl Ecol 40:176–187

Goss-Custard JD, Stillman RA, West AD, Caldow RWG, Triplet P, Durell SEALeVdit, McGrorty S (2004) When enough is not enough: shorebirds and shellfishing. Proc R Soc B Biol Sci 271:233–237

Goss-Custard JD, Burton NHK, Clark NA, Ferns PN, McGrorty S, Reading CJ, Rehfisch MM (2006a) Test of a behavior-based individual-based model: response of shorebird mortality to habitat loss. Ecol Appl 16:2215–2222

Goss-Custard JD, West AD, Yates MG, Caldow RWG, Stillman RA, Bardsley L, Castilla J, Castro M, Dierschke V, Durell SEALeVdit, Eichhorn G, Ens BJ, Exo K-M, Udayangani-Fernando PU, Ferns PN, Hockey PAR, Gill JA, Johnstone I, Kalejta-Summers B, Masero JA, Moreira F, Nagarajan RV, Owens IPF, Pacheco C, Perez-Hurtado A, Rogers D, Scheiffarth G, Sitters H, Sutherland WJ, Triplet P, Worrall DH, Zharikov Y, Zwarts L, Pettifor RA (2006b) Intake rates and the functional response in shorebirds (Charadriiformes) eating macro-invertebrates. Biol Rev 81:501–529

Grafen A (1989) The phylogenetic regression. Philos T R Soc B 326:119–157

Graham CH, Ferrier S, Huettman F, Moritz C, Peterson AT (2004) New developments in museum-based informatics and applications in biodiversity analysis. Trends Ecol Evol 19:497–503

Green JL, Hastings A, Arzberger P, Ayala FJ, Cottingham KL, Cuddington K, Davis F, Dunne JA, Fortin MJ, Gerber L, Neubert M (2005) Complexity in ecology and conservation: mathematical, statistical, and computational challenges. Bioscience 55:501–510

Gregory RD, van Strien A, Vorisek P, Gmelig Meyling AW, Noble DG, Foppen RPB, Gibbons DW (2005) Developing indicators for European birds. Philos Trans R Soc B 360:269–288

Grimm V, Railsback SF (2005) Individual-based modelling and ecology. Princeton University Press, Princeton

Grimm V, Revilla E, Berger U, Jeltsch F, Mooij WM, Railsback SF, Thulke HH (2005) Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310: 987–991

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186

Guisan A, Lehmann A, Ferrier S, Austin M, Overton JMC, Aspinall R, Hastie T (2006) Making better biogeographical predictions of species' distributions. J Appl Ecol 43:386–392

Hanski I (1999) Metapopulation Ecology. Oxford University Press, Oxford

Hartig F, Calabrese JM, Reineking B, Wiegand T, Huth A (2011) Statistical inference for stochastic simulation models—theory and application. Ecol Lett 14:816–827

Hawkins BA, Field R, Cornell HV, Currie DJ, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology 84:3105–3117

Heikkinen RK, Luoto M, Araujo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modelling under climate change. Prog Phys Geogr 30:751–777

Hopkins GW, Freckleton RP (2002) Declines in the numbers of amateur and professional taxonomists: implications for conservation. Anim Conserv 5:245–249

IUCN (2011) IUCN red list of threatened species. Version 2011.1. http://www.iucnredlist.org. Accessed 12 Oct 2011

Johst K, Brandl R, Pfeifer R (2001) Foraging in a patchy and dynamic landscape: human land use and the white stork. Ecol Appl 11:60–69

Jones MB, Schildhauer MP, Reichman OJ, Bowers S (2006a) The new bioinformatics: integrating ecological data from the gene to the biosphere. Annu Rev Ecol Evol Syst 37:519–544

Jones MJ, Fielding A, Sullivan M (2006b) Analysing extinction risk in parrots using decision trees. Biodivers Conserv 15:1993–2007

Jongejans E, Skarpaas O, Shea K (2008) Dispersal, demography and spatial population models for conservation and control management. Perspect Plant Ecol 9:153–170

Jonsen ID, Flemming JM, Myers RA (2005) Robust state-space modeling of animal movement data. Ecology 86:2874–2880

Jonsen ID, Myers RA, James MC (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. Mar Ecol Prog Ser 337:255–264

Kadoya T, Washitani I (2010) Predicting the rate of range expansion of an invasive alien bumblebee (*Bombus terrestris*) using a stochastic spatio-temporal model. Biol Conserv 143:1228–1235

Kasahara S, Koyama K (2010) Population trends of common wintering waterfowl in Japan: participatory monitoring data from 1996 to 2009. Ornithol Sci 9:23–36

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

Kearney MR, Wintle BA, Porter WP (2010) Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conserv Lett 3:203–213

Keesing F, Belden LK, Daszak P, Dobson A, Harvell CD, Holt RD, Hudson P, Jolles A, Jones KE, Mitchell CE, Myers SS, Bogich T, Ostfeld RS (2010) Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature 468:647–652

Kerr JT, Kharouba HM, Currie DJ (2007) The macroecological contribution to global change solutions. Science 316:1581–1584

Kéry M, Dorazio RM, Soldaat L, van Strien A, Zuiderwijk A, Royle JA (2009) Trend estimation in populations with imperfect detection. J Appl Ecol 46:1163–1172

Kéry M, Royle JA, Schmid H, Schaub M, Volet B, Hafliger G, Zbinden N (2010) Site-occupancy distribution modeling to correct population-trend estimates derived from opportunistic observations. Conserv Biol 24:1388–1397

Kissling WD, Carl G (2008) Spatial autocorrelation and the selection of simultaneous autoregressive models. Glob Ecol Biogeogr 17:59–71

Klaassen M, Bauer S, Madsen J, Tombre I (2006) Modelling behavioural and fitness consequences of disturbance for geese along their spring flyway. J Appl Ecol 43:92–100

Kramer-Schadt S, Revilla E, Wiegand T, Breitenmoser U (2004) Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. J Appl Ecol 41:711–723

Kühn I, Böhning-Gaese K, Cramer W, Klotz S (2008) Macroecology meets global change research. Glob Ecol Biogeogr 17:3–4

Kuroe M, Yamaguchi N, Kadoya T, Miyashita T (2011) Matrix heterogeneity affects population size of the harvest mice: Bayesian estimation of matrix resistance and model validation. Oikos 120:271–279

Lawton JH (1999) Are there general laws in ecology? Oikos 84:177–192

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Levin SA, Grenfell B, Hastings A, Perelson AS (1997) Mathematical and computational challenges in population biology and ecosystems science. Science 275:334–343

Levins R (1966) The strategy of model building in population ecology. Am Sci 54:421–431

Liaw A, Wiener M (2002) Classification and regression by random. For R News 2:18–22

Lindenmayer DB, Likens GE (2009) Adaptive monitoring: a new paradigm for long-term research and monitoring. Trends Ecol Evol 24:482–486

Lindenmayer DB, Likens GE (2011) Losing the culture of ecology. Bull Ecol Soc Am 92:245–246

Link WA, Sauer JR (2002) A hierarchical analysis of population change with application to Cerulean Warblers. Ecology 83:2832–2840

Link WA, Sauer JR, Niven DK (2006) A hierarchical model for regional analysis of population change using Christmas Bird Count data, with application to the American Black Duck. Condor 108:13–24

Ludwig D (1999) Is it meaningful to estimate a probability of extinction? Ecology 80:298–310

Maherali H, Klironomos JN (2007) Influence of phylogeny on fungal community assembly and ecosystem functioning. Science 316:1746–1748

Martínez I, Wiegand T, Julio Camarero J, Batllori E, Gutiérrez E (2011) Disentangling the formation of contrasting tree-line physiognomies combining model selection and Bayesian parameterization for simulation models. Am Nat 177:E136–E152

Martins EP, Hansen TF (1997) Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am Nat 149:646–667

McMahon SM, Harrison SP, Armbruster WS, Bartlein PJ, Beale CM, Edwards ME, Kattge J, Midgley G, Morin X, Prentice IC (2011) Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. Trends Ecol Evol 26:249–259

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: current state and trends, vol 1. Island, Washington DC

Mitchell MS, Powell RA (2004) A mechanistic home range model for optimal use of spatially distributed resources. Ecol Model 177:209–232

Mitchell MS, Powell RA (2007) Optimal use of resources structures home ranges and spatial distribution of black bears. Anim Behav 74:219–230

Moorcroft PR, Lewis MA, Crabtree RL (2006) Mechanistic home range models capture spatial patterns and dynamics of coyote teriitories in Yellowstone. Proc R Soc B Biol Sci 273:1651–1659

Morales JM, Haydon DT, Frair J, Holsiner KE, Fryxell JM (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology 85:2436–2445

Moriguchi S, Amano T, Ushiyama K, Fujita G, Higuchi H (2010) Seasonal and sexual differences in migration timing and fat deposition in the Greater White-fronted Goose. Ornithol Sci 9:75–82

Morin X, Thuiller W (2009) Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. Ecology 90:1301–1313

Mueller T, Fagan WF (2008) Search and navigation in dynamic environments—from individual behaviors to population distributions. Oikos 117:654–664

Murray KA, Rosauer D, McCallum H, Skerratt LF (2010) Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. Proc R Soc B Biol Sci 278:1515–1523

Nolet BA, Langevoord O, Bevan RM, Engelaar KR, Klaassen M, Mulder RJW, van Dijk S (2001) Spatial variation in tuber depletion by swans explained by differences in net intake rates. Ecology 82:1655–1667

Nolet BA, Bevan RM, Klaassen M, Langevoord O, van der Heijden YGJT (2002) Habitat switching by Bewick's swans: maximization of average long-term energy gain? J Anim Ecol 71:979–993

Nolet BA, Gyimesi A, Klaassen RHG (2006a) Prediction of bird-day carrying capacity on a staging site: a test of depletion models. J Anim Ecol 75:1285–1292

Nolet BA, Klaassen RHG, Mooij WM (2006b) The use of a flexible patch leaving rule under exploitative competition: a field test with swans. Oikos 112:342–352

Noss RF (1996) The naturalists are dying off. Conserv Biol 10:1–3

Olden JD, Lawler JJ, Poff NL (2008) Machine learning without tears: a practical primer for ecologists. Q Rev Biol 83:171–193

Orzack SH (2012) The philosophy of modelling or does the philosophy of biology have *any* use? Philos Trans R Soc B 367:170–180. doi:10.1098/rstb.2011.0265

Ovaskainen O, Rekola H, Meyke E, Arjas E (2008) Bayesian methods for analyzing movements in heterogeneous landscapes from mark-recapture data. Ecology 89:542–554

Patterson TA, Thomas L, Wilcox C, Ovaskainen O, Matthiopoulos J (2008) State-space models of individual animal movement. Trends Ecol Evol 23:87–94

Pearman PB, Guisan A, Broennimann O, Randin CF (2008) Niche dynamics in space and time. Trends Ecol Evol 23:149–158

Pedersen MW, Patterson TA, Thygesen UH, Madsen H (2011) Estimating animal behavior and residency from movement data. Oikos 120:1281–1290

Pennisi E (2010) Filling gaps in global biodiversity estimates. Science 330:24

Pereira HM, Cooper HD (2006) Towards the global monitoring of biodiversity change. Trends Ecol Evol 21:123–129

Peterson AT, Soberon J, Sanchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. Science 285:1265–1267

Pettifor RA, Caldow RWG, Rowcliffe JM, Goss-Custard JD, Black JM, Hodder KH, Houston AI, Lang A, Webb J (2000) Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. J Appl Ecol 37:103–135

Pocock MJO (2011) Can traits predict species' vulnerability? A test with farmland passerines in two continents. Proc R Soc B Biol Sci 278:1532–1538

Porté A, Bartelink HH (2002) Modelling mixed forest growth: a review of models for forest management. Ecol Model 150:141–188

Purvis A (2008) Phylogenetic approaches to the study of extinction. Annu Rev Ecol Evol Syst 39:301–319

Purvis A, Agapow PM, Gittleman JL, Mace GM (2000) Non-random extinction and the loss of evolutionary history. Science 288:328–330

Railsback SF, Harvey BC (2002) Analysis of habitat-selection rules using an individual-based model. Ecology 83:1817–1830

Reichman OJ, Jones MB, Schildhauer MP (2011) Challenges and opportunities of open data in ecology. Science 331:703–705

Revilla E, Wiegand T (2008) Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. Proc Natl Acad Sci USA 105:19120–19125

Revilla E, Wiegand T, Palomares F, Ferreras P, Delibes M (2004) Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. Am Nat 164:E130–E153

Reynolds JD (2003) Life histories and extinction risk. In: Blackburn TM, Gaston KJ (eds) MacroecologyBlackwell, Oxford, pp 195–217

Rodríguez C, Johst K, Bustamante J (2006) How do crop types influence breeding success in lesser kestrels through prey quality and availability? A modelling approach. J Appl Ecol 43:587–597

Root TL, Schneider SH (1995) Ecology and climate—research strategies and implications. Science 269:334–341

Rossmanith E, Grimm V, Blaum N, Jeltsch F (2006) Behavioural flexibility in the mating system buffers population extinction: lessons from the lesser spotted woodpecker *Picoides minor*. J Anim Ecol 75:540–548

Rowcliffe JM, Watkinson AR, Sutherland WJ, Vickery JA (2001) The depletion of algal beds by geese: a predictive model and test. Oecologia 127:361–371

Royle JA, Nichols JD, Kéry M (2005) Modelling occurrence and abundance of species when detection is imperfect. Oikos 110:353–359

Safi K, Pettorelli N (2010) Phylogenetic, spatial and environmental components of extinction risk in carnivores. Glob Ecol Biogeogr 19:352–362

Satake A, Rudel TK (2007) Modeling the forest transition: forest scarcity and ecosystem service hypotheses. Ecol Appl 17:2024–2036

Sauer JR, Link WA (2011) Analysis of the North American Breeding Bird Survey using hierarchical models. Auk 128:87–98

Sauer JR, Peterjohn BG, Link WA (1994) Observer differences in the North American Breeding Bird Survey. Auk 111:50–62

Schick RS, Loarie SR, Colchero F, Best BD, Boustany A, Conde DA, Halpin PN, Joppa LN, McClellan CM, Clark JS (2008) Understanding movement data and movement processes: current and emerging directions. Ecol Lett 11:1338–1350

Schiegg K, Walters JR, Priddy JA (2005) Testing a spatially explicit, individual-based model of red-cockaded woodpecker population dynamics. Ecol Appl 15:1495–1503

Şekercioğlu CH, Daily GC, Ehrlich PR (2004) Ecosystem consequences of bird declines. Proc Natl Acad Sci USA 101:18042–18047

Shultz S, Bradbury RB, Evans KL, Gregory RD, Blackburn TM (2005) Brain size and resource specialization predict long-term population trends in British birds. Proc R Soc B Biol Sci 272:2305–2311

Simberloff D (2004) Community ecology: is it time to move on? Am Nat 163:787–799

Smart SL, Stillman RA, Norris KJ (2008) Measuring the functional responses of farmland birds: an example for a declining seed-feeding bunting. J Anim Ecol 77:687–695

Snäll T, Kindvall O, Nilsson J, Pärt T (2011) Evaluating citizen-based presence data for bird monitoring. Biol Conserv 144:804–810

Starfield AM (1997) A pragmatic approach to modeling for wildlife management. J Wildl Manag 61:261–270

Stephens PA, Frey-Roos F, Arnold W, Sutherland WJ (2002) Model complexity and population predictions. The alpine marmot as a case study. J Anim Ecol 71:343–361

Stephens PA, Freckleton RP, Watkinson AR, Sutherland WJ (2003) Predicting the response of farmland bird populations to changing food supplies. J Appl Ecol 40:970–983

Stillman RA, Goss-Custard JD (2002) Seasonal changes in the response of oystercatchers *Haematopus ostralegus* to human disturbance. J Avian Biol 33:358–365

Stillman RA, Goss-Custard JD (2010) Individual-based ecology of coastal birds. Biol Rev 85:413–434

Stillman RA, Simmons VL (2006) Predicting the functional response of a farmland bird. Funct Ecol 20:723–730

Stillman RA, Goss-Custard JD, West AD, Durell SEALeVdit, Caldow RWG, Mcgrorty S, Clarke RT (2000) Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. J Appl Ecol 37:564–588

Stillman RA, Goss-Custard JD, West AD, Durell SEALeVdit, Mcgrorty S, Caldow RWG, Norris KJ (2001) Predicting shorebird mortality and population size under different regimes of shellfishery management. J Appl Ecol 38:857–868

Sullivan MS, Jones MJ, Lee DC, Marsden SJ, Fielding AH, Young EV (2006) A comparison of predictive methods in extinction risk studies: contrasts and decision trees. Biodivers Conserv 15:1977–1991

Sutherland WJ (1996) From individual behaviour to population ecology. Oxford University Press, Oxford

Sutherland WJ (1998) The importance of behavioural studies in conservation biology. Anim Behav 56:801–809

Sutherland WJ (2006) Predicting the ecological consequences of environmental change: a review of the methods. J Appl Ecol 43:599–616

Sutherland WJ, Allport GA (1994) A spatial depletion model of the interaction between bean geese and wigeon with the consequences for habitat management. J Anim Ecol 63:51–59

Sutherland WJ, Anderson CW (1993) Predicting the distribution of individuals and the consequences of habitat loss: the role of prey depletion. J Theor Biol 160:223–230

Sutherland WJ, Dolman PM (1994) Combining behaviour and population dynamics with applications for predicting consequences of habitat loss. Proc R Soc B Biol Sci 255:133–138

Sutherland WJ, Newton I, Green R (2004) Bird ecology and conservation: a handbook of techniques. Oxford University Press, Oxford

Svenning J-C, Skov F (2007) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecol Lett 10:453–460

ter Braak CJF, van Strien AJ, Meijer R, Verstrael TJ (1994) Analysis of monitoring data with many missing values: which method? In: Hagemeijer EJM, Verstrael TJ (eds) Bird Numbers 1992. Distribution, monitoring and ecological aspects. Proceedings of the 12th International Conference of IBCC and

EOAC, Noordwijkerhout, The Netherlands. Statistics Netherlands, Voorburg/Heerlen; SOVON, Beek-Ubbergen, pp 663–673
Thogmartin WE, Sauer JR, Knutson MG (2004) A Hierarchical spatial model of avian abundance with application to Cerulean warblers. Ecol Appl 14:1766–1779
Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN (2004) Extinction risk from climate change. Nature 427:145–148
Triplet P, Stillman RA, Goss-Custard JD (1999) Prey abundance and the strength of interference in a foraging shorebird. J Anim Ecol 68:254–265
Turner MG (1989) Landscape ecology: the effect of pattern on process. Annu Rev Ecol Evol Syst 20:171–197
UNEP (United Nations Environment Programme) (2002) Report on the sixth meeting of the conference of the parties to the convention on biological diversity (UNEP/CBD/COP/20/Part 2) strategic plan decision VI/26 in CBD. UNEP, Nairobi
Uniyal SK (2011) Prioritizing taxonomists. Science 332:536–537
Urban DL (2005) Modeling ecological processes across scales. Ecology 86:1996–2006
Van Dyck H, Van Strien AJ, Maes D, Van Swaay CAM (2009) Declines in common, widespread butterflies in a landscape under intense human use. Conserv Biol 23:957–965
Van Nes EH, Scheffer M (2005) A strategy to improve the contribution of complex simulation models to ecological theory. Ecol Model 185:153–164
Van Oijen M, Rougier J, Smith R (2005) Bayesian calibration of process-based forest models: bridging the gap between models and data. Tree Physiol 25:915–927
Van Strien AJ, Pannekoek J, Gibbons DW (2001) Indexing European bird population trends using results of national monitoring schemes: a trial of a new method. Bird Study 48:200–213
Vellend M (2010) Conceptual synthesis in community ecology. Q Rev Biol 85:183–206
Vickery JA, Sutherland WJ, Watkinson AR, Lane SJ, Rowcliffe JM (1995) Habitat switching by dark-bellied brent geese *Branta b. bernicla* (L.) in relation to food depletion. Oecologia 103:499–508
Waite TA, Campbell LG, Chhangani AK, Robbins P (2007) La Niña's signature: synchronous decline of the mammal community in a 'protected' area in India. Divers Distrib 13:752–760
Weiner J (1995) On the practice of ecology. J Ecol 83:153–158
West AD, Goss-Custard JD, Stillman RA, Caldow RWG, Durell SEALeVdit, McGrorty S (2002) Predicting the impacts of disturbance on shorebird mortality using a behaviour-based model. Biol Conserv 106:319–328
Whittingham MJ, Krebs JR, Swetnam RD, Vickery JA, Wilson JD, Freckleton RP (2007) Sould conservation strategies consider spatial generality? Farmland birds show regional not national patterns of habitat association. Ecol Lett 10:25–35
Wiegand T, Jeltsch F, Hanski I, Grimm V (2003) Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. Oikos 100:209–222
Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397
Wiens JJ (2004) Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. Evolution 58:193–197
Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. Trends Ecol Evol 19:639–644
Wiens JA, Stenseth NC, Vanhorne B, Ims RA (1993) Ecological mechanisms and landscape ecology. Oikos 66:369–380
Wiens JA, Stralberg D, Jongsomjit D, Howell CA, Snyder MA (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. Proc Natl Acad Sci USA 106:19729–19736
Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes JA, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR (2010) Niche conservatism as an emerging principle in ecology and conservation biology. Ecol Lett 13:1310–1324
Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu Rev Ecol Evol Syst 34:273–309
Wu J, Loucks OL (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. Q Rev Biol 70:439–466
Yamaura Y, Amano T, Kusumoto Y, Nagata H, Okabe K (2011) Climate and topography drives macroscale biodiversity through land-use change in a human-dominated world. Oikos 120:427–451